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A 150 years' celebration of darwin's book on human evolution and sexual selection: Its legacy and future prospects

Edited by
Marco Antonio Correa Varella, Jaroslava Varella Valentova, Catherine Salmon, Barnaby James Wyld Dixson, Marina Butovskaya, Anabela Pinto Pinto, Boguslaw Pawlowski and Carol Cronin Weisfeld

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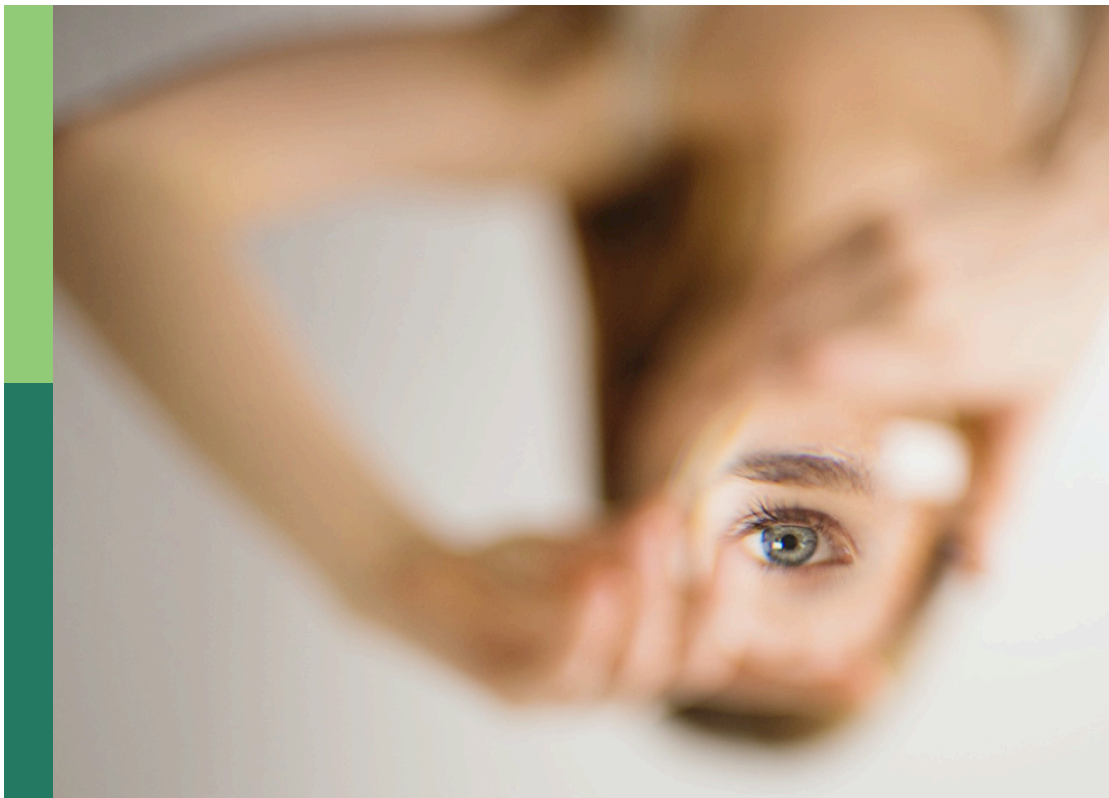

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A 150 years' celebration of darwin's book on human evolution and sexual selection: Its legacy and future prospects

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Editorial: A 150 years' celebration of Darwin's book on human evolution and sexual selection: its legacy and future prospects

Marco Antonio Correa Varella[1]*, Catherine Salmon[2], Barnaby James Wyld Dixson[3], Marina Butovskaya[4], Anabela Pinto[5], Boguslaw Pawlowski[6], Carol Cronin Weisfeld[7] and Jaroslava Varella Valentova[1]

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Editorial on the Research Topic
A 150 years' celebration of Darwin's book on human evolution and sexual selection: its legacy and future prospects

Charles Darwin is considered a great naturalist and geologist, but also a great evolutionary psychologist because of his pioneering contributions concerning the evolution of the human mind and behavior. Despite persisting misunderstandings (Varella et al., 2013), the evolutionary perspective applied to understanding human mind, behavior, and culture has greatly expanded and improved since then (Sear et al., 2007; Griffiths, 2008; Tooby, 2020). This Research Topic launched in 2021 aimed at celebrating the 150 years of Darwin's *The Descent of Man, and Selection in Relation to Sex* book from 1871, in which he offered a promising and comparative research program about human evolution and its relation to sexual selection, that has led to a variety of studies, discoveries, and scientific progress. Recently, there have been many similar initiatives for the sesquicentenary celebration, including reviews (Brooks, 2021; Fritzsche et al., 2021; Richerson et al., 2021; Harman, 2022; Rosenthal and Ryan, 2022), opinion pieces (Fuentes, 2021; Whiten et al., 2021), books (DeSilva, 2021; Bertranpetit and Peretó, 2022), and Research Topic (Gavrilets et al., 2021). The majority of celebratory texts relate to human evolution in general, and only a few touch on human psychology or even sexual selection. This Research Topic fills this gap by offering a lengthy and deep exploration of sexual selection topics related to human evolution.

The collection of 20 articles accepted and published in this celebratory Research Topic includes theoretical and empirical studies that together present an updated, diverse, and comprehensive view about the ways in which sexual selection can influence the evolution of human mind and behavior. This Research Topic offers five groups of articles: (1) Theoretical contributions related to the inner workings of sexual and social selection; (2) Contributions

focused on the evolution of human capacities for arts, creativity, music, and play; (3) Contributions concerned with parenting and alloparenting; (4) Contributions approaching sexual dimorphism; and (5) Contributions investigating signaling, mate preferences, and sexual strategies.

Theoretical contributions about sexual and social selection

This collection of articles begins with a review article by Petrie. The author provides a highly accessible review article summarizing how sexual selection has shaped the evolution of sexual dimorphism in ornamental characteristics. Petrie draws on her own iconic research demonstrating sexual selection on the peacock's train as an indirect signal of genetic benefits to discuss future directions in this field of research (Petrie, 1994). While statistical models detailing how direct and indirect mechanisms operate on sexually selected traits in non-human animals were developed decades ago (Kirkpatrick and Barton, 1997; Kokko et al., 2006), they have been slow to gain traction among researchers studying humans. Petrie presents a narrative and mathematical model demonstrating sexual selection is profoundly different from natural selection, which will help researchers studying sexual selection in humans in their future research in this growing field.

Davis and Arnocky focus their attention on a well-studied topic, mate choice and the evolution of esthetics. They emphasize that the mainstream approach to studying mate choice and attractiveness adopts the Wallacean perspective of attractive traits being possible signals of individual biological quality, while the original Darwinian approach has been mostly overlooked. In Darwin's view, female mate choice was driven by feelings based mostly on esthetics *per se*, without indicating individuals' underlying qualities (direct or indirect benefits), or even being a disadvantage to the individual, as stressed by Fisher, Zahavi, and lately by Prum, whose null hypothesis on trait-preference is described in this article. They suggest that evolutionary psychologists should expand their theoretical assumptions to consider the Lande-Kirpatrick's improvements on Darwin's original model as the null hypothesis regarding intersexual selection.

Crespi et al. review the central Darwinian mechanism of mating competition among conspecifics (sexual selection) proposed as an important evolutionary force explaining the apparent enigma of exaggerated colorful or otherwise costly traits. Darwin's concept of sexual selection was further advanced by several scholars including "runaway" selection, which could happen if choice was based on comparisons favoring relative extremes. The authors then present Alexander (1990) concept of runaway social selection arguing that an arms-race competition among individuals for social skills (and weapons) was at the core of human evolution. Runaway social selection suggests that humans generated and became their own primary selective pressures in arenas of social within-group and between-group competition, allies or partner selection, mate choice, caregiver-offspring relationships, and cultural traits and social-cultural learning. Crespi et al. argue that each of these arenas of social selection drove the evolution of different, interacting dimensions of human sociality and culture, and that they merged to shape the humans inhabiting the current world.

Papers on arts, creativity, music, and play

When Darwin argued in favor of the universality of the human mind, he highlighted the shared pleasures that populations around the world take in singing, dancing, acting, painting, tattooing, and self-decorating. Varella explored the evolved structure of artistic motivation using a large three decades-long real-life public database from university applications in Brazil. He predicted that an evolved artistic motivation would be specific, intrinsically sourced, and temporally stable. After analyzing reasons for career-choice in two studies, he found that applicants for artistic careers specifically and consistently through time reported more intrinsic reasons, such as personal aptitude, compared to applicants for non-artistic careers. He was able to provide evidence against Steven Pinker's non-adaptationist hypothesis that artistic activities are motivated by a generic "hunger for status", given that social prestige and other extrinsic reasons were quite low in applicants for artistic careers. He also found that probably there is a singular psychological mechanism for artistic motivation intrinsically influencing all different artistic modalities.

Darwin also argued that inclinations toward music, arts and creative expressions evolved in both sexes through sexual selection as a form of courtship display. Marin and Rathgeber present data on the sexual selection hypothesis for the evolution of human musicality in an instrumental music priming study in which they tested whether musical priming increased sexual attraction as assessed through ratings of facial attractiveness and dating desirability. While an increase in dating desirability was reported by both sexes, only females reported greater ratings of attractiveness on the part of males post prime. This highlights several points. It supports a link between music/creativity and mate choice but it also echoes the findings of others that multiple cues are relevant in mate choice and some cues may be more influential in female vs. male choice as seen in the stronger effects of the music prime on females.

Varella et al. expanded on the theme of sexual selection influencing the evolution of artistic and athletic propensities by performing the first direct comparison between the strength of intersexual and intrasexual selections acting on inclinations toward literary, visual, musical, and circus arts and sports. They analyzed self-perceived talent and expertise, proxies of intersexual selection such as mate value and sociosexuality, and proxies of intrasexual selection such as aggressiveness and intrasexual competitiveness in men and women from Brazil and the Czech Republic. They found that intersexual selection was related to literary, musical, visual and circus arts in women, and to literary, circus arts, and sports in men, while intrasexual selection was related to literary, musical, visual arts, and sports in women, and to literary, musical arts, and sports in men. Sexual selection was most strongly related to artistic inclination in women, and sports in men. They conclude that cross-culturally both sexes use some artistic inclinations as ornaments and armaments, although more as ornaments in women, and armaments in men; while sports function as ornaments and armaments only in men, and as armaments in women.

General creativity as a sexually selected psychological trait in women was investigated by Galasinska and Szymkow. They used a within-subject design and indirect hormonal measures to test whether creativity (i.e., fluency, flexibility, and originality of unusual uses for everyday objects) is higher during the fertile phase of the menstrual cycle. They found that Polish women had more original ideas during the ovulatory phase, despite having roughly the same number of ideas (i.e., fluency) during other phases of the menstrual cycle. When the fertile phase was compared to all non-fertile phases combined, they also found high flexibility (i.e., breaking a pattern) of ideas during the ovulatory phase. Given that their results were not mediated by arousal or positive mood, they conclude that creativity may be a mental ornament in women, which suggests possible ancestral influences of male choice on female creativity.

Novaes and Natividade narrowed it down to ornamental creativity, the psychological capacities that produce and appreciate aesthetically conspicuous manifestations. They offered an updated and comprehensive review of the converging evidence pointing to the influence of sexual selection on creative ornamentation. They pointed out that although associations between tendencies toward ornamental creativity and individual attractiveness or mating success are good indications of the power of sexual selection, it is not sufficient for establishing with high certainty the role of sexual selection. Thus, Novaes and Natividade compiled evidence stemming from proximate mechanisms such as neurobiology, heritability and hormonal influences, ontogenetic and social factors, and phylogenetic and comparative findings from other species. By considering Tinbergen's four questions and creating a nomological network of evidence they were able to empirically fundament the conclusion that sexual selection indeed influenced the evolution of human ornamental creativity in both sexes. They have presented the gaps in the knowledge and offered routes for future research.

Moraes et al. approached playfulness, play and play-like activities through sexual selection. They noticed that while sexual selection has been applied to many activities that are considered "play" (e.g., play music, role-playing, play sports), there are few studies applying sexual selection to adult play and gaming tendencies *per se*. They conceptually differentiated between the behaviors of play and the underlying psychological capacities, such as playfulness or competitiveness. They defined, differentiated, and dissected the constituent parts of the concepts of playfulness, play, and games. The result was a compilation of converging evidence supporting the notion that both play and games are evolved capacities in human nature, such as universality, precocity, and heritability, and emphasized indications of sexual selection, such as sex differences and relationship to mating success. They concluded by offering a number of suggestions, including considering the underlying psychological components of behavior, cross-cultural and inter-specific evidence, ecology validity, and the alignment of Tinbergen's questions with cultural explanations.

Papers on parenting and alloparenting

An unusual feature of human evolution is the reduction of overall body hair compared to other primates. The majority of theoretical and empirical research discusses how reduced body hair evolved for thermoregulation (Wheeler, 1992), reduced parasite loads (Rantala, 2007; McIntosh et al., 2017), and mate choice (Dixson et al., 2019). Amaral approaches how humans evolved reduced hirsutism from the novel perspective of parenting. Building on her previous research on this topic (Amaral, 2008), phylogenetic comparative analyses are employed testing the tensile properties of primate hair suggesting that infants clinging to body hair were crucial for their safety during maternal tripedal movement. Amaral emphasizes that safe infant caring and sexual selection might have influenced the evolution of bipedalism in humans. She then proposes that reduced hirsutism co-evolved with bipedalism in humans via natural selection in concert with other selective pressures (e.g., thermoregulation) and cultural solutions such as huddling developed for thermoregulation in the absence of pronounced body hair. Amaral invited researchers to approach the evolution of human bipedalism aligned with reduced hirsutism as a solution to a female problem of safe carrying infants, not so much a male acquisition for throwing stones, for instance.

Daly and Perry's article focused on what sexual selection theory brings to our understanding of stepparenting and stepfamily dynamics. Highlighting the problem first with reference to non-human animals, the decision for a new mate with regard to existing offspring can be summarized by the question "Kill, ignore, or adopt?" Research has suggested that the adopt option can be understood as a part of courtship in many species and this can be seen as the product of species typical ecologies. Despite this, within species variation exists, perhaps nowhere so much as in humans. Sexual selection and parental investment theory suggest testable hypotheses about what factors predict this variability in stepparental behavior. They review the fitness consequences not only in birds but in humans, noting the recurrent presence of step-parenting over historical time, viewing stepparenting as a special case of discriminative parental solicitude in response to ecological conditions that range from local sex ratios, mortality, resource availability, and individual child traits. They suggest that our understanding of stepfamily dynamics will benefit from hypothesis testing shaped by an understanding of sexual selection and discriminative parental solicitude.

The study by Semenova et al. contributes to the understanding of evolutionary dynamics in parental conflicts by exploring some under-researched cases. The study's conclusions highlight the importance of considering sex-biased asymmetry in potential fitness gains in understanding human reproductive behavior. Specifically, models that provide new insights into the evolution of parental care are presented. One interesting finding from the study is the possibility of population division as an evolutionary outcome of human mating interaction, where "reproductive defection" serves as the best response to any action by a potential sexual partner. The study's models are particularly pertinent to sexual conflict in humans, where child rearing is a long and costly process and partner defection can greatly disrupt parental investment. Semenova et al. suggest that under a certain payoff matrix, avoiding risky reproduction represents a relatively cost-effective decision for humans of both sexes. The final model predicts that individuals who adopt cooperative reproductive strategies could cluster together in geographically, linguistically,

or religiously structured populations, potentially leading to population clustering. The propensity for population separation, and the biological prerequisites for the emergence of morality have not yet been considered in the literature under a parental game theoretical approach. Authors hope to spark discussions among scientists from diverse fields, leading to renewed efforts to explore the evolution of parental care in diverse environments and cultures. Overall, the study offers new perspectives and avenues for future research in the field of evolutionary biology dealing with sex differences.

Papers on sexual dimorphism

The evolution of marked variation in olfactory cues, cutaneous characteristics, and somatotypes have only recently received attention among researchers studying sexual selection in humans (Štěrbová et al., 2018; Dixson, 2021; Valentova et al., 2021). Sex differences in body composition, notably muscularity and body size are some of the largest between women and men (Wells, 2007), which are often attributed to effects of sexual selection via mate choice (Dixson et al., 2010; Brooks et al., 2015). Lassek and Gaulin challenge this view using a large dataset from the NHANES and demonstrate small sex differences in stature, but marked differences in muscularity and body fat. Compared to women, men had 72% higher arm muscle, 65% greater muscle mass, and 36% greater lean muscle mass. Conversely, women store more than 1.6 times more body fat, the distribution of which is sexually dimorphic wherein women store greater gluteal femoral fat (i.e., the hips, buttock, and thighs) whereas men store more fat in the belly and midriff. Lassek and Gaulin conclude that women's body fat is naturally selected as reserves for neural development for the fetus during pregnancy, while men's muscularity and strength function for male-male competition for resources (Apicella, 2014), which may secondarily influence women's mate preferences for muscularity (Dixson et al., 2014; Lidborg et al., 2022).

One possible way to study sexual dimorphism is to view it developmentally. In a long-lived species like *Homo sapiens*, one would hypothesize that different life stages might be characterized by sexually differentiated adaptations in response to environmental challenges that impact the sexes differentially. Goetz et al. critique the field of Developmental Psychology, which, for many reasons, has minimized evolutionary and adaptationist explanations in favor of seeing socialization as explaining developmental changes. The authors argue that Developmental Psychology's failure to use ideas from Sexual Selection theory has led to an impoverished understanding of phenomena like children's playground behavior. There have, however, been some notable exceptions; Sexual Selection theory was utilized by Silverman and Eals (1992) to provide strong evidence for the hunter-gatherer theory (a truly integrative theory) of spatial skills development in children. They conclude by suggesting that an evolutionary and functional view of human mind and behavior once adopted by Developmental Psychology could take the field forward into a more accurate and robust understanding of developmental pathways.

Mezentseva et al. performed an experimental study, investigating gender differences in recognition of basic emotions (i.e., happiness, disgust, fear, and anger) among traditional Mongolian nomads of Southern Siberia, Tuvans. Unlike most previous studies, the authors reported no gender differences in the recognition of happiness, disgust, and fear in facial photographs of men and women. However, there were significant gender differences in anger recognition, where Tuvan men, compared to Tuvan women, were more accurate in labeling anger displays of men from their own population. The authors suggest a role for cultural conditioning in women's poor communication abilities. Even today, Mongolian cultural traditions encourage division of labor, where women's occupation and social environment are limited to the household, and prescribe limited contact between strangers of opposite sexes. Nevertheless, the reasons for Tuvan women's particular insensitivity to men's angry facial expressions remain poorly understood and require further research.

The results of an experimental study investigating trust and trustworthiness among strangers were presented by Rostovtseva et al.. The experiment combines a game-theoretic approach, video stimuli presentation, and the use of geometric morphometrics. In the paper, the authors have demonstrated that trust toward strangers is manifested at a remarkably high level, and is partly determined by the sex and appearance of an interaction partner. Generally, women elicited more trust in partners of both sexes, which supports previous findings. However, women more willingly trusted men with a more masculine facial appearance, while men themselves, on the contrary, did not trust them. According to the literature, men with highly masculinized faces tend to demonstrate less trustworthiness (Stirrat and Perrett, 2010). The authors suggest that one of possible explanations for the revealed female preferences could be that women find masculine male faces attractive for short-term sexual relationships, which may modulate their trusting behavior for the wrong reasons. The study illustrates the differential impact of male masculinization on the behavior of interaction partners of the same and the opposite sex. Despite a clear effect of sex and facial appearance on eliciting trust in strangers, actual trustworthiness was not associated either with sex or appearance. The revealed results raise the question of the adaptive value of the observed behavioral responses to partners' sex and sex-related facial traits.

Papers on signaling, mate preferences, sexual strategies

Mailhos et al. investigated association between such male voice parameters as frequency (F_0), formant dispersion, formant position or vocal tract length, and body size, as well as physical strength measured by handgrip strength. They confirmed some of the previous results on the relationship between vocal parameters and the key determinants of male physical formidability. They showed, for instance, that handgrip strength is negatively related to F_0. It was also true when controlled for body height or weight. The authors also studied if voices of the weakest and the strongest men differed in attractiveness assessed by females, and did not find any association between male speakers' strength and perceived attractiveness by females. This study contributes to our understanding of the meaning of human male vocal characteristics as a potential cue or signal that could be important for the assessment of a men's physiological condition.

The conceptual paper, by Gangestad and Dinh, brings together questions of how and why women's sexual interests vary across the ovulatory cycle. One reliable empirical finding is that sexual desire increases when conception is more likely. But this is not the only time that women experience sexual desire, they are also interested in non-conceptive sex. The question is how to make sense of this finding as well as others in the literature. The authors suggest that we need to place more emphasis on the strategic analysis of behavior. It is likely that the circumstances that result in greater sexual interest during conceptive and non-conceptive phases of the ovulatory cycle are different. Sex in these different phases (i.e., mid-cycle vs. other phases) can have different functions and the different sexual interests may be motivated by different goals or strategies. Taking a more design feature or reverse-engineering approach is likely to be beneficial in combination with new theories to guide, not only future research on the role of extended sexuality in women, but our interpretation of the results.

Pisanski et al. investigated if mate preferences for body height in several countries (i.e., Canada, Cuba, Norway, and USA) depend on sexual strategies. They examined this via graphic stimuli containing metric indices. They confirmed the "male taller norm" in all countries. Relative to their own body height, men preferred shorter, and women taller sexual partners. What was, however, the most interesting result was that only men showed a different preference for their partner's height in relation to their sexual strategy. When choosing a partner for short-term relationships they preferred greater sexual dimorphism (i.e., relatively shorter partner than themselves) than when choosing a long-term partner. Women preferred the same partner height irrespective of the relationship context. This study adds new cross-cultural evidence for the importance of relationship context when mate preferences are concerned.

Sexual selection theory offers an essential framework for understanding the real world dynamics of gender roles, mate selection, sexual activity, and reproductive rates. Zhao et al. investigated these interactions in a sample of young Chinese adults, focusing on the relationship between androgyny and sexual activeness, with self-reported physical attractiveness, sexual motivation, and interpersonal relationships as mediators. Results were consistent with existing evidence suggesting that indeed there is a relationship between greater androgyny (i.e., lower adherence to gender roles as self-reported) and less self-reported heterosexual activity. The mediation results provide stimulating ideas for further research on these questions.

Conclusion

This Research Topic offers new critical developments, fresh ideas, and solid results furthering Darwin's legacy on sexual selection applied to human evolution. Such accomplishment could only be possible with a large set of authors from diverse backgrounds and countries from North, Central and South America, Europe, Asia and Oceania. We present articles from a total of 56 authors from 17 countries: two from Austria, six from Brazil, seven from Canada, three from China, two from Cuba, two from the Czech Republic, one from France, two from Germany, one from Netherlands, one from New Zealand, one from Norway, three from Poland, six from Russia, four form Spain, one from the United Kingdom, three form Uruguay, and ten from the United States of America. In total, this rich combination of authors produced outputs from six different types of articles: seven original research articles, three perspective articles, two hypothesis and theory articles, four brief research reports, one conceptual analysis, and three reviews. We can safely conclude that this was the largest, most diverse, and highly promising sesquicentenary thematic issue of its kind.

Aligned with Darwin's *The Descent of Man, and Selection in Relation to Sex* original book (1871), the past celebratory pieces that followed, such as the classic centennial celebratory book titled *Sexual Selection and the Descent of Man, 1871–1971* edited by Campbell (1972), have also brought valuable insights and progress to the field. We hope we have helped assemble a strong set of empirical and theoretical articles in this Research Topic promising progress and future novel evolutionary hypotheses and conclusions.

Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Evolution by Sexual Selection

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Charles Darwin published his second book "Sexual selection and the descent of man" in 1871 150 years ago, to try to explain, amongst other things, the evolution of the peacock's train, something that he famously thought was problematic for his theory of evolution by natural selection. He proposed that the peacock's train had evolved because females preferred to mate with males with more elaborate trains. This idea was very controversial at the time and it wasn't until 1991 that a manuscript testing Darwin's hypothesis was published. The idea that a character could arise as a result of a female preference is still controversial. Some argue that there is no need to distinguish sexual from natural selection and that natural selection can adequately explain the evolution of extravagant characteristics that are characteristic of sexually selected species. Here, I outline the reasons why I think that this is not the case and that Darwin was right to distinguish sexual selection as a distinct process. I present a simple verbal and mathematical model to expound the view that sexual selection is profoundly different from natural selection because, uniquely, it can simultaneously promote and maintain the genetic variation which fuels evolutionary change. Viewed in this way, sexual selection can help resolve other evolutionary conundrums, such as the evolution of sexual reproduction, that are characterised by having impossibly large costs and no obvious immediate benefits and which have baffled evolutionary biologists for a very long time. If sexual selection does indeed facilitate rapid adaptation to a changing environment as I have outlined, then it is very important that we understand the fundamentals of adaptive mate choice and guard against any disruption to this natural process.

Keywords: natural selection, sexual selection, mate choice, mutation rate, adaptation, rate of evolution

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INTRODUCTION

The reason that Darwin (1859) published a second book after the Origin of Species was revealed in a now famous comment in a letter to Asa Gray in 1860 just a year after the publication of the Origin: "the sight of a Peacock's train whenever I gaze at it makes me sick" (Burkhardt et al., 1993). His crucial insight was that the existence of the peacock's train could not be explained by his theory of evolution by natural selection. Darwin's second book, published in 1871 (Darwin, 1871), outlined

his theory of evolution by sexual selection. In this book Darwin suggested that the costly peacock's train evolved because females prefer to mate with males that have fancy upper-tail coverts. This book was controversial at the time, and research on sexual selection only really started in earnest in the late 1970s (Hoquet, 2015). Sexual selection is still controversial (Charlesworth, 1988; Clutton-Brock, 2010; Hoquet, 2015), and the aim of this article is to ask whether Darwin was right to distinguish sexual from natural selection. Are the two processes fundamentally different, and, if so, in what way?

WHAT IS THE EVIDENCE FOR FEMALE CHOICE AND WHY DO FEMALES SHOW MATE PREFERENCES?

Tim Halliday and I provided some of the first evidence testing Darwin's idea (Petrie et al., 1991) in peafowl. The main empirical support for active female choice comes from observations of marked females visiting a lek site. Females always approached more than one male before mating and the male chosen almost invariably had the highest number of eyespots in the train of those visited (see **Table 1**). Experimental removal of eyespots resulted in a reduction in mating success (Petrie and Halliday, 1994). These results have been replicated by others, although it must be said that not all peafowl researchers are unanimous in their views on the evolution of the peacock's train (Yasmin and Yahya, 1996; Loyau et al., 2005, 2008; Takahashi et al., 2008; Dakin and Montgomerie, 2009, 2011; Harikrishnan et al., 2010).

However, this empirical support instantly raised the question; why do peahens prefer to mate with peacocks with fancy trains? Theories of female choice have proliferated but, broadly, females could either gain direct benefits from their choice, where males provide resources that directly help females successfully reproduce, or indirect genetic benefits (Kirkpatrick and Ryan, 1991), where mating with a particular displaying male results in higher offspring fitness. Female choice is a characteristic like any other, and to have evolved the benefits of choosing between males must outweigh the costs. In peafowl, there is a *prima facie* case for indirect genetic benefits or "good genes" driving the mating preferences of peahens, since peacocks classically provide no resources other than seminal fluid to aid female reproduction. They do not fertilise more eggs per female (Birkhead and Petrie, 1995), they do not courtship feed, they do not defend females from other males, they just stand displaying on the same small spot looking beautiful, and females are free to move between males (Petrie et al., 1991; Harikrishnan et al., 2010). This has led some to suggest that peahens incur few costs when choosing between males on leks and there is no need to evoke any benefits to mate choice; female choice is arbitrary and has no utilitarian function (Hoquet, 2015). However, this thinking ignores the fact that there is a huge inherent cost associated with choosing to mate with a displaying male that provides no paternal care for offspring (Petrie and Lipsitch, 1994). Moreover, given that there is marked variation in male mating success on peacock leks with most males achieving no copulations at all, it is very hard to understand how such a system could be evolutionarily stable for both males and females.

TABLE 1 | Males visited by marked individual peahens.

(1) A (147), B (161)
(2) C (155), D (152), E (157), D (152), E (157)
(3) D (152), D (152), F (141), D (152)
(4) F (141), F (141), A (147), F (141), D (152), G (141), E (157), E, E, E, E, E, E (157)
(5) F (141), D (152), E (157),E (157), D (152), F (141), D (152), C (155), E (157), G (141), D (152), D (152), E (157)
(6) D (152), D (152), D (152), E (157), E (157)
(7) F (141), H (153)
(8) A (147), F (141), D (152), D (152), E (157)
(9) H (153), D (152)
(10) G (141), F (141), D (152)
(11) F (141), A (147), B (161), B (161)

The above was originally published in Animal Behaviour in 1991. It shows the movements of 11 marked females between males on one lek site (flint pit paddock) at Whipsnade from the time that they first visited males (A–H) until they mated with the last male visited. The numbers in brackets are the numbers of eyespots in the trains of the males visited. For example, female 2 visited three different males before mating with the male E. These data provide clear evidence of active female choice. Peahens always visit more than one male before mating and, in 10 out of 11 cases, females finally mated with the male with the highest eye-spot number of those visited (best-of-n). This is good evidence that eye-spot number or something closely related to it is important for female choice. Alan Grafen kindly analysed these data to take account of the fact that several of the males appeared more than once in the choice sets but, he concluded that it was very unlikely that this result could have occurred by chance. Other models were tested, and Alan found that the only other model that could potentially explain the pattern was that the female mated with the male that had more eyespots than the last one visited. However, this condition is satisfied earlier on in many of the choice sets and he concluded that the best-of-n model provided the best fit to the data. See Petrie et al. (1991) for further details.

WHY DO FEMALES PREFER TO MATE WITH DISPLAYING MALES THAT PROVIDE NO PATERNAL CARE?

In 1994, using a game theoretical modelling approach, Mark Lipsitch and I considered why a mutant gene for caring does not invade a population of displaying males. Surely a mutation for caring which arose in an unsuccessful displaying male would spread through a population as females could increase their reproductive success with male help (Petrie and Lipsitch, 1994). We showed that the invasion and stability conditions for female choice for displaying males are satisfied only if the benefits of choice are greater than the cost of lost male care. If females are only gaining indirect genetic benefits, then these conditions are satisfied only when the amount of variation among males in genetic quality is large. However, this raises yet another serious problem for evolutionary theory as Fisher's fundamental theorem states that there is always diminishing heritable variation in fitness-related traits, because strong directional selection would quickly remove any genetic variation (Fisher, 1930). Female choice for "good genes" can only evolve and be maintained if there are genetic quality differences between males. The main problem therefore is that even if males varied in genetic quality,

strong directional selection would quickly remove it and all males should then be of similarly high quality. This is sometimes known as the lek paradox (Pomiankowski and Møller, 1995). There are a number of theories that have been proposed to explain the lek paradox and the most commonly cited is that there is variation in condition dependent traits which could potentially reflect variation in a large number of genes (Kotiaho et al., 2008).

COULD MUTATION PROVIDE THE GENETIC VARIATION REQUIRED TO MAINTAIN COSTLY FEMALE CHOICE?

Mutation is the ultimate source of all genetic variation, so could mutation provide the genetic variation required to maintain costly female choice? Mutations are mainly harmful, for every beneficial mutation with an increase in fitness there are very many more deleterious mutations which reduce fitness and some lethal mutations, so it is thought that natural selection will always act to keep the mutation rate as low as possible (Eyre-Walker and Keightley, 2007). And it is true that several DNA repair mechanisms have evolved to ensure fidelity in DNA replication.

The main problem of how genetic variation is maintained in the peacock's train is even more acute when the empirical evidence from peafowl is considered. Not only do fancy peacocks have higher mating success (Petrie et al., 1991; Petrie and Halliday, 1994), they also have higher survivorship (Petrie, 1992; Jennions et al., 2001), their offspring survive better (Petrie, 1994; Hale et al., 2009), and females lay more eggs for males with fancy trains (Petrie and Williams, 1993; Loyau et al., 2007), so strong directional selection would remove any variation pretty quickly. But, observably it doesn't (see photo **Figure 1**) and if one looks at the coefficient of additive genetic variance in sexually selected traits, we find that, in general, there is more and not less genetic variation in sexually selected characteristics (Pomiankowski and Møller, 1995; Pike et al., 2009). This fact alone demands a different sort of explanation where sexual selection **promotes** rather than depletes genetic variation.

So how could sexual selection promote genetic variation? In 1997, Tadeii et al. published a manuscript in *Nature* which described the action of a mutator gene, one that could control the rate of mutation, basically, a mutated DNA repair gene (Taddei et al., 1997). They argued that if an elevated mutation rate became associated with a beneficial mutation it could hitch-hike into a population and that this association could provide a continual source of genetic variation. However, the authors concluded that this would only be likely to be important in asexual prokaryotes because the recombination that occurs in sexually reproducing eukaryotes would quickly disrupt the genetic hitch-hiking and the mutated gene would be selected against (Taddei et al., 1997). It occurred to me that whilst this may be true in situations without sexual selection, if there is an element of female choice for males with beneficial mutations and rejection of any males with deleterious mutations, so that the level of fitness is revealed in some way by the degree of train elaboration, then maybe a higher mutation rate could be sustained in a sexually reproducing species (Petrie and Roberts, 2007).

CAN SEXUAL SELECTION MAINTAIN A HIGHER MUTATION RATE?

I visited Geoff Parker in Liverpool in 1997 to discuss this possibility and, although he had some doubts, he broadly thought it was an interesting idea and suggested I submitted a note to *Nature*. Unfortunately, it did not pass muster with the referees who were not convinced by a simple verbal model, and it took a further 10 years before the manuscript was finally published. Using a simulation modelling approach conducted by Gilbert Roberts, we showed that female choice of a male with higher fitness (higher offspring survival and mating success) was sufficient to raise the rate of mutation in a population of displaying males when compared to that sustained in a population where mating occurred at random (Petrie and Roberts, 2007). Moreover, female choice selecting the fittest of just two males was sufficient to double the rate of mutation over that seen under random mating. This process provides a self-sustaining solution to the lek paradox, as the more males females choose between, the higher the relative male fitness a female gains and, the greater mutation rate that can be sustained.

The greater the mutation rate sustained, the more it pays to choose between males and so on, thus resulting in a positive feedback loop between the level of genetic variation in the population and the level of female choice (Petrie and Roberts, 2007).

This idea is testable, and a few recent manuscripts have attempted to do this, the main predictions of the hypothesis are: -

1) Interspecific variation in the level of sexual selection will be positively related to genetic variability (Petrie et al., 1998).
2) There should be a higher mutation rate in species with more intense sexual selection (Møller and Cuervo, 2003; Ellegren, 2006; Anmarkrud et al., 2011; Baur and Berger, 2020).
3) Mutation rates should be higher in sexual as opposed to non-sexual traits (Møller and Cuervo, 2003).
4) There should be a higher rate of evolutionary change in sexually selected lineages (Lumley et al., 2015; Iglesias-Carrasco et al., 2019).

Of course, the actual tests of these predictions depend on the measures of both the degree of sexual selection and the genetic mechanism that controls the rate of mutation. Whilst I originally imagined a mutator gene as the disruption of a DNA repair gene there are several other possible mechanisms that can give rise to adaptive variation, such as that accompanying transposable elements or loss of function genes (Lynch et al., 2016; Charlesworth et al., 2017; Murray, 2020). Moreover, the different mechanisms are not necessarily always inevitably affected by recombination. There is now evidence for recombination low spots in the genome for example, classically there is very little recombination at the MHC (Nachman, 2002). There is also evidence for mutational hot spots, so any mechanism for generating mutation does not necessarily affect the whole genome (Lynch et al., 2016). Next generation sequencing opens up many possibilities for testing the idea at the genomic level. Hopefully, it

FIGURE 1 | Photograph of two unmarked lek males sitting side-by-side on a fence at Whipsnade. The photograph whilst of quite poor quality clearly shows that there is marked variation in both the length and breadth (number of feathers) in the male's trains (copyright M. Petrie).

will be possible to identify and distinguish the different signatures of sexual and natural selection.

I believe Evolution by sexual selection to be a fundamentally different process to Evolution by natural selection and that Darwin was right to distinguish the two processes. John Maynard Smith, who was my personal tutor when I was an undergraduate at Sussex University from 1972 to 1975, said amongst many other sensible things, "that if you can't write it on the back of a matchbox you haven't understood it". So, I'm now going to summarise what I think I have said mathematically, which illustrates what I believe to be the main fundamental difference between natural and sexual selection.

Under natural selection the rate of evolutionary change (E_n) in a phenotypic character is proportional to the amount of genetic variation among individuals in a population in that character, the additive genetic variance (V_A) and the strength of natural selection (S_n). Where the strength of selection (S_n) is the relative increase in the number of offspring surviving to reproduction with that character.

$$E_n \propto V_A \times S_n \tag{1}$$

Under sexual selection the rate of evolutionary change in a character (E_s) is also proportional to V_A and the strength of selection. However, the strength of sexual selection is proportional to the relative increase in the number of offspring surviving to reproduction (S_n) **and** the relative number of mates a male (N_m) with that character obtains, since the number of gene copies in the next generation is also dependent upon relative mating success.

$$E_s \propto V_A \times S_n N_m \tag{2}$$

However, under sexual selection the amount of genetic variation is also proportional to the strength of selection on the rate of mutation (μ)

$$V_A \propto \mu \times S_n N_m. \tag{3}$$

So, under Sexual selection and, substituting 3 in 2, gives,

$$E_s \propto \mu \times (S_n N_m)^2 . \tag{4}$$

The rate of evolutionary change is therefore much greater under sexual selection, where the strength of selection is potentially magnified by mating success **and** where sexual selection can promote the rate of mutation. These are, in my opinion, the fundamental differences between natural selection and sexual selection which warrant Darwin's decision to treat the two processes separately.

DISCUSSION

Sexual selection is a much more powerful evolutionary force than natural selection because variation in mating success can magnify selection and simultaneously promote and maintain novel genetic variation among individuals, which ultimately fuels rapid evolutionary change.

Interestingly, if an unsuccessful male on a peacock lek with lower-than-average fitness (as a result of deleterious mutations)

gains no mates at all (normally the majority of males on a lek), then the net rate of evolutionary change on a phenotypic character is zero. Only when the relative fitness of a male is greater-than-average (as a result of a beneficial mutation) will selection result in rapid adaptive change since only these males will gain mates. An increase in the rate of mutation via a mutator gene will therefore also only occur if the mutator gene is linked to a beneficial mutation which can hitch-hike into the population. The self-sustaining positive-feedback loop in the level of additive genetic variance that results from this process maintains the female preference for males that do nothing but show-off their good genes.

I don't think that the precise form of the mate preference function used in the model is important. Females do need to choose males and unless there are genetic differences between males there is no basis for female choice. A non-linear preference function as well as a linear preference function in relation to male quality would in my opinion produce the same qualitative result. The number of mates obtained by any one male, however, will quantitatively affect the strength of selection for the genetic characteristics of that male.

Although the natural history underlying the model is based on inter-sexual selection or mate choice for males (epitomised by the lek mating system of peafowl) with a character that reveals their underlying genetic quality, there is no reason to believe that the fundamentals of this process cannot also be applied to intra-sexual selection, where the outcome of contests between individuals of the same sex determines mating success. Wherever there is variance in mating success which is ultimately determined by variation in genetic quality then there is the opportunity for very rapid evolutionary change.

Sexual selection when viewed in this way has the potential to explain other evolutionary problems (Sheratt and Wilkinson, 2009) that are characterised by having impossibly large costs and no obvious immediate benefits and that have baffled evolutionary biologists for a long time, such as the evolution of sexual reproduction and the existence of males (Smith, 1986; Agrawal, 2001; Siller, 2001; Whitlock and Agrawal, 2009; Roberts and Petrie, 2021). The problem with the evolution of sexual reproduction can be briefly summed up as the cost of producing males. The number of offspring produced by an asexual female is twice that produced by a sexual female (producing equal numbers of male and female offspring) since males cannot produce offspring by themselves. In order to overcome this large numerical cost a sexually produced offspring must be twice as fit as an asexually produced offspring.

Only if there are genetic differences between males in a population will it pay females to outbreed in order to exchange their male genes to increase the genetic quality of their offspring. Both Agrawal (2001) and Siller (2001), modelled the effect of sexual selection on the production of males and, concluded that the function of males in a sexually reproducing population was to remove bad genes or reduce the genetic load of a population (Whitlock and Agrawal, 2009). If sexual selection functions in the way I have described above, then sexual selection for good genes will provide a short-term advantage to produce males and rapidly facilitate the evolution of sexual reproduction (Roberts and Petrie, 2021).

If sexual selection does facilitate rapid adaptation to a changing environment then it is very important that we understand the fundamentals of adaptive mate choice and guard against any disruption to this process. This is especially true when thinking about the conservation of species facing rapid climate change (Gosling and Sutherland, 2000) or adaptation to the emergence of new zoonotic diseases (Zuk, 2002) such as Covid-19.

Any process that interferes with a female's ability to discriminate between potential mates is a threat to the fitness of a population. The prevention of adaptive female choice in humans can be imposed politically or by religious doctrine and this can and does occur in human populations. Arranged marriages, forced matings and excessive control of female behaviour in societies can result in sub-optimal, maladaptive matings which in turn can adversely influence offspring health. The concomitant effect of these practices or of any environmental pollutants such as artificial chemicals and drugs on adaptive mate choice behaviour, is not routinely considered and, given the importance of gaining good genes for offspring survival to reproduction in all species, it strikes me that this is a major oversight.

We live in a rapidly changing world, I would argue that it is now imperative that in 2021, the 150th anniversary of the publication of Darwin's theory of evolution by sexual selection (1871), we finally accept that sexual selection is a major force in adaptation and evolutionary change and needs to be taken much more seriously.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Evolved Features of Artistic Motivation: Analyzing a Brazilian Database Spanning Three Decades

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Darwin explored the evolutionary processes underlying artistic propensities in humans. He stressed the universality of the human mind by pointing to the shared pleasure which all populations take in dancing, engaging in music, acting, painting, tattooing, and self-decorating. Artistic motivation drives/reinforces individuals to engage in aesthetically oriented activities. As curiosity/play, artistic behavior is hypothesized as a functionally autonomous activity motivated intrinsically through an evolved, specific, and stable aesthetic motivational system. The author tested whether artistic motivation is rather intrinsically sourced, domain-specific, and temporally stable using a large decades-long real-life public Brazilian database of university applications. In Study I, the author analyzed reasons for career-choice responded to by 403,832 late-adolescent applicants (48.84% women), between 1987 and 1998. In Study II, the author analyzed another career-choice reason question responded to by 1,703,916 late-adolescent applicants (51.02% women), between 1987 and 2020. Music, Dance, Scenic Arts, Visual Arts, and Literary Studies, in combination, presented a higher percentage of individuals reporting intrinsic factors (e.g., personal taste/aptitude/fulfillment) and the lower proportion reporting extrinsic motives (e.g., the influence of media/teacher/family, salary, social contribution/prestige) than other career groups. If artistic motivation were a recent by-product of general curiosity or status-seeking, artistic and non-artistic careers would not differ. Overall, intrinsic motives were 2.60–6.35 times higher than extrinsic factors; among artistic applicants' were 10.81–28.38 times higher, suggesting domain-specificity. Intrinsic motivation did not differ among artistic careers and remained stable throughout the periods. Converging results corroborated a specific, stable, and intrinsically sourced artistic motivation consistent with its possible evolutionary origins.

Keywords: arts, aesthetic behavior, motivation, career-choice, evolutionary psychology, domain-specificity, creativity, creative professions

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INTRODUCTION

In Darwin's currently sesquicentennial book "The Descent of Man, and Selection in Relation to Sex" (1871), he not only expands his theorization about human origins and common descent, but also addresses the evolution of many psychobehavioral tendencies of our species (Campbell, 1972; Richerson et al., 2021). The evolution of our artistic propensities was an important part of the book (Menninghaus, 2019). He stressed the artistic universality by saying that the close similarity between all human populations in "tastes, dispositions and habits" is revealed by

"the pleasure which they all take in dancing, rude music, acting, painting, tattooing, and otherwise decorating themselves" (p. 232). Darwin considered the human aesthetic and artistic tendencies both influenced by cultural and evolutionary factors, so he has opened fruitful lines of research that have since flourished.

Over the last decades, a growing body of literature considers artistic tendencies as part of human natural endowment, focusing on aesthetics (Voland and Grammer, 2003; Chatterjee, 2013), music, and dance (Wallin et al., 2000; Mithen, 2005; Ball, 2010; Bannan, 2012; Honing, 2018), literature and poetry (Carroll, 1995; Gottschall and Wilson, 2005; Boyd, 2009; Gottschall, 2012), visual arts (Coe, 2003), and arts in general (Dissanayake, 1988, 1992, 2000; Eibl-Eibesfeldt, 1989; Martindale et al., 2007; Dutton, 2009; Davies, 2012; Sütterlin et al., 2014; Hogh-Olesen, 2018; Menninghaus, 2019; Richards, 2019). However, there are also non-adaptive hypotheses, in which artistic activities would be a pleasurable technology (i.e., an unspecialized by-product of pre-existing capacities recently co-opted) (Pinker, 2004; Souza, 2004; Panksepp, 2009; Patel, 2010; Verpooten and Nelissen, 2012; Hodgson and Verpooten, 2015). To move beyond eventual "just-so stories" (Varella et al., 2013) and anecdotal evidence (Varella et al., 2017) on both sides, more high-quality empirical studies are still needed to tell apart adaptive and non-adaptive hypotheses about artistic propensities (cf. Andrews et al., 2002; Varella et al., 2012).

Many definitions of artistic-like activities stress manipulations performed to capture the attention, emotion, and imagination of others (cf. Varella et al., 2011, 2017). Varella et al. (2011) put together four independent lists of specific manipulations that artists employ to aesthetically enhance objects and behaviors to super-stimulate perceivers' appreciation. In effect, the interpersonal dynamics of artistic activities are akin to the multimodal signaling and communicative process (Varella et al., 2011; Valentova et al., 2017, 2019; De Tiège et al., 2021). The stimulating artistic activities are a result of human "artisticality"; a term that generically encompasses the propensities to ontogenetically develop psychological faculties that underlie a whole array of multimodal and extraordinary aesthetically enhancing activities, including behaviors, its products, and appreciations across cultures, historical periods, and species (Varella et al., 2017; Varella, 2018).

As for musicality (Bispham, 2009), artisticality has at least three main psychological components: capacities for (re)creative production (executive), aesthetic appreciation (perceptive), and artistic motivations (drive) (Varella et al., 2011, 2017; Watanabe, 2013). Artistic motivations are related to "the pleasures that we all take in" (p. 232) engaging in aesthetic/artistic activities, as Darwin (1871) has stressed. Artistic motivations drive and reinforce individuals to start and maintain engagement in artistic activities, both production and appreciation. Artistic motivation rewards and impels individuals to use their level of artisticality to actively or passively engage in aesthetically oriented activities with some level of commitment. Artistic motivation concerns both the drive to directly reach the final goal of producing and appreciating arts, and the drive to reach non-artistic commitments and sub-goals (e.g., face the traffic jam to visit the art museum, or to pass exams for an artistic career) which lead to the final goal of appreciating and producing arts.

Motivation can be broadly described as a modulating and coordinating influence on the direction, vigor, and composition of behavior that arises from a wide variety of internal, environmental, and social sources, and is manifested at many levels of the behavioral and neural organization (Shizgal, 2001). Traditionally, motivating factors are broadly divided into internal and external. Activities that provide their own inherent reward are considered intrinsically motivated (Deci and Ryan, 2000; Ryan and Deci, 2017). Whereas, extrinsic motivation refers to individuals' engagement in an activity to obtain some instrumentally distinct consequence, such as money or status (Deci and Ryan, 2000; Ryan and Deci, 2017).

The existence of specific feelings, desires, pleasures, or intrinsic motivation for a given activity possibly signals ancestral biological advantages and can be seen as an indicator of its evolved nature (Thornhill, 2003; Huron, 2005). To be converted into behavioral action, the outputs of cognitive mechanisms require motivational processes (Berridge, 2012; Anselme, 2016), which coevolve with the respective cognition (Ermer et al., 2008). The functional/adaptive significance of a given set of behaviors is dependent on the underlying cognitive capabilities and on the factors that motivate/sustain performance in appropriate contexts (Bispham, 2009). Thus, the behavioral expression of appreciative and executive artistic capacities needs to have a coevolved correspondent underlying motivational system. Uncovering the motivational basis of artistic propensities is a fundamental aspect of evolutionary theorization (cf. Merker et al., 2015).

Similar to curiosity and play, artistic behavior can be hypothesized as a functionally autonomous activity motivated rather intrinsically through an evolved and specific aesthetic motivational system. For instance, Morris (1962) concludes that the shared picture-making motivation in apes and humans has an element of self-rewarding activation. Csikszentmihalyi (1996) conceptualizes creativity as an autotelic activity that is enjoyable in itself. Watanabe (2013) concludes that the self-reinforcing power of the art-like behavior and the artistic product for the artist and conspecifics are mostly unique to humans. Darwin (1871) and Dutton (2009) considered the direct and universal artistic pleasure, and (Dutton, 2009) concluded that it is one of the main evolved features of human artistic instinct. Hogh-Olesen (2018) refers to the universal necessity to embellish the human body and surroundings and the desire to fill time and space with song, music, dance, and stories as the aesthetic impulse, a primary impulse inherent to human nature. These do not exclude the possibility that some external factors, such as social belonging or mate attraction, coul has stressed. Artistic motivations d also be important, and possibly even evolved, extrinsic motivations activating artistic tendencies (cf. Winegard et al., 2018).

Different lines of evidence seem to suggest the existence of an intrinsic motivational drive underlying artistic manifestation. Some evidence shows that a deep motivation toward artistic self-expression is uninhibited when the communicative channel of language fails following neurological damage (Zaidel, 2014).

In the majority of these neurological cases, patients increase the production of art, occasionally prolifically, emerging even if never previously expressed (i.e., *de novo* artist) (cf. Midorikawa and Kawamura, 2015), despite the damage's laterality or localization (Zaidel, 2014). The emergence of *de novo* artists after brain damage is not short-lived and the engagement in artistic expression tends to be compulsive and highly sustained (Abraham, 2019).

Another strategy to assess the importance of intrinsic motivation is to administer an external reward and evaluate whether it has negative effects on the behavior. Morris (1962) described when a chimpanzee once received food reward as drawing encouragement. However, the drawing aesthetic value was impaired; the ape took less interest in the drawing lines; any scribble would do and then it would immediately hold out its hand for the extrinsic reward. Similarly, intrinsically motivated paper collages done by 7–11 years old girls were evaluated as higher on creative expression than the extrinsically motivated group, which, in turn, was higher on the technical level (Amabile, 1982). Moreover, collages made by preschool children with a free choice of materials were judged by artists as more creative than those made by children for whom the experimenter chose the materials (Amabile and Gitomer, 1984). Further, non-rewarded artistic activity (collage-making, storytelling) is evaluated as more creative than the rewarded activity among both children and adults (Amabile et al., 1986).

Intrinsic motivation is also frequently assessed in terms of freely pursued activities. According to Cushman and Laidler (1990), leisure activity is pleasurable and intrinsically motivated, being an end in itself and valuable for its own sake. Aesthetics and artistic activities are among the most frequently spontaneously pursued free-time activities and hobbies (Kleiber et al., 1986; Chalip et al., 1996; Walker and Scott-Melnyk, 2001; Chamorro-Premuzic and Furnham, 2004; Furnham and Chamorro-Premuzic, 2004; McManus and Furnham, 2006; Mosing et al., 2015).

Intrinsic and extrinsic motivations can be explored by analyzing the explicit reasons for individuals' engagement with activities. Frequent participants of arts and cultural activities declare they want to support important community organizations and events through their participation, learn more about other cultures, and experience high-quality art (Walker and Scott-Melnyk, 2001). McCarthy and Jinnett (2001) found that personal interest in the artistic material itself, the desire to express themselves artistically, opportunity for social interaction, interest in learning more about the arts, education, enrichment, and accompanying a friend or a family member are among the reasons for taking part in artistic organizations. Swanson et al. (2008) found that recreation, aesthetics, social interaction, escape, education, and self-esteem were the reasons for attending performances of theater, comedy, and vocal popular music. Chong (2010) found that the reasons for enjoying singing were self-expression, aesthetic experience, interpersonal relationships, stress reduction/mood change, spirituality, empowerment/identity, and self-actualization. Despite not explicitly distinguishing between intrinsic and extrinsic factors, notably, some intrinsic factors are among the top-ranked reasons followed by some extrinsic factors related to social interaction. These findings strengthen the case for an evolved rather intrinsic artistic motivation.

Further, modularity, domain-specificity, or functional autonomy/specialization have been considered a hallmark of mental adaptation because different information-processing problems usually require different procedures for their successful solution (Cosmides and Tooby, 1994; Andrews et al., 2002; Barrett, 2008; Tooby and Cosmides, 2015). Thus, specialization was selected because it pays off in terms of solving problems faster and more efficiently (Cosmides and Tooby, 1994; Tooby and Cosmides, 2015). Watanabe (2013) stresses the functional autonomy of art-like behavior among animals, particularly in humans. Although no study has focused on how specific is artistic motivation, the cases of *de novo* artists following brain damage (e.g., Abraham, 2019), the cases of exceptional and unexpected artistic talent in young autistic individuals dissociated from their learning difficulties (e.g., Gordon, 2005; Zaidel, 2014; Paola et al., 2020), the domain-specificity of musical and aesthetic creativity (Feist, 2004), and the spontaneous choices of artistic leisure activities (e.g., McManus and Furnham, 2006) together indicate some level of specificity in artistic motivation. Thus, it is plausible that artistic motivations would present signs of domain-specificity.

Furthermore, the comparative evidence of homology indicates a deep-seated stable motivational tendency for aesthetic display. Great apes and humans share an element of self-rewarding activation during picture-making (Morris, 1962). Captive male orangutans spontaneously perform premeditated long nocturnal calls (Samson et al., 2014). Chimpanzees exhibit a spontaneous tendency toward entrainment and rhythmic synchronization (Hattori et al., 2013; Large and Gray, 2015), and in their natural environment, chimpanzees exhibit episodes of rain-dancing, pant-hoot chorusing, or "carnival displays" (Dufour et al., 2015). No study has investigated the temporal stability or long-term trends of artistic motivation; however, artistic interest is stable over individual ontogeny (e.g., Waller et al., 1995), early paleo art is antique and its occurence is somewhat constant since Middle Paleolithic (Henshilwood et al., 2018), and artistic manifestations have universal aspects, which indicates a stable motivational core for this tendency across-cultures (Brown, 1991; Dissanayake, 2008). Hence, it is also probable that artistic motivation is to a certain degree, temporally stable across generations, possibly detectable even in small time scales of a few decades.

Although corroborating, the existing literature has many limitations that hinder wide-ranging conclusions about the psychological structure of artistic motivation, regarding its source, specificity, and stability. Previous studies focus on a limited range of artistic activities, have relatively small samples, and tend to be restricted to one or a few North American or West European locations. This is far from representative of the diversity of human species (Henrich et al., 2010), which requires a more inclusive science of the human mind across cultures (Barrett, 2020), focusing particularly on less-studied populations such as in Africa and Latin America (Rad et al., 2018). In order to overcome these limitations, I investigated reasons for artistic commitment using a decades-long real-life

massive database from late adolescents applying to a public university in Brazil.

THE PRESENT STUDY

I tested whether artistic motivation is rather intrinsic, domain-specific, and temporally stable using explicit reasons for choosing a career through a university degree. Individual variation in vocational interests is among the most stable of all psychological constructs (Low et al., 2005), and during young adulthood there is an increase in interests related to "people" which comprises artistic, social, and enterprising (Hoff et al., 2018). Career choice is associated with many factors including individual cognitive style (Varella et al., 2016). The choice of artistic careers is a real-life situation and a crucial intermediary step toward an increased commitment to and engagement with artistic activities.

There is a socio-demographic questionnaire required upon registering for the entrance exams which had two multiple-answer questions about motives/reasons for choosing the main career: Study I focuses on the short-lived question (1987–1998) and Study II addresses the longstanding question about reasons for career application (1987–2020). The comparison among different classes of reasons for applying to a university degree indicates whether artistic motivation is more intrinsically or extrinsically sourced. The comparison between artistic and non-artistic careers and within artistic careers allows measuring how specific is the artistic motivational profile. The correlation between the examination year and classes of reasons indicates possible long-term temporal trends or stability (cf. Varella et al., 2016).

A non-adaptive hypothesis would likely predict that the intrinsic motivational factors related to artistic activities would be a direct and undifferentiated by-product of general curiosity. As such, it would predict no difference from non-artistic careers since curiosity arguably contributes to the choice of all careers. Further, Pinker (2004) stated that art (other than narrative) could be a by-product of three distinct pre-existing mental adaptations: the aesthetic pleasure of experiencing adaptive objects and environments (perception); the ability to design artifacts to achieve desired ends (production); and the hunger for status (motivation). Thus, according to Pinker (2004), the artistic activity would not be an end in itself, but rather another means to obtain social status and prestige. If that is true, I would find more extrinsic factors such as "influence of the family," "influence of the educational advisor," "social prestige," and "job market," and "ample possibilities of salary" as the main reasons for seeking artistic careers. Moreover, since the general hunger for status can possibly influence the choice of any career, there would be no profile difference between artistic and non-artistic careers. Finally, because the popularity and prestige of careers can change over the years, the non-adaptive hypothesis would predict that artistic motivation to be as influenced by historical and societal changes as non-artistic careers exhibiting long-term trends and being temporally unstable within the three decades' timeframe.

Aims

I tested whether artistic motivation is rather intrinsic, domain-specific, and temporally stable, as predicted for an evolved trait. Based on the above-mentioned literature, artistic activity is hypothesized as a functionally autonomous activity motivated rather intrinsically through an evolved, specific, and temporally stable underlying aesthetic motivational system. However, if the main motivational factors are general curiosity and/or general status-seeking, it is hypothesized that artistic motivation would be balanced between intrinsic and extrinsic factors, there would be no differences between artistic and non-artistic careers, and the interest in artistic career would trend upwards or downwards along with non-artistic careers following recent socio-historical factors. The author examined reasons for applying to an artistic career using a decades-long real-life massive database from late adolescents applying to a prominent public university in Brazil.

STUDY I

Materials and Methods

The author accessed public data available online from the *Comissão Permanente para os Vestibulares* (COMVEST) website.[1] COMVEST runs the entrance examinations to the University of Campinas (UNICAMP), one of the three main public São Paulo State universities (Brazil). UNICAMP is one of the most desired places to study and it involves real-life choices and implications, which gives an ecologically powerful measure of motivation and vocation. At the website (e.g., for 1998)[2] the data were collected from "vestibular" (i.e., university entrance exam), from "all cities," "all kinds of public" (including "open concurrence" and "quotas"), and from all individuals "applying" for the entrance exam, not only those who were later approved and actually signed up for the chosen career, because being approved requires more than only interest/motivation (e.g., preparation, competitiveness, good previous education).

The short-lived question about motives/reasons to apply for a university career lasts 16 years (1987–2003), but after 1999 all answer options indicating intrinsic motivations were removed, which made the test comparing intrinsic and extrinsic reasons unfeasible. Thus, the author used data only until 1998 (11 years' period). During this period, applicants could take the examination in up to 18 different medium-sized to large Brazilian cities (viz. Bauru, Campinas, Jundiaí, Limeira, Piracicaba, Presidente Prudente, Ribeirão Preto, Santo André, Santos, São José do Rio Preto, São Jose dos Campos, São Paulo, and Sorocaba, all from São Paulo State, and 5 other state capitals': Brasília/DF, Belo Horizonte/MG, Curitiba/PR, Rio de Janeiro/RJ, and Salvador/BA). This includes four out of the five Brazilian regions and six out of the 26 Brazilian states. Between 1987 and 1998, the phrasing of this specific question was: "What is the predominant motive for your choice of the course [career] for which you are applying as the 1st option?" In Brazil, the application involves two or three options of careers ranked

[1] www.comvest.unicamp.br

[2] http://www.comvest.unicamp.br/estatisticas/1998/quest/quest1.php

according to the interest of the applicant. The initial answer options were: "blank" (*missing*), "I've always liked it," "research done at school," "conversations with colleagues," "information obtained from the communication media," "influence of the family," "results of vocational testing," "influence of the teacher," "influence of the educational advisor," "the only one that is accessible to me," and "other." In 1989, the answer option "research done at school" was substituted by "personal aptitude for the fundamental courses of the career." In 1991 the option "other" was removed from the COMVEST questionnaire, which did not change till 1998.

Between 1987 and 1998, 403,832 late-adolescent applicants (77.11% between 17 and 20 years old, 9.02% between 21 and 23 years old, 3.53% between 24 and 29 years old; 51.16% men and 48.84% women) answered about the single predominant reason for the first choice of the career application. Among the answer options, "I've always liked it" and "personal aptitude" were categorized as intrinsic motives, while "research done at school," "conversations with colleagues," "information obtained from the communication media," "influence of the family," "results of vocational testing," "influence of the teacher," "influence of the educational advisor," and "the only one that is accessible to me" were categorized as extrinsic motives, following conceptualizations of Deci and Ryan (2000) and Ryan and Deci (2017). Even if the options categorized as extrinsic include some traces of intrinsic factors, to avoid confirmation bias the author kept as "intrinsic factor" only those options which show an unambiguous intrinsic aspect. Because there is a portion of participants that chose "other" or left it "blank," the percentage of intrinsic and extrinsic categories do not necessarily add up to 100%. **Table 1** presents the averaged percentage of choices for each answer option for all participants throughout the period.

Online data was manually collected as the given percentage of individuals marking each answer option, including the option "blank," for each year and career, tabulated into Excel along with the total individuals answering the questions. Using percentages controls for natural variation in the actual number of applicants in each career and year. Given the restricted nature of available data (i.e., percentage of individuals answering each option of each question), I do not have data per individual or sex, but only per year and career.

I collected data from all artistic careers offered at UNICAMP until 1998 (viz. Music, Dance, Scenic Arts, and Artistic Education). The different career modalities of music (viz. instrument [erudite], composition, teaching, conducting, and popular) were averaged together to create the overall Music career. All artistic careers contemplate both the analytical domain of history/theory/criticism and the creative production/performance domain. For comparison, I also collected data from some non-humanities careers (Chemistry, Dentistry, Physical Education), from some humanities non-artistic careers (History, Philosophy, Pedagogy, Social Sciences), and from "All careers" combined, which is the only aggregate option available online (44 different careers in 1998; treating Music modalities as two careers since most others are either integral and nocturnal or teaching and bachelor). The other aggregated groups (non-humanities, humanities non-artistic, and artistic) were created by averaging the percentage of respondents who chose each answer option across careers. **Table 2** displays the numbers of individuals per career group throughout the period. Most mentioned careers had already existed since 1987. Philosophy and Popular Music started in 1989. The non-artistic careers for comparison were chosen to approximately match artistic careers in terms of the time of existence, sex composition, application interest, and perceived societal recognition/application. The same website (e.g., for 1998, see text footnote 2) contains those parameters among the many questions of the socioeconomic questionnaire. The chosen courses include classes in the morning and the afternoon (i.e., full-time), but not during the evening. Integral courses require longer daily dedication, are normally the oldest and the most preferred ones, which ensures more representative and larger samples.

TABLE 1 | Averaged percentage of choices for each answer option for all participants between 1987 and 1998 in the basic order of appearance.

Answer options	Mean percentage of participants (Standard Deviation)
"Blank"	2.42% (2.36)
"I've always liked it"	46.39% (6.78)
"Personal aptitude"	32.78% (2.66)
"Research done at school"	0.22% (0.51)
"Conversations with colleagues"	1.58% (0.40)
"Information obtained from the communication media"	5,73% (0.96)
"Influence of the family"	1.52% (0.13)
"Results of vocational testing"	1.32% (0.32)
"Influence of the teacher"	0.42% (0.08)
"Influence of the educational advisor"	0.25% (0.08)
"The only one that is accessible to me"	2.13% (0.56)
"Other"	5.24% (0.57)

Analyses and Results

After checking for transcription errors and creating each pooled averaged group of careers, the author created the two classes of motives (intrinsic and extrinsic) by adding the percentage of each correspondent and respective answer option (i.e., "I've always liked it" and "personal aptitude" as intrinsic and the remaining as extrinsic, see **Table 1**). The percentages of "blank" and "other" were ignored for their indeterminacy regarding the class of motives. Thus, intrinsic and extrinsic motives are not mere opposite measures, they do not even correlate [$r(12) = -0.336$, $p = 0.285$]. The author further created a ratio between the classes of motives by dividing the averaged intrinsic percentages by the averaged extrinsic percentages (i.e., In/Ex). This ratio indicates how many times intrinsic motives are higher than extrinsic motives, it creates a composite measure for an overall motivational profile, it enables group comparisons of the motivational profile, and it enables an integrated discussion of both intrinsic and extrinsic motives. Although the ratio of intrinsic to extrinsic factors is correlated to both with intrinsic [$r(12) = 0.627$; $p = 0.029$], and with extrinsic motives

TABLE 2 | Number of individuals per career group from whom answers were accessed in the short-lived (1987–1998) question about reasons to apply for a career.

Career group		All careers	Non-humanities	Humanities non-artistic	Artistic
Number of individuals	Between 1987 and 1998	403,832	48,778	15,536	10,163

[$r(12)$ = -0.942; $p < 0.001$], the degree of relationship is only strong enough to constitute a necessary condition for multicollinearity in the case of extrinsic factors (Schroeder et al., 1990). Further, the data was transferred into SPSS 20 (IBM Corp., Armonk, NY, United States) for group comparisons using the multivariate General Linear Model (GLM). To overcome this one case of multicollinearity, within the GLM I followed the more conservative Pillai's Trace test, which has the highest power, thus being robust and indicated for this situation (Sarma and Vardhan, 2019). Bonferroni *post-hoc* test was used for main effects and Partial Eta-squared (η_p^2) as effect size estimator. I also performed Pearson correlation analyses. Zero percentages were treated as missing values because the COMVEST site presents zero percentages whenever there was any number of participants below five.

The author performed a multivariate GLM with the two classes of motives (intrinsic × extrinsic) and the intrinsic to extrinsic ratio as dependent variables, the groups of careers as independent factors (total of careers in the period, non-humanities careers, humanities non-artistic careers, and artistic careers), and the year (12 consecutive application period) as a covariate. The model [Pillai's Trace = 1.045, $F(12, 129) = 7.658$, $p < 0.001$, $\eta_p^2 = 0.348$] showed that the combined artistic professions presented significantly higher percentage of individuals reporting intrinsic motives [$F(3, 43) = 11.36$, $p < 0.001$, $\eta_p^2 = 0.442$], lower percentage of individuals choosing extrinsic motives [$F(3, 43) = 54.55$, $p < 0.001$, $\eta_p^2 = 0.792$], and higher intrinsic to extrinsic motives ratio [$F(3, 43) = 48.79$, $p < 0.001$, $\eta_p^2 = 0.773$] than all other career groups.

The Bonferroni *post-hoc* test showed differences between Artistic careers and all other career groups in the intrinsic motives. Specifically, Artistic careers differed from All careers ($p = 0.001$), from non-humanities careers ($p = 0.031$) and from Humanities non-artistic careers ($p < 0.001$). Artistic careers further differed from all other careers in extrinsic motives (all p's < 0.001), and in the intrinsic to the extrinsic ratio (all p's < 0.001). Moreover, a lower percentage of individuals within non-humanities careers reported extrinsic motives for career choice than in the all non-artistic career group ($p = 0.005$). There was no other difference among the groups (see **Figure 1**). The intrinsic to extrinsic ratio showed that the total of applicants' intrinsic motives ("I've always liked it" and "personal aptitude") was 6.35 times higher than combined extrinsic factors ("research done at school," "conversations with colleagues," "information obtained from the communication media," "influence of the family," "results of vocational testing," "influence of the teacher," "influence of the educational advisor," "the only one that is accessible to me"). The mean ratio between intrinsic and extrinsic motives was 8.42 for non-humanities and 6.67 for Humanities non-artistic. However, among the artistic career applicants'

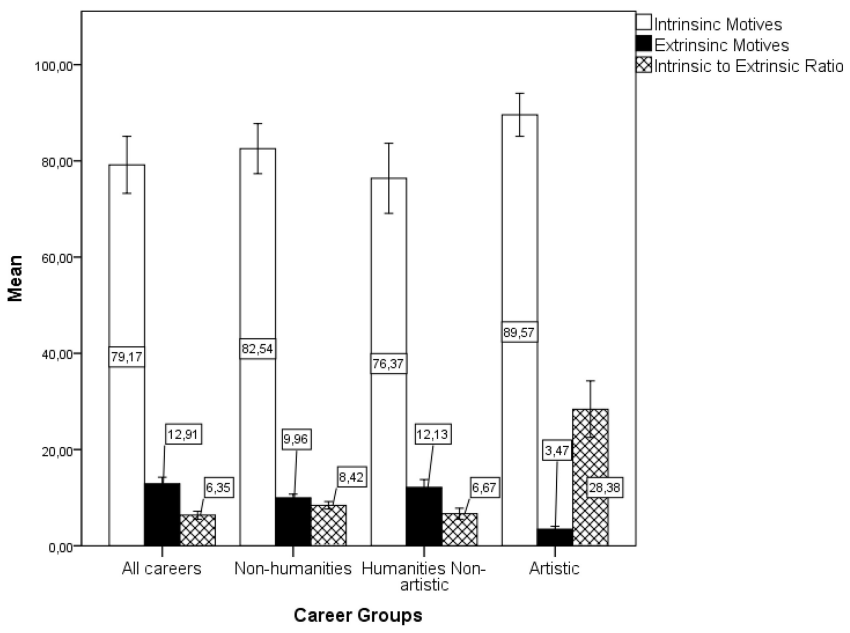

FIGURE 1 | Averaged percentages of individuals indicating intrinsic or extrinsic motives of career choice by the cluster of careers in the short-lived question (1987–1998). Error bars are ± 2 Standard Errors (SEs).

intrinsic motives were 28.38 times higher than the extrinsic ones, suggesting a specific motivational profile.

In **Figure 1**, the cluster **"All careers"** includes up to 44 different careers; **"non-artistic"** includes Chemistry, Dentistry, Physical Education, History, Philosophy, Pedagogy, and Social Sciences; **"Non-humanities"** includes Chemistry, Dentistry, and Physical Education; **"Humanities Non-artistic"** includes History, Philosophy, Pedagogy, and Social Sciences; **"Artistic"** includes Music, Dance, Scenic Arts, and Artistic Education.

Although the multivariate GLM model [Pillai's Trace = 0.671, $F(3, 41) = 27.826$, $p < 0.001$, $\eta_p^2 = 0.671$] has indicated a positive effect of the year only on intrinsic motives throughout the 12 consecutive application periods [$F(1, 43) = 87.24$, $p < 0.001$, $\eta_p^2 = 0.670$], the observed effect was an artifact of the official substitution of the answer option "research done at school" (extrinsic) by the option "personal aptitude" (intrinsic) in 1989 and the removal of the answer option "other" in 1991, which then probably induced more individuals to mark one of the popular intrinsic options. Thus, in order to account for these distortions, from the 12 consecutive application periods the author selected the 7 years after 1991 when the answer options remained unchanged. Pearson correlation showed that the years did not actually interact with intrinsic motivations [$r(32) = 0.058$, $p = 0.752$], neither with the extrinsic ones [$r(32) = -0.151$, $p = 0.410$], nor with the intrinsic to extrinsic ratio [$r(32) = 0.071$, $p = 0.698$], suggesting its overall temporal stability (see **Figures 2**, **3**).

The author further compared the classes of motives among the artistic careers to test whether there is uniformity of pattern within the artistic career group and performed a multivariate GLM with the artistic careers as independent factors (Music, Dance, Scenic Arts, Artistic Education), the two classes of motives (intrinsic × extrinsic) and the intrinsic to extrinsic ratio as dependent variables, and the year (12 consecutive application periods) as a covariate. The model [Pillai's Trace = 0.474, $F(9, 123) = 2.562$ $p = 0.010$, $\eta_p^2 = 0.158$] showed no difference among the artistic courses in the intrinsic motives [$F(3, 41) = 1.22$, $p = 0.313$, $\eta_p^2 = 0.082$], but showed differences in extrinsic motives [$F(3, 41) = 6.06$, $p = 0.002$, $\eta_p^2 = 0.307$] and in the intrinsic to extrinsic ratio [$F(3, 41) = 7.22$, $p = 0.001$, $\eta_p^2 = 0.346$]. The *post-hoc* with Bonferroni correction showed that a lower percentage of individuals reported extrinsic motives for Dance than for Artistic Education ($p < 0.001$). Moreover, Dance had higher intrinsic to extrinsic motives ratio than Scenic Art ($p = 0.010$) and Artistic Education ($p < 0.001$) (see **Figure 4**).

Although the multivariate GLM model has indicated a positive effect of the year on intrinsic motives throughout the 12 consecutive application periods [Pillai's Trace = 0.607, $F(1, 41) = 20.117$, $p < 0.001$, $\eta_p^2 = 0.607$], again, there was no temporal effect after restricting analyses to the period when the answer options remained unchanged (between 1991 and 1998). The Pearson correlation between the 7 years after 1991 and the percentage of individuals reporting each class of motives or the intrinsic to extrinsic ratio showed no temporal changes to intrinsic motives [$r(32) = -0.136$, $p = 0.459$], to the extrinsic ones [$r(30) = -0.058$ $p = 0.762$], or to the intrinsic to extrinsic ratio [$r(32) = 0.049$, $p = 0.792$].

STUDY II

Materials and Methods

Similar to Study I, I assessed online the public data available at the COMVEST website. The collected data were the given

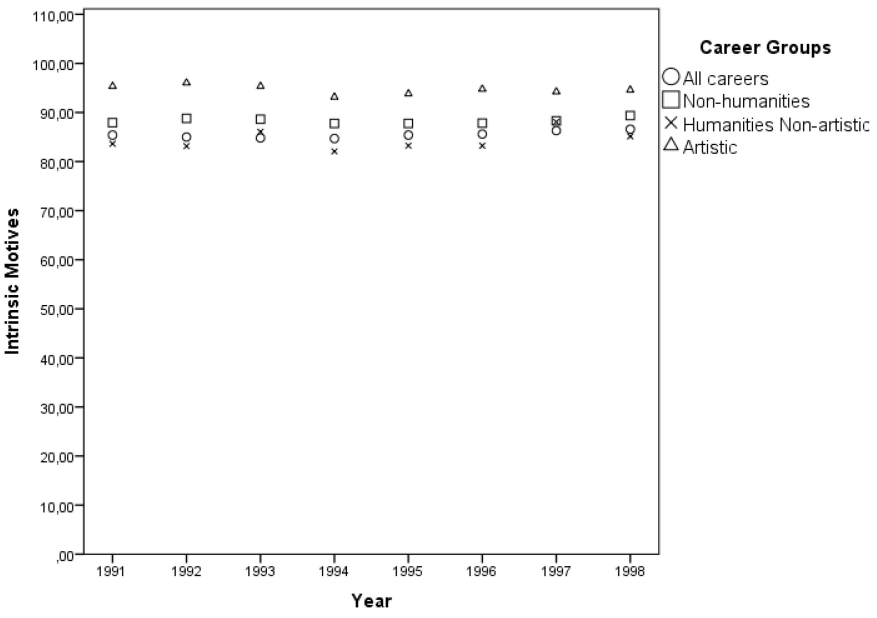

FIGURE 2 | Dispersion of the averaged percentages of individuals indicating *intrinsic* motives of career choice by the cluster of careers throughout the years 1991 and 1998.

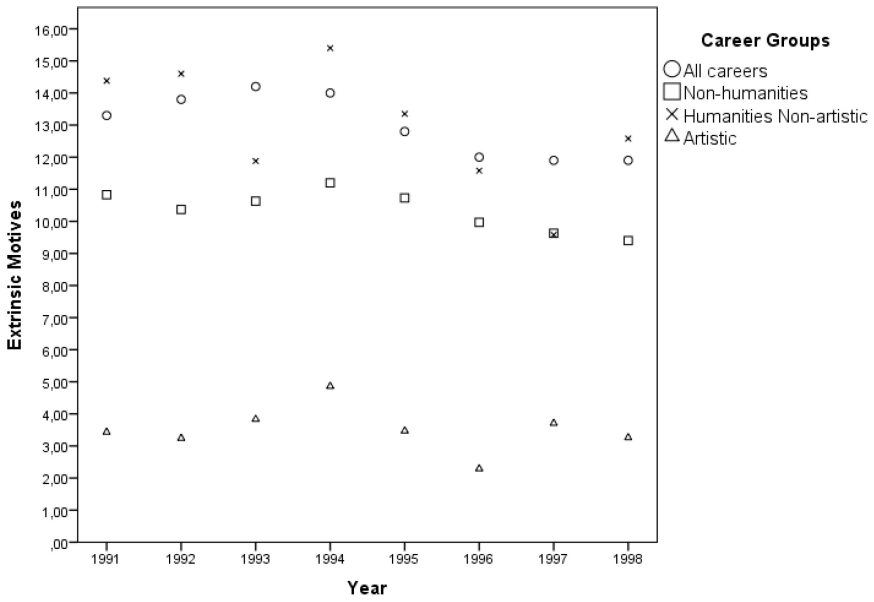

FIGURE 3 | Dispersion of the averaged percentages of individuals indicating *extrinsic* motives of career choice by the cluster of careers throughout the years 1991 and 1998.

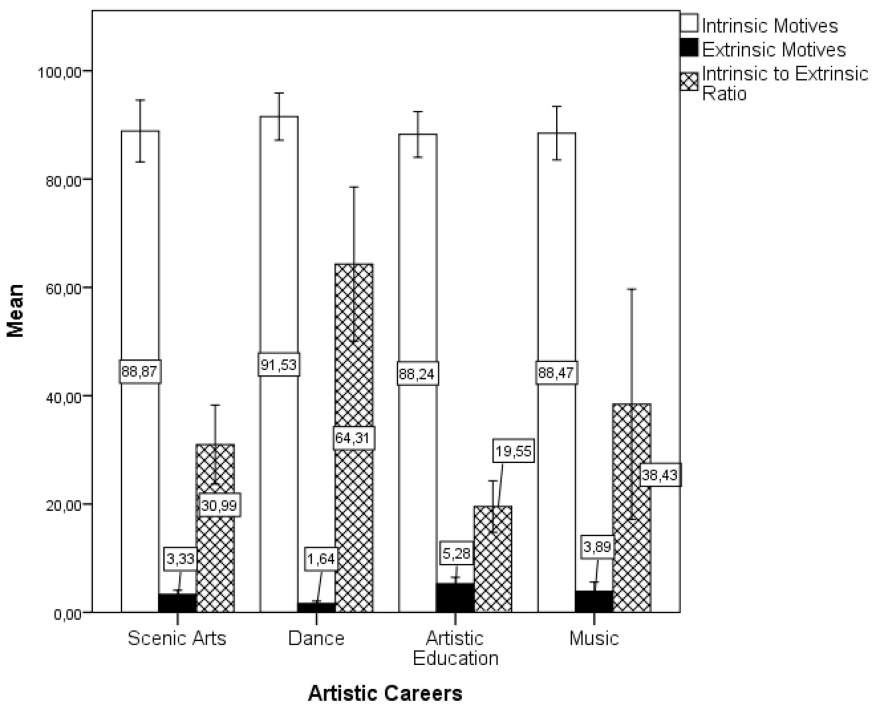

FIGURE 4 | Averaged percentages of individuals indicating intrinsic or extrinsic motives of career choice by artistic careers in the short-lived question (1987–1998). Error bars are ± 2 SEs.

percentage of individuals marking each answer option, including the option "blank," for each year and career, and for "vestibular" (i.e., university entrance exams), "all cities," "all kinds of public" (including "open concurrence" and "quotas"), and from "all applicants." The applicants could take the examination in 35 different Brazilian cities until 2020, 30 from the São Paulo State, and capitals of 5 other Brazilian states (viz. MG, DF, PR, CE, and BA).

The long-lasting question about reasons to apply for a career between 1987 and 1998 was phrased as follows: "You chose the

TABLE 3 | Descriptive statistics for the percentage of choice for each answer option for all participants between 1987 and 2020.

Answer option	Mean percentage of choice (Standard Deviation)
"Blank"	3.39% (7.75)
"Personal aptitude"	38.54% (10.10)
"Social prestige	2.00% (0.64)
"Job market"	8.43% (1.94)
"Social contribution"	14.20% (5.36)
"Lower concurrence"	1.10% (0.30)
"Ample possibilities of salary"	0.70% (0.57)
"Personal fulfillment"	26.20% (7.95)
"Other"	5.50% (3.44)

This is the order in which the answer option appears between 1999 and 2020.

career or course for which you are applying as the 1st option based on:," and the initial answer options were "blank" (*missing*), "job market," "social prestige of the profession," "adequacy for personal aptitude," "low concurrence of the positions," "ample possibilities of salaries," "other motive." Since 1989, the answer options "possibility of social contribution," and "possibility of personal fulfillment" were added. Since 1999, the phrasing of the question turned to "What is the predominant motive for your choice of the course (career) for which you are applying as the 1st option?" and remained the same until nowadays, and the answer options remained the same. The only exception was the option "ample possibilities of salaries" that was permanently removed in 1999, possibly because of the lower adherence of respondents (see **Table 3**). The order of the answer options changed only once in 1999 and remained the same since then. Until 1999, "job market" appeared in second place (the current place of "personal aptitude"), and "personal aptitude" appeared in fourth place (the current place of "job market"). Although the exact specific phrasing of the question changed once, the main theme of the question and the majority of answer options remained basically the same throughout the 33 years.

Between 1987 and 2020, 1,703,916 late-adolescent applicants (84.52% between 17 and 20 years old, 9.14% between 21 and 23 years old, 4% between 24 and 29 years old; 48.98% men and 51.02% women) answered about the predominant reason for the first choice of the career application. **Table 4** shows percentages of applicants per career group. Among the answer options, "personal aptitude" and "personal fulfillment" were categorized as intrinsic motives, while "social prestige," "social contribution," "lower concurrence," "job market," and "ample possibilities of salary" were categorized as extrinsic motives, following conceptualizations of Deci and Ryan (2000) and Ryan and Deci (2017). Again, the percentages of "blank" and "other" were ignored for their indeterminacy regarding the class of motives, thus although negatively correlated, [$r(136) = -0.767$; $p < 0.001$], intrinsic and extrinsic motives are not the mere opposite. Although the ratio of intrinsic to extrinsic factors is correlated to both with intrinsic, [$r(136) = 0.661$; $p < 0.001$], and with extrinsic motives [$r(136) = -0.798$; $p < 0.001$], the degree of relationship is not strong enough to constitute a necessary condition for multicollinearity (Schroeder et al., 1990). In 2020, the examinations occurred until the end of January, hence it was before the pandemic alert in Brazil which occurred in March. **Table 3** displays averaged percentage of choice for each answer option for all participants throughout the period.

I collected data from all artistic careers offered at UNICAMP so far (viz. Music, Dance, Scenic Arts, Artistic Education/Visual Arts, and Literary Studies). Artistic Education became Visual Arts in 2007, and Literary Studies was created in 2006. In the same way as the other artistic careers, Literary Studies also contemplates both the analytical domain of history/theory/criticism and the creative production/performance domain. After 1999, beyond the standard disciplines that were tested before the entrance, those applying for Music, Dance, Scenic Arts, and Artistic Education/Visual Arts had also required for each career a tailored theoretical and practical test of specific abilities. For comparison, I also collected data from the same comparison careers as in Study I (non-humanities careers: Chemistry, Dentistry, Physical Education; humanities non-artistic careers: History, Philosophy, Pedagogy, Social Sciences, and All careers combined—up to 62 in 2020). The pooled groups (non-humanities, humanities non-artistic, artistic, and overall Music) were created by averaging the percentage of respondents that had chosen each answer option across careers. Consistent with Study I, I also collected data only for full-time careers (i.e., including classes in the morning and the afternoon). **Table 4** presents the number of individuals per career group throughout the period.

Analyses and Results

Data treatment and statistical analyses were similar to Study I. The author checked for transcriptions errors, created each aggregate averaged group of careers, created the two classes of motives (intrinsic and extrinsic) by adding the percentage of each correspondent and respective answer option (i.e., "personal aptitude" and "personal fulfillment" as intrinsic and the remaining as extrinsic, see **Table 3**). The percentages of "blank" and "other" were ignored for their indeterminacy regarding the class of motives. The author further created the intrinsic to the extrinsic ratio which indicates how many times intrinsic motives are higher than extrinsic motives, creates a composite measure for an overall motivational profile, enables groups comparison of the motivational profile, and enables an integrated discussion of both intrinsic and extrinsic motives. Then, the data was transferred into SPSS 20 (IBM Corp., Armonk, NY, United States) for group comparisons using the multivariate GLM. To overcome another case of multicollinearity, within GLM I kept relying on the more

TABLE 4 | The number of individuals per career group from which answers were accessed in long-standing (1987–2020) question about reasons to apply for a career.

Career group		All careers	Non-humanities	Humanities non-artistic	Artistic
Number of individuals	Between 1987 and 2020	1,703,916	112,305	59,039	49,215

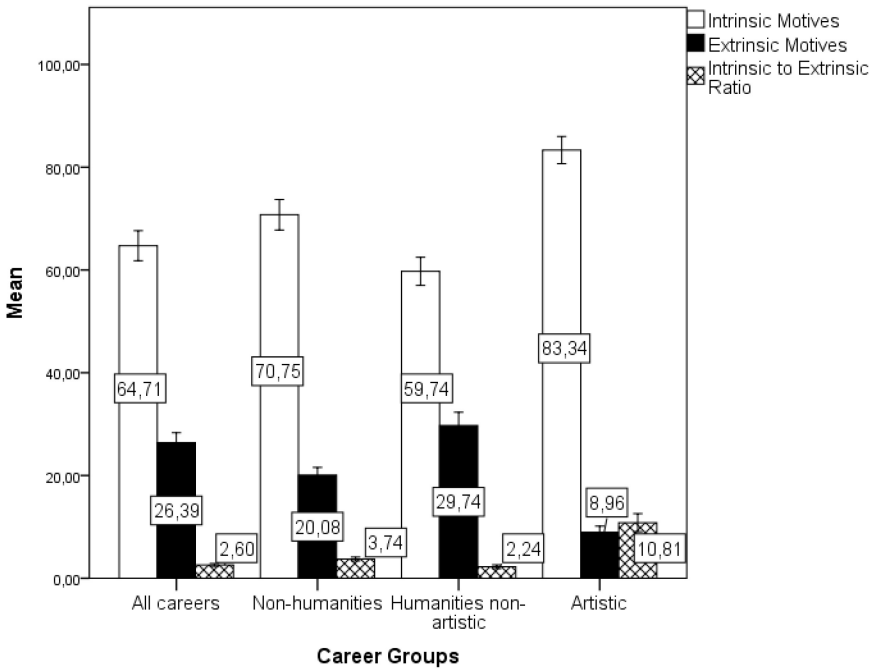

FIGURE 5 | Averaged percentages of individuals indicating intrinsic or extrinsic motives of career choice by the cluster of careers in the long-standing question (1987–2020). Error bars are ± 2 SEs.

conservative Pillai's Trace test, which has the highest power (Sarma and Vardhan, 2019). Bonferroni *post hoc* test was used for testing the main effects, effect size estimator was Partial Eta-squared (η_p^2). The author ran Pearson correlation analyses. Zero percentages were considered missing values.

The author performed a multivariate GLM with the two classes of motives (intrinsic × extrinsic) and the intrinsic to extrinsic ratio as dependent variables, the groups of careers as independent factors (total of careers in the period, non-humanities careers, humanities non-artistic careers, and artistic careers), and the year (33 years' period) as a covariate. The model showed that the career categories differ in intrinsic, extrinsic, and in the ratio of intrinsic to extrinsic factors [Pillai's Trace = 0.928; $F(9, 393) = 28.83$, $p < 0.001$, $\eta_p^2 = 0.309$]. Compared with all career groups, the combined artistic professions presented significantly higher percentage of individuals marking intrinsic motives [$F(3, 131) = 51.76$, $p < 0.001$, $\eta_p^2 = 0.542$], lower percentage of individuals marking extrinsic motives [$F(3, 131) = 129.74$, $p < 0.001$, $\eta_p^2 = 0.748$], and higher intrinsic to extrinsic ratio [$F(3, 131) = 84.27$, $p < 0.001$, $\eta_p^2 = 0.659$] (for details, see **Figure 5**).

The *post-hoc* test with Bonferroni correction showed differences between Artistic careers and all other career groups in intrinsic motives (all p's < 0.001), in extrinsic motives (all p's < 0.001), and in the intrinsic to the extrinsic ratio (all p's < 0.001). Similarly, a higher percentage of individuals within non-humanities careers reported intrinsic motives for career choice than All careers group ($p = 0.019$), and Humanities non-artistic careers ($p < 0.001$). The Non-humanities careers group also presented a lower percentage of individuals reporting extrinsic motives than the All-careers group, and Humanities non-artistic (all p's < 0.001). There was no other difference among the comparison groups. Among all applicants, the intrinsic to extrinsic ratio showed that intrinsic motives ("personal aptitude" and "personal fulfillment") were 2.60 times higher than extrinsic factors ("social prestige," "social contribution," "lower concurrence," "attractive job market," and "attractive salary"). Among Non-humanities careers the intrinsic to extrinsic ratio was 3.74, among Humanities non-artistic careers it was 2.24, but among applicants for artistic careers, intrinsic motives were 10.81 times higher, which suggests a specific overall motivational profile (see **Figure 5**).

In **Figure 5**, the cluster **"All careers"** includes 62 different careers; **"non-humanities"** include Chemistry, Dentistry, and Physical Education; **"Humanities Non-artistic"** include History, Philosophy, Pedagogy, and Social Sciences; **"Artistic"** include Music, Dance, Scenic Arts, Artistic Education/Visual Arts, and Literary Studies.

The multivariate GLM model indicated no effect of the year on intrinsic motives [$F(1, 131) = 0.357$, $p = 0.551$, $\eta_p^2 = 0.003$], but an effect on extrinsic motives [$F(1, 131) = 48.34$, $p < 0.001$, $\eta_p^2 = 0.270$], and on the intrinsic to extrinsic ratio [$F(1, 131) = 17.43$, $p < 0.001$, $\eta_p^2 = 0.117$] throughout the 34 consecutive application period [Pillai's Trace = 0.370; $F(3, 129) = 25.29$, $p < 0.001$, $\eta_p^2 = 0.370$] (see **Figures 6**, **7**). The Pearson correlation confirmed that the years did not correlate with intrinsic motivations [$r(136) = 0.35$, $p = 0.683$], but was positively associated with the extrinsic ones [$r(136) = 0.292$,

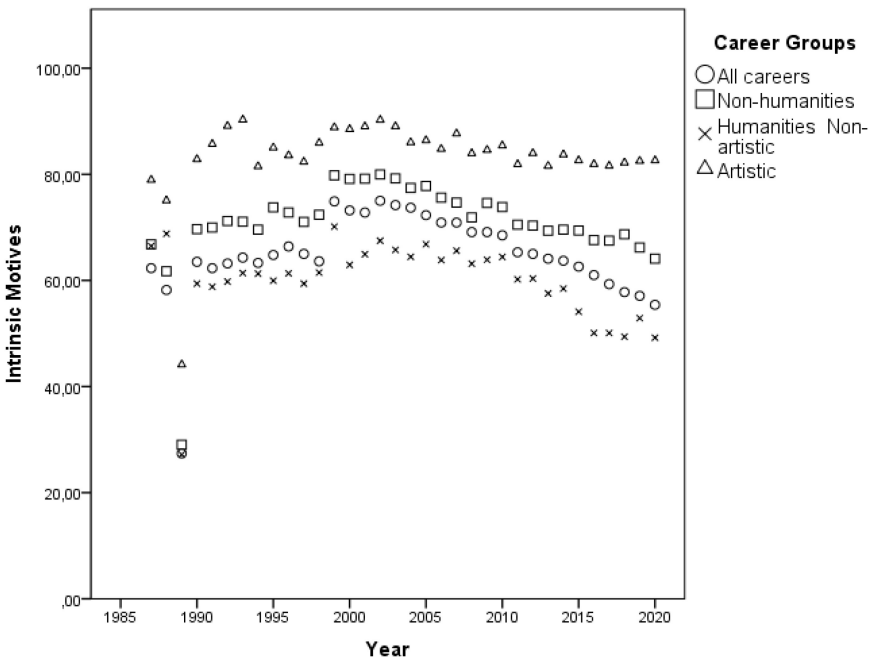

FIGURE 6 | Dispersion of the averaged percentages of individuals indicating *intrinsic* motives of career choice by the cluster of careers throughout the years 1987 and 2020.

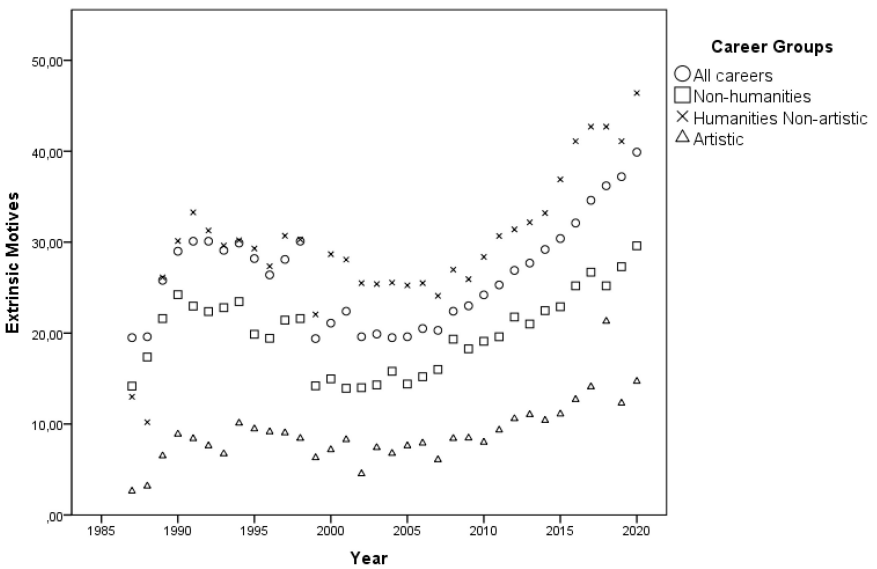

FIGURE 7 | Dispersion of the averaged percentages of individuals indicating *extrinsic* motives of career choice by the cluster of careers throughout the years 1987 and 2020.

$p < 0.001$] and negatively with the intrinsic to extrinsic ratio [$r(136) = -0.208$, $p = 0.015$], suggesting the overall temporal stability of intrinsic motives (see **Figures 6**, **7**).

Finally, the author compared the motives among the artistic careers to test for the uniformity of pattern within the artistic career group. The author also performed a multivariate GLM with the two classes of motives (intrinsic × extrinsic) and the intrinsic to extrinsic ratio as dependent variables, the artistic careers as independent factors (Music, Dance, Scenic Arts, Artistic Education/Visual Arts, and Literary Studies), and the year (34 consecutive application periods) as a covariate. The model showed no difference [Pillai's Trace = 0.101; $F(12, 432) = 1.26$, $p = 0.241$, $\eta_p^2 = 0.034$] among the artistic courses in the intrinsic motives [$F(4, 144) = 0.659$ $p = 0.621$, $\eta_p^2 = 0.018$]

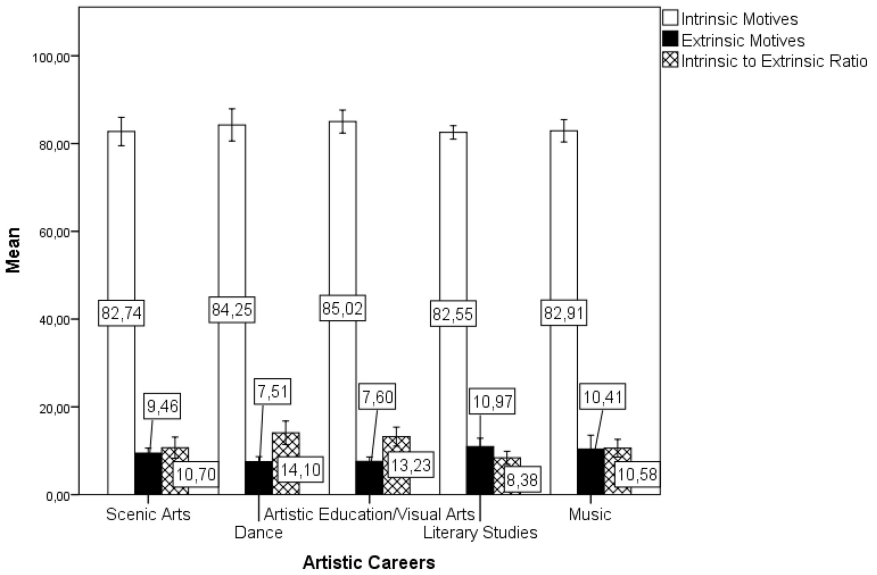

FIGURE 8 | Averaged percentages of individuals indicating intrinsic or extrinsic motives of career choice by Artistic careers in the long-standing question (1987–2020). Error bars are ± 2 SEs.

extrinsic motives [$F(4, 144) = 2.574$, $p = 0.040$, $\eta_p^2 = 0.067$] or the intrinsic to extrinsic ratio [$F(4, 144) = 2.333$, $p = 0.046$, $\eta_p^2 = 0.065$]. Although the subsequent univariate tests indicated a small marginally significant difference among artistic careers in extrinsic motives and the intrinsic to extrinsic ratio the Bonferroni *post hoc* showed no differences among them (lowest $p = 0.091$) (for details, see **Figure 8**).

The same multivariate GLM model showed no effect of the year (34 consecutive application periods) [Pillai's Trace = 0.371; $F(3, 142) = 27.924$, $p < 0.001$, $\eta_p^2 = 0.371$] on intrinsic motives [$F(1, 144) = 2.704$, $p = 0.102$, $\eta_p^2 = 0.018$], but an effect on extrinsic motives [$F(1, 144) = 46.423$, $p < 0.001$, $\eta_p^2 = 0.244$] and on the intrinsic to extrinsic ratio [$F(1, 144) = 46.482$, $p < 0.001$, $\eta_p^2 = 0.244$]. The Pearson correlation confirmed that the years did not interact with intrinsic motivations [$r(150) = 0.177$, $p = 0.155$], but only positively with the extrinsic ones [$r(150) = 0.495$, $p < 0.001$] and negatively with the intrinsic to extrinsic ratio [$r(150) = -0.504$, $p < 0.001$], suggesting the temporal stability of the intrinsic motives. Interestingly, among artistic careers there was no correlation between intrinsic and extrinsic factors [$r(150) = -0.131$, $p = 0.109$] (see **Figures 6**, **7**).

DISCUSSION

The author tested whether artistic motivation as reflected from the reasons to apply for university artistic courses is intrinsic, domain-specific, and temporally stable in two studies using each different question of a large decades-long real-life public Brazilian database from university entrance applications. Using an unobtrusive method, the author analyzed the primary reasons to apply for a career according to a question involving 403,832 late-adolescents between 1987 and 1998 from 44 different careers and 18 different Brazilian cities (Study I); and according to a question involving 1,703,916 late-adolescents between 1987 and 2020 from 62 different careers and 35 different Brazilian cities (Study II). It comprised the artistic areas of Music, Dance, Drama, Visual Arts, and Literary Studies. General results from both studies supported a domain-specific, temporarily stable, and intrinsically sourced artistic motivation, consistent with its possible evolved nature. Across both studies, individuals applying for the combined artistic professions presented a significantly higher percentage of intrinsic factors (e.g., personal taste/aptitude/fulfillment) and a lower percentage of extrinsic factors (e.g., the influence of media/teacher/family, ample possibilities of salary, social prestige/contribution) than other careers groups. Among the total of applicants, the intrinsic to extrinsic ratio showed that intrinsic motives were 2.60–6.35 times higher than extrinsic factors, but among artistic applicants they were 10.81–28.38 times higher, suggesting a specific overall motivational profile. There was no difference in intrinsic motivation among different artistic careers suggesting a single-core global artistic motivational profile. Overall, the period interacted only with extrinsic motivations in only the longstanding question, suggesting that intrinsic factors are more temporally stable than extrinsic ones.

Both studies supported the hypothesis that artistic motivation is rather intrinsic, by showing that the combined artistic professions presented significantly higher intrinsic and lower extrinsic motivations than other groups of careers. These results corroborate studies showing that intrinsic reasons, such as personal interest in the artistic material itself, desire to express themselves artistically (McCarthy and Jinnett, 2001), recreation and aesthetics (Swanson et al., 2008), and self-expression and aesthetic experience (Chong, 2010) are among the primary

reasons individuals report when engaging in artistic activities. This is in line with other evidence showing intrinsic artistic motivation, such as the intrinsically spontaneous, compulsive, and higher sustained artistic production in some patients with brain-damage (Zaidel, 2014; Midorikawa and Kawamura, 2015; Abraham, 2019). Further, experimental studies show that unrewarded motivation leads to better aesthetic value, while extrinsic motivation is somewhat detrimental (Amabile, 1982; Amabile and Gitomer, 1984; Amabile et al., 1986). Moreover, aesthetics and artistic activities are among the most popular choices of the spontaneously pursued free-time activities (Chalip et al., 1996; Walker and Scott-Melnyk, 2001; Chamorro-Premuzic and Furnham, 2004; Furnham and Chamorro-Premuzic, 2004; McManus and Furnham, 2006; Chong, 2010). The convergence of results from various lines of investigation makes a strong case in support of the rather intrinsic nature of artistic motivation as predicted from an evolutionary perspective (Morris, 1962; Dutton, 2009; Hogh-Olesen, 2018).

It is noteworthy that the effect size was bigger for the low extrinsic artistic motivation than for the high intrinsic artistic motivation. Thus, together with the increased intrinsic motivation, there is a major lack of external rewards for deciding to be a professional artist, which contradicts the "hunger for status" non-adaptive hypothesis (Pinker, 2004). Proximate sociocultural factors might also play a role in contributing to the obtained pattern of results. In Brazil and much of North America, art courses are elective as extra-class activities in high schools, hence favoring intrinsic interests and lacking the mandatory aspect of the core disciplines. In fact, in order to be approved in the test of specific artistic abilities, applicants needed to take elective preparatory courses. Further, being labeled talented or gifted by others might offer better opportunities, teachers, and curriculum (Berlin, 2009). This positive social context might reinforce the students' perception of innate artistic talent (Evans et al., 2000), which can further positively influence their high intrinsic motivation. There is also a pervasive notion that arts are not a lucrative or sensible career path (Abbing, 2008), so much so that music students report that family and friends actively discourage their musical development (Evans et al., 2000), which can contribute to the obtained result of low extrinsic artistic motivation. Although relevant, the sociocultural factors likely do not fully explain the pattern of present results. That is because in some instances there was no correlation between intrinsic and extrinsic measures, and there are indeed important biological components to artistic talent including strong intrinsic motivation, referred to as "rage to master" (Winner and Drake, 2018), including multigenerational continuity (Perrone et al., 2010), and medium to high heritability in the choice of creative professions (Roeling et al., 2017). A twin-based study even showed that as musical ability, a musical practice also is substantially heritable (40–70%), and the association between both practice and ability was predominantly genetic so that identical twins differing in the amount of practice did not differ in their ability (Mosing et al., 2014). Therefore, it is most likely that both biological and cultural factors converge and complement each other (cf. Varella et al., 2012) affecting both intrinsic and extrinsic motivational aspects generating to the obtained overall pattern of results, as captured by the artistic specificity of the intrinsic and extrinsic ratio.

Both studies supported the hypothesis that artistic motivation is domain-specific by showing that the intrinsically sourced motivational profile of individuals applying for artistic careers is uniquely increased and distinct from other non-artistic careers: humanities, non-humanities, and also the total of careers. Across the two studies and investigated questions, the relative proportion between intrinsic and extrinsic reasons is around 4–4.5 times higher among applicants for artistic careers than for the total of applicants. Furthermore, the intrinsically sourced motivational profile did not differ among different artistic careers, which indicates that the same specific artistic motivation is globally underlying different artistic modalities. These findings support various taxonomies and classificatory schemes that consider artistic/aesthetic as a specific and legitimate domain within the field of vocation interests (Kuder, 1948; Guilford et al., 1954; Moloney et al., 1991; Holland, 1997; Su et al., 2019), of leisure practices (Dumazedier, 1988; Scott and Willits, 1998; Mingo and Montecolle, 2014), and even of engagement with beauty (Diessner et al., 2008). The convergent evidence pointing to domain-specificity is a hallmark of mental adaptation (Cosmides and Tooby, 1994; Andrews et al., 2002; Barrett, 2008; Tooby and Cosmides, 2015) that should be taken into account when analyzing the evolved nature of artistic propensities (cf. Varella et al., 2010; Valentova et al., 2019, focusing on musicality).

The hypothesized temporally stability also received support from both questions. The time period of 8 and 33 years, respectively, did not interact with intrinsic motives from both questions and with extrinsic motives from one question, suggesting overall temporal stability, particularly of the intrinsic motivation, at least within the three decades' time scale. The historical stability is aligned with studies showing lifetime individual stability of interests. Ranging from the highly sustained artistic expression of some patients with brain damage (Abraham, 2019), passing through the stability of vocation interests (Lubinski et al., 1995; Waller et al., 1995), stability of leisure interests (Waller et al., 1995), and stability of engagement with artistic beauty (Diessner et al., 2008) throughout periods of individuals' life. Similarly, particular interests reflecting hands-on physical activities and self-expressive/artistic activities tend to be even more stable than scientific, social, enterprising, and clerical interests (Low et al., 2005). Moreover, the earliest human artistic manifestations date back to the Middle (d'Errico et al., 2009; Henshilwood et al., 2018) and Lower Paleolithic (Bednarik, 2014), which gives enough time for artisticality to get specialized and well stabilized (cf. Starratt and Shackelford, 2010).

The overall pattern of results did not support the non-adaptive hypothesis based on general curiosity, or "hunger for status," as put forward by Pinker (2004). Contrary to the by-product predictions there were differences between artistic and non-artistic careers, intrinsic factors were more relevant than extrinsic ones, and the period mostly did not influence artistic motivation. This fails to corroborate the non-adaptive hypothesis does not mean that curiosity and status-seeking are not related to the

artistic domain, only that there might be a more basic and specific underlying motivational factor at play. The confluence of present results from both studies together with related previous evidence in corroborating the hypotheses that artistic motivation is rather intrinsic, domain-specific, and at least three decades historically stable offers solid empirical support for the notion that artistic motivation is an evolved aspect of human nature (cf. Morris, 1962; Dutton, 2009; Hogh-Olesen, 2018).

Moreover, the present study found that the same intrinsic motivational factors influence the five artistic modalities (viz. Scenic Arts, Visual Arts, Literary Studies, Music, and Dance). This offers further evidence to consider art as a legitimate global and coherent dimension in which the different modalities evolved together served by the same motivational mechanisms (Dutton, 2009). Furthermore, analyzing a huge sample size, real-life data, unobtrusive method, and a considerable temporal span, the present study for the first time establishes that the average general vocational interest is around twice as often motivated by intrinsic than extrinsic reasons, though there is a general recent historical trend decreasing this ratio.

There are some limitations in the present study. The entrance exam system (i.e., COMVEST) did not maintain perfect consistency in the questions phrasing, the order, or the number of answer options. However, the official changes were minor and performed only once throughout the period, which was accounted for in the analyses. Further, the entrance exams system rounds the percentages of the data up to only one decimal place, so the author expects a .1 error rate in the given percentages. Also, the system does not show frequency results when there are less than five candidates in a given career of a given year. Hence, in some years, some music instrument modalities, such as clarinet or trombone, could not be added to the other modalities to create the overall Music career. Importantly, although the data were taken from a Latin American country, a non-Western English-speaking area, the data do not represent the general Brazilian (or world) population given its circumscribed location (7 Brazilian states out of 26, but mostly São Paulo state). The studies were also age-limited mostly to late-adolescents applying for full-time diurnal, but not nocturnal courses. Future studies should try to account for and expand beyond these limitations to replicate and further explore the design features of human artistic motivation in real-life scenarios.

CONCLUSION

I aimed to celebrate the 150 years of Darwin's legacy from "The Descent of Man, and Selection in Relation to Sex" (1871) by advancing the evolutionary knowledge regarding the nature, scope, and structure of artistic motivation. The author has analyzed massive sample sizes of real-life data, a three decades' time span, and a diversity of artistic and non-artistic careers. The convergent results across both studies indicated a distinctive and highly intrinsically based artistic motivation, that is specific to all arts and temporally stable within the three decades' time span. This is supported in the literature by various lines of investigations.

Although less prominent, extrinsic factors also play a role, particularly the decreased reliance on extrinsic factors of individuals applying to artistic careers. Socio-historical factors including the structure of the educational system which leaves artistic courses as elective, and the difficult career prospects in the job market may also contribute to the obtained pattern of results. Thus, both biological and sociocultural factors converge and complement each other influencing both intrinsic and extrinsic motivational aspects akin to what Darwin has put forward in 1871.

Therefore, the author concludes that artistic motivation presents at least three predicted features consistent with its possible evolved nature; it is highly intrinsically sourced, has domain-specificity, and has some temporal stability. Future studies should explore these features using different indicators of motivation and use different methodological approaches to probe for these and other possible aspects.

DATA AVAILABILITY STATEMENT

The data source for this research is *per se* open, so anyone can access http://www.comvest.unicamp.br/estatisticas-comvest/vestibulares/vestibulares-anteriores/ to choose which year one wants to access. The specific data used for this research were gathered from the socioeconomic questionnaire (e.g., for the year 2019 is http://www.comvest.unicamp.br/estatisticas/2019/quest/quest1.php) within COMVEST webpage at the session about statistics. One only needs to select the course and which question to access each part of the data per year. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MV conceived and designed the studies, searched the literature, gathered the data, organized and analyzed the data, and wrote the manuscript.

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Substantial but Misunderstood Human Sexual Dimorphism Results Mainly From Sexual Selection on Males and Natural Selection on Females

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Human sexual dimorphism has been widely misunderstood. A large literature has underestimated the effect of differences in body composition and the role of male contest competition for mates. It is often assumed that sexually dimorphic traits reflect a history of sexual selection, but natural selection frequently builds different phenotypes in males and females. The relatively small sex difference in stature (~7%) and its decrease during human evolution have been widely presumed to indicate decreased male contest competition for mates. However, females likely increased in stature relative to males in order to successfully deliver large-brained neonates through a bipedally-adapted pelvis. Despite the relatively small differences in stature and body mass (~16%), there are marked sex differences in body composition. Across multiple samples from groups with different nutrition, males typically have 36% more lean body mass, 65% more muscle mass, and 72% more arm muscle than women, yielding parallel sex differences in strength. These sex differences in muscle and strength are comparable to those seen in primates where sexual selection, arising from aggressive male mating competition, has produced high levels of dimorphism. Body fat percentage shows a reverse pattern, with females having ~1.6 times more than males and depositing that fat in different body regions than males. We argue that these sex differences in adipose arise mainly from natural selection on women to accumulate neurodevelopmental resources.

Keywords: stature, cephalopelvic disproportion, body fat, muscle mass, disruptive natural selection, neurodevelopmental resources, contest competition

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INTRODUCTION

In this manuscript we argue that sexual selection acting on males and disruptive natural selection (acting differently on males and females) have made humans a highly sexually dimorphic species, albeit in unique ways. After considering the ways in which these different forms of selection have been understood, we first discuss the modest sex differences in human stature and the critical relationship of paternal and maternal stature to pregnancy outcomes. We then contrast modest

sex differences in stature and body mass to the marked sex differences in lean mass, muscle, and strength, and in the percentage and distribution of body fat. We argue that sex differences in muscle and strength are largely the result of sexual selection for male-male competitive traits, whereas females have increased body fat (in place of muscle) due to natural selection for maternal investment capacity in the context of our unusually large brains. Our approach is multifaceted and involves synthetic review of previously published material, some systematic compilations and analysis of data from the literature, and some tests of new hypotheses using new data sets.

Darwin (1859, 1871) distinguished two evolutionary processes of *natural* and *sexual* selection, and much theoretical and empirical work has built on this distinction (for review see Andersson, 1994; Andersson and Iwasa, 1996). Conventional definitions of sexual selection emphasize that it can produce adaptations useful in the mating arena that would not be favored by natural selection (e.g., Darwin, 1871, V1, p. 279). This emphasis is traceable to Darwin's justification for positing an adaptive force beyond natural selection; if natural selection explains everything, why bother to define an additional process? But he also acknowledged in both 1859 and 1871 that some traits (he used the example of sense organs) could be useful to individuals both in "their ordinary habits of life" and in securing mates, and hence would be favored by both kinds of selection. In other words, adaptive evolution is driven by differentials across an array of fitness components, and that dynamic process has no obligation to be tidy in terms of any particular theoretical framing of natural vs. sexual selection.

Recently, Shuker and Kvarnemo (2021) have attempted to redefine sexual selection as "any selection that arises from fitness differences associated with non-random success in the competition for access to gametes for fertilization" (p. 783). We dislike this formulation because (as explained below) gametes are not always the limiting factor precipitating mating competition, and hence a definition based on them will yield somewhat paradoxical conclusions.

Any definition (or theory) of sexual selection must attend to the fact that mating competition tends to be imbalanced, being more intense in one sex than in the other. That sex is usually, but not always, the male. In anisogamous species, female gametes are larger and thus typically produced in smaller numbers than male gametes. Because it would be expected for males to compete for scarce eggs, but not for females to compete for abundant sperm, sexual dimorphism in gamete size would set the evolutionary stage for disproportionate mating competition among males.

But how would we explain species where female mating competition is more intense; are sperm somehow in short supply? In a ground-breaking paper, Clutton-Brock and Vincent (1991) argued that neither gametes, nor parental investment (*sensu* Trivers, 1972) are the limiting factor driving sexual selection. Instead, they suggested that the sex with the higher potential reproductive rate would inevitably find the "slower" sex in short supply because there would usually be fewer of the slow sex ready to begin a new reproductive venture and they would thus constitute a limited resource for the "faster" sex. Unlike gamete size, where there is a universal sex difference, sex differences in reproductive rate could cut either way, with males or females being the slow sex.

Matching the predictions of Clutton-Brock and Vincent's (1991) theory, in species where males are the slow sex (e.g., phalaropes), females have evolved to be larger, more brightly colored, and more active in courtship—traits typically associated with mating competition in males. Shuker and Kvarnemo's (2021) definition would require us to recognize such traits as due to sexual selection when they help males acquire female mates (whose gametes are scarce), but as due to natural selection when they serve the same function for females seeking male mates (because male gametes are not the target of competition). Because that kind of conceptual cleavage seems discordant with Darwin's original framing of sexual selection as favoring traits useful in mate acquisition, we adopt Andersson's (1994) widely used definition: "Sexual selection is the differences in reproduction that arise from variation among individuals in traits that affect success in competition over mates and fertilizations" (p. 31).

More generally, adaptive evolution is driven by reproductive differentials between different phenotypes. Those differentials are logically attributable to three fitness components: viability, fecundity, and mating success. Individuals must survive long enough to reproduce and traits that promote such survival are targets of *viability selection*. Among those who survive to reproductive age, some may produce more or better-endowed gametes; some may have better machinery for fostering, protecting or nourishing their young; and some may be more physiologically efficient at converting food into progeny. Such differentials would be targets of *fecundity selection*.

But among those who survive and have efficient, well-formed reproductive machinery, some will get more (or better) mates—because they are more attractive to the opposite sex or because they are better at excluding members of their own sex from mating or a combination of both. These differentials are targets of *sexual selection*. In the terms relevant to this article, viability selection and fecundity selection are both aspects of natural selection, and they stand in contrast to sexual selection. While the conceptual distinction between natural and sexual selection is clear in these terms, the specific fitness differentials shaping any particular dimorphic trait may not be so easily separable because they may not be limited to a single fitness component.

Based on the preceding discussion, it should be clear that disruptive natural selection can produce sexual dimorphism when the ecology of males and females is sufficiently different that viability and/or fecundity selection favor different traits in the two sexes. For example, features of the uterus, placentation, and hormonal support for pregnancy obviously contribute to female reproductive success in ways that would not similarly benefit a male. But these sex differences are the product of natural (more specifically, fecundity) selection, because they benefit female reproduction directly, rather than via any advantage they provide in attracting mates or excluding sexual competitors (although males may subsequently evolve to prefer traits that enhance female reproductive success). Thus, as Darwin (1871) highlighted, the mere existence of a sex difference is not by itself evidence of sexual selection. With these distinctions in mind, we will consider the possible roles of natural and sexual selection

in shaping a set of anatomical and physiological differences between women and men.

MATERIALS AND METHODS

Data Relating to Human and Primate Sexual Dimorphism

We used information from seven databases, some previously published and some new. These include data for 260 separate population samples from non-industrial countries with body fat estimated from two skinfolds (Wells, 2012a), a sample of 6,421 persons from 29 countries including 3 in South America, 6 in Africa, and 9 in Europe from 1981 to 2019 (Pontzer et al., 2021), and data on body weights in primates (Smith and Jungers, 1997; Gordon, 2006a,b). From other published data, we also compiled a new dataset of 191 separate population samples that reported values for total mass, fat mass, and lean body mass by sex based on a variety of non-skinfold methods, including underwater weighing, total body water, dual-energy x-ray absorptiometry (DEXA), bioelectrical impedance, MRI, 4-compartment measures, and total body potassium. These 191 samples included 6 foraging populations, 12 horticultural populations, and 23 nations, including some industrial nations (see **Supplementary Table 1**). In addition, we analyzed data extracted from the 2013 US natality database, the Third National Health and Nutrition Examination Survey (NHANES III, 1988–1994), and from four NHANES surveys for 1999–2006, as detailed below.

Maternal Stature and Risk of Emergency C-Section

The risk of emergency primary C-section in relation to self-reported maternal stature was determined using logistic regression for 3,550,445 live births, including 1,122,782 primiparas, from birth certificate data from the 2013 US natality database. An emergency C-section was a C-section done in relationship to one or more complications of labor and delivery. Mothers with an elective or repeat C-section were excluded. Control factors included age, parity, race, ethnicity, and birth weight. The relationship between maternal stature and birth weight was also determined with the same controls (except for birth weight).

Difference in Maternal and Paternal Stature and Risk of Cephalopelvic Disproportion

Data from the NHANES III was used to determine the joint effect of maternal and paternal stature on the risk of cephalopelvic disproportion (CPD). This national U.S. sample included birth certificate data for 10,414 children < 15 years of age, and the presence or absence of a diagnosis of CPD at delivery for 3,190 children. These children were matched to their mothers' and fathers' records using the family number, resulting in complete data for 2,918 parent-child triads.

Sex Differences in Body Composition in the US Based on National Health and Nutrition Examination Survey

Data from NHANES for 1999 to 2000, 2001 to 2002, 2003 to 2004, and 2005 to 2006 were combined into a single data set. Data from dual-energy x-ray absorptiometry (DEXA) were used to assess the amount of fat-free lean tissue, percent body fat, and the ratio of leg fat to trunk fat for 5,273 males and 5,271 females aged 15–49 with a non-obese body mass index of < 30. Sex differences in fat and lean body mass for 10,537 males and 11,536 females aged 18 and older were determined with linear regression controlling for age, race, ethnicity, height, and weight.

Data for 3,878 males and 4,565 females aged 15–39 from NHANES III were used to determine sex differences in waist/hip ratio. In this survey, waist circumference was measured 1 cm above the iliac crest (not at the smallest waist) and hip circumference was measured at its maximum. Comparisons of the two methods of measuring waist circumference in another sample showed that the minimal waist circumference averages 10% less than the "NHANES waist" (Lassek and Gaulin, 2016). Also from NHANES III we determined sex differences in four skinfolds for 16,539 US adults > 17 years old (measured in tenths of millimeters): triceps, subscapular, suprailiac, and thigh.

RESULTS

Stature Dimorphism

The various extant primate species differ greatly in body size dimorphism (typically measured as weight—a dimension discussed in more detail below). Most comparative analyses conclude that primate size dimorphism is associated with elevated male contest competition for mating opportunities (Gaulin and Sailer, 1984; Frayer and Wolpoff, 1985; Ely and Kurland, 1989; Plavcan and Schaik, 1997b; Plavcan, 2012a,b). However, there are many other factors—fecundity, life history, feeding niche, predation risk, locomotor substrate, infanticide frequency—that could favor increases or decreases in body size for one or both sexes (Leutenegger and Kelley, 1977; Plavcan and Schaik, 1992; Ford, 1994; Gordon, 2006a,b; Plavcan, 2012a; Cassini, 2020). While undoubtedly important in some cases, these factors tend to be taxon-specific and thus tend not to explain a significant amount of variance in broad comparative studies. As a result, in his comprehensive review Plavcan (2012b) concluded, "to date, male agonistic contest competition is the only factor that has consistently received support from comparative analyses in explaining why males are larger and have larger canine teeth than females in non-human anthropoid primates" (Plavcan, 2012b, p. 52).

A recent meta-analysis across a wide array of taxa is especially relevant because it uses body length dimorphism and is thus comparable to human stature dimorphism (Janicke and Fromonteil, 2021). In their phylogenetically controlled analysis, across 59 species and 95 effect sizes, these authors found a significant positive association between their index of the intensity of pre-copulatory competition for mating partners and

the magnitude of length dimorphism. Sexual selection for mating opportunities is a pervasive enough effect that it manifests even when widely diverse taxa—with their unique ecologies and genetic backgrounds—are considered together.

Whereas comparative analyses are an evolutionist's essential tool for highlighting factors that operate across diverse taxa and circumstances, taxonomically broad relationships do not automatically illuminate particular cases, such as *Homo sapiens*. Forty years ago, J. Patrick Gray compiled world-wide data on human stature dimorphism. Various analyses of that database (Gray and Wolfe, 1980; Wolfe and Gray, 1982a,b; Gaulin and Boster, 1985, 1992, Rogers and Mukherjee, 1992) suggest that the cross-cultural variance in stature dimorphism is both small and uncorrelated with population differences in marriage patterns, subsistence ecology, or mean stature. Sample size, however, is a reasonable predictor: The more males and females were measured in a society, the more its stature dimorphism converged on 1.073 (Gaulin and Boster, 1985).

Wells (2012b) compiled a data set including 96 non-Western populations and also reported a mean stature dimorphism of 1.073. In a larger sample of 137 non-industrialized societies, Wells (2012a) found a mean stature dimorphism of 1.067. In our US sample of 16,343 adults 18–64 from NHANES 1999 to 2006, the ratio is 1.083 (**Supplementary Figure 1**). The consistency of human stature dimorphism was revealed in a longitudinal context by a study examining Swedish data from the tenth to seventeenth centuries; although mean stature increased as a result of increased nutrition, the magnitude of stature *dimorphism* was unchanged (Gustafsson et al., 2007). In other words, contemporary humans show a very consistent—perhaps genetically constrained (Rogers and Mukherjee, 1992)—level of stature dimorphism, with males significantly taller than females in all known societies.

Importantly for our evolutionary analysis, while the magnitude of stature dimorphism seems to have been relatively stable over recent centuries, it has not been constant over the longer history of the human lineage. Although sexual dimorphism is significantly more difficult to diagnose in the past compared to the present (e.g., Plavcan and Schaik, 1997a; Plavcan, 2012a,b), a consensus persists that sexual dimorphism has decreased over the last 3 million years of hominin evolution (e.g., Richmond and Jungers, 1995; Plavcan and Schaik, 1997a; Lockwood et al., 2007; Gordon et al., 2008). Early, unambiguously bipedal hominins (e.g., members of the genera *Australopithecus* and *Paranthropus*), were apparently more dimorphic in stature (or in the size of their post-cranial skeletons) than are contemporary *Homo sapiens*. A commonly cited benchmark is that these extinct hominins were roughly as dimorphic as extant gorillas (McHenry, 1991a,b; Richmond and Jungers, 1995; Harmon, 2006; Gordon et al., 2008; Plavcan, 2012b, 2018; Masao et al., 2016; Villmoare et al., 2019)—a species with intense male contest competition for mates.

Reno et al. (2003) disagreed, suggesting that *Australopithecus afarensis* showed a human-like pattern of dimorphism, but their analysis has been methodologically criticized on multiple grounds, and a reanalysis concurs with the more frequent view that pre-*Homo* hominins were significantly more dimorphic than *Homo sapiens* (Plavcan et al., 2005). Furthermore, recent analyses suggest that early members of the genus *Homo* (approximately 1.5 million years ago) exhibited skeletal dimorphism levels intermediate between *Australopithecus* and contemporary humans (Villmoare et al., 2019).

Many anthropologists, aware of the apparently significant role of sexual selection is shaping sexual dimorphism across species (above), may have been too quick to interpret decreasing sex differences in stature during hominin evolution as evidence for a progressively more monogamous human mating system, and a concomitant decrease in male mating competition. We believe this interpretation deserves more scrutiny because, as demonstrated below, there is significant natural selection on women related to obstetric issues.

Effects of Male and Female Stature on Human Parturition

What this predominant sexual-selection perspective neglects is that, as suggested by several primatologists (Leutenegger and Kelley, 1977; Plavcan and Schaik, 1992, 1997b; Ford, 1994; Gordon, 2006a,b; Plavcan, 2012a,b; Cassini, 2020), other fitness components beyond mating competition may be relevant to the evolution of male and female size. A relatively uncontroversial but seldom remarked feature of the transition to *Homo*, is that both sexes increased in stature, but females grew disproportionately larger (McHenry and Coffing, 2000; Carretero et al., 2012; Plavcan, 2018). In other words, stature dimorphism decreased, not because males got smaller (as might be expected if the sexually competitive advantages of large size diminished due to monogamy), but because females increased in stature more than males did. This suggests a need to focus on selection pressures acting uniquely on females, which in turn points to selection components relevant to the female role in reproduction.

Birth weight has fitness consequences for altricial human infants. If they can fit through their mother's birth canal, heavier infants survive better (Lummaa, 2003). Taller women are advantaged in this respect: In the US natality data set, each centimeter of maternal stature increases birth weight by 11.4, 95% CI [11.3, 11.5] grams. For all births, the risk of having a neonate with low birth weight decreased by 2.6%, 95% CI [2.5, 2.6] for each cm of maternal stature. Without attempting to determine the causal pathway, other studies have found higher reproductive success in taller mothers in Gambia (Sear et al., 2004) and Guatemala (Pollet and Nettle, 2008). A comparative study in 42 developing countries found lower child mortality in the offspring of taller mothers (Monden and Smits, 2009).

Such selective differentials would likely have favored increased female stature, but would they have done so more in *Homo* than in *Australopithecus*? A recent meta-analysis across 60 species of mammals found a strong positive effect of infant birth weight on subsequent survival, with a one SD increase in birth weight increasing the odds of offspring survival by 71% (Ronget et al., 2018). Given the generality of the birth-weight advantage, it would likely have favored increased maternal stature in earlier hominin genera as well as in *Homo*, and thus would not explain a stature-dimorphism reduction in *Homo*. There is, however,

another positive selection pressure on female stature that would have operated more strongly in later, larger brained hominins.

The "obstetric dilemma" (Washburn, 1960) arises because selection pressures for efficient bipedal locomotion narrowed the human pelvis in a way that constricted the birth canal. Because the head is the largest part of a fetus, a mismatch between fetal head size and pelvic size—cephalopelvic disproportion (CPD)— became increasingly problematic as hominins evolved larger brains. Human infants are notoriously altricial (helpless) compared to those of our great ape cousins, and this trait is proposed to be an evolutionary compromise to the opposing selection pressures arising out of bipedality and delivering large-brained infants: Deliver the infant earlier in development, before its brain is too large (Krogman, 1951; Rosenberg, 1992; Trevathan, 2010).

While there has been some debate about the obstetric-dilemma explanation for human altriciality (Dunsworth et al., 2012; Haeusler et al., 2021), two key facts are undisputed: Human infants are very large relative to their mothers' birth canals, and this tight fit is relevant to female fitness (Haeusler et al., 2021; Lassek and Gaulin, 2021). For example, as recently as 1990, there were seven countries (with limited access to surgical delivery) where a woman's lifetime risk of dying in childbirth was between 8 and 14% (WHO, 2015). The risk of CPD is especially high for a woman's first birth (Lassek and Gaulin, 2021). Most studies attempting to assess this obstetric risk at different time points in the past and across different types of subsistence ecology agree that the hurdle of delivering a human infant has been an enduring selective agent (Dobbie, 1982; Hogberg and Brostrom, 1985; Arriaza et al., 1988; Headland, 1989; Hill et al., 2007; Haeusler et al., 2021).

Because giving birth is so risky in humans, related selective differentials must have had important influences on the evolving female phenotype. Although bipedality was well established more than 4 million years ago, significant brain expansion began only about 2 million years ago, with the emergence of the genus *Homo*. Evidence of birth canal expansion in a 1.5-million-year-old female *Homo erectus* pelvis from the Afar region of East Africa (Simpson et al., 2008) is consistent with the idea that selective differentials related to obstetric challenges have been reshaping female anatomy for many millennia, and some studies suggest that the female pelvic shape of *Australopithecus* already showed some obstetric-related adaptations (Berge et al., 1984; DeSilva, 2011).

Pelvic expansion is one kind of evolutionary adjustment to the obstetric dilemma but there are biomechanical reasons to think that solution will be constrained by its effects on bipedal locomotion. A wider pelvis increases the valgus angle where the distal femur articulates with the tibia, and that increase places additional stress on the anterior cruciate ligament (ACL). In a college sample, women had an 20% larger tibiofemoral angle than men (Nguyen and Shultz, 2007); and when landing from a short drop, women have a 5–6-degree difference from men in the valgus angle at landing and a 12–13-degree difference in maximum valgus (Russell et al., 2006; Vogt, 2017).

As a consequence of this biomechanical sex difference, women experience two to eight times more ACL tears than men when engaged in the same activities (Arendt and Dick, 1995; Arendt et al., 1999; Gwinn et al., 2000; Agel et al., 2005; Alahmad et al., 2020), and the valgus angle seems to be predictive of such injury in females (Hewett et al., 2005; Russell et al., 2006). A torn ACL would likely have been fatal for an ancestral hominin, thus seriously limiting the net fitness advantages of further pelvic expansion. As typically happens when fitness effects are in opposite directions, selection has traded off the risks of CPD and ACL tears, as evidenced by the fact that both are still relatively frequent.

Selection is opportunistic in the sense that any mutation that, in net, augments fitness will be favored. It seems that increased stature was one such evolutionary innovation. Taller females have, on average, larger pelves without increasing their valgus angles (Adadevoh et al., 1989; Imai et al., 2020). Thus, increases in female stature should reduce the birthing problems associated with the obstetric dilemma. If this view is correct, we would expect a strong positive relationship between female stature and successful delivery of a healthy infant.

We used the occurrence of an emergency (i.e., non-elective) primary C-section as a proxy measure for CPD. Using logistic regression with birth certificate data for 3,550,445 live births from the 2013 US natality database, we determined the risk of such C-sections in relation to self-reported maternal stature. As predicted, the risk of a problem delivery decreases with increasing maternal stature. Controlling for maternal age, parity, race, ethnicity, and infant birth weight, the risk of emergency primary C-section declined by 3.2%, 95% CI [3.1, 3.2] with each cm of increase in maternal stature. The uncontrolled risk is shown in **Figure 1** and, for first births, declines from more than 22% to about 11% from the shortest to the tallest women. For all births, over the same range of maternal stature the risk declines from more than 10% to about 6%. (First births are of course most relevant because they are the most difficult and because, ancestrally, mothers who did not successfully deliver their first infant never delivered a second.) This result is consistent with smaller studies showing a higher risk of CPD and emergency C-section with shorter maternal stature (Durjardin et al., 1996; Cnattingius et al., 1998; Brabin et al., 2002;

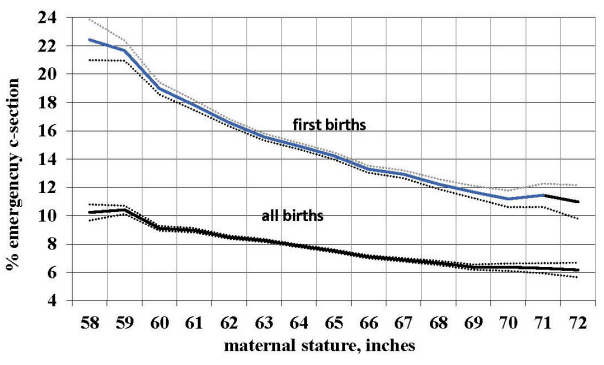

FIGURE 1 | Relationship of mean maternal stature to the risk of an emergency C-section for 3,550,445 total births and 1,122,782 first births with 99% confidence intervals, US, 2013 (without controls).

Sheiner et al., 2005; Benjamin et al., 2011). Moreover, taller women have a pelvic shape that better accommodates larger-headed fetuses (Fischer and Mitteroecker, 2015).

Because of the contribution of paternal genes to fetal growth rates, the mother and fetus of a union between a taller father and shorter mother should be at increased risk of CPD. Consistent with this prediction, prior studies have shown that larger differences in maternal and paternal stature predict serious complications of labor and delivery. One case-control study (Connolly et al., 2003) found that a one cm increase in maternal stature decreased the risk of CPD (odds ratio 0.91, 95% CI [0.84, 0.98]) while paternal stature was positively related to risk (odds ratio 1.2, 95% CI [1.1, 1.4]), implying that taller fathers and shorter mothers would have the highest risk. This was directly tested in another study (Stulp et al., 2011) which examined the risk of an emergency C-section in relation to the paternal-maternal stature difference and found a significant linear increase in risk as the parental stature difference increased.

For a similar investigation, we constructed a matched dataset of parents and children with birth certificate information for 2,918 mother-father-child triads. Based on logistic regression, for each cm the father was taller than the mother, the risk of CPD increased by 8%, 95% CI [3–13].

The hypothesis that stature dimorphism decreased in order to increase successful delivery was further tested in a cross-national study by Guegan et al. (2000). Since most maternal deaths are due to complications of labor and delivery which are more frequent in shorter mothers, they hypothesized that in populations where there is a high birth rate exposing mothers to more obstetric risk and a high per-birth risk of maternal mortality, there will be a selective pressure for a reduction in stature dimorphism. This hypothesis was supported in an analysis of data from 38 populations. Controlling for other variables, stature dimorphism was lower in populations with higher fertility and maternal mortality.

The results presented above support the idea that as males increased in stature over the last two million years of hominin evolution, female stature increased proportionately more due to natural selection pressures relating to the challenges of delivering larger-brained infants. It was *these combined female and male changes that reduced human stature dimorphism.* Hence, the pervasive belief that the reduction in human stature differences was caused by a parallel reduction in male contest competition is undermined by our analysis of the evolutionarily important relationship between stature and successful parturition. Moreover, other lines of evidence (below) support the idea that sexual selection on males has not abated in the hominin lineage.

Body Mass Dimorphism

Although sex differences in human body composition confound simple comparisons (see section "Sex Differences in Lean Body Mass, Muscle Mass, and Strength," below), we review overall body mass because it is the most frequently used measure of sexual dimorphism in studies of other animals. Because of its advantage in aggressive contests, body mass has long been recognized as providing sexually selected benefits for the sex experiencing stronger mating competition (Darwin, 1871; Gaulin and Sailer, 1984; Andersson, 1994; Puts, 2010). Body mass dimorphism is characteristic of non-monogamous primates (Gaulin and Sailer, 1984; Ely and Kurland, 1989; Plavcan, 2012b). Frayer and Wolpoff (1985) cross-tabulated primate body-weight dimorphism by mating system and taxonomic subgroup. In terms of overall body mass, they found that monogamous species ranged from 0% dimorphism among the prosimians to 3.5% among the lesser apes; in contrast, polygamous primates ranged from 10% dimorphism among prosimians to 44% among apes and Old World monkeys.

In contemporary human populations men range from 12 to 25% heavier, on average, than women (Pheasant, 1983; Lindle et al., 1997; Kyle et al., 2005; Xiao et al., 2005). In a notably large sample of 473 Hadza hunter-gatherers, almost equally divided by sex, men averaged 14.9% heavier than women (Sherry and Marlowe, 2007). In samples of 96 non-industrialized populations Wells (2012b) and a sample from 129 nations (Pontzer et al., 2021), men averaged 14.2 and 12% heavier than women. In our dataset of 191 samples, men averaged 21% heavier, and in the US NHANES DEXA database, men were 13.9% heavier. Because women are more likely than men to be obese (Kelly et al., 2008), where obesity is less prevalent, the sex difference in human body mass tends to be larger, as reflected in the larger differences in earlier US samples (Stoudt et al., 1965).

For comparison with related species, males are 10% heavier in gibbons (*Hylobates lar*), 11–32% heavier in common chimpanzees (*Pan troglodytes*), 72–88% heavier in olive baboons (*Papio anubis*), and 66–146% heavier in gorillas (*Gorilla gorilla*) (Smith and Jungers, 1997; Gordon, 2006b). These observed sex differences in overall body mass suggest that *Homo sapiens* falls between monogamous gibbons and promiscuous chimpanzees.

But total body mass provides only a crude picture of the forces shaping these sex differences because, on average, men and women allocate that mass much differently (Plavcan, 2012b). Women have considerably more fat and men have more lean (and muscle) mass (Pond, 1998; Kyle et al., 2005; Wells, 2007, 2012a,b; Lassek and Gaulin, 2009; Hill et al., 2017; Puts et al., in press). Because these sex differences in body composition are present but significantly less pronounced in infants and children and increase dramatically with puberty (Wells, 2007; Kirchengast, 2010; Taylor et al., 2010), this is an ontogenetic sign that they are related to the different reproductive strategies of the two sexes, as explored below.

Sex Differences in Lean Body Mass, Muscle Mass, and Strength

In contrast to the moderate sex difference in overall body mass, human males have a substantially more (fat-free) lean body mass than females, averaging between 30 and 42% more across the four data sets (**Table 1**). The overall average of the mean lean body masses was 55.2 kg for males and 40.6 for females, with males having 36% more. For the last two datasets (where they can be calculated), the effect sizes are 1.86 and 2.67. For 96 non-industrial samples (Wells, 2012b), the lean body mass means for males and females were 50.8 $\pm$ 1.29 and

TABLE 1 | Lean body mass (kg) and percent body fat from four data sets with ratios and effect sizes (*d*) where available.

		Lean body mass, kg					Fat%				
Source	**Samples**	**m**	**f**	**m/f**	**f/m**	***d***	**m**	**f**	**m/f**	**f/m**	***d***
Wells (2012a)	260	51.6	39.7	1.30	0.77		17.0	28.1	0.61	1.66	
Africa	55	47.9	38.3	1.25	0.80		14.9	23.1	0.65	1.55	
Asia	67	45.1	35.0	1.29	0.78		15.5	24.2	0.64	1.56	
Oceania	46	49.9	37.9	1.32	0.76		15.0	24.2	0.62	1.62	
Polynesia	21	60.3	47.6	1.27	0.79		24.6	37.9	0.65	1.54	
S. America	39	50.7	38.0	1.33	0.75		15.6	28.4	0.55	1.81	
Arctic/Subarctic	32	55.5	41.5	1.34	0.75		16.3	30.7	0.53	1.89	
This paper (**Supplementary Table 1**)	191	58.1	42.1	1.38	0.72		20.1	30.5	0.66	1.60	
Foragers	6	45.9	36.5	1.26	0.80		21.4	32.3	0.63	1.64	
Horticulturalists	12	53.9	38.4	1.41	0.71		13.3	24.6	0.53	1.95	
Non-WEIRD (5)	8	51.4	38.0	1.36	0.74		18.2	31.9	0.57	1.77	
India	8	34.5	26.9	1.28	0.78		18.7	27.2	0.69	1.47	
Japan	8	52.1	37.3	1.40	0.72		18.6	28.7	0.64	1.62	
Canada	8	60.6	43.1	1.41	0.71		19.9	30.2	0.65	1.57	
United States	90	61.9	44.4	1.39	0.72		22.1	32.7	0.68	1.56	
Europe (12)	47	60.6	43.6	1.39	0.72		18.6	28.3	0.66	1.58	
Oceana	8	62.5	45.0	1.39	0.72		21.7	30.8	0.70	1.47	
Pontzer et al. (2021)	129	59.1	44.0	1.34	0.74	1.86	22.8	35.1	0.65	1.55	1.38
16–19	314	57.1	42.5	1.34	0.74	1.96	21.5	32.3	0.67	1.50	1.14
20–25	385	60.3	43.3	1.39	0.72	2.04	19.6	33.6	0.58	1.71	1.56
25–29	467	60.0	43.4	1.38	0.72	2.04	22.3	34.4	0.65	1.54	1.31
30–34	387	59.1	45.2	1.31	0.77	1.68	24.0	36.7	0.65	1.53	1.42
35–39	399	58.9	45.5	1.30	0.77	1.58	26.4	38.4	0.69	1.45	1.48
NHANES 1999–2006*	5,434	56.6	39.8	1.42	0.70	2.67	20.7	32.5	0.64	1.57	2.54
15–19	3,149	53.6	38.6	1.39	0.72	2.32	18.8	31.3	0.60	1.66	2.77
20–25	784	56.3	39.5	1.43	0.70	2.66	19.7	32.2	0.61	1.64	2.78
25–29	541	57.2	40.1	1.43	0.70	2.74	21.4	32.3	0.66	1.50	2.23
30–34	488	57.9	40.4	1.43	0.70	2.75	21.4	33.1	0.65	1.55	2.40
35–39	472	58.2	40.4	1.44	0.69	2.88	22.1	33.5	0.66	1.52	2.50

**BMI < 30, see section "Materials and Methods".*

38.7 ± 0.77, with males having 29% more with an effect size of 2.34. The human sex difference in lean mass is similar to the 11–32% sex difference in weight for chimpanzees (which have significant contest competition) (above). The sex difference in lean body mass in the NHANES DEXA sample is illustrated in **Supplementary Figure 2**.

Lean body mass includes organs, muscle, and bone which, in aggregate, should naturally increase with greater overall body mass. Of these, differences in muscle would be more informative about possible divergent selection pressures on males and females. To assess how much of the lean-mass differences are due to differences in muscle, we compiled 29 samples that measured muscle mass using a variety of methods (**Supplementary Table 2**) and included new DEXA data from NHANES 1999 to 2006. The mean ratio of male to female muscle mass was 1.65 and the mean effect size (for the 25 studies reporting this statistic) was 2.70.

Perhaps most relevant to aggressive competition in humans is the sex difference in upper-body muscle mass. We have identified 8 studies of sex differences in arm muscle including new data for this paper (**Supplementary Table 3**). The mean ratio of male to female arm muscle was 1.72 and the mean effect size for 5 studies was 2.91. This is similar in magnitude to the sex difference in lean body mass in gorillas (1.79), the most sexually dimorphic primate (Zihlman and McFarland, 2000). Sex differences in the DEXA sample are illustrated in **Supplementary Figure 3**. Sex differences in leg muscle mass are somewhat smaller (**Supplementary Table 3**), but still substantial; data from 14 samples (including new US data) give an average ratio of 1.48 and an average effect size in 11 samples of 2.71.

Contemporary phenotypes suggest that selection has favored larger body size in men than women. Given that background, selection for body-composition differences can be compellingly demonstrated by examining those differences in men and women statistically matched for both height and weight (**Table 2**). In that controlled analysis, males still have 9.8 kg more lean mass, 2.3 kg more arm muscle, 2.7 kg more leg muscle, and 4.2 kg more lean trunk mass. Thus, human sex differences in body composition are not a mere byproduct of size differences.

Muscle mass is a target of selection primarily via the amount of strength it yields. Several relevant meta-analyses of sex differences in strength are available (Sackett and Wilk, 1994; Hough et al., 2001; Courtright et al., 2013) that examine comparable

TABLE 2 | Fat and lean body mass differences in 10,537 males and 11,536 females aged 18 and older based on linear regression controlling for age, race, ethnicity, height, and weight, US, NHANES 1999–2006, all $p < 001$.

Measure	Coefficient, 95% CI
Total lean, kg	−9.81 (−9.67, −8.92)
Arm lean, kg	−2.29 (−2.26, −2.31)
Leg lean, kg	−2.74 (−2.68, −2.79)
Trunk lean, kg	−4.20 (−4.13, −4.27)
Fat percent	12.08 (11.94, 12.22)
Total fat, kg	9.81 (9.69, 9.93)
Arm fat, kg	1.31 (1.29, 1.34)
Leg fat, kg	4.92 (4.85, 5.00)
Trunk fat, kg	3.69 (3.61, 3.77)

dimensions of strength. All examine muscular tension (exerting force such as pushing, pulling, lifting), muscular power (exerting force quickly), and muscular endurance (exerting force over time), and all measure sex differences not as ratios but as effect sizes (*d*, the number of standard deviations separating males and females), the normal output of meta-analysis. Effect sizes for muscular tension in the three studies were 2.28, 1.86, and 2.13, and for muscular strength in the last two, 1.66 and 1.71.

In addition, Courtright et al. (2013), partitioned their effects by upper-body (arms, chest) vs. lower-body (legs), and found that the sex difference was greater in the upper body (*d* of 1.98 vs. 1.68). All of these effect sizes are very large by conventional standards, in some cases approaching or exceeding two standard deviations. Representative studies from these meta-analyses show that males have twice as much upper body strength as females and 66% more leg strength. When present in other animals, sex differences in physical strength would usually be interpreted as a sexually selected adaptation to aggressive mating competition (Andersson, 1994). Since male muscles are also used in hunting, the possible role of disruptive natural selection related to divergent female and male foraging strategies is also considered in Discussion section "Can Natural Selection Explain Dimorphism in Stature, Mass, and Strength?".

Sex Differences in Total Body Fat

Data for the four body-composition datasets (**Table 1** and **Supplementary Table 1**) are in close agreement concerning sex differences in percent body fat: Overall, women have between 1.55 and 1.66 times as much body fat as men. For ages 20–25, the effect size is 1.56 in the sample of Pontzer et al. (2021) and 2.78 in the larger NHANES DEXA sample (illustrated in **Supplementary Figure 4**). Women not only have substantially more body fat than men, but the average of 30.8 percent fat across the four samples is extraordinarily high compared to mammals generally (Pond, 1978, 1998). Even women undergoing starvation still have significant amounts of body fat. Two groups of women with severe anorexia nervosa (and BMI's of 16.8 and 16.2) still had 17.2 and 15.2% body fat (Golden et al., 1997).

When adult American males and females are matched for height and weight using regression (see above), females have 12.1% (9.8 kg) more body fat (**Table 2**), with 1.3 kg more arm fat, 4.9 kg more leg fat, and 3.7 kg more trunk fat (which includes some of the gluteal region). The 12% difference is similar to the samples in **Table 1** and gives a female/male ratio of 1.46 for percent fat.

The female body fat percentages in **Table 1**, persistent over the post-pubertal life cycle, are extraordinarily high compared with most other mammals and primates. Although species differences in body fat are sometimes large (Pond, 1978; Wells, 2006), they are correlated with the unique energy demands of (1) hibernation, (2) long-distance migration, especially in birds, or (3) brief, concentrated reproductive effort (Pond, 1998), none of which apply to humans. Across all mammals for which there are data (including the fatter migratory and hibernating species) mean body fat averages around 7% (Pond and Mattacks, 1985). Thus, men are 2–3 times fatter, and women 3.5–4.5 times fatter (**Table 1**) than the mammalian average, on a percentage basis, and very much fatter than other species that evolved in tropical savanna environments (Pond, 1978, 1998; Wells, 2006; Puts et al., in press). Possible reasons for women's larger amount of body fat are the focus of the section "Why Do Women Have so Much Fat?" of the Discussion.

Sex Differences in Body-Fat Distribution

Not only do men and women differ in the amount of body fat they store, they also differ in where they deposit it. Men deposit most of their fat viscerally whereas women deposit much of theirs peripherally and subcutaneously, especially in the gluteofemoral region (Tichet et al., 1993; Lassek and Gaulin, 2007, 2008; Taylor et al., 2010), giving them a characteristically low waist/hip ratio (WHR). **Table 3** shows differences in fat distribution in various national samples. Standard deviations are relatively high because WHR is strongly correlated with BMI, which varies with age. Across the samples, women have 9% lower waist-hip ratios and in the NHANES 1999–2006 sample, a 23% higher ratio of leg fat to trunk fat. There is more than a twofold difference in the depth of the thigh skinfold (**Table 3**), a measure of subcutaneous gluteofemoral fat, with an effect size of 1.87. Possible reasons for the sex difference in regional fat are the topic of the section "Possible Reasons for Sex Differences in Regional Fat Distribution" of the Discussion.

DISCUSSION

As stressed throughout, reliable sex differences are not, by themselves, evidence of sexual selection. As in some other species, natural selection may favor differences between females and males. For example, in raptorial birds the conflicting effects of larger size—increasing fecundity in the sex that lays the eggs, but compromising agility in the sex doing (more of) the hunting—has led to disruptive natural selection such that females are larger than males in many species. This females-larger pattern has evolved independently in the Accipitriformes, Falconiformes, and Strigiformes, groups now known to not be closely related (Schoenjahn et al., 2020).

There are at least two potential sources of divergent natural selection pressures on women and men that might broadly

TABLE 3 | Sex differences in waist-hip ratio (WHR) and other measures of fat distribution.

Source	Country	n	Ages	Measure	Female	Male	*f/m*	*d*
Wietlisbach et al. (2013)	27 countries	40,480	35–64	WHR	0.81	0.92	0.88	
Tichet et al. (1993)	France	18,393	17–60	WHR	0.79 ± 0.07	0.91 ± 0.07	0.87	1.73
*NHANES III	US	8,080	15–39	WHR	0.84 ± 0.07	0.90 ± 0.07	0.93	0.85
Qiong et al. (2017)	China	2,286	20–29	WHR	0.79 ± 0.06	0.84 ± 0.06	0.94	0.83
Bacopoulou et al. (2015)	Greece	1,610	12–17	WHR	0.73 ± 0.06	0.79 ± 0.06	0.92	1.00
Taylor et al. (2010)	New Zealand	206	20–26	WHR	0.78 ± 0.08	0.85 ± 0.07	0.92	1.00
Fredriks et al. (2005)	Dutch	690	18	WHR	0.75 ± 0.07	0.82 ± 0.06	0.91	1.08
Ahmad et al. (2016)	Malaysia	669	18 +	WHR	0.86 ± 0.08	0.90 ± 0.08	0.96	0,50
Ley et al. (1992)	UK DEXA	234	31–55	Waist fat	12.0 ± 1.9	18.1 ± 2.9	0.66	2.54
				Hip fat	19.4 ± 2.3	18.1 ± 1.8	1.07	0.65
				Ratio	0.62	1.00		
*NHANES 99-06	US DEXA	9,359	15–49	Leg/trunk	1.02 ± 0.31	0.83 ± 0.24	1.23	0.63
*NHANES III	US skinfolds	16,539	>17	Triceps	23.7 ± 8.7	12.6 ± 6.2	1.88	1.48
	mm			Subscap.	22.6 ± 9.5	19.0 ± 7.8	1.19	1.19
				Suprailiac	21.9 ± 10.3	20.9 ± 10.0	1.05	0.09
				Thigh	28.4 ± 9.2	13.3 ± 7.0	2.12	1.87

**New analyses (see section "Materials and Methods").*

parallel this avian situation: (1) being the sex that gestates and lactates, women might experience certain survival or fertility differentials that are not relevant to men (section "Increase in Female Stature to Accommodate Larger Brained Fetuses"), and (2) a widespread and apparently ancient sexual division of labor might favor different phenotypes in the two sexes, as discussed below.

Can Natural Selection Explain Dimorphism in Stature, Mass, and Strength?

In addition to sexual selection, natural selection can also produce sex differences in body size, though it seldom favors larger males. For example, natural (i.e., fecundity) selection can favor larger female size, notably in insects and fishes (Perrone, 1978; Thornhill and Alcock, 1983; Andersson, 1994), as realized by Darwin (1871). Likewise, divergent foraging niches can also produce sexually dimorphic body size, perhaps the best examples being raptorial birds where, again, females are consistently larger than males (Newton, 1979; Andersson and Norberg, 1981; Schoenjahn et al., 2020).

A sexual division of labor, with males concentrating on hunting mobile prey and women focusing on immobile plant foods is nearly universal among human foragers (Murdock, 1937; Gurven and Hill, 2009) and possibly primitive in the chimp-human clade given that hunting, while rare, is a nearly exclusive male activity in common chimpanzees (Mitani and Watts, 2001; Mitani et al., 2002). It has been suggested that this ecological sex difference could have generated natural selection for sexual dimorphism in human body size (Kaplan et al., 2000).

Evidence from modern hunter-gatherer groups suggests that male hunting provided a major portion of calories, fat, and protein to their families (and other families of their group through meat sharing) during human evolution (Cordain et al., 2000; Gurven and Hill, 2009). Given that men's hunting ability correlates positively with their muscle mass (Apicella, 2014) perhaps *natural* selection played a role in shaping both the sexual division of labor and sex differences in muscle mass.

The evidence on this issue is scant and indirect. Wolfe and Gray (1982b) conducted a cross-cultural analyses of stature dimorphism in relation to mode of subsistence. They found that, compared to hunter-gatherers, agriculturalists (whose sexual division of labor is less marked) actually exhibit more stature dimorphism and that, overall, a more equal division of labor was not associated with a reduction in stature dimorphism.

Based on a different cross-cultural sample, Holden and Mace (1999) used a sophisticated analytical strategy that controlled for both cultural and geographic relatedness among their sample populations. In their analyses, foraging populations showed the same levels of stature dimorphism as farming populations. However, dividing their cases differently, they found that cultures where women provide a higher proportion of food than men (regardless of how food is procured) showed less stature dimorphism. They suggested that this was the result of female offspring being better nourished in populations where women are the primary providers. In support of this interpretation they showed that sex biases in juvenile mortality showed a parallel pattern—juvenile males survive better where men contribute more to subsistence and juvenile females survive better when women contribute mere.

Using a genomic approach (Arner et al., 2021), examined allelic differences associated with a number of sexually dimorphic human phenotypes including height and body mass. They found no evidence of post-agriculture changes in the intensity of selection at these loci. In other words, the available evidence indicates that changes in subsistence have not had appreciable effects of human dimorphism, suggesting that human dimorphism is not primarily shaped by selection related to subsistence.

Dimorphism and Male Mating Success

Sexual selection arising out of competition for mates can cause a wide array of sex differences, but they broadly cluster into two major types: those that increase attractiveness to the opposite sex, and those that increase the ability to exclude same-sex competitors from mating (Andersson, 1994). The reasons why mating competition takes one form or the other are not fully understood (but see Gaulin and Sailer, 1984; Puts, 2010 for some suggestions), but the former is predominant in birds and the latter predominant in mammals.

How are we to assess the relationship between dimorphism and male mating success over the course of human evolution? A meta-analysis of the relationship between "status" (measured variously as physical formidability, hunting ability, material wealth, and political influence) and several male fitness components across 33 non-industrial societies found a consistent positive effect, but a weaker effect than in non-human primates (von Rueden and Jaeggi, 2016) which could be taken to indicate a weakening of male contest competition in extant humans accompanying the spread of monogamous marriage systems. A study of Y-chromosome distribution found evidence of a recent shift from polygyny to monogamy (Dupanloup et al., 2003).

However, contemporary fitness effects may not be relevant to explaining the selective forces that produced the extant pattern of human sex differences. It is a cornerstone of evolutionary explanation that current traits are the result of selection pressures that operated in ancestral populations (Tooby and Cosmides, 1990). Thus, if the present is different from the past, the fitness differentials that produced the trait may no longer obtain. Of possible relevance to reconstructing selective regimes, we can discover no law prohibiting polygamy earlier that the (British) Bigamy Act 1603.

Because we have no direct evidence of the human matting system during the period when human patterns of dimorphism were shaped, it seems reasonable to give more weight to the genetic evidence provided by the Y-chromosome. Genetic studies uniformly find much less genetic diversity in the human Y-chromosome than in human mitochondrial DNA which is passed only through females. This is consistent with a smaller effective male population size and higher variability in male than female reproductive success (Destro-Bisol et al., 2004; Wade and Shulter, 2004; Wilder et al., 2004a,b; Shriver, 2005; Hammer et al., 2008, 2010; Favre and Sornette, 2012; Heyer et al., 2012; Balaresque et al., 2015; Karmin et al., 2015; Poznik et al., 2016). This is also reflected in demographic data showing higher variance in male reproductive success across a range of tribal societies (Betzig, 2012).

Although a sexual division of labor might generate natural selection for hunting ability, there is substantial evidence that dimorphism related to hunting ability has been under *sexual* selection. In Hadza hunter-gatherers, upper-body strength predicts hunting success, prestige, and reproductive success (Apicella, 2014) and there are similar benefits in the Tsimane (Gurven and von Rueden, 2006) and Ache (Hawkes, 1991). Successful hunters achieve elevated reproductive success through a number of pathways (e.g., Kaplan and Hill, 1985; Smith, 2004). Hunting may provide males a costly signaling venue to display traits attractive to females (Bliege-Bird et al., 2001). In other words, sexual division of labor itself may be, at least in part, a consequence of disproportionate male mating competition. The same muscular attributes useful in hunting may also have been sexually selected by providing advantages in aggressive competition among men (or groups of men, see Zeng et al., 2018) for access to mates.

In addition to male muscularity serving a direct role in competing with other males, a number of studies have shown that it is also associated with female judgments of male attractiveness (Horvath, 1981; Dixson et al., 2003; Fan et al., 2005; Geary, 2005; Dixson and Dixson, 2007; Frederick and Haselton, 2007; Honekopp et al., 2007; Dixson et al., 2010b) and with reproductive success in China (Schooling et al., 2011), although men may overestimate how much muscle mass is optimally attractive (Lei and Perrett, 2021). These female preferences would have evolved only if there were preexisting fitness benefits to male muscularity (e.g., in contest competition for mates or in hunting).

Sex differences in body mass, muscle mass, and strength are typical outcomes of sexual selection in mammals generally and primates in particular. Their frequency in related species does not guarantee that they were caused by the same sexual-selection processes in humans. However, our confidence that they were will be increased if we see evidence that male mating competition had produced sexual dimorphism in other traits that are not obviously related to hunting.

We can begin with the observation that males are the "fast" sex (*sensu* Clutton-Brock and Vincent, 1991) in humans, returning to the mate pool more quickly and thus more likely to find mates scarce. Quantitative evidence indicates that more men are excluded from fatherhood than there are women excluded from motherhood, the essential consequence of differential mating competition. For example, there is higher variance in male than female reproductive success across a range of societies and that variance difference increases as populations become more sedentary (Betzig, 2012).

If men evolved to exclude competitors from mating they should have psychological traits designed for that purpose, such as increased aggression, and many kinds of data indicate that men are more physically aggressive than women (Archer, 2009). An indication of how pervasive fighting between young males is in the US can be is found in the results of biennial surveys of American high school students. From 1993 to 2019, an average of 39% of males vs. 23% of females in grades 9–12 in American schools were involved in one or more physical fights in the previous 12 months (NCES, 2021).

A number of studies have found a positive relationship between male reproductive or mating success and aggression (Sadalla et al., 1987; Chagnon, 1988; Connolly et al., 2000; Charles and Egan, 2004; Llaurens et al., 2009) and physical dominance (Puts et al., 2006; Gangestad et al., 2007; Markey and Markey, 2007; Bryan et al., 2011) supporting the idea that human male aggression is the result of sexual selection (Archer, 2009; Georgiev et al., 2013), as it in other mammals (Gómez et al., 2016). Human females are more prone to choose aggressive and combative males as mates when they feel in danger from other males (Snyder et al., 2011).

The more extreme the nature of the violence, the more extreme are the observed sex differences. Because it is less likely to be an effect of differential socialization by sex, the least contaminated assay of evolved sex differences in aggressive tendencies is same-sex homicide outside of warfare (within-society homicides), because they are nowhere condoned for either sex. Nevertheless, a very large sex difference remains. Men are much more likely to kill a man than a woman is to kill a woman; the discrepancy is large and relatively stable across time and across different modes of subsistence, with males accounting for approximately 95% of all same-sex homicides (Daly and Wilson, 1990). The most common "motive," according to standard federal reporting criteria, is not robbery but "incident of trivial origin"—status competition that went further (perhaps) than the competitors expected (Daly and Wilson, 1988).

Homicide related to mating competition is a frequent occurrence in many hunter-gatherer societies (Kruger and Fitzgerald, 2012; Allen and Jones, 2014), including the "harmless"! Kung, in which most homicides are related to competition for women (Lee, 1993). In the Gebusi, for example, a group with a very high homicide rate of 7 per 1,000, the professed cause was to punish sorcery but the actual cause was to increase male control of marriageable women (Knauft, 1987). Across cultures, time, and species, lethal male-male aggression is strongly related to mating competition (Kruger and Fitzgerald, 2012).

In that context it is relevant that men's (but not women's) proneness to anger and history of physical aggression are both correlated with their own physical strength, suggesting psychological mechanisms for the strategic deployment of aggression against conspecifics (Sell et al., 2009); "don't start it unless you can win it."

Of course, in addition to competition between individual men within groups, there is also substantial evidence for persistent violent competition between groups in the form of warfare or raiding, which is the most common form of killing seen in chimpanzees (Bowles, 2009; Puts, 2010; Allen and Jones, 2014; Puts et al., 2015; Puts, 2016; Hill et al., 2017; Mann, 2018). Competition between patrilineal groups has been suggested as the cause of a post-Neolithic Y-chromosome bottleneck (Zeng et al., 2018).

When men attack each other (in the absence of weapons) fists slamming into faces is a common pattern. Sexual selection may have been at work in this domain as well. The particular facial bones most frequently fractured in such altercations evolved greater robusticity such that they have been for several million years, and continue to be, the most sexually dimorphic elements of the human skull (Carrier and Morgan, 2015), suggesting that such conflict was predominantly a male-male affair.

If faces are targets of attack in male contest competition, selection may have produced beards as adaptive protection. Beards are a notably derived (e.g., compared to chimpanzees, where the area around the mouth is one of the least hairy regions), and highly dimorphic feature of human anatomy (Darwin, 1871). Facial hair is morphologically distinct from scalp hair in ways that may allow it to deflect and/or absorb blows to the face (Beseris et al., 2020). Men perceive potential competitors with full beards as more dominant (Puts, 2010; Dixson and Vasey, 2012; Dixson et al., 2017a). As we would expect if it plays a role in male contest competition, beardedness is more prevalent in countries with male-biased sex ratios (Dixson et al., 2019), under crowded conditions (Dixson et al., 2017b), and where economic inequality is high (Dixson and Lee, 2020; Pazhoohi and Kingstone, 2020). Compared to clean-shaven faces, beards enhance judgments of male facial masculinity, dominance, and aggressiveness, irrespective of underlying facial structure (Sherlock et al., 2017; Mefodeva et al., 2020). Likewise, beards enhance the speed and accuracy of detecting an angry facial expression (Craig et al., 2019; Dixson et al., 2021).

If beards are a sexual display, which sex are they displaying to? Several studies that compared the effects of beards on dominance or aggressiveness judgments by men with their effects on attractiveness judgments by women found the male-male effects significantly stronger (Puts, 2010; Dixson and Vasey, 2012; Dixson et al., 2017a). Still, there is some evidence for female preferences, notably that beardedness is more common where pathogen stress is high (Dixson and Lee, 2020; Pazhoohi and Kingstone, 2020), suggesting female choice for good-genes benefits.

Other sexually dimorphic features are even less plausibly related to an adaptive specialization for hunting but apparently related to aggressive male-male interactions. The one-octave sex difference in habitual voice pitch is an example (Puts et al., 2006). Lower voice pitch is much more strongly related to male dominance perceptions than to female attractiveness perceptions (Puts et al., 2007; Hodges-Simeon et al., 2010; Rosenfield et al., 2020), and situational lowering of male voice pitch elevates listeners' perceptions of the speaker's aggressive intent (Zhang et al., 2021).

The strong sexual dimorphism in both voice pitch and facial hair results in what animal behaviorists would call male sexual ornaments. Comparative research suggests that men are roughly as ornamented as males in polygynous primate species with large, fluid social groups (Dixson et al., 2005; Grueter et al., 2015). Beards and low-pitched voices are especially relevant to our analysis because an array of experimental studies links them to aggressive male-male competition in a way that they cannot be plausibly linked to the alternative hypothesis of selection for hunting abilities.

Lastly, ontogeny also provides relevant evidence about the evolution of human sexual dimorphism. The sex differences that are the focus of our article—stature, body mass, body fat and lean mass, fat distribution, muscularity and strength—all emerge or are significantly amplified around sexual maturity. This timing suggests they are related to reproduction rather than to sex-specific ecological adaptations.

Increase in Female Stature to Accommodate Larger Brained Fetuses

Gestation and lactation are demanding mechanically, energetically, and in terms of supplying particular nutrients to the fetus (e.g., calcium for the skeleton, fat for the brain). Because males do not face these demands it would be surprising if disruptive natural selection had not caused female and male

phenotypes to diverge with respect to these demands. We have suggested two such adaptations.

One is the increase in female stature relative to males. With the transition to larger-brained *Homo* from earlier *Australopithecus*, sexual dimorphism in stature decreased. This decrease is widely regarded as indicating a shift to a more monogamous mating system with a concomitant decrease in male mating competition (a sexual-selection explanation). But this explanation ignores potentially relevant facts: The decrease in stature dimorphism was accomplished via size increases in both sexes, with the female size increase being relatively greater than the male.

We interpret these facts as indicating some novel selection pressure on females, and specifically highlight the difficulty of delivering a large-brained infant.

Our analyses of contemporary data show that taller women, and women closer in stature to their mates, are less likely to experience an emergency Caesarian section (a proxy for the kinds of birthing difficulties that would have reduced female fitness during hominin evolution). To the extent that our data are relevant, the current level of human stature dimorphism seems: (1) to have been significantly shaped by viability and fecundity selection on women and, (2) consequently, underestimates the intensity of sexual selection on males.

Why Do Women Have so Much Fat?

The second adaptation in human females likely brought about by natural selection is the increase in the percentage of body fat. Currently, there is no scientific consensus about why women (and to a lesser extent men) have such high levels of body fat. Fat is heavy and, unlike muscle, does not contribute to its transport costs. For this reason, no animal should store more fat than it needs.

One suggestion is that hairlessness increased our need for insulation against hypothermia (Kushlan, 1980) although, even if correct, this idea would not explain the sex difference. Pond (1992) has presented comparative mammalian evidence from the *Carnivora*, an order with species in a wide array of habitats from tropical to polar, and found no support for the idea that fat deposits evolved primarily for insulation. Moreover, hominins were a tropical lineage throughout most of their history with relatively little need for insulation. If insulation were the main purpose of human fat we should have very little, or there should be large population differences in body fat—correlated with latitude—that evolved as our ancestors began moving out of Africa.

Wells (2012a) shows a very weak positive correlation between peripheral body fat (as assayed by triceps skinfold) and latitude, but only when he omits the Polynesian populations from his sample. Regardless, tropical African hunter-gatherers such as the Hadza at 10.6–13.5% body fat for men and 19.0–20.9% body fat for women (Sherry and Marlowe, 2007; Pontzer et al., 2012) have far too much adipose to support the insulation hypothesis for high levels of human fat deposition.

The obesity epidemic, while real, is also not the explanation, because Wells's (2012a) sample of non-industrial populations (**Table 1**) and our sample of foragers and horticulturalists (**Table 1** and **Supplementary Table 1**) show that high levels of body fat are human universals.

Because only women gestate and lactate, this sex difference is widely assumed to have favored their disproportionate fat deposits (e.g., Frisch, 1984; Power and Schulkin, 2008; Kirchengast, 2010). But if this were the correct explanation, all mammals should exhibit similar sex differences in body fat. In contradiction to this expectation, significant sex differences in total fat deposition are not the norm in mammals (Pond, 1978; Pond and Mattacks, 1985) nor in primates, and sometimes are skewed in the opposite direction with males being fatter (*Macaca fasicularis*: Pond and Mattacks, 1987; *Papio anubis*: Eley et al., 1989; *Papio cynocephalus*: Altmann et al., 1993; *Macaca mulata*: Colman et al., 1998; *Callithrix jacchus*: Power et al., 2001; *Macaca fuscata*: Hamada et al., 2003; *Propithecus verreauxi*: Lewis and Kappeler, 2005; Raman et al., 2005).

Could the higher fat levels in human females be due to their needing more energy during pregnancy and lactation than other primates? This seems unlikely. Studies show that the energy costs of pregnancy and lactation in relation to maternal weight in humans are similar to other primates and apes, and primate females typically deal with the energy costs of pregnancy and lactation by increasing food intake (Dufour and Slather, 2002).

Although primates generally have longer gestations than other mammals, thus decreasing their daily energy requirement, the length of gestation in humans in relation to the mother's weight is close the primate regression line (Dufour and Slather, 2002) and daily maternal energy investment is also on the regression line for other apes (Ulijaszek, 2002). Human lactation costs are also similar to other primates. The lactation period for human females (based on the !Kung) is below the regression line for primates and apes (Dufour and Slather, 2002). The relatively dilute concentration of nutrients in human milk is similar to other primates (Dufour and Slather, 2002) and the calories per gram are lower than in baboons and other monkeys (Oftedal, 1984). Women's cost of lactation in relation to weight is much lower than in many other mammals and similar to baboons (Prentice, 1988). In other words, species differences in the *energetic* costs of reproduction would not seem to demand greater stored resources in women than in our primate relatives.

In species with well-defined breeding periods, males may seasonally accumulate additional fat to facilitate aggressive competition for mates (Boinski, 1987; Bercovitch, 1992) or females may do so to support their maternal investment (Hamada et al., 2003). But in her comprehensive review of fatty tissues in wild vertebrates, Pond (1978) remarked that the *perpetually* large fat deposits in human females are very unusual.

The exceptional nature of women's high fat storage is further underscored by a comparative analysis across 87 mammal taxa which showed that, in species with alloparental care—whether by the father or others—females store less fat (Heldstab et al., 2017) presumably because, by providing some resources, fathers and allomothers reduce the demands on mothers. It has been estimated that alloparenting decreases the lifetime reproductive effort of human females by 14–29% compared with other mammals (Bogin et al., 2014). Thus, to be as large they are, to manifest relatively early in development, and to be so permanent in a species with significant alloparental care, women's fat deposits must have been shaped by both strong and relatively unique selection pressures.

Perhaps women's higher percentage of fat is explained by another unique human trait: our large brains. All female mammals must provision the development of their fetus and infant, but none must build as large a brain in proportion to their own body size. Brains not only consume large amounts of energy from glucose, but they require significant amounts of quite specific fats—notably, long-chain omega-6 and omega-3 polyunsaturated fatty acids—as major building blocks.

On a dry-weight basis, the human brain is about 60% fat (Bradbury, 2011), and two rare long-chain fatty acids, the omega-3 docosahexaenoic acid (DHA) and omega-6 arachidonic acid, each constitute about 10% of brain fatty acids (Makrides et al., 1994), with DHA playing the most critical role in brain development and function (Lauritzen et al., 2016). These essential fatty acids cannot be synthesized by humans and thus must come from the diet and be stored until needed.

The percentage of DHA in stored fatty acids reflects the percentage in the long-term diet and is seldom more than 0.4% of total adipose (Knutsen et al., 2003; Luxwolda et al., 2014). However, when there is less DHA in the diet, the concentration of DHA in stored adipose is consequently lower, and the only way to store more DHA is to increase the total amount of adipose (and hence BMI). Women with less DHA in the diet thus tend to have more fat: Female BMI is inversely related to the amount of DHA in the blood (Sands et al., 2005). Contemporary studies indicate that DHA is preferentially stored in gluteofemoral fat and then mobilized during pregnancy and lactation (see "Possible Reasons for Sex Differences in Regional Fat Distribution" below).

This neuro-developmental perspective potentially explains why human mothers need more fat than mothers of other mammalian species (Cunnane and Crawford, 2003; Lassek and Gaulin, 2006, 2007, 2008; Wells, 2006) and also explains why human neonates have so much body fat (Cunnane and Crawford, 2003; Correia et al., 2004). Because the amount of various fatty acids that can be stored is proportionate to their occurrence in the diet, and because critical omega-3 fatty acids are dietarily scarce, fat stores must be large to contain significant amounts of this critical brain-building fat (Lassek and Gaulin, 2006).

This perspective, if correct, has the advantage of uniting under one explanatory umbrella three highly derived human states: exceptionally large brains, higher levels of body fat than any non-hibernating, non-migrating mammal, and greater sexual dimorphism in body fat than any other mammal. Other hypotheses, such a need for protection against hypothermia, do not fit the comparative data and do not explain the large sex difference. From our perspective, sex differences in the percentage of body fat would be explained by disruptive natural selection favoring larger fat stores in women.

This view contrasts to some degree with the prevailing literature, where women's fat stores are often viewed as the outcome of sexual selection acting via male choice. Given the extensive evidence concerning male mating preferences for female body shape, there is no doubt that such selection has occurred, but two issues require attention. First, the male preference should not have evolved unless it was targeting existing viability or fecundity differences among females (in other words, such preferences evolved to track what natural selection on females was already favoring). Second, as many studies make clear, the relevant target of male choice is female body-fat *distribution*, as discussed below.

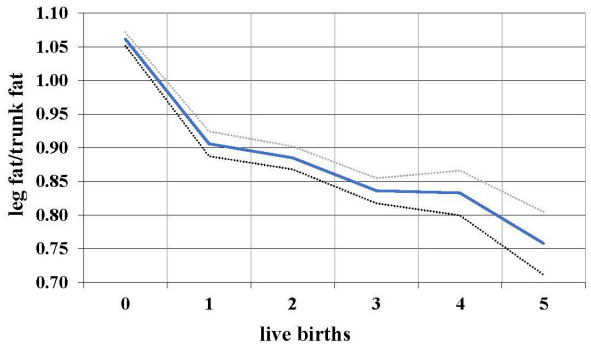

FIGURE 2 | Relationship between live births and leg/trunk fat ratio in 7,753 women 12–49, with 95% confidence intervals, NHANES 1999–2006.

Possible Reasons for Sex Differences in Regional Fat Distribution

The evolutionary reasons for the sex difference in adipose storage are not fully understood. Mechanically, adding weight in the form of body fat to a limb increases the force required to move it, without increasing strength, so peripheral fat must compromise the agility and power of the arms and legs. That mechanical effect could *dis*favor peripheral fat deposits in the sex competing more intensely for mates—males, as we have argued in the human case. But why would peripheral fat be favored in women? And why should it be localized to a few depots, rather than deposited as a smooth sheath beneath the skin of the whole body?

Various answers have been offered to one or both questions. Positioned near the center of mass of the body, the gluteofemoral depot may stabilize locomotion and provide a counter-balance to the frontal mass of a developing fetus (Pawlowski, 2001; Pawlowski and Grabarczyk, 2003). Another suggestion is that women may shunt fat from visceral to subcutaneous depots to increase the available space for gestation and to reduce intra-abdominal pressure on the fetus (Abrahim, 2021).

Another line of thinking connects to the neurodevelopmental explanation for women's high levels of body fat (section "Why do Women Have so Much Fat?" above). Relative to other depots, the gluteofemoral depot is protected against use for ordinary energy needs but is then systematically drawn down during late pregnancy and lactation (Rebuffe-Scrive et al., 1985; Rebuffe-Scrive, 1987; Lassek and Gaulin, 2006)—the key period of fetal and infant brain growth.

During lactation most of the long-chain fatty acids in maternal milk come from stored fat rather than from the mother's current diet (Lassek and Gaulin, 2006), and the gluteofemoral depot seems to be the primary source of the omega-3 and omega-6 fats that are essential for fetal and infant brain development (Lassek and Gaulin, 2007). Women who have adequate food supplies eat substantially less than they need to caloricly support lactation and instead mobilize stored fat. Is that to provide critical *materials* stored in that fat?

During the female reproductive lifespan, there is a decrease in the relative amount of gluteofemoral fat with parity (Lassek and Gaulin, 2006). Based on data from NHANES 1999 to 2006, the ratio of leg fat to trunk fat (which is highly correlated with the waist-hip ratio, but measures actual fat) drops with each successive birth (**Figure 2**), suggesting that gluteofemoral resources are differentially consumed in reproduction. Women with a higher thigh/waist ratio have higher levels of DHA, the omega-3 fat found at high levels in the brain (Lassek and Gaulin, 2019). These polyunsaturated fats—especially the omega-3s—are relatively unstable and possibly best stored in cooler subcutaneous rather than warmer visceral locations.

All of the effects on body fat mentioned thus far would result from natural selection, through the more efficient locomotion of the woman or through the production of infants with better-provisioned brains. However, once such selective differentials existed, sexual selection might begin to operate via evolved male preferences for women whose subcutaneous fat deposits indicated superior brain-building potential (Lassek and Gaulin, 2008). A similar argument was advanced by Cant (1981), noting that concentrated fat depots (e.g., buttocks and breasts) more effectively advertised a woman's stored maternal resources, but did not explicitly identify neurodevelopmental resources as limiting. One study (Szalay and Costello, 1991) attributes all sexually dimorphic fat to sexual selection, but that explanation is incomplete; some pre-existing adipose-related fitness gradient in women is a precondition for the evolution of male preferences that track the gradient.

This logical requirement suggests there was prior natural selection on females for discrete fat depots, perhaps sorted by type of fatty acid and/or intended usage—with male preferences simply evolving to differentially attend to the depots most relevant to female mate quality. Currently, the gluteofemoral depot is the primary source of brain-building fats (above). That fact is consonant with the extensive psychological literature showing that men selectively attend to women's waist/hip ratios in evaluating female attractiveness (e.g., Singh, 1993; Sugiyama, 2005; Singh and Randall, 2007; Dixson et al., 2010a,b,c, 2011; Brooks et al., 2015), with some researchers arguing that preference data suggest the waist/hip ratio is a supernormal stimulus (Marković, 2017). Several reviews have evaluated and rejected the idea that waist/hip ratios broadly track health and fertility (Lassek and Gaulin, 2018a,b; Bovet, 2019), thus suggesting it provides more specific information content.

SUMMARY

Over the last two million years of hominin evolution, both sexes increased in body size, but females increased proportionately more. These combined changes produced relatively low levels of stature dimorphism in contemporary humans, a fact that is widely interpreted as indicating a reduction in the intensity of male contest competition for mates over the same time period. But that interpretation fails to recognize the substantial sex differences in human body composition. Men's much greater lean body mass, muscle mass, and muscular strength (with effect sizes of 2.7–2.9) indicate a degree of dimorphism comparable to other primate species with intense male mating competition. Based on current obstetric evidence, females likely increased in stature relative to males in order to accommodate increasingly large-brained neonates. In parallel, women added body fat (rather than muscle) to provide more of the long-chain fatty acids that are critical for fetal and infant neurodevelopment.

Summarizing these ideas in the light of the two forces of natural and sexual selection: (1) sexual dimorphism in stature, fat mass, and fat distribution have been significantly shaped by disruptive natural-selection regimes operating on females and males, with some likely overlay of subsequent sexual selection acting via mate choice in the case of fat distribution; (2) sexual dimorphism in lean mass, muscle mass, and strength are largely due to sexual selection arising from a long history of aggressive male mating competition, with the some possible influence of divergent natural selection due to sex differences in foraging ecology; and (3) a large literature seems to have overemphasized the role of mate choice, and underestimated the role of male contest competition for mates, in shaping human sex differences.

DATA AVAILABILITY STATEMENT

Data analyzed from the National Health and Nutrition Examination Survey (NHANES), including the NHANES III and the NHANES 1999–2000, 2001–2002, 2003–2004, and 2005–2006, are available at https://wwwn.cdc.gov/nchs/nhanes/default.aspx. US natality data for 2013 are available from the Period-Linked Birth-Infant Death File for 2013 at https://www.cdc.gov/nchs/data_access/vitalstatsonline.htm.

AUTHOR CONTRIBUTIONS

WL compiled the various databases and performed the statistical analyses. SG wrote the first draft of the article. WL and SG jointly developed the ideas presented and edited the article to its final form. Both authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.859931/full#supplementary-material

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The Road Not Taken: What Developmental Psychology Might Learn From Darwin's Insights Concerning Sexual Selection

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Developmental Psychology is the branch of psychology that studies, not only human behavior, but how and why human behavior changes over time. This essay seeks to review to what extent Developmental Psychology has failed to perceive human behavior through the lens of evolutionary theory in general, and in particular sexual selection as first described by Darwin and later elaborated on by many, including Robert Trivers and Geoffrey Miller; the essay asserts that this failure has resulted in many wrong turns and missed opportunities. In some cases, major developmental theorists (e.g., Freud, Erikson) were bedeviled by sex-based differences which they saw but could not explain and which compromised the parsimony of their stage theories. In the case of stage theories of moral development, some major theorists (e.g., Piaget, Kohlberg) were able to offer simpler explanations of moral development only by limiting their studies to male subjects. And, while Developmental Psychology textbooks thoroughly describe sex differences in the timing of morphological changes in puberty, writers seldom discuss why the timing is different in the two sexes, universally, and functionally. On the other hand, several domains of developmental focus, including play, mate choice, parenting, and spatial cognition, have seen successful research efforts that utilized sexually selected predispositions as foundational assumptions. The essay concludes with a discussion of how a more evolutionary and functional view of human behavior might move the field of Developmental Psychology to an even more robust and accurate understanding of how humans change over the course of a lifetime.

Keywords: sexual selection, sex differences, developmental psychology, developmental pedagogy, stage theories, adaptationism

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INTRODUCTION

As we mark 150 years since Darwin's publication of *The Descent of Man, and Selection in Relation to Sex,* it is fitting that we reflect on Psychology's limited ability to benefit from Darwin's insights. Eloquent essays have been written on the broad failure to integrate Evolutionary Theory into the Social Sciences, including Psychology (Tinbergen, 1963; Pinker, 2004; Barkow, 2006; Segerstråle, 2006). Expectations for integrating Evolutionary Theory might have been particularly high for Developmental Psychology, which aims to explain changes in human behavior over the lifespan;

those expectations have not been met either (MacDonald, 1988; Charlesworth, 1992). Looking at Sexual Selection as contrasted with Evolutionary Theory more generally, one is even more struck by Developmental Psychology's stubborn resistance; Sexual Selection has been a fearsome lightning rod indeed.

There are many reasons for Developmental Psychology's failure to integrate ideas from Sexual Selection Theory. These causes include Western philosophy's history of dualism, a combination, culturally, of ignorance and arrogance about sexual matters, a focus on practical measures to improve people's lives (meliorism), and suspicion of biology coming from both United States political wings. The result has been an emphasis on socialization and other culture-specific environmental factors in the development of human behavior, as opposed to species-wide biological factors. Above all, developmental psychology has failed to explore functional explanations for universal human behaviors and sex differences. Though the reasons for this failure are numerous, one prominent cause may be the misperception that because functional explanations imply genetic causation, extragenetic influences on phenotype development are relatively trivial, a position which is inconsistent with a dynamic systems theory perspective (Lickliter and Honeycutt, 2003; Badcock, 2012; Al-Shawaf et al., 2021; Narvaez et al., 2021)[1]. While a focus on ultimate explanations can lead to an overemphasis on biological causation (Narvaez et al., 2021), it is important to note also the benefits of theory in building a coherent science (Eronen and Bringmann, 2021). Like many before us (e.g., Ploeger et al., 2008; Bjorklund, 2018), we believe that a Darwinian approach holds great potential, in conjunction with other theoretical approaches (e.g., developmental systems theory), as a metatheory for a mature developmental psychological science.

This essay will not dwell on why there is this powerful bias toward nurture-based explanation; the dynamics have been amply described in prior work. Rather, this essay will briefly summarize some basic ideas from Sexual Selection Theory with relevance for Developmental Psychology. The essay will then describe the path taken by Developmental Psychology, as reflected in major textbooks used in higher education courses, and point out failures in theory and research resulting, arguably, from failing to recognize the importance of Sexual Selection. The essay will end with examples of successful integration of Sexual Selection insights into developmental research and call for more such efforts.

Sexual Selection Theory: Concepts Relevant to Developmental Psychology

Darwin was puzzled by the consistency of the sex difference in animals whereby males compete for sexual access to females. In 1972, Trivers solved the conundrum by providing a theory to explain this pattern (Trivers, 1972). He recognized that the female is usually the more nurturant sex, and the males compete for access to this essential, limiting asset, often resulting in the evolution of larger, aggressive males. Males can reproduce merely by inseminating a female, whereas in mammals most notably, the female must invest much more energy, providing internal fertilization, pregnancy, parturition, and lactation. Therefore, females are selected to be judicious in choosing a mate, a pattern discernable in humans as well as most other mammals. Mammals' internal fertilization also means that pair-bonding males are prone to uncertainty about paternity, so selection favors males' guarding their mates against sexual interlopers (Mealey, 2000). Correspondingly, pair-bonding females' interests are more threatened by desertion by their mate.

Evolutionary theorists seek functional explanations for species-wide traits, including sex differences in behavior. They are interested in these "why" (ultimate; Mayr, 1961; MacDougall-Shackleton, 2011) questions that even intrigue young children but don't seem to puzzle mainstream psychologists. Developmental psychology textbooks seem not to recognize the extent to which human behavioral sex differences can be explained by extensions of what Trivers calls the theory of sexual selection and parental investment.

While some have questioned the usefulness of posing "why" questions (e.g., Laland et al., 2011), we see value in their inclusion. First, functional explanations provide heuristic and inductive value for hypothesis generation at the proximate (how) level of explanation. Knowing that the heart acts as a pump immediately suggests how components of the system might interrelate. Second, functional explanations can help define categories of behavior providing ontological clarity. For instance, the form of a behavior often belies its function. Both an infant's smile and cry, while differing in form (and state) function to reduce the distance between him and his caregiver. Likewise, the form of status-seeking behavior can include both prosocial and antisocial behaviors, yet serve functionally identical purposes (Hawley, 1999, 2016). Functional explanations can also distinguish between behaviors that share form (e.g., maternal aggression vs. reactive aggression). Third, functional explanations can provide an additional type of support (or lack thereof). Both proximate and ultimate explanation ought to be concordant. Forth, a functional understanding can improve targeting of developmental guidance (Ellis et al., 2012). Finally, our understanding of a given phenomenon is simply much richer if both levels of analysis are addressed. Knowing that male birds sing due to rising testosterone levels during the breeding season (proximate explanation) is categorically different than knowing that male birds sing to attract mates (ultimate explanation), but knowing both can be quite satisfying. See MacDougall-Shackleton (2011) for further discussion.

Returning to ultimate explanations derived from Sexual Selection theory, patterns of size dimorphism can be understood from this perspective. For instance, as in other species with male sexual competition, men are taller and stronger than women on average in all populations, maturing a year or two after girls. Adolescent boys and men are more aggressive and competitive than girls and women across cultures (e.g., Schlegel, 1995).

[1]It is important to note that a functional explanation does not imply (hard) genetic determinism. While it does posit selection of genes, and a role of genes in development, it does not speak to the questions of canalization, that is robustness or plasticity, of phenotypes. It merely asserts some role of genetic causation and can explain species-typical patterns of behavior. It has long been observed that extragenetic developmental adjustments can alter behavioral phenotypes. For instance, Kuo (1960) demonstrated that breed-typical behavior could be extinguished via developmental adjustments.

Around the world, boys exhibit more play fighting than girls in order to practice combat and to establish dominance relations.

Men's greater desire for status and resources for acquiring mates is linked to men's higher violent crime rates (Wilson and Daly, 1985) and putatively responsible for men's greater strength, especially upper body strength useful for fighting. Whereas men often react to a threat of attack by mobilizing physiologically for a fight, women and other female mammals often act to protect their young or to seek help, a reaction partly mediated by oxytocin (Taylor, 2006).

The sex differentiation in reproductive behavior is mediated in part by hormones. Accordingly, Sexual Selection Theory has come to incorporate elements of endocrinology, utilizing more elements of endocrinology than were available to Darwin.

Female mammals are exposed to little or no androgenic influence before birth, resulting in less play fighting than males. Girls with abnormally high exposure to androgens before birth show more play fighting than control girls, and less interest in doll play and marriage (Hooven, 2021). At puberty, interest in babies rises in both sexes, especially among females (Goldberg et al., 1982). At puberty, girls are feminized, mostly by estrogens. In both sexes, high levels of sex-typical gonadal hormones contribute to sex differentiation and hence in traditional evolutionary models are assumed to contribute to sexual attractiveness (Law Smith et al., 2006; Lidborg et al., 2022).

A woman's level of several parental hormones during pregnancy or after birth is correlated with her bonding and nurturant tendencies. In mammals, maternal motivation is driven by hormones, exposure to young, filial emotional displays, competence, learning, and imitation. Men's level of testosterone falls, and their level of prolactin rises when their mate becomes pregnant and when the baby is born (Storey et al., 2000). The greater these changes, the more paternal behavior the father exhibits (e.g., Gettler et al., 2011). Thus, parental behavior is shaped partly by hormones and experience in both sexes, but the hormones differ.

The parental roles are somewhat specialized by gender. Around the world, fathers tend to defend the nuclear family from attack (Opie et al., 2013), and fathers are expected to be more productive economically. Women, however, perform labor outside the home, prehistorically having gathered plant food (Friedl, 1975). Tribal cultures exhibit clear sex differentiation of labor, avoiding disputes over task assignment and redundancy and gaps in training during childhood.

Girls living in stressful or father-absent homes tend to reach menarche earlier than controls (Ellis, 2004). Boys in abusive homes and who possess a certain gene on the X chromosome, are at risk of antisocial behavior, and more at risk than girls. Abuse, including sexual abuse and homicide, is more likely when an unrelated male, such as a boyfriend or stepfather, resides in the home (Daly and Wilson, 1988). In general, development by any measure is better when both biological parents are in the home.

Many other human reproductive behaviors do not differ between the sexes but are universal and hence may have an evolved basis. Almost all tribal cultures are extended-family cultures in which three generations live together or in proximity. These universals are of interest because of their relevance to survival and reproductive success. Comparatively, biparental species tend to show marked reductions in sexual dimorphism compared to promiscuous or polygynous ones, a trend visible in our hominin ancestors (Grabowski et al., 2015). Pair-bonding emotions e.g., amorousness seems to be monotropic and qualitatively isomorphic and correlates of marital satisfaction are shared (Weisfeld et al., 2018). Both sexes compete for dominance, albeit males more so (Weisfeld, 1986), with forms of aggression also differing (Campbell, 1999; Pellegrini and Archer, 2005). Correlates of divorce, such as infertility are shared between the sexes, although earnings, financial independence, and infidelity differentially impact divorce across the sexes (Betzig, 1989). By many indications, including the fact that almost all people, around the world, seek to marry, marriage is a reproductive adaptation (Weisfeld et al., 2018).

Teaching Life-Span Developmental Psychology

We three authors have altogether taught various courses in Developmental Psychology for over 85 years. In teaching Developmental Psychology, we have sought to use texts that integrate causal explanations for behavior, reasoning that heredity and socialization interact throughout the lifespan. That is, after all, the charge of Developmental Psychology, understood from the time that the journal by that name began publication in the 1960's: *to explain changes in behavior as a function of time.* As the first editor, Boyd R. McCandless, wrote, this would surely require integrating nature and nurture, including accounting for sex differences (McCandless, 1969). Yet published research and textbook writing certainly veered off that path early and often. Our own difficulty in finding truly integrative Developmental Psychology textbooks is reflected in the data provided in **Table 1**. In preparing this table, we created a list of concepts from Sexual Selection Theory that are relevant to Developmental Psychology, and we searched the subject index from 10 mainstream texts to see if the topic appeared (Fitzgerald, 1986; Berk, 2001; Rice, 2001; Broderick and Blewitt, 2003; Boyd and Bee, 2009; Feldman, 2009; Sigelman and Rider, 2018; Kuther, 2020; Kail and Cavanaugh, 2021; Kraynock et al., 2022). In many cases, whether or not the topic was found in the index, we searched further in the text to see whether the connection to sexual selection was made; if yes, we marked it as included, and if not, we marked it not included. For example, "breastfeeding" was mentioned in some books in terms of how long it's recommended by U.S. pediatricians, but the functional reasoning, in terms of how milk varies with the nursling's age and gender, was not presented. We included one text published before the year 2000 (Fitzgerald, 1986, which never went into second edition), because we considered it to include good integrative reasoning for its time. The text box below enumerates, for each concept, what percentage of the 10 texts made connections to the relevant concepts from Sexual Selection Theory.

As is apparent, 9 of the 10 texts acknowledge that cross-cultural research and naturalistic observation are important methodologies in Developmental Psychology. Only 3 books

discussed human evolution as a source of useful information. All 10 of the books describe gender-related similarities and differences in play, but explaining why they occur cross-culturally varied widely, in terms of integrating biological and socialization explanations. For example, Boyd and Bee (2009) present sex differences in toddlers' play as the product of males' identity development; in contrast, Fitzgerald (1986) and Kuther (2020) discuss the roles of prenatal hormones and environmental effects as inseparable influences. Out of the 36 concepts, 14 are not mentioned at all, and 9 are mentioned in one text. In addition to what appears in **Table 1**, the term Sexual Selection Theory (Darwin, 1871) was not found in any text; Parental Investment Theory (Trivers, 1972) was presented incorrectly in 1 text. As Surbey put it in her 1998 essay, our intention is not to admonish teachers of Developmental Psychology, but, rather, to encourage teachers to be open to integrating additional information into the way they think about development and the way they present it to students.

What if? How Theories Might Have Benefited From Sexual Selection Ideas

Stage theories are a major contribution from Developmental Psychology, as they function as path models, aiding our ability to predict behavioral changes over time. Dozens of stage theories have been proposed, but only a handful are generally familiar: those proposed by Freud (psychosexual development); Erikson (psychosocial development); Piaget (cognitive development); and Kohlberg (moral development). In each case, save perhaps Piaget's, the theorist was handicapped by a failure to deal with sex differences.

Freud's great contribution may be seeing that much human behavior is driven by unconscious forces (Miller, 2016); but Freud's developmental stages (oral, anal, phallic, latency, genital) are generally not supported by empirical data (Rutter, 1971). Indeed, Freud admitted his frustration at not being able to fit female experience into his theory of the Oedipal Complex—through which a boy's castration anxiety leads to identification

TABLE 1 | Topics for sexual selection usually missing from mainstream texts on developmental psychology.

Devlopmental topic	Missing relevant sexual selection concepts (Percentage of 10 texts* including concept)
Basic theories and research methods	(90%) Importance of cross-cultural research (30%) Research on foragers, or hominid evolution (90%) Naturalistic observation
Genes, environment, and development	(0%) Sexual and asexual reproduction (20%) Evolution of sex chromosomes; genomic imprinting (0%) Sexual selection pressures on the sexes at different ages
Prenatal development and birth	(0%) Evolutionary theories of post-partum depression (0%) Primate pattern of nocturnal births (0%) Evolution of lactation, weaning conflict, variation of milk with developmental age and sex (20%) Role of pregnancy and lactation in lowering risk of breast cancer for women
Physical growth (brain, body, and health)	(10%) Function of sex differences in maturation rate (0%) Function of secondary sex differences (hairiness, etc.) (0%) Pubertal behavioral changes and their relevance to sexual selection: Competitiveness, nurturance, libido, risk-taking, pair-bonding, jealousy (0%) Role of obesity and family stress in accelerating menarche
Sensation and perception	(0%) Function of general female superiority in sensation (10%) Evolution of sex differences in visual-spatial skills
Cognition and intelligence	(0%) Role of parents and older peers as teachers of sex-specific skills (50%) Role of elders across cultures as repositories of knowledge
Language and education	(10%) Implications and consequences of cross-national decline in male education and achievement
Self and personality	(10%) Sex differences in achievement motivation (0%) Role of testosterone in raising/lowering self-confidence
Sex and gender roles	(40%) Integration of role of hormones throughout lifespan (e.g., heterochrony) (70%) Life expectancy differences (e.g., males die earlier, due to both hormonal and lifestyle factors) (0%) Grandmother hypothesis (females may live longer to increase reproductive success of their own offspring) (50%) Occupational sex differences (70%) Genetic, olfactory, and hormonal correlates related to sexual orientation
Moral development	(70%) Major theories and their difficulties with explaining gender differences and cultural differences
Attachment, social relationships, and family	(10%) Role of oxytocin in attachment (0%) Sex similarities and differences in hormones and brain areas involved in parenting behaviors (100%) Gender-related similarities and differences in play (10%) Sex differences in mate criteria (10%) Factors affecting marriage rate and age at first marriage (0%) Advantages of biological father being present
Psychopathology	(10%) Sex differences in internalizing vs. externalizing pathologies (10%) Sex differences in perpetrators and victims of homicide, rape
Aging, death, and grieving	(70%) Sex differences in reactions to death of a spouse

with the father figure and elaborated moral functioning via a mature superego. Eventually, Freud (1925) proposed (1925) that because females never experience castration anxiety, females have compromised superegos, and therefore females' moral reasoning and civil functioning can never be as mature as what males offer. As Gilligan concluded, "Thus a problem in theory became cast as a problem in women's development, and the problem in women's development was located in their experience of relationships" (Gilligan, 1982, p. 7). Several neoanalytic theorists (e.g., Chodorow, 1974) endeavored to reframe Freud's theory in a way that does less violence to female development, by focusing less on anatomical differences and more on sex role differences.

One major example of such reframing is seen in the stage theory of Erikson (1980), who departed from Freud's focus on anatomy and sex, again turning to relationships. But Erikson's fifth psychosocial stage (identity vs. role confusion) and sixth stage (intimacy vs. isolation) seemed to lose their clarity when he discussed females; as Gilligan (1982) pointed out, identity and intimacy may be simultaneous developmental processes, and this seems especially so for females. Gilligan's insights into weaknesses in Eriksonian theory make even more functional sense if one considers that females everywhere tend to marry at a younger age than males do partially due to limitations on female reproductive potential.

Piaget (1936, 1945) constructed a theory of cognitive development in children and adolescence that has largely stood the test of time, cross-culturally (Bjorklund, 1995; Miller, 2016) and provided the groundwork for research on adult cognition (Sinnott, 1996). As MacDonald observes, Flavell once commented that, "if one wants to understand how Piaget conceived the child, one simply has to ask how evolution would have designed an optimal learning machine" (MacDonald, 1988, p. 14). MacDonald points to the young child's intrinsic motivation and responsiveness to general features of the environment. It would be difficult to argue that Piaget's cognitive development theory would have substantially benefited from his paying more attention to Sexual Selection. It is a different matter, however, with Piaget's theory of moral development (Piaget, 1932). Both Piaget and his intellectual heir, Kohlberg, were so bedeviled by gender differences in their findings that they chose to do most, if not all, of their morality research on males (Gilligan, 1982). Baron-Cohen (2005) addressed gender differences in social decision-making directly, when he modified his own theory of mindreading to make a "model of empathizing." This model describes development in children up to age four, but its predictions fit with patterns of findings across ages and cultures. Both sexes are more likely to empathize than to systemize. However, males, on average, systemize more (attend to physical detail, construct, and organize systems) than females do. Females empathize (use eye contact, decode non-verbal expression, and respond empathetically) more than males do. Baron-Cohen (2005, p. 481) concluded that, "From an evolutionary perspective, sex difference in empathizing and systemizing are likely to have been shaped by sexual selection and follow, at least in part, from sex differences in reproductive strategies." More research is warranted, but this is a promising start toward addressing questions about moral development.

One could argue that early theorists were anxious to see Developmental Psychology recognized as an independent science, distinct from the biological disciplines that were refining their methods at the same time (Charlesworth, 1992). But, once the path was defined as one that did not include biological influences, most developmentalists marched down the path without looking back, leaving the landscape littered with missed opportunities. Surely important opportunities were missed when stage theorists failed to recognize the implications of sexually dimorphic characteristics (often related to Life History processes such as gestation, lactation, and weaning) seen throughout human development.

What if? How Research Might Have Benefited From Sexual Selection Ideas

Generally, discussion of human sex differences has been met with resistance from Developmental Psychologists. Consider that the number of citations (according to Google Scholar) for Maccoby and Jacklin (1974) volume *The Psychology of Sex Differences* is close to 15,000. The book emphasizes socialization factors involved in sex differences in most behaviors, including aggression. By 1998, Maccoby (1998) had reconsidered biology's role, describing an interactive process whereby biological factors nudged children toward sex segregation, which increased sex differences in aggression, etc. Yet despite the earlier edition being twice as old, it has garnered five times the number of citations. Similarly, books by Mealey (2000); Lippa (2005), and Geary (2020) have not found wide acceptance within Developmental Psychology.

Typically, Developmental Psychology textbooks document sex differences in the timing of morphological changes in puberty. With few exceptions (Weisfeld and Billings, 1988; Weisfeld, 1999), writers seldom discuss why the timing is different in the two sexes, universally, and functionally. Boys retain their child-like morphology longer, to gain experience and strength before their physical characteristics engender competitive responses from mature males (see Dunsworth, 2020, for an alternative, proximate explanation). Darwin had seen this sex difference in functional terms, when he described how young boys around the world practice wrestling, often not marrying before the age of twenty "as before that age they cannot conquer their rivals" (Darwin, 1871, p. 872). Only a handful of developmentalists (Aldis, 1976; LaFrenière, 2013) have pointed out that, while boys do more rough-and-tumble play, both sexes engage equally in chase games, honing escape abilities—demonstrating the utility of extending Sexual Selection Theory to understand functional patterns of universal and divergent patterns of play.

Again, the play literature tends to see bullying behavior in cases of what is arguably normal playfighting in preadolescent children. Weisfeld and Weisfeld (2013) refer to the work of Aldis (1976) who described playfighting between siblings as the typical scenario, where actors represent different ages and sizes, and where the larger actor frequently switches roles to let the smaller actor "win"—all with smiles and laughter as expressions of functional play. Since the work of Olweus (1978) this has been confused with bullying. The result is not only

poorly conceptualized research leading to wasted resources and ineffectual programs (Merrell et al., 2008); the confusion has also led to reducing recess and punishing behaviors that may be developmentally normal and functional.

Where Has Sexual Selection Theory Benefited Developmental Psychology?

One can find intriguing examples of research that recognizes sex differences and explores those differences as part of the Developmental Psychologist's challenge. Both Charlesworth and his student, LaFrenière, did observational research on children's play and observed marked sex differences (Charlesworth and Lafreniere, 1983). Applying a functional lens, LaFrenière et al. (2002) were able to document those sex differences in 10 cultures showing that girls expressed more empathy and social competence, while boys' behavior exhibited more physical aggression and dominance. Later LaFrenière (2013, p. 183) would write, "For boys especially, rough-and-tumble play in early childhood provides a scaffold for learning emotion regulation skills related to managing anger and aggression." Thus, LaFrenière identified both an ultimate function for the behavior (male-male competition for future reproductive success) and a proximate function (social success with peers in childhood). As Mealey had observed earlier, "...the existence of two physical sexes virtually ensures the existence of two psychological sexes" (Mealey, 2000, p. 40).

Recognizing sex differences is fundamental for understanding the development of visual-spatial skills (Maccoby and Jacklin, 1974; Hoyenga and Hoyenga, 1993; Kimura, 1999; Geary, 2020). Silverman and Eals (1992) and Eals and Silverman (1994), in a series of observational experiments, found that male undergraduate students were superior at wayfinding, while female undergrads were superior at remembering objects and their placement in a two-dimensional array. They explained this through the "hunter-gatherer hypothesis" which attributed the differences to survival-related skills developed in humans' hunter-gatherer past and inherited as predispositions seen in males and females today. As hunters, the theory explains, men utilized three-dimensional skills traveling great distances in search of prey and then finding their way back home. As gatherers, women covered shorter distances but remembered where they saw signs of edible plants on the ground—so that they could return and harvest what was ready to eat. Thus, the differences in visual-spatial skills are highly specialized, for functional reasons. Later, this theory was confirmed with data from 40 countries (Silverman et al., 2007). Interested in when these differences appear developmentally, Choi and Silverman (2003) designed experiments showing that some sex differences are apparent in 9-year-olds, but elaborated sex differences do not appear until about 3 years later. This suggests roles both for pubertal hormones, and for refining differentiated strategies through practice.

Life History Theory, developed in evolutionary ecology in the 1950's (Stearns, 1976), and later applied to the human lifecycle (Hill and Kaplan, 1999), attempts to explain life-history strategies (e.g., sexual debut) in terms of selective forces, some of which challenge the sexes differentially. Falling within Life History Theory, the concept of sex ratio, the ratio of males to females, affects a wide range of behaviors. While the human primary (before birth) and secondary (at birth) sex ratios are approximately 1:1, the tertiary sex ratio, by early adulthood, is skewed toward females, because males often suffer higher mortality in childhood and adolescence, partially due to intrasexual competition (Mealey, 2000) and "risky behavior" (Daly and Wilson, 1983). Being the scarcer sex, males are then better able to impose their mating priorities. When females are in short supply, the converse applies. For instance, Pollet and Nettle (2008) did archival research on a U.S. population with low numbers of women; these women were able to marry young and marry well, securing husbands who had a higher SES than competing males. Conversely, when young males were scarce, they were less likely to be married, presumably because they were better positioned to pursue short-term mating; however, a higher proportion of these scarce men are married later in life (Kruger and Schlemmer, 2009). This topic deserves more research, especially given current patterns of sex differences in educational attainment (US Census Bureau, 2020), considered alongside tendencies for homophily and hypergamy (c.f., Sassler and Lichter, 2020). The sex ratio is skewed even more when fewer males present as attractive choices. Furthermore, patterns of marriage mobility—female educational hypergamy and male hypogamy (marrying someone with more vs. less education)—are no longer apparent (Qian, 2017; Van Bavel et al., 2018). Data from 28 countries drawn from the European Social Survey indicate that women, rather than remaining unpartnered, will often chose to "cast a wider net," partnering with men whose socioeconomic status falls short of their own (De Hauw et al., 2017). Similar patterns have emerged in Latin America (Esteve et al., 2016) and the United States (Qian, 2017; Lichter and Qian, 2019).

CONCLUSION

Many books document human sex differences ably (e.g., Maccoby and Jacklin, 1974; Hoyenga and Hoyenga, 1993; Mealey, 2000; Lippa, 2005; Geary, 2020). We see heuristic value when a book provides, not just a massive listing of such sex differences, but a story told by the differences. It is the "orderliness" of behavior that is of interest, as Archer (1992) put it. We benefit most from research that recognizes patterns in sex differences and offers an overarching explanatory theory.

We need honest discussion regarding sex roles and implications for salaries and work environments, while simultaneously avoiding rigid normative judgments and outright dismissal of potential bias. Sex segregation in the labor force and gender inequality in pay continues, with the gender gap narrowing slowly in most countries that provide relevant data (Ponthieux and Meurs, 2015). One could argue for breaking down all professional sex segregation; but a stronger argument might be made for raising salaries of predominantly female occupations and reducing barriers in the workplace, so that atypical boys and girls feel comfortable pursuing divergent paths.

For those Developmental Psychologists who would like to read more about Evolutionary Theory and its application to human development, particularly in childhood, *The Origins of Human Nature* (Bjorklund and Pellegrini, 2002) is an important introduction, as are *Human Infancy* (Freedman, 1974), *Ethology and Human Development* (Archer, 1992), and *Adaptive Origins* (LaFrenière, 2010; see also Geary and Bjorklund, 2000; Salmon and Shackelford, 2007; Ellis et al., 2009; Konner, 2010; Geary and Berch, 2016; Bjorklund, 2020; Geary, 2020; Hart and Bjorklund, 2022). Many articles offer good introductions to Sexual Selection theory and its relevance to human development (e.g., Buss, 1995; Miller, 1998; Bjorklund and Pellegrini, 2000; Schmitt, 2005; Puts, 2016; Wilson et al., 2017).

What might be gained by incorporating Darwin's insights into our work in Developmental Psychology? More complete understanding? More satisfying understanding? Better positioning for making decisions on a personal and societal level? More of a sound basis for arguing for equality of opportunity if we are so inclined? A sounder footing for educating the next generations of teachers, nurses, psychologists, and others who study Developmental Psychology? We argue, simply, yes.

AUTHOR CONTRIBUTIONS

SG, GW, and CW conceived of the manuscript idea. GW designed the manuscript outline. GW and CW prepared the first draft. SG restructured and added additional content in the subsequent drafts, proofread, formatted, and submitted the manuscript. All authors contributed to the article and approved the submitted version.

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CONCEPTUAL ANALYSIS
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Darwin Versus Wallace: Esthetic Evolution and Preferential Mate Choice

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Dominant theorizing and research surrounding the operation of intersexual selection in evolutionary psychology tends to be guided by an adaptationist framework and aligned with models of sexual selection involving direct benefits (e.g., parental care) and indirect "good gene" and condition-dependent benefits. In this way, evolutionary psychologists more often espouse Alfred Russel Wallaces' utilitarian viewpoint that traits become attractive because they honestly signal vigor and vitality, which gives priority to natural selection. In doing so, Darwin's esthetic perspective originally articulated in *The Descent of Man* and alternative models of sexual selection (e.g., Fisherian runaway), are given less consideration. This is despite some informative reviews on the topic in evolutionary psychology. In the current conceptual analysis, we discuss the potential of Prum's Lande-Kirkpatrick (LK) null model of sexual selection to help make sense of some of the mixed evidence regarding the links between attractive traits and purported markers of phenotypic and genetic condition. We then consider how the implications of the LK null model can help to shift theoretical assumptions and guide future work in evolutionary psychology on intersexual selection.

Keywords: intersexual selection, mate choice, Lande–Kirkpatrick null model, evolutionary psychology, good genes, costly signaling

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INTRODUCTION

Both Darwin and Wallace agreed that sexual selection involves competition between same-sex conspecifics for access to reproductive opportunities (i.e., intrasexual competition; Miller, 1998; Hoquet and Levandowsky, 2015). However, they proposed competing ideas regarding the action of intersexual selection and what drives the evolution of esthetic appreciation and preferential mate choice in humans and non-human animals. Darwin believed that some traits could become attractive for nonfunctional reasons, whereas Wallace argued that traits primarily become attractive because they honestly advertise phenotypic quality, such as vigor and viability. The "Wallacean approach" has been favored in theorizing and research in evolutionary psychology for decades, but evolutionary biologists have begun to take seriously Darwin's original stance on preferential mate choice that was first articulated in *The Descent of Man* (1871). In the current conceptual analysis, we delve into the various evolutionary processes that purportedly shape mate preferences, including Fisherian selection, sensory biases, good genes, and Zahavian handicaps. We further explore Prum's (2010, 2012) Lande-Kirkpatrick (LK) null model of sexual

selection, whereby trait–preference genetic correlations manifest without the influence of natural selection on mate preferences. We discuss the implications of the LK null model for adaptationist programs of research that predominate evolutionary psychology, whereby attractive phenotypes are often assumed to communicate underlying quality of the organism. We identify gaps in the literature on trait–preference coevolutionary dynamics and the need for more direct empirical work examining markers of health, developmental stability, and immune function in relation with salient phenotypic characteristics, such as facial features, breast morphology, and vocal register.

Darwin and Wallace on Sexual Selection

Darwin (1871) observed that male conspecifics often battled with each other for access to females (i.e., intrasexual competition) who had the power to choose their preferred mates (i.e., intersexual selection). Darwin also documented instances of female–female rivalry, such as in some species of emu (*Dromaius*): a genus of large flightless birds. Across species, he noted that males more often possessed elaborate ornaments and competed more vigorously for access to selective female mates. In support of this idea, Bateman (1948) demonstrated how discriminating mate choice in females could produce greater reproductive variance in males and so encourage greater short-term mating effort. Trivers (1972) later provided an explanation for sex differences in sexual selection dynamics, which was based on variance in obligatory parental investment: the sex that devotes more resources to parental investment (typically females) is more discriminating in their mate choice and the less investing sex (typically males) devotes more energy to short-term reproductive effort and engages in more direct, risky, and potentially lethal intrasexual rivalry. Among the less investing sex, there is higher reproductive variability, the influence of sexual selection is stronger, and the development of conspicuous sexual characters is more apparent. This still leaves unanswered the reason(s) *why* females preferentially value certain phenotypic characteristics over others in mates. In *The Descent* Darwin proposed that females seem to possess an enigmatic "taste for the beautiful":

> Why certain bright colours should excite pleasure cannot, I presume, be explained, any more than why certain flavours and scents are agreeable; but habit has something to do with the result, for that which is at first unpleasant to our senses, ultimately becomes pleasant, and habits are inherited (p. 94).

Darwin's contemporary, Alfred Russel Wallace (1823–1913) vacillated on the importance and operation of sexual selection. At first, he agreed with Darwin on the causes of sexual dimorphism and the vibrant coloration of plumage in male birds (Kottler, 1980). This can be seen in the following passage from Wallace (1868):

> It would appear from the numerous cases in which both sexes are adorned with equally brilliant colour (while both sexes are rarely armed with equally developed offensive and defensive weapons when not required for individual safety), that the normal action of "sexual selection" is to develop colour and beauty in both sexes, by the preservation and multiplication of all varieties of colour in either sex which are pleasing to the other (p. 82).

However, from about 1876 onward, he appeared to reject sexual selection (Kottler, 1980). From this point on in his career, he adhered to a more "utilitarian" perspective and discounted the importance of females selecting males based on differential male ornamentation (Hoquet and Levandowsky, 2015). For instance, Wallace (1889) stated as:

> In like manner, female birds may be charmed or excited by the fine display of plumage by the males; but there is no proof whatever that slight differences in that display have any effect in determining their choice of a partner (p. 286–287).

Wallace viewed esthetic features, such as brightly colored and prominent ornaments, as largely the products of natural selection. He believed that these traits were honest cues to vigor and vitality and were principally involved in species recognition and intimidating predators, not mate attraction. Relatedly, Wallace posited that the drab coloration of many females was not merely a default condition but served an important survival function to avoid predation (discussed in Caro, 2017). Darwin's "esthetic" view was aligned with the notion that ornaments could become attractive for reasons that have little to do with phenotypic condition (a "taste for the beautiful"). Therefore, Darwin and Wallace expressed divergent ideas regarding the evolution of sexual dimorphism and secondary sexual characteristics (Miller, 1998; Prum, 2012; Hoquet and Levandowsky, 2015). Wallace disagreed that non-human animals could possess an "esthetic sense" and was opposed to Darwin's position that naturalistic explanations should be used to understand human cognitive, emotional, and esthetic capacities. Unlike Darwin, Wallace argued for the power of natural selection in driving preferential mate choice and largely dismissed the influence of sexual selection (Prum, 2017). Wallace attributed various human psychological processes, such as consciousness and esthetic pleasures, to God and mystical phenomena (Fisher, 1930; Hoquet and Levandowsky, 2015).

Adaptationism and Mate Choice

Despite more attention being given to Darwin's ideas on the operation of sexual selection, research on preferential mate choice, particularly among evolutionary psychologists, has been notably "Wallacean." A cursory reading of popular writing and research in evolutionary psychology on intersexual selection provides insight into how the field tends to be guided by an adaptationist bias—that mental faculties are, first-and-foremost, adaptations and the direct products of selection (Schulz, 2013). Strong adherence to adaptationism can result in ignoring or discounting the possibility that psychological traits may be exaptations instead of adaptations (Gould, 1991). Exaptations denote heritable traits that were originally selected to perform one function but have since been co-opted to perform other unrelated functions that may, nonetheless,

still enhance fitness (Buss et al., 1998; Havlíček et al., 2015). Psychological characteristics that promote an organism's survival and reproduction in its current environment might also be by-products of adaptations that have no direct functional significance (i.e., a spandrel). To be sure, adaptationist thinking has, and will continue to be, essential for delineating the functional significance of purported psychological adaptations (Daly and Wilson, 1995). However, simply because a mental faculty is useful at "achieving something" that can be mapped on to indices of reproductive success should not be taken as sufficient evidence that it was shaped by selection for that specific functional purpose.

Adaptationist programs of research in evolutionary psychology tend to be aligned with the assumption that many historically and cross-culturally consistent mate preferences were selected in the ancestral environment because they provided accurate information about an individual's phenotypic condition. Therefore, it is often assumed that: (1) particular traits become attractive because they honestly communicate "good genes," health, reproductive value, and/or parental investment and (2) that secondary sexual characteristics correlate reliably with markers of genetic condition and phenotypic quality (Prum, 2010, 2012, 2017). In this way, evolutionary psychologists deviate from Darwin's esthetic perspective propounded in *The Descent* and conform more to Wallace's utilitarian viewpoint on mate choice. This bias in favor of neo-Darwinian (i.e., Wallacean) thinking likely manifests because researchers are not learning about Darwin's original ideas, which is an important consideration for educators teaching evolutionary theory. These assumptions can be problematic. First, attractive traits may not actually qualify as adaptations and may instead be better conceptualized as exaptations or spandrels. Second, it neglects the other evolutionary processes that influence intersexual selection dynamics. In the following sections, we describe prominent models of sexual selection that tend to be favored in evolutionary psychology to explain mate preferences.

Models of Sexual Selection

Good Providers, Good Genes, and Costly Signaling

Several models have been proposed to help account for preferential mate choice, specifically female choice, that vary according to the kinds of benefits that can be acquired by the selecting sex (Andersson, 1994; Jones and Ratterman, 2009). Females may acquire *direct* benefits by selecting males who are more fertile, as well as those possessing a greater capacity to invest material resources (e.g., food) and parental care (Gangestad and Thornhill, 1997; Kokko et al., 2003). Selecting males for their ability to provision resources for mates and offspring is known as the "good-provider" model of sexual selection (Hoelzer, 1989). Males may also provide direct benefits in terms of protection from predators or from other males (Frederick and Haselton, 2007). Health status may also indicate an enhanced capacity to compete for and provide ongoing resources and parental investment, and so could be desired as a good-provider indicator (Tybur and Gangestad, 2011).

Other models of sexual selection involve conferring potential *indirect* benefits to offspring *via* genetic inheritance. The model of indirect benefits commonly adhered to by evolutionary psychologists is the *good genes model*, whereby females prefer males possessing heritable traits associated with genetic quality that can be transmitted to offspring to enhance their reproductive success (reviewed in Gangestad and Thornhill, 1997). A salient issue debated by evolutionary scientists regarding the good genes model is that directional selection would presumably eliminate genetic variance for viability (i.e., the lek paradox; Kirkpatrick, 1982). However, it is clear that there exists considerable genetic variance in display traits that are under the influence of sexual selection (Prokop et al., 2012). Some have argued that heritable viability could potentially be maintained *via* mutations with the introduction of new genetic variants (Rice, 1988). Although this idea is rarely directly tested by researchers using the good genes model. Another potential issue with the good genes model is that as the selective environment changes over time so too would the viability indicators (Gangestad and Thornhill, 1997). The ongoing evolutionary arms race between pathogens and their hosts helped to delineate how markers of viability could change alongside selective pressures in the environment, and provided another mechanism through which genetic variability might be maintained (Anderson and May, 1982). Individuals selecting mates with cues to pathogen resistance could transmit better pathogenic immunity to their offspring (Hamilton and Zuk, 1982). This "parasite model" is the dominant model of good genes sexual selection adhered to in evolutionary psychology (e.g., Pazhoohi and Kingstone, 2020).

Despite its popularity in evolutionary psychology as the driving force of intersexual selection, previous meta-analytic work provided equivocal support for the role of good genes across species (Prokop et al., 2012). More recently, Achorn and Rosenthal (2020, p. 216) have argued that "For conspicuous display traits, weak signals of good genes should be the rule". These scholars propose that when the genetic influences on viability indicators are strong, the likelihood of preferences for good genes being maintained decreases because it diminishes genetic variation *via* sexual selection. Achorn and Rosenthal (2020) take the position that the good genes model is inadequate in explaining the evolution of elaborate sexual display traits and preferences for those ornaments.

Fluctuating asymmetry (i.e., subtle deviations from bilateral symmetry) in physical characteristics has garnered much attention from evolutionary psychologists as a viability marker that is purportedly shaped by exposure to parasites, pathogens, toxins, and deleterious mutations (Møller, 1990). Morphological traits with lower fluctuating asymmetry are posited to be attractive because they reflect *developmental stability*—A heightened capacity to withstand genetic and environment perturbations during development (Møller, 1990; Møller and Thornhill, 1997). Individuals with higher fluctuating asymmetry have been found to suffer lower fecundity and greater mortality (Watson and Thornhill, 1994), and males with low fluctuating asymmetry, including human men, appear to benefit from greater mating success (reviewer in Gangestad and Thornhill, 1997). It is important to mention that a previous review of 40 published meta-analyses on fluctuating asymmetry in evolutionary biology indicated that about 20% of the research findings could

be attributed to publication bias and that effect sizes across studies were very small (Jennions and Møller, 2002). Indeed, evolutionary researchers often overstate the importance of asymmetry in determining the attractiveness of human traits (Van Dongen, 2011). There is an evident shortage of research on sexually dimorphic secondary sexual characteristics involved in mate choice, such as the female breast, and whether fluctuating asymmetry in these characters are actually tied to phenotypic condition (Locke and Arnocky, 2021).

Zahavi (1975) argued that genetic variability in fitness could be maintained through attractive male secondary sexual characteristics that purportedly reduce survivability. Characteristics constituting *Zahavian handicaps* involve extravagant traits that are "wasteful" or produce a cost to the organism in terms of reduced survivability, and so may be honest cues to an organism's genetic and phenotypic condition (discussed in Penn and Számadó, 2020). There are, however, some salient issues associated with the handicap hypothesis. It may be assumed that viability in males will consistently correspond to greater health (discussed in Frederick et al., 2013). However, investing in putatively costly traits can decrease an individual's health (Kokko et al., 2002). Therefore, any evidence for a positive, negative, or neutral relation between a trait and health could be taken as evidence in favor of the handicap hypothesis. The handicap hypothesis also assumes that mate preferences are adaptive and enhance offspring viability, and evidence indicates that non-adaptive female preferences emerge under various conditions (e.g., when the development of the handicap is caused by non-heritable factors; Kirkpatrick, 1986). Furthermore, robust indicators of health and immunity are unlikely to diversify once evolved, which runs in contrast to the diversity of ornaments predicted *via* Darwin's theory of sexual selection (Prum, 1997, 2012). The hypothesis also comes in a variety of different versions, but none seem capable of adequately explaining male sexually dimorphic ornaments (Számadó and Penn, 2018). The handicap hypothesis also tends to carry the assumption that extravagant ornaments can only be produced by genetically fit males and that these traits carry some cost to survival.

The peacock's (*Pavo cristatus*) vibrant train was used by Zahavi (1975) to explicate the hypothesis, and it is a classic example used in evolutionary psychology as evidence of the power of sexual selection to produce complex and costly ornaments. Indeed, peacocks with a greater number of train-feather eyespots (i.e., ocelli) appear to have greater mating success (Petrie and Halliday, 1994), they help to produce larger offspring with greater survivability (Petrie, 1994), and they enjoy better health status (Loyau et al., 2005). In a study by Møller and Petrie (2002), train length, but not the number or size of the eyespots, was positively linked to body condition (body mass) and some markers of immune function (heterophil–lymphocyte ratio) but negatively related to others (humoral immunity). Other studies also indicate that there is insufficient variability in train-feather eyespot number among feral peacocks to account for variance in male mating success (Dakin and Montgomerie, 2011). The long, elaborate peacock train also does not appear to reduce locomotor performance (Askew, 2014). And because of the dichromatic nature of the visual systems of most mammalian predators that hunt birds, the peacocks colorful feathers are actually quite inconspicuous (Kane et al., 2019). These results cast some doubt on the idea that the peacocks elaborate plumage is a signal that carries a cost to survival. It is important to consider that the peacock train may not be a single ornament, but a trait that carries multiple independent signals (e.g., number of ocelli, symmetry, and vibrance of plumage; Van Doorn and Weissing, 2004). But this still does not entail that these multiple signals carry a cost to survival.

The handicap hypothesis was extended to propose that secondary sexual characteristics are honest indicators of an individual's condition because their development is mediated by sex hormones (e.g., testosterone) that are believed to have a negative impact on the functioning of the immune system (i.e., the *immunocompetence handicap hypothesis*; Folstad and Karter, 1992). Therefore, women choosing men with well-developed sexual characters could presumably pass on these genetic and phenotypic benefits to their offspring.

The models of sexual selection reviewed so far revolve around direct benefits, good genes, and costly signaling which coincide with Wallace's notion of utility that natural selection plays a primary role in preferential mate choice. These models are well represented in research in evolutionary psychology on the operation of mate preferences. Alternative models intended to account for female choice that resonate more with Darwin's esthetic view have been reviewed in evolutionary psychology (e.g., Gangestad and Thornhill, 1997; Miller, 1998; Gangestad, 2001; Frederick et al., 2013), but they are given comparatively less consideration among researchers in the field.

Fisherian Runaway and Sensory Biases

Individuals may acquire indirect benefits for their offspring *via* mate choice that are unrelated to good genes, health, costly signals, and/or greater pathogen resistance. This was the position articulated by Darwin in *The Descent* that trait–preference covariation may result for relatively nonfunctional reasons. This model (see Gangestad and Thornhill, 1997) was elaborated upon by Fisher (1930) who argued that a female preference for a particular male ornament could become genetically correlated and co-evolve with the ornament (i.e., *Runaway selection*). This trait–preference correlation is argued to manifest because of linkage disequilibrium (i.e., non-random association of different neighboring alleles; Hosken and Wilson, 2019). Consequently, males possessing the conspicuous ornament would gain a mating advantage, and so daughters carrying the trait preference and sons possessing the ornament would increase in frequency in future generations. This results in a positive feedback process whereby the female preference and the male secondary sexual characteristic become exaggerated, which is halted and balanced by countervailing costs to survival associated with the exaggerated ornament (Fisher, 1915, 1930). Of note, coevolution is not restricted to Fisherian selection, and in nature a genetic trait–preference correlation could be at play with direct benefit and good genes models (Kokko et al., 2002).

Although the different models of sexual selection for indirect benefits tend to be pitted against one another,

Kokko et al. (2003) argued that there are commonalities between them and that it is problematic to view them as mutually exclusive. For instance, it is possible that only males possessing markers of viability and good phenotypic condition can manage to produce more extravagant traits as a consequence of runaway selection (discussed in Frederick et al., 2013). Females may then express a preference for males embodying indicators of good genes presumably required for these extravagant characteristics. It can also be challenging to differentiate between the influence of direct and indirect benefits. For instance, physical formidability (e.g., greater musculature) in males may signal the ability to provide protection (Frederick and Haselton, 2007), a direct benefit, but male musculature is also considered to be an indicator of good genes (Gangestad et al., 2007), or females may select muscular males simply to provide a reproductive advantage to their offspring (i.e., Fisherian selection; Frederick et al., 2013). Although, it is worth mentioning that the evidence supporting male muscle mass as a trait that women find attractive as a signal to protection in long-term relationships is lacking (Fajardo et al., 2022). Instead, research indicates that muscular men tend to pursue short-term sexual strategies (Frederick and Haselton, 2007), and women do not appear to perceive muscular men as high in indicators of long-term partner mate value (e.g., "good father"; Gangestad et al., 2007).

Fisherian co-evolution provides a compelling alternative to other previously discussed models of sexual selection. However, it raises the question of why females display an initial preference for traits that are unrelated to viability. Across species, females appear to display a desire for more exaggerated and novel display traits, such as larger, brighter, and more colorful plumage, that can evoke stronger sensory stimulation (Ryan and Keddy-Hector, 1992; Miller, 1998). Females may also express pre-existing perceptual biases in non-mating contexts that become intertwined with sexual selection (discussed in Miller, 1998). Runaway selection (Fisher, 1915, 1930) may then amplify these sensory biases. For instance, *sensory trap* involves a female responding to an "out-of-context" stimulus provided by males during courtship, which mimics a signal that evolved to elicit a response for reasons unrelated to mate attraction (Christy, 1995). And *sensory exploitation* (Ryan and Keddy-Hector, 1992) describes how pre-existing sensory biases in females may be exploited by male courtship signals. Importantly, the idea that sensory biases could be driving preferential mate choice still necessitates appealing to natural selection along the causal chain (Prum, 2010). Invoking sensory biases to explain runaway selection also deviates from Fisher's (1915, 1930) original position that any conspicuous trait associated with reproductive success that varies among members of a population can initiate the runaway process. These display traits can emerge through different kinds of stochastic processes, such as *genetic drift*—chance events causing fluctuations in the frequency of alleles across time in a population—such as *a bottleneck*—a sudden reduction in a population resulting in a genetically unrepresentative subsample—and *founder effects*—a random subsample of members from the original population splintering off to form a new isolated population (Kitchen, 2018). It is this position that Prum (2010) posits should serve as the null model of sexual selection.

Darwin and the Lande-Kirkpatrick Null Model

Prum (2010, 2012, 2017) advances the idea that, in contrast to adaptationist thinking, which is often afforded epistemic privilege in evolutionary psychology, scientists should not assume that natural selection is the key mechanism governing mate choice dynamics. Following the logic of Fisherian runaway, Lande (1981) and Kirkpatrick (1982) proposed indirect models of intersexual selection whereby the strength of the genetic trait–preference correlation relative to the degree of genetic variation in the trait would dictate whether a population would proceed toward stable equilibrium (trait–preference correlation < trait genetic variance) or non-equilibrium states (trait–preference correlation > trait genetic variance). The latter condition represents the Fisherian runaway process, where a stronger correlation between the preference and trait increases the likelihood of runaway selection and a positive feedback loop that can produce extreme ornaments that must be halted by stabilizing selection (i.e., pushing a population toward intermediate phenotypes). When the trait–preference correlation is greater than the amount of genetic variance in a trait, stochastic evolutionary processes (e.g., genetic drift) may trigger runaway selection (Lande, 1981). As stated by Prum (2010, p. 3087), "…substantial evolutionary elaboration of trait and preferences can occur through drift away from a stable equilibrium and the evolution of a population toward a new equilibrium rather than a return to the former state". Collectively, these dynamics constitute what Prum (2010) called the LK model, which he likened to the Hardy–Weinberg equilibrium: in the absence of other evolutionary forces, there exists variation in trait–preference genetic correlations. The LK model suggests that highly elaborate ornamental secondary sexual characteristics can evolve without the influence of natural selection on mate preferences and that we do not need to appeal to models of sensory bias to understand the initiation of Fisherian runaway. The action of natural selection on display traits is still encompassed within the LK model, but, unlike good gene and direct benefits models of sexual selection, it does not require the influence of natural selection on preferences for those traits. The LK model aligns with Darwin's esthetic view of female choice, and unlike dominant approaches to intersexual selection in evolutionary psychology, it does not assume additional selective pressures beyond the trait–preference correlation or a positive association between viability and attractive characteristics (Prum, 2010). Prum (2012) stated that a truly Darwinian approach to intersexual selection should appeal to utilitarian good genes and phenotypic condition explanations only when the evidence does not support the LK null model and influence of pre-existing sensory biases. The practicality of this approach is further supported by meta-analytic work showing that Fisherian

selection is likely a more important part of mate choice than the good genes model of sexual selection (Prokop et al., 2012).

In the following section, we document important mixed findings in the literature on mate preferences regarding secondary sexual characteristics commonly purported to be markers of genetic and phenotypic condition. Following Prum (2010, 2012, 2017), we believe that it is in these literatures that the utility of the LK null model may be most apparent for evolutionary psychologists.

Secondary Sexual Characteristics, Health, Immunocompetence, and Viability

To date, limited empirical work has directly addressed questions of (1) whether human secondary sex characteristics reflect individual differences in genetic quality or immunocompetence, and (2) whether the development and maintenance of these traits truly entail an immunologic or energetic cost. Nevertheless, the role of secondary sexual characteristics in signaling heritable immunocompetence has often been framed in research literature and textbooks as being well established (see Scott et al., 2013 for review). Some work has supported a positive phenotypic correlation between secondary sex characteristics and specific markers of immunocompetence. For instance, Arnocky et al. (2018) found that in men, vocal masculinization was positively correlated with both self-reported health and salivary immunoglobulin-A (SIgA; a marker of mucosal immunity), which itself was positively correlated with testosterone (T). Given vocal physiology and corresponding fundamental frequency are influenced by T (Dabbs and Mallinger, 1999; Hodges-Simeon et al., 2021), it is possible that low pitch is attractive to females (Feinberg et al., 2005; Hodges-Simeon et al., 2011) because it serves as a costly signal of underlying immunocompetence (Arnocky et al., 2018). Listeners also rate men's voices with a lower fundamental frequency as healthier (Albert et al., 2021). However, health may constitute a direct or indirect benefit (Tybur and Gangestad, 2011; Frederick et al., 2013), and these results could be taken as evidence in favor of either direct or indirect benefit models of sexual selection. Furthermore, evidence indicates that non-heritable factors play a more important role than heritable factors in shaping immune system functioning (Brodin and Davis, 2017).

Attractive facial characteristics have also been considered from an immunocompetence signaling perspective (see Arnocky et al., 2014 for review). Shackelford and Larsen (2000) found that facial asymmetry correlated with negative health markers (see also Jones et al., 2001; Borráz-León et al., 2021). Results regarding men's facial masculinity have been more thoroughly studied but are equivocal (Scott et al., 2013). Rhodes et al. (2003) found that rated masculinity in the faces of young males correlated modestly with actual health. Boothroyd et al. (2005) did not support a link between women's preferences for facial masculinity and preferences for apparent health, and there were ambiguous results regarding the relation between perceived masculinity and health. Similarly, Boothroyd et al. (2007) did not support a link between facial masculinity and health and showed how women and men perceived healthy and masculine faces to be associated with divergent personality characteristics (e.g., ambition, faithfulness, and parenting skill). Across three samples, Boothroyd et al. (2009) showed that women's preferences for facial masculinity were negatively correlated with their preferences for facial symmetry and unrelated with their preferences for health and facial averageness. Using anthropometric measurements, Boothroyd et al. (2013) found that men's facial masculinity predicted better past health, but worse reported health over a ten-week follow-up period. Another study examining other-rated facial sexual dimorphism found that facial masculinity was related to semen quality, but not with a salivary immune response to *Escherichia coli* or with salivary lysozyme response to *Micrococcus lysodekticus* (Foo et al., 2017). Thornhill and Gangestad (2006) found men with masculinized faces experienced fewer respiratory illnesses and less use of antibiotics. However, facial masculinization appears unrelated to heterozygosity of the major histocompatibility complex (MHC); a series of genes whereby heterozygosity is linked with broader immune recognition of pathogens and parasites (Zaidi et al., 2019). Relations between T and facial masculinity are also unclear. A meta-analysis found no association between the facial width-to-height ratio (FWHR) and circulating T in men (Bird et al., 2016), yet some evidence has linked T to the FWHR in peri-pubertal samples (Welker et al., 2016).

Male height has also been considered as a signal of underlying genetic quality. Despite positive assortative mating for height, women prefer men who are *relatively* taller than they are in laboratory studies, national surveys, and personal ad responses (Pawlowski and Koziel, 2002; Pawlowski, 2003; Stulp et al., 2013). Male height appears unrelated to circulating T, but rather has been linked positively to T response during exertion (Kowal et al., 2021). Height has been also linked to MHC heterozygosity (Zaidi et al., 2019). Height positively predicted men's response to a hepatitis B vaccine up to about six feet tall, after which the trend reversed (Krams et al., 2014), whereas other research has found no links between height and immune markers in an energy-rich Western sample (Pawłowski et al., 2017). In a high pathogen threat subsistence-based sample, height for age was lower among those higher in immune markers, suggesting a potential trade-off between growth and immune function (Garcia et al., 2020) that correspond with recent evidence linking early pubertal development with less MHC heterozygosity (Arnocky et al., 2021).

The signaling properties of secondary sex characteristics have also been applied to females. Human males can benefit their reproductive fitness *via* long-term mating with healthy females, and females will benefit from outcompeting rivals for the most desirable males (Arnocky and Vaillancourt, 2017). Recent work has examined female breast symmetry, as one of our species' most sexually dimorphic traits that have seemingly evolved to be larger than necessary for feeding young. Locke and Arnocky (2021) found that regardless of size or volume, women with symmetrical breasts were higher in salivary immunoglobulin-A (SIgA).

As demonstrated above, positive phenotypic correlations between immune markers and ornaments could be interpreted as evidence in support of parasite models (Reid et al., 2005). However, parasite

models assume a causal mechanism where one is not typically tested, and most studies fail to consider specific genetic mechanisms that might underlie observed relations between immunity and physical features (Reid et al., 2005). Research would benefit from examining immune function x hormone interactions during key developmental periods in relation with downstream phenotypic development, instead of relying solely on cross-sectional assessment of these variables in adulthood. The complexity of measuring immunocompetence, in which varying systems and processes may relate differently to testosterone (Roberts et al., 2004; Hau, 2007; Nowak et al., 2018), further contributes to the challenge of interpreting the role of immune-linked traits as costly simply because they are T-dependent. Some immune markers, such as SIgA, appear to be positively related with testosterone, which could suggest that T-linked traits that correlate positively with SIgA act more as an index signal than a costly signal. The study of parasite models is further complicated by debate about directional interpretation of links between both T and immune function, and phenotypic traits and immune function, as supporting evidence, whereby negative, positive, or even null relationships could be argued as evidence of a trade-off between immunity and "costly" androgens resulting in the development or maintenance of a trait (Getty, 2002; Scott et al., 2013). Although written a decade ago, Scott et al. (2013) interpretation that "at present, there is no clear evidence of a general, cross-species link between testosterone, genetically mediated immunity, phenotypic health and trait size, from which patterns among humans can straightforwardly be inferred" hold true today (p. 581).

Collectively, these findings cast some doubt on the conclusion that well-developed secondary sexual characteristics (e.g., facial masculinity) are attractive because they evolved to signal the provisioning of direct benefits (e.g., the good-provider model) or indirect genetic benefits in the form of good genes and pathogen resistance that can be transmitted to offspring. Here the Wallacean utilitarian perspective and the importance of natural selection in governing mate choice is given prominence in adaptationist programs of research. This favoritism deviates from Darwin's esthetic view, what Prum calls the "beauty happens hypothesis," and alternative models of sexual selection, such as Fisherian selection, are given little attention. Particularly regarding men's secondary sexual characteristics, there is likely value in following Prum's (2010, 2012) LK null Model: first assuming that these traits may have incidentally evolved to be attractive because of stochastic evolutionary forces (e.g., genetic drift), and/or due to their coincidence with a third, unaccounted variable (e.g., sensory bias).

Recommendations for Researchers Moving Forward

The LK null model itself is a quantitative genetic model with specific parameters in line with Fisherian selection (see Appendix in Prum, 2010). This is not the typical kind of empirical research and modeling undertaken by evolutionary psychologists. This raises the question of how evolutionary psychologist can apply the insights of the LK null model in their work? Part of the value of Prum's proposal involves a theoretical shift that investigators should first not assume that mate preferences for display traits are underpinned by "extrinsic factors" such as good genes, condition-dependence, parasite avoidance, parental investment, and/or sensory bias—What Prum (2010, p. 3086) refers to as additional sources of "natural selection on mating preferences". It involves considering that the mere existence of genetic variability in ornaments and preferences paired with assortative mating creates direct selective pressure on display traits, in addition to indirect selective pressure on the preference because of its genetic linkage to the ornament (so-called "intrinsic" forces of selection; Prum, 2010, p. 3088). Prum argues that the LK null model is more parsimonious and that we should presume that preferences for particular characteristics are the products of runaway co-evolution until there is compelling evidence favoring the operation of extrinsic factors. Consequently, the LK null model encourages scholars to raise the standard of evidence required to adhere to models of sexual selection that predominate adaptationist programs of research, such as the good genes model.

Indeed, there are ways to improve existing good genes and phenotypic condition research. For example, much of the empirical work on good genes has been centered on inconspicuous morphological characteristics (e.g., asymmetry in finger length) that are likely inconsequential to intersexual selection. It is more sensible to study heritable well-developed sexually dimorphic secondary sexual characteristic that are evidently involved in mate choice (e.g., breasts) to test for the presence of good genes and condition-dependence (Møller and Pomiankowski, 1993; Locke and Arnocky, 2021). Furthermore, characteristics that show considerable cross-cultural variability in attractiveness are unlikely to honestly communicate information about good genes, health, reproductive value, fecundity, or fertility. For instance, it is commonly believed that facial dimorphism (i.e., facial femininity and masculinity) is an honest and reliable signal of good genes and greater immunocompetence, but most of the evidence in support these ideas are based in developed and urbanized Western contexts (see Scott et al., 2013). Cross-cultural research, however, indicates substantial variability in facial dimorphism (Kleisner et al., 2021) and preferences for facial dimorphism (Scott et al., 2014) that contrast with predictions from the "parasite model." This variability is arguably more in line with Fisherian co-evolutionary dynamics embodied within Prum's LK null model. More cross-cultural research of a similar vein on various secondary sexual characteristics is needed.

Furthermore, when studying the links between attractive display traits, health, and immunocompetence, the focus of research should be on markers of immune function that are meaningfully tied to health outcomes, such as chronic inflammatory activity (Cunningham et al., 2022). It is also necessary to examine the collective action of multiple markers of health, rather than a small number of isolated indicators (Foo et al., 2017). For example, Mengelkoch et al. (2022) found sex-differentiated links between multiple direct *in vivo* (e.g., inflammation) and *in vitro* (e.g., growth of *Staphylococcus aureus*) markers of immune function with perceptions of facial

attractiveness. Nonetheless, there seems to be limited compelling evidence to date in support of the argument that facial attractiveness is an honest and reliable signal of greater immunocompetence (Jones et al., 2021).

There is also a need for longitudinal work examining the development of phenotypic characteristics and their links with markers of good genes, health, and immune function over time during pivotal periods of development, such as late childhood and early adolescence. This kind of research is necessary to decipher the relative costs and benefits of expressing display traits and will help to clarify some of the equivocal relations between these traits with viability indicators. For instance, do markers of genetic quality predict the expression of well-developed secondary sexual characteristics? Researchers could also examine downregulation in the expression of display traits in relation to health status. For example, darker manes on male lions are preferentially desired by females perhaps as a signal of greater phenotypic condition, because darker manes might carry a cost to survival in terms of less efficient heat dissipation (West and Packer, 2002). Some indirect evidence indicates that male lions with poor nutritional status have lighter colored manes (West and Packer, 2002). Among mammals, being sick and having poor nutrition might reduce hair growth and coloration; making hair look unhealthy. Others are skeptical about the evidence in favor of this idea and note that pelage does not always correlate with nutritional status in mammals (Hill and McGraw, 2003). Like the manes of lions, men's beards constitute a sexually dimorphic secondary sexual characteristic that women display cross-culturally variable preferences for (Dixson and Brooks, 2013). Despite some speculation (Dixson and Vasey, 2012), there is very little research supporting that beards are immunologically "costly" and that they advertise superior immune functioning.

Criticisms of the LK Null Model

Not all evolutionary scientists, however, agree with Prum's "beauty happens" hypothesis and the proposal that the LK null model should be the default model of sexual selection (Kempenaers, 2017; Borgia and Ball, 2018). For example, Patricelli et al. (2019) argued that Prum ignored other hypotheses for sexual displays other than Fisherian selection and stated that "Mate choice learning, as well as mutation-order divergence, sensory drive, and bias, sexual conflict, and male–male competition all provide testable nonmutually exclusive alternatives to both Fisherian and indicator models" (p. 120). Borgia and Ball (2018) also drew attention to meta-analytic work whereby little evidence was found to support genetic correlations between male sexual displays and female preferences (Greenfield et al., 2014). Although, some have pointed out that most empirical work examining trait–preference correlations have been statistically underpowered (Sharma et al., 2017). It has also been contended that because Fisher's process has testable causal relations that it is an inappropriate null model for intersexual selection (Patricelli et al., 2019). For instance, like good genes models of sexual selection, Fisherian selection requires that: (1) a mate preference is heritable and has a genetic basis, (2) a preference is reliably linked to a specific display trait, and (3) that there is a genetic correlation between the display trait and the preference for that trait (i.e., that they are in disequilibrium). However, a null *hypothesis* is not the same as a null *model* (discussed in Kovaka, 2020). A null hypothesis is that there is no statistically significant association between observed variables (i.e., no effect). Null modeling involves comparing the most parsimonious model including a focal set of variables intended to explain some pattern in nature against a model with an additional process or mechanism (Bausman, 2018).

It is also worth mentioning that some authors have advanced alternative hypotheses that run in contrast to sexual selection. For example, Roughgarden (2012) has argued that, contrary to sexual selection, social selection offers a framework whereby mate choice functions principally to create the social conditions necessary to support offspring development. From this viewpoint, the factors implicated in nurturing and rearing offspring guide mate choice: "Social selection as presented here offers an alternative to sexual selection both as an explanation for the evolution of ornaments and as a general approach to mating behavior and parental investment" (Roughgarden, 2012, p. 2301). It is an intriguing proposal but needs to be reconciled with decades of evidence showing how humans select mates based on short-term mate value characteristics that have little to do with creating favorable conditions for offspring development (Schmitt et al., 2001).

CONCLUSION

Despite cogent reviews of the various evolutionary processes that can drive sexual selection and mate preferences (e.g., Gangestad and Thornhill, 1997; Miller, 1998; Gangestad, 2001; Frederick et al., 2013), research in evolutionary psychology still appears to be guided by the assumption that traits principally become attractive because they constitute adaptations that are reliably associated with direct benefits (e.g., parental investment) and indirect genetic benefits (e.g., good genes). In doing so, the possibility that such traits may be exaptations or spandrels is discounted (Gould, 1991), as well as whether attractive features are desired because they play off pre-existing sensory biases. This approach also deviates from Darwin's original stance articulated in *The Descent* that mate preferences can evolve for somewhat arbitrary reasons, which is captured in certain indirect benefit models of sexual selection (e.g., Fisherian runaway). But this position regarding mate choice is not given serious consideration as a competing explanation for the evolution of human mate choice. Prum (2010, 2012, 2017) advocates that the LK model should be the true null model for sexual selection and that only in the face of compelling evidence for the role of genetic and phenotypic condition should these alternative positions be favored. This may be particularly relevant for research on the attractiveness of various secondary sexual characteristics and morphological traits. The insights provided through the LK null model can help to acknowledge problematic assumptions underlying adaptationist frameworks that predominate evolutionary psychological research and to guide future work on the various models of sexual selection that collectively shape trait–preference co-evolutionary dynamics.

AUTHOR CONTRIBUTIONS

AD and SA wrote and edited the manuscript draft. All authors contributed to the article and approved the submitted version.

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Safe Carrying of Heavy Infants Together With Hair Properties Explain Human Evolution

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As a physicist, my scientific career was interrupted by maternity, and afterward retaken, with a parallel independent personal perspective on human evolution. My previous published contributions are reanalyzed as Hypothesis and Theory. The focus is on safe infant carrying in primates, sexual selection among Hominoidea, fur reduction in hominins, and tensile properties of hominoid hairs, justifying the necessary change to bipedal locomotion from the overwhelming selective pressure of infant survival. The Discussion starts with analysis of existing bias against acceptance of these new ideas, first with rational arguments on bias existing between Exact Sciences and Biological Sciences. A reanalysis of data on elasticity of hominoid hairs is made, based on published differences between statistical analysis of measurements in exact and inexact sciences. A table constructed from the original data on hair elasticity allows a simplified discussion, based on statistics used in Physics in the study of "known samples," adding extra information to the available data. Published data on hair density in primates and mammals allow the conclusion that hair elastic properties might have evolved correlated to the pressure of safe carrying of heavy infants, with an upper limit of 1 kgf/cm^2 for safe infant clinging to primate mother's hair. The Discussion enters then on the main ideological bias, related to the resistance in the academy to the idea that bipedalism could be connected to a "female problem," that means, that it was not a "male acquisition." Tripedal walk, occurring naturally among African Apes carrying their newborns, unable to support themselves by ventral clinging, is the natural candidate leading to evolution of bipedal locomotion. Tripedal walk as an intermediate stage to bipedalism was in fact theoretically proposed, but ignoring its role in primate transportation by ape mothers. The Discussion proceeds to a proposal of phylogenetic evolution of Hominoids, the usual focus on the males changes to the role of females with infants, allowing an integrated view on Hominin evolution, with fur reduction and thermoregulation of the naked skin, with subcutaneous insulating fat layer. The model for earliest hominin social structures is based on huddle formation and hormonally defined rites of passage.

Keywords: infant carrying, survival of heavy infants, hair properties, nakedness, bipedalism, thermoregulation, huddle, early social structure

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INTRODUCTION

The Frontiers Research Topic "A 150 Years' Celebration of Darwin's Book on Human Evolution and Sexual Selection: Its Legacy and Future Prospects" included explicitly "Among other possibilities, we also encourage researchers to submit biographical comments about the significance of Darwin and his book to one's career, and how it has impacted one's research interests." My article starts with biographical comments on the impact of Darwin's Sexual Selection on me.

I came in contact with Darwin's book (Darwin, 1871) by chance, in 1975, while walking in the street where I then lived. I crossed the street exactly in front of a bookshop, where the book was exposed in the showcase, since it was published the year before in my language, Portuguese. I decided to buy it because I was recovering from a crisis which changed completely my life, and the subject fitted exactly in what I was looking for, without even knowing it.

Since childhood, I had facility in mathematics, but difficulties with social relations, so I chose graduation in Physics and started to do scientific research still as a student, in a Nuclear Research Reactor, where I got a job immediately after graduation. I worked there for more than a decade doing hard science, and have been sent abroad for a 15 months stage in Sweden in 64/65. After my return to São Paulo, Brazil, I started to publish scientific articles, got married, completed my Master's degree in Nuclear Science, and started to work in my Ph.D. thesis (on Molecular Physics). After getting the data, I discovered that I was pregnant, started to write the thesis, and my daughter was born (December 1972) 5 days after my thesis defense.

The next year was terrible, I had not enough time to stay with my baby, rebelled against male authoritarianism at work, and finally decided to quit my full time job, family and personal life became priority. After some months at home I was invited to start a new part time compromise, and returned to the Physics Institute of the University of São Paulo (IFUSP), giving classes and starting to work in a new research project. I succeeded in making a proposal to start a new Laboratory (X-ray Crystallography) in a new research field (Liquid Crystals). But marriage collapsed, and some months later I did have a personal breakdown, with a slow recovery.

The period from January 1974, when I left the Reactor, to August 1976, when I won a contest for tenure at IFUSP, defined a change in life perspective, together with Darwin's book. It was completely different than what I had learnt at school, when only natural selection was mentioned in biology. I underlined all important points of Darwin's text (715 pages), striking for me were the human skin and sexually dimorphic vocalizations, besides the evidence on animals. The idea of esthetic female choice was especially intriguing for me. I read also in Portuguese "the naked ape" (Morris, 1967). All these ideas about Biological Evolution were then mixed with studies of psychoanalysis (Freud and several authors), pedagogy (Piaget) and anthropology (Levi Strauss and Roger Bastide). In 1976 my daughter went to the kindergarten, the new Laboratory was installed at USP and I could conciliate my academic duties with time for private studies satisfying my curiosity.

For the next decades my research evolved in the interfaces physics/chemistry/biology/education at IFUSP, where I became Full Professor in 1991. My independent studies lead in parallel to three papers in Human Evolution (do Amaral, 1989, 1996; Amaral, 2008).

The next item gives a personal perspective on the development of ideas and literature on Evolution from the 19th to 21st centuries. After that, the section on Results presents the basic knowledge necessary for the Discussion made later on in this article.

PERSPECTIVE SINCE THE 19TH CENTURY

The interest of Charles Darwin on human mind and instincts existed before his book on Natural Selection (Darwin, 1859), but he was very cautious and prudent in expressing these ideas. Only in his book on Sexual Selection (SS) (Darwin, 1871) he discusses explicitly our species, as one among others, and immediately after that comes his book "The expressions of the Emotions in Man and Animals" (Darwin, 1872), where he exposes more of his private life, in family photos. He considered the three books as a trilogy, and in fact his ideas prepared the modern disciplines of ethology and psychology.

It should be stressed the existing ideas in the 19th century. The term "biologie," derived from greek (Aristotle), was already defined by 1800. The term "evolution," referred to the development of the individual embryo, and started to be used for species change.

The British philosopher and positivist scientist Herbert Spencer, a decade younger than Darwin, introduced "social Darwinism" and the concept of "struggle for existence ruled by survival of the fittest," which appears in Darwin's book. Spencer central ideas emphasized the social organism and the social self-consciousness of individuals (Offer, 2019). The dualism individual versus society is indeed a permanent philosophical and practical problem.

In Darwin's time only the proposal of natural selection caused real impact, since the intellectual ambient was already prepared to absorb it. His proposal of sexual selection, particularly in relation to female choice received strong resistance, and his book on Expression of Emotions became popular, but did not receive much scientific credit.

In Darwin's autobiography written for his family he states what was already in SS: he considered that Natural Selection needed several corrections. He was since childhood interested in collecting things, as a systematic naturalist, but also as a very ordinary boy. After his 3 years in Cambridge he joined the Beagle as a Naturalist without pay, for 5 years (1831–1836). The way this voyage defined his latter work was much discussed (Sulloway, 1982), but I prefer to stay with his own words, on pg. 119/120 of his autobiography (Darwin and Barlow, 1958):

– *My first note-book was opened in July 1837. I worked on true Baconian principles, and without any theory collected facts on*

a wholesale scale, more especially with respect to domesticated productions, by printed enquiries, by conversations with skillful breeders and gardeners, and by extensive reading. . ..
– *I soon perceived that selection was the keystone of man's success in making useful races of animals and plants. But how selection could be applied to organisms living in a state of nature remained a mystery to me.*

Clearly, artificial selection, by breeding intentionally, was the first obvious mechanism drawing Darwin's attention. In pg. 121 starts his telling about receiving in summer 1858 Wallace's essay "On the Tendency of Varieties to depart indefinitely from the Original Type," with similar ideas. He joined his ideas with Wallace's essay, published together in the Journal of the Proceedings of the Linnean Society 1858, p. 45. He says on p. 122 of his autobiography:

– *Nevertheless our joint production excited very little attention. . ..*
– *In September 1858 I set to work by the strong advice of Lyell and Hooker to prepare a volume on the transmutation of the species. . ..*
– *It was published under the title of the Origin of Species, in November 1859. . .. . .*

Darwin ideas on artificial selection became the first chapter on his book on natural selection. As discussed later (Brown, 2010) variation under domestication was the paradigm. Soon later Darwin published "The Variation of Animals and Plants under Domestication," expanding that first chapter, and this book (Darwin, 1868) became one of the foundation of scientific plant breeding.

Darwin did have ideas on "heredity," but he accepted Lamarck's views on heredity of acquired characteristics, which was at his time the only systematic theory of biological evolution (Lamarck, 1809). In the Origin of the Species he accepts the inheritance of acquired characteristics as one of the factors contributing to evolution.

An interesting review (Jordanova, 1986) criticizes the first English translation of Lamarck's book.

Genetics came later on and there is evidence that Gregor Mendel, younger but contemporary of Darwin, knew about Darwin, while Darwin did not know about Mendel (Fairbanks, 2020). The meaning of Mendel's work on heredity, published in 1866, became clear only in the beginning of the 20th century, when it was rediscovered (Keynes and Cox, 2008) (Simunek et al., 2011).

Regarding the following scientific progresses it should be stressed the contributions of Ronald Fisher, British mathematician, statistician and geneticist, first in his work on sexual selection as a genetic runaway process (Fisher, 1915) and later on his analysis of Mendel's data on experimentation with pea plants (Fisher, 1936), which originated a hot debate later on (Franklin et al., 2008).

Modern Genetics paved the route for the Modern Synthesis, defined by the union of natural selection with genetics, in the period between the two Great Wars. The large amount of work of this period can be seen from a perspective of some decades later, in some specific references:

– Evolution: The Modern Synthesis (Huxley, 1942), and a Definite Edition, with a Foreword (Pigliucci and Müller, 2010).
– Genetics of the Evolutionary Process (Dobzhansky, 1970), with a Book review (Harrison, 1972).
– Origins of the Modern Synthesis: *The Evolutionary Synthesis*. Perspectives on the Unification of Biology (Mayr and Provine, 1980), with a book review (Ruse, 1981).

It should be stressed that the Modern Synthesis had two problems:

– The whole field of fetal development and embryogenesis (a direction strong in Germany) was discarded in favor of population genetics.
– Sexual selection became only objective reproduction with competition between males, and female sexuality was ignored.

From Darwin's ideas on animal behavior emerges the work on ethology, by Konrad Lorenz and Niko Tinbergen, influencing psychology already in the 30's. A perspective on their work can be found in a book (Burkhardt, 2005) with a review (Clucas, 2006). Lorenz and Tinbergen, together with Karl von Frisch (who worked on bees), received the Nobel Prize for Physiology and Medicine in 1973.

The revival of Darwin's ideas on Expression of Emotions occurs only with psychologist Paul Ekman, almost hundred years after Darwin. In 1954 he begins his research on facial expression and body movements, including hand gestures, followed by non-verbal behavior and micro-expressions. He discovers universal facial expressions and publishes books and articles (Ekman, 1999, 2007, 2016). The field of Evolutionary Psychology develops, together with Emotions (Cosmides and Tooby, 2000).

In the centenary of Darwin's book on sexual selection 11 essays were published in a book (Campbell, 1972), with a review (Williams, 1973). There the parental investment theory (Trivers, 1972) expands sexual selection and predicts that the sex that invests more in its offspring will be more selective when choosing a mate, and the less-investing sex will have intra-sexual competition for access to mates.

Detailed studies in sexual selection flourished in the last decades, both on animals and plants (Andersson, 1994; Andersson and Iwasa, 1996; Andersson and Simmons, 2006).

Regarding sexual selection among humans, the specific proposals of Darwin were retaken more recently in psychological academic papers, focusing physical attractiveness (Dixson et al., 2007, 2010, 2011; Valentova et al., 2017), based usually on attractiveness of male or female figures, eye tracking and also questionnaires to volunteers.

Regarding sexual selection among monkeys, Darwin published a very interesting article on Nature (Darwin, 1876). My first article (do Amaral, 1989) quotes the frontier literature at that time, and this article discusses again the subject.

The following item presents the results necessary to proceed in this article on Hypothesis and Theory, focusing safe carrying of heavy infants together with hair properties as a possible explanation of Human Evolution.

RESULTS OF INTEREST TO THIS PROPOSAL

My Previous Initial Contribution to Human Evolution

In this item I synthesize my three papers on Human Evolution (HE), mentioned in the Introduction. It must be stressed that the present focus on the subject "bipedal locomotion" is a consequence of development of objective criteria to define, from the existing bones, if a given fossil was a biped or not. Locomotion is of course important, but all anthropoids are able to bipedal walk for short periods, the point is to understand why such peculiar form of locomotion became necessary in Human Evolution.

Paper 1—Global View

My original proposal (do Amaral, 1989). Joins "hypothesis and theory," with the view I had at that time. The complete text (with 60 references) is available in pdf image format. I copy the abstract and make some comments.

Abstract

Hindrances against bipedalism evolution are localized in obstetrical constraints, maternal mortality rates, infant birth trauma and unsafe pregnancy. Analysis of infant survival probability shows that a shift to bipedalism could occur as a necessary consequence of the process of body fur reduction, in a balance between such hindrances and safe infant transportation. Fur reduction is proposed to correlate with cooling mechanism in intra-species physical fights. The triggering of a feed-back mechanism connecting reduction of body fur to canine reduction would be responsible for a passage from threat displays to actual physical fights. The proposed scenario for such changes is the transition from uni-male to multi-male social structures among Hominoidea. The implications of the approach adopted are discussed.

Comments

The paper is based on the discovery of Lucy (*A. afarensis*), proving that bipedality was established 4 MYA, at the forest fringe, under a vegetable diet. The main reference (Berge et al., 1984) proposed that Lucy already had obstetrical traumatism, with rotation and flexion of the neonate in a ventrally oriented pelvic outlet, even with a small neonate fetal skull size. I added a further argument: bipedality is also unfavorable to safe pregnancy since it might favor abortion accidents, and presents problems of locomotion in the last months of pregnancy. Maternal and child mortality at birth ought to have been a major problem, and this will be discussed in this paper.

My original proposal evolved in two connected arguments:

- *The reproductive success was proposed to be proportional to the total infant survival probability, given by the product of two factors: Probability of survival of mother and fetus from conception to birth (obstetrical factor So) and probability of neonate survival during infancy (pediatric factor Sp).*
- *Reduction of body fur in hominids is the more natural candidate for the parallel process inducing bipedality, with a strong selective pressure for carrying infants on the arms of their mothers.*

A simple analysis, given in the paper, shows that body fur reduction brings bipedality as a NECESSARY CONSEQUENCE, before the condition of total nakedness is attained. A body fur reduction responsible for about 15% decrease in Sp, in relation to chimpanzee, would be enough to start to favor bipedalism.

Five basic references on physiology of hairs and skin support that reduction of body hairs comes before bipedalism: (de Beer, 1962; Schultz, 1968; Montagna, 1982, 1985; Ebling, 1985).

A main reference for my views on social structures of primates was published in Science (Eisenberg et al., 1972). Also interesting a short article on connections between canine reduction and the danger of canine wounds (Hutchinson, 1963), helping my proposal.

Paper 2—on Nakedness

The second paper (do Amaral, 1996) discusses the thermoregulatory advantages of hominid bipedalism combined with naked skin and larger body size. Published in Current Events, it does not have an abstract, it has 26 references and 6 Tables with numerical results of calculations. I question results from a specific paper favoring bipedalism after nakedness (Wheeler, 1992), with calculations for haired *vs.* naked bipeds and quadrupeds, crossing the four alternatives. I have reproduced several published curves using a scanner and Microsoft Windows on a PC computer, and performed numerical integration, making detailed discussions. I focus arguments of an earlier paper (Newman, 1970), that concludes "the obvious time and place where progressive denudation would have been least disadvantageous is the ancient forest habitat." A critique to Wheeller's ideas suggested that the advantages of bipedalism had little or no adaptive significance to thermoregulation (Chaplin et al., 1994).

I choose here some phrases that synthesize my Paper 2:

"Although it is widely accepted that naked skin facilitates dissipation of body heat, the circumstances favoring its evolution are quite unclear. The point made in this paper is that although Wheeler's calculations demonstrate the thermoregulatory advantages of bipedalism over quadrupedalism and of increased body size in savanna environments, the results do not indicate that the initial step in the denudation process occurred in open hot environments, nor that bipedality preceded body-hair reduction."

"Wheeler's work did made the point that nakedness has thermoregulatory advantages regarding water consumption at $T_{200} = 30°C$. However, this is interpreted here as suggesting that nakedness evolved in a more forested environment, and possibly, before or together with bipedality, not after it."

"A more dry forest, which is one of the forest types of tropical regions. . .. . ., could be a possible candidate as a habitat for the emergence of earlier hominids.

These conclusions were confirmed with discoveries of fossils in following years, and are integrated in the accepted views on HE today. The origin of the process of hair reduction

remains, however, unknown and continues to be attributed to thermoregulatory requirements. Recent revivals of this problem should be mentioned, and will be discussed in this paper.

Paper 3—on Infant Carrying

In order to give support to my proposals I needed to have experimental results, but it was not trivial to get samples of hominoid hairs. I went to a congress in France, and took the occasion to contact Dr. Christine Berge (Museum National d'Histoire Naturelle, Paris, France), and she gave me 3 pieces of skin with hairs, making this work possible (Amaral, 2008).

This paper has free access from internet. It has 50 references, 5 figures, 2 Tables. The relevance and pertinence of this original analysis for Human Evolution will be focused in the following items of Results. Here I make some general remarks on hairs as natural fibers.

Mechanical studies of animal fibers have been extensively performed because of interest in textile production, mainly wool (Feughelman, 1997) as well as cosmetics for human head hair (Robbins, 1994). Animal hair is composed of three parts: an external thin cuticle, a thicker cortex with fibrous proteins, and a central porous medulla.

Ape hair viewed under an optical microscope is similar in structure to wool and human head hair, as seen in **Figure 1**.

Mechanical properties of natural fibers are defined by the cortex of the fiber and are due to the molecular structure of keratin, which constitutes the cortex. Extensive work during decades evidenced the dependence of mechanical properties essentially on the cross-sectional area of the fiber, thus enabling basic research to be conducted on relatively few single fibers, eliminating the need for statistical methods on a large number of samples (Feughelman, 1997).

The Problem of Infant Carrying

The following items give results from literature on infant carrying by primates, and also more details of the results obtained in my paper 3 (Amaral, 2008) in the context of biophysical analysis of the carrying problem.

The Importance of Infant Carrying in Primates

All higher primates (except humans) carry their young clinging to their fur from birth. The correlation between infant carrying and the form of locomotion of adult primates is clear, but no detailed study had focused on the mechanics of the problem, until my detailed study from the point of view of biophysics of the carrying problem (Amaral, 2008), where references to infant carrying in primates can be found: (DeVore, 1965; Jolly, 1972; Tuttle and Watts, 1985).

Here some recent references are added, and the details necessary for an easy understanding by human scientists are given.

It is clear that safety in infant carrying imposes limits on the weight of infants, especially among Hominoids (our lineage), characterized by increasing body size. Accepted hominoid phylogeny places the branch to the Lesser Apes (gibbon) as the oldest, followed by the Great Apes, with the older branch to the arboreal orangutan and the branch originating terrestrial gorilla and chimpanzee coming later, together with biped hominins. Some discussion remains on the relative position of humans and the Apes (Ruvolo et al., 1994; Lockwood et al., 2004).

Among non-human primates, there is a change in the carrying pattern of infants by adults (mostly by the mother) as the infant grows. Newborns are carried clinging in close ventro-ventral contact, often with additional support from the mother. Change to infant support over the adult body (dorsal or lumbar clinging) occurs some months later (typically for infants heavier than 5 Kg) in all non-human higher primates and extends for years in apes. Besides all previous references, interesting results refer to evolution of infant carrying in primates (Ross, 2001) and co-evolution between infant carrying and grasping behavior (Peckre et al., 2016).

Examples of infant carrying by primates, to illustrate the comparison between monkeys (primates with tail) and Apes (primates without a tail), were given in (Amaral, 2014).

Monkeys carry the newborn clinging to the body hairs of adults in a ventral position for some months, until the infant is able to change to the mounting position. The tail of the infant is

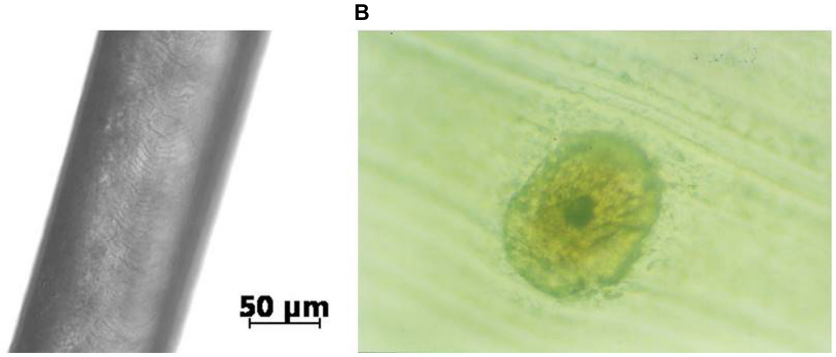

FIGURE 1 | An example of ape hair (from orangutan) view in a microscope, Amaral (2008). The external appearance with the cuticle scale structure is shown in panel **(A)** and the cross-section inner structure in panel **(B)**.

rolled up around the tail of the adult, usually the mother among African monkeys, helping the stability on movement (Figure 1A; Amaral, 2014). The Lesser Apes (gibbon) has a unique situation, with bipedal walk in tree branches and acrobatic movements of mothers with infants, easily found in internet photos, and also in a text posted by Sojourner (2011). The bigger arboreal Asian Orangutan (Great Ape) is suspended in a tree, but the mother holds the infant with one arm (Figure 2; Amaral, 2014). The larger terrestrial African Gorilla (Great Ape) mother is transporting the infant in the mounting position (Figure 1B; Amaral, 2014).

The sketch in **Figure 2** is a simplification of the mechanical problem of the infant in an inclined plane, in the dorsal clinging to the gorilla mother (Amaral, 2008). Adult gorilla is much heavier than adult human, but their newborns have only half the weight of human babies. In the first 1 or 2 months, the infant gorilla is supported manually by its mother as she walks tripedally or bipedally.

As shown in **Figures 3A,B**, the same occurs for chimpanzee babies, unable to support their own weight by clinging prior to 2 months of age. Change from quadruped to triped or biped motion occurs systematically among all great apes when infant safety requires manual support. Slow and careful locomotion of female chimpanzees while carrying young infants has been reported, and two primary causes of mortality have been found among infant chimpanzees: inadequacy of the mother–infant bond and injuries caused by falling from the mother (van Lawick-Goodall, 1967).

It is clear that infant carrying is crucial and depends on not trivial behavior among African great apes.

Mechanics of the Carrying Problem

The mechanical analysis of infant carrying among Hominoids has been made along two directions (Amaral, 2008) with results shown also here.

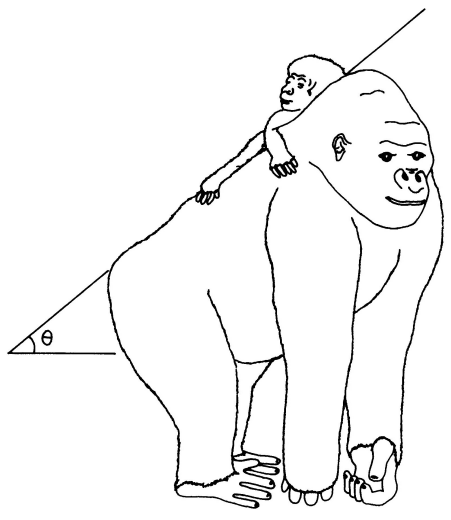

FIGURE 2 | Drawing (done by João Carlos Terassi) of the simplified mechanical problem, with an angle of inclination, discussed in the text and also in Amaral (2008).

Hair Tensile Properties

The results to be discussed in detail came from three pieces of skin with hairs, each with about 200 cm^2 area, obtained from 3 individual animals (one gibbon, one orangutan, and one gorilla—chimpanzee was not available), as already described (Amaral, 2008). The elasticity and the resistance capacity of the hairs are measured in stress/strain curves, one for each hair, as displayed in **Figure 4**.

Stress-strain curves for Ape hairs and human hairs for comparison: (**Figure 4A**) human, (**Figure 4B**) gorilla, (**Figure 4C**) gibbon and (**Figure 4D**) orangutan. The curves give the deformation (given as a fraction of the original elongation) due to the applied force (given in Newtons), until the breakage of the individual hair. Ten hairs of each individual have been measured. In **Figure 4A**, the region E corresponds to the linear region, P to the plastic plateau, PY to the "pos-yield" region, until the break of the hair. The insertion in **Figure 4A** is an amplification of the linear region, permitting to obtain the elastic force F_E and the linear coefficient α.

The curves display all the classical regions of animal hair. There is an initial elastic region, following a linear Hooke law, until about 1% deformation (elastic limit F_E), followed by a plastic region, due to changes in the conformation of the keratin molecule, which is influenced by the amount of water, and a final break of the hair.

Curves are typical of all natural fibers, and in the human hair reveal the treatment given to it. The regression coefficient of the initial linear region α gives the Young modulus of elasticity Y, in units of pressure (GPa = 10^9 N/m^2), through the relation $Y = \alpha/A$, where A is the area of the cross section of the hair, Ø its diameter, so that $A = \pi\ (Ø/2)^2$. The elastic limit F_E is the limit that the hair can stand, in order to be able to support the pressure given by infant clinging to the hair. From each curve it is possible to measure the values of α and F_E (as shown in the insert in the figure), and also the values at the rupture point (force Fr and strain Sr). The force to rip out the hair from the skin has also been measured (20 hairs in each sample) and it is a little larger than the elastic limit.

It should be stressed the dependence between the hair diameter and the Young's modulus of a particular animal species (Šimková et al., 2013).

It is clear from **Figure 4** that the results are different for each hominoid species. Furthermore, the skin and hair from the different ape species are easily recognized by appearance and texture: Gibbon hairs are black, thin and smooth silky, those from orangutan are reddish, thicker and rough, while those of gorilla are black with intermediate thickness and texture.

The important point to emphasize is that properties of hairs are "species characteristic," and therefore even a single individual is enough to obtain meaningful results, extensive to that species. In the original paper (Amaral, 2008) the conventional statistical analysis, used in biology, has been made, since hairs are a "natural biological sample." Differences between species are statistically significant, in the comparison of each pair of species, and also in the Anova test for the 3 ape species. An extensive discussion on the implications of the results regarding safety of infant carrying

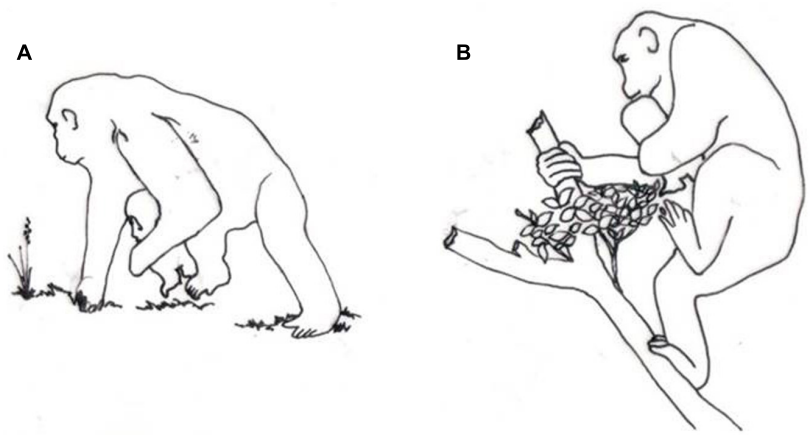

FIGURE 3 | Drawings (done by João Carlos Terassi) inspired in photos (van Lawick-Goodall, 1967) of chimpanzee mother using tripedalism. **(A)** Using one hand to hold infant, walking in terrestrial substrate. **(B)** Using one hand to hold infant, walking in arboreal substrate.

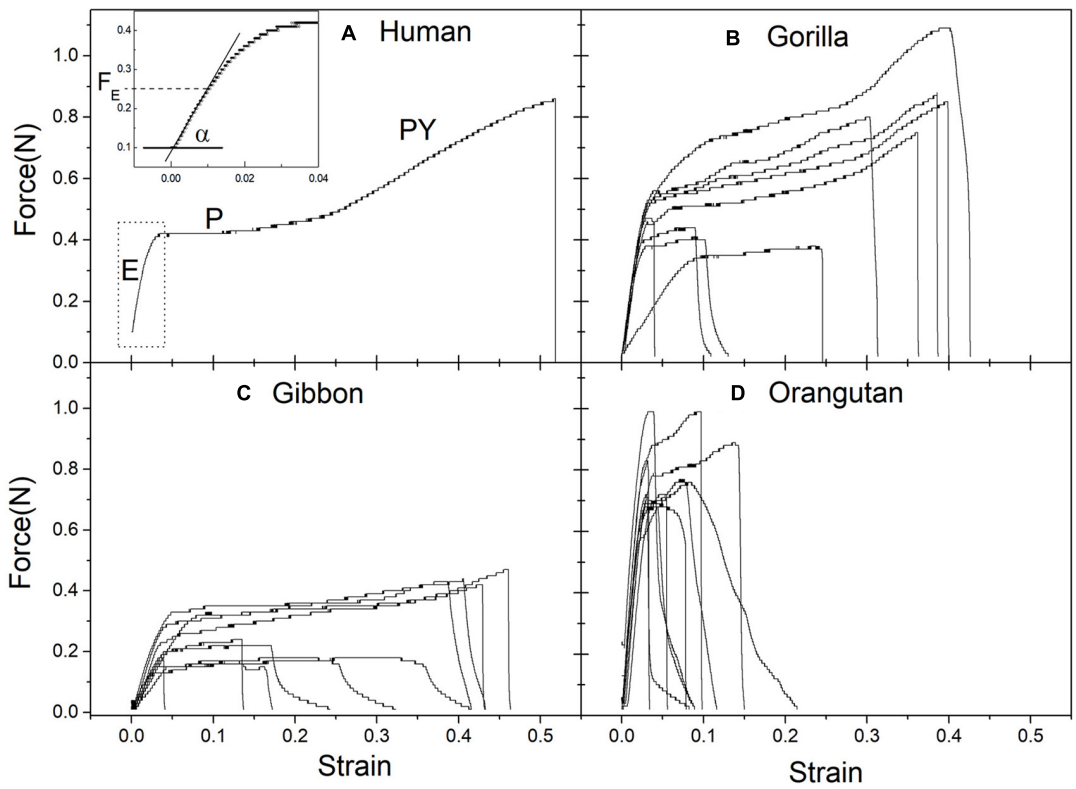

FIGURE 4 | Experimentally obtained stress (Force) strain (relative deformation) curves for single hairs: **(A)** humans **(B)** Gorilla **(C)** Gibbon **(D)** Orangutan. Typical regions are seen: elastic (E), plastic (P) post yield (PY) and final break. In panel **(A)** the insert shows the linear region with coefficient α. See text for explanations.

along our evolutionary line was already published and will not be repeated here.

Mounting Position of Gorilla Infants

Let us analyze the dorsal clinging position, following paper 3 (Amaral, 2008). **Figure 2** is a sketch of the mounting position in African apes, showing the angle θ of the inclined plane where the infant stands. In the sketch the angle θ coincides with the angle defined by the usual knuckle-walking position of African great apes, this just helps to capture the forces in action. The total infant weight, in the vertical direction, has two components, one in the inclined plane, favoring slipping, and one normal to the inclined plane, responsible for the friction force opposing slipping, which depends on the friction coefficient. In

the absence of clinging, slipping on the body surface of contact starts for a critical value θ_c and the infant falls down. Both friction and clinging are thus essential to hold heavy infants in the mounting position.

It should be stressed that this is a necessary condition for infant survival and therefore also for species continuation. It is a very robust requirement of basic mechanics for equilibrium. The ape hair–hair friction coefficient μ must be known to analyze the actual ape situation, and it was actually measured and discussed. This simplified mechanical analysis is able to explain the observed angle θ presented by Gorillas (estimated in about 26°) (Amaral, 2008).

A reference to my paper (DeSilva, 2011) mentioned *"the elimination of dorsal riding as an option for infant hominids,"* in the context of bipedality. deSilva work proposed a shift toward birthing relatively large infants early in human evolution, analyzing the infant/mother mass ratios in Australopithecus females.

DISCUSSION: HYPOTHESIS AND THEORIES

There exist bias strongly acting against acceptance of new ideas coming from "outsiders" (my case) and their integration in the *status quo* of the main stream in "academic knowledge." This is quite obvious regarding Human Evolution, strongly connected with religion and social habits and costumes. But what became clear to me now is that a main bias seems to exist also between Exact Sciences and Biological Sciences, and it has to do with a belief on the power of Mathematics to solve any problem, what is of course not true. Any theory relies on initial assumptions, taken for granted as intuitive and without proofs. This forms a very rigid body of ideological beliefs, not open to real debate.

This discussion will first enter on rational arguments, and only later will attempt to overcome such bias.

Infant Carrying and Human Birth

Let us discuss proposals that go also in the direction of "infant carrying" leading to bipedalism, with connections with the obstetrical problem.

Iwamoto (1985) recalled examples of facultative bipedalism among monkeys and speculated that the "decisive factor (for habitual bipedalism) may have been some everyday necessity to carry something in both hands." After criticizing proposals in which the "something" is food, Iwamoto suggested that the "something" could be their helpless babies. However, this proposal has been dismissed under the hypothesis that babies became helpless only with increase of brain in Homo.

The work by Berge et al. (1984) showed that babies were helpless before increase of the brain, but her work focused in "obstetrics," did not enter really on the connection to bipedalism. The same is valid for all later studies on parturition. The very detailed paper by Rosenberg (1992) enters on birth in non-human primates and on the evolution of modern childbirth with its overwhelming importance in human evolution. But she also did not come to the point of proposing a direct connection to the evolution of bipedalism.

The correlations between changes in the pelvis, occurring in the earlier stages of evolution of erect posture and the obstetrical mechanism of females had been pointed out long time ago (Robinson, 1972). A very interesting discussion (Robinson et al., 1972) made on the difference in bipedal efficiency of pongids and hominids, suggested that "*the evolution of erect bipedality appears to have occurred in two phases, the: first of which was primarily concerned with re-positioning the center of gravity to reduce the energy cost of frequent use of bipedality, and the: second concerned the development of a speed-oriented striding and running mechanism.*"

Such two phase process is now very well established, since bipedality evolved much before the erect position.

At the same time that my third paper was available in the internet (Amaral, 2008) the paper on fetal load and the evolution of lumbar lordosis in bipedal hominins was also published (Whitcome et al., 2007): *"human females have evolved a derived curvature and reinforcement of the lumbar vertebrae to compensate for this bipedal obstetric load. Similarly dimorphic morphologies in fossil vertebrae of Australopithecus suggest that this adaptation to fetal load preceded the evolution of Homo."*

However, the connections between these findings on lordosis and my proposal on infant carrying were clear only for me:

– The problem is evident only in the three last months of pregnancy. But of course infant carrying would represent a much bigger and long lasting effect.

From this perception, I went in two different directions. In my university I proposed collaboration with a physicist working at the Faculty of Sports, in a Laboratory of Biomechanics. My idea was to study the locomotion of mothers carrying their babies and the effects on their movement, focusing on the pelvic and spinal posture and the displacement of the body's center of gravity.

The second direction came from my direct contact with Karen Rosenberg (United States), who proposed a Symposium on Infant Carrying in Human Evolution at the 78th annual Meeting of the American Association of Physical Anthropologists, Chicago, April 2009. The 15 invited persons for oral presentations included me and Katherine Whitcome. So I attended the meeting, with an abstract published (Amaral, 2009). In that meeting I met an American anthropologist and started collaboration with him. In the following year I attended also the 79th meeting, in Albuquerque, New Mexico, April 2010, also with a published abstract (Williams et al., 2010).

But it became clear to me that my original proposal, focusing the correlation with reduction of body hairs, was not evolving internationally. The collaborations I could start extended over years, in parallel with my regular activities in Physics, leading to two articles in HE:

– Sex differences in forearm proportions (Williams et al., 2015).
– Effects of transporting an infant on the posture of women (Junqueira et al., 2015).

I decided then to turn to divulgation of my proposal in my ambient, with two papers in Portuguese (Amaral, 2014; do Amaral, 2015). I also started to present seminars on HE, when invited by colleagues who knew my activities in Physics. I gave such seminars in the Institutes of Chemistry, of Pharmacy, in Medical Schools, even in the Biology. The Institute of Theoretical Physics invited me only within the Divulgation seminars, not in the official ones, and in my own Institute of Physics also.

I noticed then that the audience could be very receptive to my proposal, when the scientists did not have compromises with the mainstream in HE. Moreover, women in general accepted it as "obvious," while men in general "laughed" as hearing a joke! The "structural chauvinism" became very clear. I then entered in the problems related to History of Science and the terrible difficulties due to the mainstream blockage, of social nature.

When the pandemic arrived a very long time at home started, working alone in my computer. But online events started to exist all over the world, opening new opportunities.

Looking Again at Data From Hominoid Hairs

My data on Hominoid Hairs, shown and discussed in previous items could be published (Amaral, 2008) only after I did all the conventional statistics used in Biology, which are not used in Physics. I started then to think seriously on the differences between statistics used in Physics and statistics used in Biology and Human Sciences. They are based on different principles, and I started to study the problem from a historical perspective, already in the 2 years before the pandemic. Then in 2021 appeared the opportunity to attend an online meeting on Statistics, I presented an oral paper, published in the Proceedings (do Amaral, 2021), on Statistical Analysis of Measurements in Exact and Inexact Sciences, which are in fact an Open Problem until today, and I copy here its Abstract:

Abstract

Differences between statistical analysis of measurements in exact and inexact sciences are the focus of this work. The early and independent beginning of Probability and Statistics had a theoretical synthesis, with an initial development based in Physics and Astronomy. This lead to Error Theory, used in Statistics of Measurements in Exact sciences, with defined criteria of validity. This direction of Mathematical Physics resulted in the progresses and achievements in Classical Physics, and also on established ways of treating measurements of physical properties. It is discussed that Exact Sciences treat only Inanimate Matter, and things that can be defined and measured, in terms of only seven fundamental physical quantities, with the definition of the International System of Units (SI). On the other hand a direction of Mathematical Statistics emerged later on, based on "Sampling," to study properties of a population, with criteria of significance, within validity intervals, which depend on the size and characteristics of the studied sample, and on the inferences to be made in the research. These are two very different approaches, but both use probability density functions related to hypothesis about data. The modern inferential sampling statistics can be applied to all practical problems, in particular in Biology and Humanities, where there are "models," but not Theories as in Physics. The word "theory" is many times used in a mistaken way. Life and Human Sciences use this modern type of Statistics. This paper discusses a particular case, in which the same ensemble of experimental results in samples of biological origin (hairs from hominoids) can be analyzed with the two different statistical approaches, in a proposal for Human Evolution, and the conditions for inference of accurate conclusions are discussed. A philosophical discussion between subjective and objective criteria of the researcher is made, and also of the concept of knowledge.

Reanalysis of Data

Here previously obtained data on hairs (Amaral, 2008) is re-analyzed with presentation of **Table 1**, constructed from the original data, allowing a more simplified discussion, as presented in that recent conference (do Amaral, 2021).

The symbols for the variables in the first column were given, when explaining the stress/strain curves shown in **Figure 4**. The legend on **Table 1** explains the values shown in this Table.

I stress here what is necessary to a better understanding of the issue. The more important variables obtained from the stress/strain curves are:

- elastic limit F_E (N), which can also be given in units of gf (gram-force $\sim$ 0.01 Newton), a direct measure of the weight the single hair can stand without a permanent deformation.
- regression coefficient α of the initial linear region, which together with hair diameter $\emptyset$ (μm) gives the Young modulus of elasticity Y.

The values given in the columns show the average values obtained from the 10 measured curves, with $\pm$ the "error" (standard deviation of the mean). In parentheses is the variation coefficient, related to the broadness of the distribution.

This table allows an interesting comparison with the statistical analysis required in biology, in the published paper (Amaral, 2008).

The sampling statistics used in biology is certainly very helpful, but many times the amount of available samples does not allow a decision only on basis of a "large amount of data." In this case there are solid arguments in favor of accepting the approach used in physical sciences, when the study is made on "known samples." It corresponds to adding "extra known information" to the available data.

That is indeed the case for "hairs":

- it is well established that analysis of hair properties is used in legal forensic science to determine the animal species, and this is valid also for human hairs, as seen in a book (Robertson, 1999), with a book review (Tridico, 2001) and also on a review published by FBI (Oien, 2009).
- it is well established that measurements can be performed in relatively few single fibers (Feughelman, 1997).

In physical sciences the research is usually made in one sample of a known material, with repetition of measurements of a physical property. So that 10 independent measurements of hairs from one individual may represent a sufficient ensemble, since it

TABLE 1 | Thickness of the skin and length of hair (estimated) average values of the measured values of the hair diameter Ø, of the linear regression coefficient α, of the elastic limit F_E, and from Young modulus Y.

	Gorilla	Gibbon	Orangutan	Human
Skin thickness (mm)	∼1.5	∼0.6	∼2.3	
Hair Length (cm)	∼6	∼4	∼10	
Ø (μm)	66 ± 2 (21%)	52 ± 2 (19%)	120 ± 4 (24%)	60–80 ethnic determined
α (N)	17 ± 2 (25%)	6.0 ± 0.6 (33%)	32 ± 1 (13%)	
F_E (N)	0.38 ± 0.03 (30%)	0.18 ± 0.02 (36%)	0.49 ± 0.02 (12%)	0.28 ± 0.02 (29%)
Y (GPa)	5.0 ± 0.6 (42%)	2.8 ± 0.3 (43%)	2.8 ± 0.2 (36%)	2.9 ± 0.2 (33%)
Weight Adult (Kg)	150–250	7	50–90	
Hair Density hairs/cm^2	100	1,000	∼200	

Constructed from original data (Amaral, 2008; do Amaral, 2021). Averages show the standard deviation of the mean, in parentheses the coefficient CV = 100 × standard deviation/average value. Final lines show the weight of the adult animals and the density of hairs of each species.

is known for sure that the individual is from a specific ape species. Extra information enters the statistical ensemble of data, since it is known and accepted that the 3 individuals represent each one a separate species.

In physics it is not usual the use of statistical analysis in terms of the parameter "*t* of student" as function of the degree of freedom and confidence level. Analysis uses simply Gaussian function, when applicable, since the probability of the distance of a measurement to the average value depends on the standard deviation σ, in a known way:

– 68.2, 95.4, and 99.7% probability for the measure to be within, respectively, 1σ, 2σ, and 3σ from the average value.

Comparing **Table 1** above with the previous sampling statistics (Table 2 of Amaral, 2008) it is possible to say that the "thumb rule" of a physicist holds:

– if two independent average values differ by more than 3 × "error" they are most probably NOT measuring the same thing.

The same inference can be made here, since there is enough separation between the values of all measured parameters for the different species.

This discussion needs some more information regarding the two last lines of **Table 1**, showing the weight of the adult animals and the density of hairs of each species.

Hair Density in Primates

Reference to the work of Shultz on hominoid primates was mentioned already in my first paper (Schultz, 1968). In my third paper the question of density of hairs in non-human primates was discussed in detail, with reference to the extensive work of Schultz showing that hair density values on the back of primates vary, from over 1,000 hairs/cm^2 for smaller species (monkeys and gibbons), down to about 100 hairs/cm^2 for great apes (Schultz, 1931).

This very large amount of data was analyzed 50 years later (Schwartz and Rosenblum, 1981) resulting a scaling law with a negative allometry of relative hair density (rhd = hair density/total surface area), as seen in their paper. There is a decreasing scale law among primates, relating the log of the relative density of hairs rhd with the log of total surface area (cm^2). And it is clear that "*chimpanzees apparently have a lower rhd than would be expected for their body volume.*"

These results were integrated in the discussion made in my paper 3. Among Hominoidea, the small and light Gibbon is very hairy, while the big and heavy Gorilla has a density of hairs 10 times smaller. This represents a clear problem in the usual primate infant transportation, clinging to the mother's hairs.

In order to make now a more complete discussion on the problem of infant carrying the weight of the adult animals and the density of hairs of each species are added in the last lines of **Table 1**.

Moreover, a recent communication with a detailed comparison with mammals (Sandel, 2013) confirmed a significant negative correlation between hair density and body mass. Results indicate that all primates, and chimpanzees in particular, are relatively hairless compared to other mammals. Humans are covered with small fine vellus hairs, not counted as terminal hairs. The meaning of this clear scaling law is not yet completely understood. But its effect on the problem of infant carrying is very clear. There is a defined increase in weight along phylogenetic evolution: gibbon—orangutan—gorilla, infants became heavier, but the density of hair decreases, and safe carrying of heavy infants becomes THE problem to be solved.

Taken into account all the available information, it is possible to infer a pattern about evolution, from the obtained results of hairs of the three species. The increase in size and weight in the Asian line occurs with the same young modulus Y, with large increase in hair diameter Ø (μm) and elastic limit F_E (gf) from Gibbon to Orangutan. The African direction, with the much heavier Gorilla, required a larger value of the Young modulus Y, allowing for not so large increase in hair diameter Ø (μm) and elastic limit F_E (gf). The case of chimpanzee will be discussed later on.

Figure 5 display a double sketch of the evolution in terms of the important parameters obtained from mechanical analysis of hair properties of the three hominoid species: the hair diameter (in μm), the elastic limit (in gf) and the Young modulus of elasticity (in GPa) in the upper sketch, and the lower one with the weight (in kg), the hair density (in hairs/cm^2) and the geographic location.

The same Young modulus was obtained for gibbon and orangutan, along arboreal evolution in Asia, while a much larger

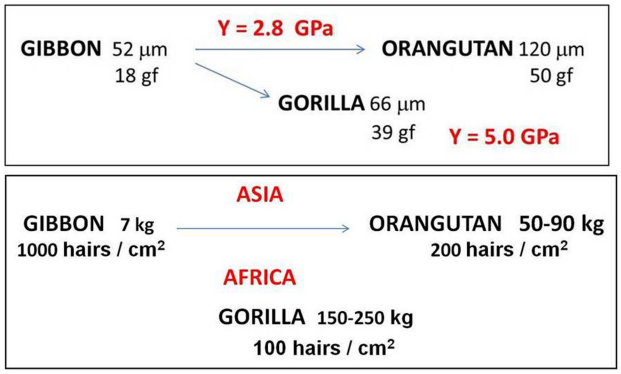

FIGURE 5 | Sketch of evolution among Hominoidea: upper focusing the Young modulus, down the species location. See text for complete explanation.

Young modulus was obtained for terrestrial largest Gorilla. So that Gorilla hair can stand much more weight than orangutan hair. Of course all this is just an "indication" and much more studies are necessary.

The discussion in Amaral (2008) considered also that the bunch of hairs available for clinging depends also on hair length and infant hand size, so that bunches of about 100 hairs are necessary to carry infants weighing a few kilogram-force. To simulate the real load effect in the actual clinging situation a bunch of hairs on about 1 cm^2 ($\pm$ 10%) of gorilla skin under load was observed, still on the skin. The bunch of hairs broke, detaching from the skin, and **Figure 6** shows the bunch after detachment from the skin. This occurred under a static load of 7 kg, compatible with the values of force at rupture (Fr) from the stress/strain curves of **Figure 4**.

– An upper limit of 1 kgf/cm^2 for clinging without problems on the hominoid skin may be deduced from this simple experiment.

Humans cannot be placed in the primate scale law regarding fur, the denudation process is unexplained, but chimpanzee already deviates, having the same density of hairs as gorillas, but being much smaller, with weight about 1/3 of the gorilla.

Conclusion: Hair physical properties might have evolved correlated to the pressure of safe infant carrying, considering the change from arboreal to terrestrial locomotion.

It should be stressed that dermatology encompass both skin and hairs but they are physically different. Human skin, with all its unique properties, will be mentioned later on.

Ideological Bias Prevent Understanding of Human Evolution

As mentioned in the beginning of this Discussion, after rational discussion, it is now necessary to enter on the problem of ideological bias. First point is related to the tripedal locomotion of gorillas and chimpanzees, discussed in the text and shown in **Figure 3**.

FIGURE 6 | Result of experiment to test the weight limit for the bunch of hairs. See text for complete explanation.

The small gibbon has ten times more hair density than the large gorilla, and about 30 times less weight than the Gorilla. Gibbon infants are safely carried, clinging to the mother's hairs, while the Gorilla newborn requires that the mother hold it with one hand, walking tripedally for some months, until the infant is able to adopt the mounting position.

It seems clear that tripedal walk, occurring naturally among African Apes carrying their newborns, unable to support themselves by ventral clinging, is the natural candidate leading to evolution of a bipedal locomotion.

The idea of tripedal walk as an intermediate stage to bipedalism was in fact theoretically proposed (Kelly, 2001), based on the fact that human anatomy is more asymmetric than in the Great Apes, but with the hypothesis that it came from the need to through stones for defense. In other words, rational arguments are mixed with a focus only on males!

I start now to make new proposals, not published yet, as HYPOTHESIS:

– Reduction of body hairs extended the length in time of tripedal locomotion, initially of some months, to the point that it became more effective to adopt bipedalism.

This hypothesis joins the tripedal theory worked by Kelly to the theory I formulated in my paper 1, considering the reproductive success to be proportional to the total infant survival probability, given by the product of two factors, as proposed in do Amaral (1989) and mentioned previously here.

In previous items the difficulties between methodology of Exact Sciences and Biological Sciences have been rationally discussed in the context of results on mechanical properties of Hairs. But it is necessary now to face the main ideological problem:

– There has been always a very strong resistance in the academy to the idea that bipedalism could be connected to a "female problem," that means, that it was not a "male acquisition."

Models are in fact developed from the point of view of the adult male individual. Here it will be instead focused the female perspective, including the connection with infants, which is the most important for reproduction and survival. With such perspective this discussion returns to Sexual Selection.

Sexual Selection Among Hominoids

There is a pattern in the evolution of hominoid socio-sexual structures, of not easy explanation, as discussed in my first paper: Gibbons are small and mainly monogamous, larger Orangutans are solitary and heaviest Gorillas have harém, but none of them accept coexistence with other adult male. Growth in size, together with large sexual dimorphism, indicates sexual selection among Orangutan and Gorilla. Chimpanzees have a fission–fusion promiscuous system, males are genetically related in their groups, while Humans are flexible. The whole process of initial separation of humans from the ape lineage is unknown.

From the global overview on the problem, my proposal published more than 30 years ago was:

"The proposed scenario for such changes is the transition from uni-male to multi-male social structures among Hominoidea".

This discussion intends to show that the scenario proposed 30 years ago remains compatible with all knowledge accumulated with the extensive theoretical and experimental work done on primates in the last decades. **Figure 7** shows a sketch of phylogenetic evolution of Hominoids, including Lesser Apes, Great Apes and Humans. Most primate groups of Old World monkeys are organized among related females while among Great Apes genetic relations are between males.

Let us discuss the global picture that emerges from comparison of some recent reviews with very detailed results on primates: (Plavcan, 2001; Dixson, 2012; Fleagle, 2013). What becomes clear is that all primates must be considered, in comparison with humans, in order to detect what is common and what is specific. There is not total agreement on the exact phylogenetic tree, there is preference for placing Humans separated from chimpanzees, stressing similarities between humans and all primates, since the correlation between genes and behavior is not clear and some parts of the human genome are more similar to that of gorillas than chimpanzees. The total percentage of equal genes says nothing about specific differences. More agreement exists on the definition of "species."

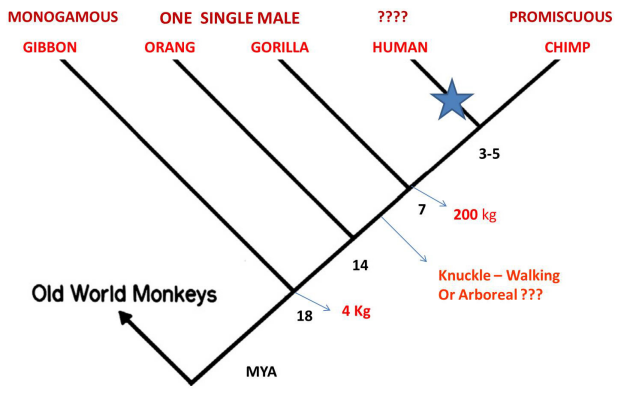

FIGURE 7 | Accepted phylogenic evolution, based on DNA analysis (Lockwood et al., 2004) placing Homo between Gorilla and Chimpanzees. Extra information pertinent to this discussion is shown in red. See text for the proposed explanation for split of the hominin lineage.

These recent reviews agree that the socio-sexual behavior of primates is very flexible, with space to work indefinitely in all the details deviating from the averages in humans as well as in all primate species, but my aim is to understand the basic trends, in order to achieve a general view able to overpass the existing bias. The most obvious secondary sex differences among primates are body mass dimorphism, and canine tooth size dimorphism, but pelage dimorphism is also present in several species and can be quite impressive. In fact the genitalia and secondary sexual traits evolve in both sexes for effective reproduction.

It is worth stressing some specific outcomes from these recent reviews:

– Plavcan stresses that sexual dimorphism is the product of changes in both male and female traits, and each sex compete agonistically in the context of coalitions (Plavcan, 2001).
– Dixson's second edition book emphasize that there is not a rigid dichotomy between the "sexual" and "socio—sexual" functions of behavior and discusses the effects of hormones in the sexual behavior (Dixson, 2012).
– Feagle's third edition book stresses that all great apes build nests for sleeping and resting, but share few unifying features in their social behavior, and describe non-trivial male–female sexual encounters among Orangutan (Fleagle, 2013).

Proposal for the Split Toward the Human Lineage

The term hominin refers to species on our branch of the hominoid tree after the split with the chimpanzee and bonobo line, including all of the extinct species and evolutionary side branches (Wood and Lonergan, 2008).

The proposal presented here is that the hominin lineage evolved from a critical transition from unimale to multimale social groups, with intense tension between sexes and rather complex intra-sexual and inter-sexual interactions. Intense socio—sexual behavior might correlate with bursts of internal heat, requiring less hair density for body cooling. Thus an initial reduction of body hairs occurred in the ancestors of both chimpanzees and naked bipeds, related to intra species aggression.

A clear result from fossil evidence is the very early reduction of canine size in the hominin lineage, correlated with changes in the socio-sexual interactions. Reduction of canine size does not correlate with monogamy, since monogamous gibbons have large canines in both males and females, and also because fossils indicate large sexual dimorphism in early hominins. Here it is recalled the idea (Hutchinson, 1963) that canines are a too

dangerous weapon when successive generations started to coexist within a group, particularly if an early process of fur reduction increased the danger of canine wounds. The inevitability of the process was stressed by Hutchinson.

Hypothesis: reduction of body hairs came together with canine reduction, correlated with passage from threat displays to actual socio-sexual physical fights, with body contact. Such intra species physical fights are much more frequent among humans than among other mammals.

Reduction of body hairs together with bipedalism means that females must carry infants on their arms, have no free hands to get food, and need help to survive. The more natural solution is the formation of female kin groups, with males floating around the periphery, and mating occurring at special times. This is coherent with considering the split toward the hominin lineage within the whole primate behavior. It is from this perspective that the basic question of the naked skin is discussed in the next item.

Thermoregulation and the Naked Skin

The still unsolved question connecting naked skin with thermoregulation must now be faced. More recently the modeling of heat balance was extended to consider a running hominin, with the conclusion that *"only when hair loss and sweating ability reach near-modern human levels could hominins have been active in the heat of the day in hot, open environments"* (Ruxton and Wilkinson, 2011a,b). This can be conciliated with a very early fur reduction, considering that earlier hominins lived still in a forest ambient.

The model was again retaken, considering the altitude at which australopiths actually lived (David-Barrett and Dunbar, 2016). This last argument trying to place hair reduction after bipedalism mentions: *"cool night time temperatures would have made it impossible for substantial hair loss to have evolved in species occupying the sites where Australopiths appear to have lived in the absence of cultural (*e.g.*, shelter, clothing) or other behavioral (nesting, group sleeping) developments"* (David-Barrett and Dunbar, 2016). In order to keep a very early process of hair reduction, the solution is indeed to focus on the possibility of behavioral nesting and group sleeping associated with a primitive shelter. Two arguments can be invoked now:

- Chimpanzees, and large bodied hominoids, construct every day their nests inclusive -with thermoregulatory capacity (Samson and Hunt, 2014).
- Along the last decade the concept of social thermoregulation among humans evolved in the psychological literature, with a defined theory (IJzerman et al., 2015).

This discussion turns now to the physiology of animals (Davenport, 1992; Schmidt-Nielsen, 1997) and humans (Bruck, 1989) giving support to arguments on biological thermoregulation as a physiological dynamical process. The practically constant basal metabolic rate (BMR), the minimal rate of energy expenditure per unit time by endothermic animals at rest, is very well known. The thermoneutral zone (TNZ) is defined as the range of ambient temperatures where the body can maintain its core temperature. The typically small tropical thermoneutral zone (TNZ), between 27°C and 30°C, represents a very small range of temperature tolerance in both directions, and the problem of altitudes in the tropics means that night temperatures of the order of 10°C must be considered.

Non-shivering thermogenesis (NST) is the increase of individual basal metabolism below the minimum critical temperature of the TNZ and participates in the chemical thermoregulation of mammals, especially neonates, connected to the metabolism of the brown adipose tissue (BAT). Extensive studies on tolerance to coldness show that NST can be induced by adaptation to cold and its molecular basis was found (Lowell and Spiegelman, 2000). A recent study has shown the shift of TNZ in a mamal (hamster) acclimated to different temperatures: cold (5°C), warm (21°C) and hot temperatures (31°C) (Zhao et al., 2014). A naked human shows increased heat production as environmental temperatures falls, and Davenport (1992) gives at 10°C a factor two in heat production in relation to TNZ. The conductance responsible for the blood flow from the core to the skin in humans can change by a factor 4 to 7 (Bruck, 1989), depending on the rate of blood change, and the thickness of the body shell and of the subcutaneous fat layer.

The real question to be discussed is how already hairless Australopithecus could solve the problem of coldness in the altitudes where they seem to have lived. Naked Australopithecus could be biologically well adapted to the tropical altitudes by a combination of NST (with a factor 2–3 over BMR), and primitive shelters made of natural materials, where a single naked adult individual may survive. However, for females with infants a real problem exists. A naked neonate has a high NST but a surface/body ratio ∼3 times higher than that of an adult and requires high ambient temperatures for survival (Bruck, 1989).

- The solution here proposed is that females with infants must huddle together for thermal cooperation.

Biological adaptations to coldness in many animal species include the cold-induced huddling, i.e., individuals together to regulate energy saving processes. This happens from penguins living in arctic conditions (Ancel et al., 1997; Gilbert et al., 2008), to penguins and birds in different l altitudes (Black et al., 2016) and also for small mammals, as studied in detail with rat pups (Alberts, 1978) and mouse development (Harshaw and Alberts, 2012; Harshaw et al., 2014) with very defined experimental results. The situation in a huddle corresponds to N bodies with individually negative heat flows, but the huddle body as a whole may have positive heat flow, as can be seen in thermographs of real biological huddles [for instance Figure 1 in Harshaw et al. (2014)].

The body surfaces of individuals in direct contact do not contribute to the huddle surface. For $N = 2$ the individuals are half within the huddle and half at its surface. For $N = 3$ the individual in the middle is really protected inside the huddle. These minimal huddles are compatible with the estimated efficiency of primitive shelters. The shelter efficiency defines the number N

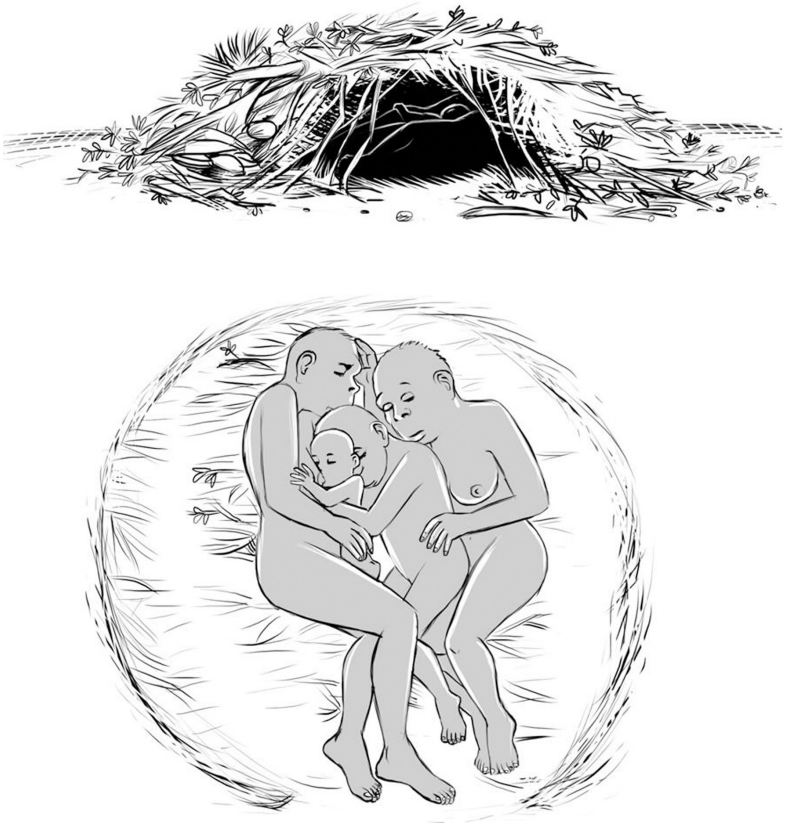

FIGURE 8 | Sketch of the possible solution for earlier naked hominins: huddle with female family for thermoregulation in a primitive shelter of natural materials (done by Carlinhos Muller, following my original idea, see details in the text).

of individuals huddling, and only in good shelter and insulation conditions individuals may be independent.

It is possible now to discuss a very peculiar characteristic of the human skin, the clear sexual dimorphism regarding distribution of hair and also fat in the bodies of males and females. In order to arrive to a solution, it is necessary to discuss the thermoregulatory difference between a furred and a naked skin.

Thermoregulation of Furred and Naked Skin

In furred animals the fur acts as an insulator, and the surface temperature of the fur can be equal to ambient temperature, depending on fur density and thickness, by trapping air, which is a good insulator. There is therefore no difference between surface and ambient temperature, with minimal heat losses to the ambient. The fur insulation value and the variation of metabolic rate with temperature define the adaptability of the species, in a very large interval of ambient temperatures (figures 7.7–7.9 in Schmidt-Nielsen, 1997). In the case of the human skin there is an insulating fat layer below the skin surface, and the heat balance is controlled by the flux of blood. The fat insulation can be bypassed for heat dissipation (figure 7.14 in Schmidt-Nielsen, 1997), and this is not possible in a furred animal, which uses other processes for change in body conductivity for heat balance. Clearly the human fat insulation evolved in the context of skin-air contact, not in skin-water contact, since the conductivity of water is 25 times higher than the air conductivity (Toner and McArdle, 1996), and the fat layer of normal humans is not so thick as the blubber of water mammals, neither does it exist in the whole body surface as it does in marine mammals.

Thermoregulation of human naked skin is thus defined by the flexibility of blood bypassing the subcutaneous insulating fat layer, allowing both insulation and refrigeration, in order to cope with hot and cold daily variations.

The crucial point to be stressed is that effective skin contact for the huddle solution is attained by naked skin in both mothers and infants. A recent study examined gender difference in human response to temperature step changes and results indicate that females differ from males in human response to sudden temperature changes from the perspectives of psychology, physiology and biomarkers (Xiong et al., 2015). Females are more prone to show thermal dissatisfaction to cool environments while males are more likely to feel thermal discomfort in warm environments. This result and similar ones performed recently give support to the proposal made here of an original huddle with only females with their children. This explains that loss of fur evolved together with the fat layer below the surface skin in females, and neonates.

A sketch of this proposal is shown in **Figure 8**. Neonates and infants must be protected in the microclimate inside the huddle, and the minimal solution for hairless Australopithecus survival consists of few females, related by kinship, embracing and protecting infants in a primitive shelter. The infant bodies are smaller than the bodies of the adult females, so that they are in close contact with the female cores at ∼37°C. The infant bodies, with a high NST, have high temperatures, so that the female bodies receive also thermal protection.

This *biological* solution is in fact expected from primate social behavior, since all Great Apes live in small groups, but with different strategies in the two sexes.

Hypothesis for a Theory

- It is already known that Bipedalism evolved in two steps, the first one in australopithecines, the second one in Homo Erectus.
- The proposal made here is that reduction of hairs evolved also in two steps. The first one in Australopithecines, with nesting and group sleeping associated with a primitive shelter and close physical contact between few females, related by kinship, embracing and protecting infants in a primitive shelter. The second one in Homo Erectus, when conditions for walking and even running with locomotive efficiency, and sweating rates to be active in the heat of the day in hot, open environments.

Model for Biological Evolution of Earliest Hominin Social Structures

The chimpanzee/bonobo lines arrived to some sort of socio-sexual equilibrium, stabilizing the reduction of body hairs, and keeping large canines. But the lineage of naked bipeds did not reach easily such stabilization, embarking in the direction of further reduction of body hairs, small canines, bipedalism, and separation of female and male sociality under specific sex defined behaviors.

The proposal made here is that naked Australopithecus evolved with different social structures for females and for males. Relations between sexes were possibly occasional and violent.

In female families, the naked females developed strong bonds with their naked infants, with permanent physical body contact, care and attachment, and kinship cooperation in female sociality. Breasts have a clear function for mother-infant contact, for nutrition and increase of warm skin contact. The basic biological changes in both sexes are directly related to efficient reproduction, the attractiveness comes as a consequence. Hominin females are more selective because they are extremely "K-selected," in the modern concept of life-history evolution (Reznick et al., 2002) with large and long maternal investment on a single newborn.

A rite of passage from infancy to adulthood must have been the first basic rule of such groups, deeply imprinted in the psyche of naked Australopithecus, and biologically determined by hormone release, not by consciousness or intellectual capacity.

- The male infant changed pitch of voice with growth, and this defined the exit from the original female family to become a young adult male, either solitary or in bands of males.

These biological changes probably defined the structuring rites of passage already in naked Australopithecus, and subsist in all human primitive groups even today (van Gennep, 1909). A revision of anthropology and social sciences is in order, as done by Szakolczai and Thomassen on their book, where the first chapter is "Arnold van Gennep—Liminal Rites and the Rhythms of Life" (Szakolczai and Thomassen, 2019).

An example of study on evolutionary psychology discussing intrinsic versus extrinsic motivations in humans is given in a recent paper (Varella, 2021) on artistic motivation using a large decades long database of university applications together with career-choice reasons.

Considering all that is known about primate and human behavior, it can be argued that only in Homo males started to help the transport of older infants in their shoulders, and groups of males together with females could be formed.

DARWIN'S LEGACY AND FUTURE PROSPECTS

The definition of Biology as a modern Science is due to Darwin and his ability to see the overwhelming importance of sexual reproduction in animals and plants, as a mystery of Nature, as well as to grasp the selectiveness of females from what he knew about emotions. The origin of sex differences in humans has been attributed by social scientists to socialization and cultural influences, and only more recently biological influences, especially sex hormones are being considered (Geary, 2006).

The 21st century sees a revolution in Biology that stays, however, inside the specialized scientific community. It refers to the question of "gene expression," which is changing completely the naive idea of DNA definition of everything "by principle." DNA expression depends on the chemical exterior circumstances, and this represents almost a revival of a modern Lamarckism based on "chemical ambient."

A meeting held in United Kingdom brought together evolutionary and biomedical researchers working on early-life effects, and demonstrated that experiences during early development can trigger developmental switches that shape anatomy, physiology and behavior for a lifetime, while potentially also affecting future generations (Kuijper et al., 2019). It is time to focus on embryologic development, abandoned in the modern synthesis for ideological reasons.

Acceptance of biological basis for human behavior is coming together with acceptance of flexibility and even "culture" on non-humans, particularly the anthropoid primates (Whiten, 2005). This corresponds also to a movement in direction of bringing humans closer to nature, and a possible integration of the Nature vs. Culture dichotomy.

The previous items discussed objective arguments for efficient reproduction and infant survival, based on physical properties

of hominoid hairs. It is time now to face Darwin's intriguing idea, considered really "dangerous," of esthetic reasons for female choice in sexual reproduction. Many papers exist on this question, but I mention only a recent article (Ryan, 2021) that discusses interesting aspects of this question, starting from fitness advantages through mate choice, followed by sensory ecology and signal design, investigations of neural circuits, neurogenetics, and neurochemistry underlying sexual attraction and more recently human studies in psychophysics, behavioral economics, and neuroaesthetics of its higher-order mechanisms, and finally cognitive ecology. This corresponds indeed to an integration of Nature with Culture.

The influence of culture is of course immense in most aspects of human societies, but there is a field connected to the body of females where biology crosses with esthetics and beauty: the integumentary system, which besides the skin also includes the hair, nails, and exocrine glands. This complex includes health, medicine and commerce since antiquity, as can be seen for instance in the Project Archeology (Ludlow, 2020). Darwin was able to foreseen this complex in connections with sexual reproduction in Life.

From the genetic front, four structural protein genes associated with the epidermal basement membrane zone or elastic fibers in the dermis were identified and were expressed significantly greater in humans than in non-human great apes (Arakawa et al., 2019) and may enhance the strength of adhesion between the epidermis and dermis in human skin. But it is necessary to focus also skin properties.

The subject of skin color has been extensively studied by Jablonski showing that the primary biological role of human skin pigmentation is protection against ultraviolet radiation (UVR). A recent review article (Jablonski, 2021) shows that the evolution of human skin pigmentation involved the interactions of genetic, environmental, and cultural variables, related to UVR and also vitamin D. Jablonski mentions indigenous groups with female pigmentation lighter than male, and suggests the importance of increased cutaneous vitamin D production potential, and therefore lighter skin, in order to facilitate absorption and redistribution of dietary calcium to the developing fetus and nursing neonate. Selection related to sexual reproduction, attractiveness coming as a consequence.

It is time now to focus on elastic properties of the human skin, much more complex than the study of hair, but it is necessary to enter now on this subject also. Scientific studies on the skin of rat started in the 80's, extension to the human skin came on the 90's and an article from this period gives an initial approach to the experimental techniques (Edwards and Marks, 1995). Many *in vitro* and *in vivo* experiments have been performed and it can be clearly stated that skin shows extremely complicated viscoelastic behavior. It could be concluded that the strength and elastic properties of skin are determined by the collagen content and visco elastic properties arise largely from the fluid (blood, lymph) and water content of skin. The large amount of results with many different techniques awaited some modeling for interpretation. But up to now there has been no convergence in the scientific literature on efficient modeling of human skin under all the experimental conditions.

The next step was given in 2021 by articles connected to the industry of beauty: A model of 3D dermal microtissue to study the skin's elastic properties—Premium Beauty News, easily find on the internet. Therefore it seems to be approaching the crossing foreseen by Darwin between necessity and esthetics.

It is still necessary to join human skin with the skin of the Great Apes. Human skin was compared with skin of other primates by Montagna (1972, 1982, 1985). Human skin is known to be thicker than that of furred mammals and there are similarities with skin of chimpanzees and gorillas (Montagna, 1985).

It is possible now to advance in this subject with my own contribution. From the obtained estimation of 1 kg/cm^2 as the safe limit for pressure on hominoid skin (Amaral, 2008) previously mentioned and shown in **Figure 6**, it can be now made here a very crude estimate of the Young modulus of elasticity of Hominoid skin as 0.1 MPa.

The result of 0.1 MPa here estimated for hominoid skin is not easily compared with existing studies of human skin elasticity, which varies with region of the body, age, sex, and other circumstances. But evidence the necessity of this type of investigation in order to clarify Human Evolution.

Human skin is the largest organ in the human body, responsible for our unique properties of sensibility and tactile body communication. It defines a unique interface between our inside and the outside, and such interface makes us Humans.

The essential legacy of Darwin on Sexual Selection remains on his focus on Human Skin, and the differences in relation to the skin of other primates. Darwin's ideas shall be rescued as selection due to interactions between individuals within the species, besides interactions with the external ambient. Qualitative arguments on positive natural selection (sometimes called anecdotal evidence) may be meaningful from their clear function. It is time to recognize that both harmony and strength are pursued by Nature for their own intrinsic values, not for an ultimate finality.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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REVIEW
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Runaway Social Selection in Human Evolution

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Darwin posited that social competition among conspecifics could be a powerful selective pressure. Alexander proposed a model of human evolution involving a runaway process of social competition based on Darwin's insight. Here we briefly review Alexander's logic, and then expand upon his model by elucidating six core arenas of social selection that involve runaway, positive-feedback processes, and that were likely involved in the evolution of the remarkable combination of adaptations in humans. We discuss how these ideas fit with the hypothesis that a key life history innovation that opened the door to runaway social selection, and cumulative culture, during hominin evolution was increased cooperation among individuals in small fission-fusion groups.

Keywords: social selection, human evolution, cooperation, runaway processes, cumulative culture

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> *"There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection"*
>
> Charles Darwin [1871: 166]

> *"Why are we all alone [in]... our tendency and ability to cooperate and compete in social groups of millions?"*
>
> Richard Alexander (1990: 1)

INTRODUCTION

In 1871–2 Charles Darwin tackled two major challenges to his theory of evolution: costly displays and weaponry used in courtship, and the descent of humans. He proposed that mating competition among conspecifics — sexual selection — was a potent evolutionary force that could explain the apparent enigmas of bright plumage, antlers, even the great horn of the Rhinoceros beetle. Sir Ronald Fisher (1930) furthered Darwin's concept of sexual selection by positing that intraspecific competition could involve a process of "runaway" selection if choice was based on comparisons favoring relative extremes. Crook (1972) and West-Eberhard (1979, 1983) expanded Darwin's and Fisher's concepts to include selection from all aspects of social interaction among conspecifics, termed "social selection." Humphrey (1976) and later Dunbar (1993) and Tomasello (1999) suggested that intelligence could evolve in the context of social competition and cooperation among conspecifics: cleverness in the "social chess game." Alexander (1990); (see also Alexander, 1974, 1979, 1989) integrated these ideas into a comprehensive model of "How humans evolved" involving a process of "runaway social selection" where hominins "increasingly became their own principal hostile force of nature," with cooperation and coalitions posited as crucial and complementary aspects of hominin social environments (Alexander, 1987, 2006; Wrangham, 1999).

We use the term "runaway" selection here to refer broadly to selection that involves either: (1) arms races within species, whereby competition-based selection between individuals and groups leads to reciprocal, escalating trait expression and elaboration across evolutionary time, or (2) positive feedback between the selection pressures and evolutionary changes in one trait (e.g., a phenotype subject to choice), and selection pressures and evolutionary changes in a second trait (e.g., choice of the phenotype), such that evolutionary changes in both traits become mutually reinforcing across generations (e.g., Nesse, 2007; Nakamaru and Dieckmann, 2009; Piantadosi and Kidd, 2016; Bailey and Kölliker, 2019). As such, runaway selection can apply to a wide variety of sets of phenotypes, including aspects of social interactions, in addition to those involved in female choice and sexual selection (e.g., Bailey and Kölliker, 2019). Alexander focused on a process of "runaway social selection" involving arms-race competition among individuals for "social cleverness" (including language abilities, social skills, aptitudes for cultural information, coalition building, and multiple other types of intelligence) that became increasingly important in human evolution (Alexander, 1990; Flinn and Alexander, 2007). There are other plausible models of human evolution involving social competition (e.g., Hrdy, 2009; van Schaik and Burkart, 2010; Wrangham, 2019); our main objective here is to describe, extend and expand upon Alexander's runaway social selection model, which connects to both Darwin's (1871) ideas about selection associated with competition among conspecifics and his model of human descent. As such, we consider runaway social selection involving both competitive arms races, and positive feedbacks driven by mutually reinforcing selection during choice-trait coevolution.

DARWIN AND THE DESCENT OF HUMANS

Darwin (1871) suggested an evolutionary scenario for humans involving a positive feedback loop between tool use and intelligence. Initially a "smart ape" began to use tools; this advantage led to further selection for intelligence and more sophisticated tools, and eventually to upright bipedal locomotion, precision hand control, reduced dentition, social cooperation, morality, and other human traits. Evidence from hominin paleontology and archeology over the past 150 years has not supported Darwin's tool use model as he presented it. Fossils indicate that Australopithecines and perhaps even earlier hominins were habitual bipeds for >2 MY prior to significant changes in brain evolution (McBrearty and Brooks, 2000; Antón et al., 2014; Almécija et al., 2021). Tool use also predates increases in cranial capacity by at least 1 MY (McPherron et al., 2010), it is not restricted to hominins and it is not subserved by specialized neurobiological mechanisms (Geary and Huffman, 2002; Geary, 2005; Sherwood et al., 2008; Bruner, 2021). Although technology is clearly a significant part of the human evolutionary story (Osiurak and Reynaud, 2020), it apparently does not account for our extraordinary social mental aptitudes including such traits as empathy, language, mental time-travel, consciousness, and mind-reading (Herrmann et al., 2007; Haber and Corriveau, 2020), or for the uniqueness of the hominin evolutionary trajectory.

Darwin recognized that culture — socially transmitted information and materials — was also a key selective pressure in human evolution. Indeed, he noted (1871, pp. 78–79) that "the formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel." Aptitudes for language, learning, and the sociality underpinned acquisition of information were increasingly important for hominin survival and reproduction, eventually resulting in the extraordinary Anthropocene niche that we inhabit today. Why humans are "the uniquely unique species" (Alexander, 1990) who developed such extraordinary cognitive and cultural abilities remains an elusive evolutionary puzzle (Tomasello, 1999; Henrich and McElreath, 2003; Laland and Seed, 2021). The problem is further complicated by inherent biases of humans trying to understand themselves (Alexander, 1987; Varella, 2018).

ALEXANDER AND RUNAWAY SOCIAL SELECTION

An important universal trait of mammals is maternal care of altricial (helpless) offspring. Many mammalian species, including most primates, also have varying levels of alloparental support and protection by relatives. Beyond these shared features, however, humans exhibit a suite of highly unusual traits (Alexander, 1990; Chapais, 2009), many of which appear adaptively responsive to variable conditions. Humans are the only species characterized by the *combination* of stable breeding bonds; flexible and extensive alloparenting and considerable male parental effort within multi-male groups; lengthy childhoods; cryptic ovulation; extended bilateral, multi-generational, and affinal kin recognition; grandparenting; influence of relatives over mate choice; language; variable group composition and inter-group relationships; and a suite of other human-elaborated traits.

Alexander's model of how hominins evolved this combination of traits is based on the concept that hominin evolution became an increasingly autonomous and self-reinforcing, runaway process. A key selective pressure on hominins was thus interactions with other hominins, particularly with regard to its selective effects on brain evolution (Alexander, 1990; see also Flinn et al., 2005). Concomitant with the increased importance of competition and cooperation among conspecifics was an increase in "ecological dominance," whereby predation and competition from other species became weaker and weaker selective forces on hominin phenotypes.

We describe a set of revisions and extensions to Alexander's model, in the light of recent work on human social and sexual evolution and behavior. First, we discuss an explanation for the initial split in the evolutionary trajectories of hominins and *Pan*, and how it underpinned the divergence of the two lineages. Second, we operationalize Alexander's model of runaway social evolution by explicitly describing the relevant arenas of social selection and social competition, what traits were selected for

and how, and how different arenas and forms of social selection contributed to runaway effects.

HOMININ ORIGINS

Hominins and Panins last shared a common ancestor about 6.5–9 MYA (Andrews, 2020; Almécija et al., 2021). From an orthograde last common ancestor, Hominins and Panins initially diverged into distinct niches, with associated changes in locomotion leading to upright bipedalism in hominins, and knuckle-walking in *Pan*, similar to *Gorilla*s. Arguably, the shift to bipedalism implies a more terrestrial niche, with different foraging opportunities and predation pressures (Harcourt-Smith, 2007; Almécija et al., 2021). Early hominins likely developed a fluid sociality similar to that characteristic of contemporary hunter/gatherer societies, involving tolerance of, and interaction with, individuals from other small, local, low-density groups (in contrast to chimpanzees and gorillas; more similar in some but not all aspects to bonobos as discussed below), eventually encompassing flexible alliances and coalitions in their fission-fusion context (Walker et al., 2011; Apicella et al., 2012; Macfarlan et al., 2014; Migliano et al., 2017, 2020). Such alliances may have been beneficial, at least initially, in terms of cooperative foraging, food-sharing, and protection from predators (Allen-Arave et al., 2008; Smith et al., 2016). This initial difference, possibly linked to the gradual shift to a more open and mobile, terrestrial niche, would have enabled a series of subsequent evolutionary changes: (1) a flexible, distinctive pattern of extended family relationships that supported longer periods of child development (Washburn and Lancaster, 1968; Lovejoy, 1981; Hrdy, 2009, 2014; Hawkes, 2020); (2) critical aspects of the fluid and complex coalitional sociality posited above (Gavrilets et al., 2008; Chapais, 2009, 2011; Hawkes et al., 2018); and (3) an environment in which cultural innovations were increasingly important for foraging, defense against predators, and success in cooperation and competition with conspecifics (Hill et al., 2011; Lotem et al., 2017; Flinn, 2021; Garg et al., 2021).

Early hominins also diverged from *Pan* in which other sets of individuals were most important to them. For female hominins, relationships with mothers, sisters, daughters, aunts, and grandmothers were of increasing importance. But so too were fathers, mates, brothers, and sons. From the male hominin perspective, relationships with paternal relatives — fathers, brothers, and sons — were of increasing importance for cooperative defense and foraging. As posited above, female relatives — wives, mothers, sisters —, and children benefited from this crucial support from males.

Hence the conundrum, analogous to the "matrilineal puzzle" proposed by Richards (1950); (see also Irons, 1983; Macfarlan et al., 2014; Dyble et al., 2015) emerges. How can males and females be with kin who reside in different places? How to help both your sister and your wife? And how to effectively avoid inbreeding problems if male and female relatives — father-daughter, brother-sister — co-reside? The solution is found in most hunter-gatherer foraging-band societies: flexible, fluid camp residence and social networks. Individuals can choose to stay or visit with whomever is most useful to them at a particular time. With inter-camp group tolerance and cooperation, hominins got the best of both worlds; help from maternal and paternal kin, mates and affines. This pattern of "exploded fission-fusion" sociality (Marlowe, 2004; Foley and Gamble, 2009; Macfarlan et al., 2014) stands in stark contrast to that of all other hominids.

A key consequence and benefit of this fluid interactive social system was an open door for cumulative culture and language. Socially transmitted information could move easily and rapidly across the hominin social landscape (Hill et al., 2011, 2014; Walker et al., 2011; Gowlett et al., 2012). A good idea ("meme") would spread fast and far (go "viral"). "Good ideas" were not limited to tools, engineering, and technology, but include social tactics and strategies (e.g., Coward and Grove, 2011). And, as described below, such a complex matrix of self-selected interactions provides excellent opportunities for social selection to exert its runaway effects, by the various mechanisms, in the various contexts, that typify human cognition, behavior and culture.

PSYCHOLOGICAL MECHANISMS OF SOCIAL SELECTION

Selective arenas represent specific contexts within which social selection mediates variation in inclusive fitness among individuals. The primary psychological mechanisms of social selection, within these contexts, are cognitive and emotional. Thus, an individual will benefit the most in inclusive fitness under social selection if they can:

(1) Individually recognize all of the persons in their group;

(2) Discern the relationships of kinship, friendship, and sexuality among all interacting individuals in their group;

(3) Figure out, consciously or unconsciously, how each individual person who they interact with could best be manipulated, cooperated with, or competed with, in what way, to maximally increase their own lifetime inclusive fitness;

(4) Discern and infer, consciously or unconsciously, how any other individual would be expected to respond to these possible actions toward them, from being able to take their mental perspective regarding their strategies and abilities to maximize their own inclusive fitness.

Each other person in a group thus has some potential inclusive fitness value to a focal individual, that could be maximized by success in providing benefits, imposing costs, or taking control of behavior away. Ability to achieve this potential will be some function of asymmetries in information, physical and intellectual power, alliances, and leverage (control of a resource or service that cannot be taken by force; Strassmann and Queller, 2010; Watts, 2010; Bissonnette et al., 2015). An individual would also benefit tremendously from knowing their own abilities and best strategies for increasing inclusive fitness, in this complex

multidimensional web of social interactions and their mental representations.

The cognitive challenges of being able to most-effectively maximize inclusive fitness *via* the four steps described above are open-ended and almost unimaginably complex, for any extended human group of reasonable size, such as 50 to 150. As a result, social selection and responses to the selection, in the context of evolving human social-cognitive-emotional abilities, can proceed virtually without limit, being constrained only by human neural computing power, manifest in brain size and modular specializations, and being driven by multiple forms of runaway social selection, as described in detail below.

The psychological mechanisms of social selection can be applied in a wide variety of specific contexts, or arenas, whereby pairs and larger sets of humans interact. These arenas can, in turn, delineate the different forms of runaway social selection that lead to accelerated human evolution for cognitive and cultural traits, and the remarkable suites of adaptations that result.

ARENAS OF SOCIAL SELECTION

Arenas of human social selection exemplify the different contexts of human interactions that contribute to runaway human social evolution under the broad umbrella of Alexander's (1989; 1990) model. These arenas have been discussed before, but not integrated together, and they have not been considered in the framework of how humans evolved since their divergence from a shared ancestor with the genus *Pan*. The "runaway" component of runaway selection is especially important because it can help to account, *via* positive feedbacks, for the extraordinary rapidity of human cognitive and social evolution.

Arenas of social selection help to indicate the mechanisms of social interactions that can lead to the enhanced brains and more-complex social cognition and emotion that characterize humans. They represent pairs or larger sets of human interactions, ordered by sex and age and number and nature of groupings, that have been postulated to involve runaway effects. The key question in particular is how runaway social selection is expected to work in fluid populations of early humans, in terms of how increased social abilities can translate into higher inclusive fitness of individuals, and enhanced survival and proliferation of groups, and in terms of evolutionary dynamics across generations.

The First Arena: Arms Races

Most generally, runaway social selection effects within generations can be driven by social competition, social cooperation or social choice. The first arena of social selection described here is *direct, symmetric and asymmetric arms-race competition within a group*, whereby two or more individuals are engaged in some fitness-related conflict where the individual with better social skills (social "weaponry") wins. Such competition represents a classic arms race, where the selective pressure is autocatalytic across generations, because the selective cause is persistent and self-reinforcing. Arms races are normally thought of in physical terms, where they become limited, across many generations, by the costs of armament and tradeoffs with other components of fitness. This limitation may apply to brain size, over the long term, due to the high costs of neural tissue. However, psychological arms races *per se* should be subject to no such constraints, since they are governed by "software" — neural organization — that can, in principle, complexify indefinitely, and involve cumulative learning and culture. In hominins, brains concomitantly evolved to become both larger and more "socialized" (specialized for social cognition), with material culture lagging behind (Geary, 2005; Gowlett et al., 2012; Rilling, 2014), as expected under autocatalytic models driven by social selection.

Possible examples of psychological arms races would be enhanced abilities to read emotions and intentions in others, levels in metacognition and theory of mind ("I think that they think that I think," etc.), ability to gain status (and recruit partners in reciprocity, as discussed below) through displays of cognitive abilities, and skills involved in strategically "out-thinking" adversaries in conflicts (e.g., Byrne and Whiten, 1988; Dunbar, 2014). The arsenal of social weapons would also include a broad range of cognitive and emotional phenotypes whose expression reciprocally selects on each other within and across generations, mainly in the general context of motivating other individuals to behave more, and more often, in the inclusive-fitness interests of the actor. A number of studies have examined coevolutionary arms races in the context of social selection and intelligence (e.g., McNally et al., 2012; dos Santos and West, 2018; Coen, 2019), and have supported the conclusion that such arms races can drive higher levels of intelligence, cooperation, and social complexity. Indeed, as noted by Darwin (1871, p. 97) "natural selection, arising from the competition of tribe with tribe, would, under favorable conditions, have sufficed to raise man to his high position."

Among males, psychological arms races should be most prominent where males are evenly matched physically, such that simple muscular dominance cannot determine competitive outcomes. Among females, it may commonly involve indirect forms of (non-physical) aggression, such as manipulations of social status and abilities in competition for allies (friends) and social support. Competition for useful allies is also likely to have been very important to males.

Mental arms races are the psychosocial equivalent of Darwin's (1871) sexual selection by male-male competition. Such simple, one-on-one psychological arms races should ramify easily into one-on-multiple and multiple-on-multiple interactions, given the fluidity of human groups and kin-structured and reciprocity-structured organizations. Indeed, the high fluidity and organizational complexity of human groups are likely, in part, end products of such arms races as well. The "multiples" of these interactions are presumably allies of some sort, who can join psychological and physical forces to better increase their inclusive fitness at the expense of others. Once a competitive dyad expands, however, the dynamics

necessarily change. Indeed, a pair of competing individuals may themselves be allies in some domains and adversaries in others. How they became so is a matter for the next selective arena.

The Second Arena: Partner Choice

The second arena of social selection is *partner choice* in the context of cooperative traits, which can lead to runaway choice-trait coevolution under a variety of conceptual and mathematical models (e.g., Nesse, 2007, 2010; Debove et al., 2015). Here, "partner" refers to social partners, with whom one preferentially interacts, over a relatively long period, due to various benefits that accrue especially *via* mutualism and reciprocity, sometimes combined with kinship. In the same way that classical sexually selected mate choice is driven by attractive displays by one individual to others, social partner choice is driven by attractive social displays, usually involving demonstrations of prosocial traits such as honesty, reliability, cooperative cultural and religious beliefs, and generosity through social, informational and material assistance in times of relative need or potential for benefit (Nesse, 2007, 2010). There are some interesting parallels here between social selection and classical Fisherian runaway selection (typically involving choice of a few "top-ranked" individuals) and "complementary" mate choice (such as for immune system gene compatibility). Thus, for example, social selection may entail tradeoffs between choosing the "best" partner (i.e., individuals that are highly socially intelligent or skilled in some area), versus choosing individuals who will remain committed to, and focus on, the relationship, even when mutualistic reciprocal relationships demand consistent effort and attention, limiting the ability to engage effectively in many of them. The latter type of relationship should also be promoted by complementarity of different social (and other) abilities between members of a dyad, which increases the benefits accruing to both.

Social partners are, of course, conventionally regarded as "friends," who in evolutionary terms represent allies who both gain inclusive fitness benefits, over the longer term, from their continued association. The partnerships can be of any dyadic combination of the two sexes, or can involve larger groups united through multiple partner choice events, merging into and overlapping with other such groups in complex social networks. Choice of partners in various contexts can also generate "markets" for partners, with complex dynamics that can enhance the competitive nature of the processes involved (Barclay, 2016; Eisenbruch and Roney, 2017). Smith and Apicella (2020) describe how partner choice, for traits that include generosity and foraging ability, mediates campmate preferences among Hazda hunter-gatherers.

The long duration of the human lifespan makes social partnerships, in principle, highly beneficial to inclusive fitness, especially if they involve complementary abilities, knowledge or resources (Nesse, 2007, 2010). In humans, choices regarding memberships in coalitional groups, based on the traits of the group and its leader, should also be notably important (Boyd and Richerson, 2009), and could themselves synergize with group against group arms races, as discussed in more detail below.

Partner choice, like arms races, can result in the runaway evolution of socially selected traits. By this process, the expression of the chosen trait, and the choice of the trait, come to be positively genetically associated with one another across generations (Sachs et al., 2004), as they both increase rapidly in frequency. Cultural analogs of this process can also lead to culturally inherited patterns of association that do not require genetic change, although such changes can themselves impose selection for genetic change and gene-culture coevolution (Richerson and Boyd, 2005; Lotem et al., 2017).

Nesse (2007, 2010) described how runaway partner choice may have promoted a whole suite of uniquely human or elaborated-in-humans traits, including theory of mind, extreme forms of cooperation, capacities for morality, the importance of building and protecting one's reputation, and self-domestication of the recent human species as a whole. Most generally, partner choice, and choice of leaders and groups, should select for finer and finer abilities to discriminate the socially salient qualities of other individuals and groups, in terms of if and how much interacting reciprocally with them, compared to alternatives, will result in gains to inclusive fitness. In humans (and possibly dolphins) the complexity of cooperation (and the intelligence required to negotiate alliances) increased dramatically in the context of triadic interactions among groups in nested hierarchies (Connor, 2007; Gerber et al., 2021). The risk/reward ratio and the number of options (and potential outcomes) were probably critical with regard to selection for enhanced intelligence, and these increased dramatically with expansion in the number of levels in a nested hierarchy of interacting entities (individuals, groups, groups within groups, etc.) and associated potential alliances. As such, this arena of social selection should result in notably enhanced abilities to judge character, truthfulness, morality and social abilities, as well as the ability to display and communicate these sorts of traits, even if they sometimes conflict with one's ability to maximize inclusive fitness by alternative, relatively selfish, and self-serving means.

The Third Arena: Mate Choice

The third arena of social selection, human mate choice, was, of course, originally formalized by Darwin (1871). It represents a subset of partner choice that is sufficiently special and distinct to warrant its own domain. Classical Fisherian mate choice by sexual selection (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982) involves a process whereby choice by one sex (in animals, usually females) for one or more fitness-related traits in the other sex (usually males) results across generations in a positive genetic correlation between stronger choice for the trait (typically in females) and higher level of trait expression (typically in males) — a runaway process that stops only when the trait is so highly developed that it incurs strong costs in terms of some other component of fitness, typically survival. This dynamic appears responsible, at least in part, for the rapid evolution and high diversity of sexually selected, mate-choice-related traits among many non-human animal groups (Arnold, 1983).

Human mating systems have diverged substantially from the Fisherian paradigm, in that (a) females, as well as males, exhibit forms of sexually selected "beauty," that may be chosen by the

opposite sex; (b) mate choice is commonly more or less joint and reciprocal, with both sexes engaging in choice of a partner based on some criteria (though often with social constraints on choice); and (c) mate choice engenders relatively long-term pair-bonding, with mutual contributions to the rearing of offspring (e.g., Miller, 2000; Buss and Schmitt, 2019; Geary, 2021).

For human mate choice, the main considerations in the second arena apply, specifically, to the situation where males and females each choose one individual of the other sex by some criteria. Individuals are thus under selection to display socially selected traits (e.g., intelligence, cleverness, humor, conversational ability, kindness, a variety of social skills), and to choose some overlapping constellation of such traits in others (Etcoff, 1999; Miller, 2000). Choice of a good opposite-sex partner for mating, reproducing, providing, and parenting is probably a much more challenging task than making and maintaining a same-sex friend, and thereby should represent a stronger socially selective filter. Pair-bonded males and females are thus selected to be able to successfully navigate the psyche of their mate, in a much more intimate, cognitively complex, and fitness-salient way than for friends. Indeed, among animals, comparative analyses by Dunbar and Shultz (2007) have demonstrated that among carnivores, artiodactyls and bats, larger relative brain size is associated with pair-bonding, and that in primates it is linked with complex, enduring social relationships even more broadly (as well as with larger group size); they argue that these findings reflect "the cognitive demands of the behavioral coordination and synchrony that is necessary to maintain stable pair-bonded relationships." Humans appear to represent an extreme of social selection and bonding effects on relative brain size and behavioral coordination, especially given the partially divergent optimal mating and parenting strategies of the two sexes, and the complex mixtures of confluence and conflicts of inclusive-fitness interest that ensue.

From an evolutionary perspective, mutual mate choice in humans becomes subject to runaway dynamics due to genetic correlations of socially selected pair-bond related traits with choice of these traits; for example, females choose kind, caring males, males with genes for these traits are selected for, and the genes for the choice and the traits become associated and rise in frequencies across generations. For this type of sexual-social selection, it remains unclear if there are evolutionary brakes on the process equivalent to those operative during natural selection by predation against, say, too-large of a train in peacocks. Possibilities for such "brakes" might be over-expression of choice (such that no or few individuals are deemed suitable for a mate), or expression of prosocial, altruistic, or parenting-related traits to such a degree that they became maladaptive in the context of maximizing inclusive fitness as a whole.

The Fourth Arena: Caregiver-Offspring Choice and Signaling

Runaway coevolution between social signals and their choice includes not just cooperation partners, and female-male pairs, but also offspring interacting with their caregivers, specifically mothers, alloparents, and fathers (West-Eberhard, 2003, p. 467; Hrdy, 2013). By this mechanism, offspring benefit from producing signals, such as high levels of subcutaneous fat, vigorous crying, smiling, eye contact, and other social interactions with caregivers ("other-regarding" in Hrdy's term), that represent indicators of their phenotypic and genetic "quality" (inclusive fitness value) and that prompt increases in feeding and engagements that enhance social-emotional cognition and learning. Such signals are expected to be predominantly honest indicators of offspring value, but may include manipulative elements (West-Eberhard, 2003), as in other models of signal-receiver interaction, that could reinforce increased discriminability of cues by receivers. Social selection and evolution should thus increase maternal, alloparental, and paternal sensitivities to offspring cues (to better reward higher-value offspring, invest less in lower-value ones, and tell honest from dishonest signals), and increase offspring aptitudes and success at solicitation. As for the other forms of signal-choice system, the result is genetic and/or cultural correlations and coevolution by a self-reinforcing runaway process (West-Eberhard, 2003).

Runaway social selection between caregivers and offspring represents an integral component of the human life history evolving toward increased alloparental and paternal care, shorter interbirth intervals and higher reproductive rates, larger-brained offspring (which are more expensive to produce and rear), and neural precocity and plasticity combined with physical altriciality (Alexander, 1990; Hrdy, 2009; Piantadosi and Kidd, 2016; Sherwood and Gómez-Robles, 2017). Neural precocity, in turn, forms part and parcel of social precocity and the evolution of greatly enhanced human social and emotional cognition, the acquisition of which is inherently developmental and centers around the elongated human childhood and adolescence (Bogin, 1990; Flinn et al., 2011; Ponzi et al., 2020). This selective arena is especially important given that infant mortality has long represented such a substantial component of variation in fitness among humans, and that such mortality can be reduced in a variety of socially salient ways, including effective offspring solicitation, alloparental contributions to maternal nutrition and infant care, paternal augmentation of food supplies, and broader social support in the group for mothers who warrant or earn it. For example, in many human groups, there is evidence of strong positive associations of lower child mortality with higher cognitive abilities of the mothers (e.g., Sandiford et al., 1997; Piantadosi and Kidd, 2016).

The Fifth Arena: Cultural Traits and Social-Cultural Learning

A final arena of within-group social selection is culture, the human-created material and information-based aspects of the environment that underpin tools, customs, religion, arts, and beliefs (Flinn and Alexander, 1982). All human phenotypes derive from interactions of genes with environments — especially cultural and social ones — but culture is special because it can be transmitted both vertically (like genes, or language as noted by Darwin, 1871) and horizontally (as memes), with horizontal transmission potentially proceeding

at a very rapid pace. As such, human traits can evolve due to "gene-culture coevolution" (interactions of genetically based human phenotypes with cultural aspects of environments; Laland and Seed, 2021), commonly due to differential human adoption and perpetuation of different cultural phenotypes and culture acting as a causal agent for selection (Whiten et al., 2017; Richerson et al., 2021).

Cultural change can proceed under a runaway process, whereby increases in cultural complexity and sophistication (the "traits") generate environments that select for enhanced social-cultural learning and more-effective adoption of cultural behaviors (the "choices"), especially by young individuals, leading to runaway coevolution (e.g., Alexander, 1979; Flinn and Alexander, 2007; Boyd and Richerson, 2009; Rendell et al., 2011; Legare and Nielsen, 2015; Legare, 2017; Lotem et al., 2017; Muthukrishna et al., 2018; Markov and Markov, 2020). This process, coupled with "arms race" elements of cultural change, may have been especially effective in driving the recent and accelerating human cultural change that has so complexified human social environments. As such, and given the cumulative nature of human cultural change, this arena of social selection should be exerting stronger and stronger effects on human evolution as time proceeds, relative to the other four (Birch and Heyes, 2021; cf. Wadley, 2021).

The Final Arena: Between-Group Competition

The five arenas of runaway social selection described above all operate within human groups, where groups may be delineated by various terms including families, bands, villages, tribes, or ethnic, linguistic, or cultural groups, of any sizes, that each has some conception of "us" in relation to "them." Whereas social selection and competition occur extensively within such groups, their evolution should be constrained by demographic, ecological and anti-cooperative effects that weaken the group in the context of their competitive interactions with other groups (Lahti and Weinstein, 2005). As such, a final, higher-level arena of social selection operates between groups, as described by Darwin (1871) in terms of competition between human "tribes," and by Alexander specifically in terms of runaway imbalances of power. In particular, Alexander posits, following from Darwin's (1871) views that conflict between tribes selects for within-tribe cooperation and morality, that human social evolution has been driven, in large part, by group against group competition that selects for enhanced within-group cooperation as a means to counter external threats (Alexander, 1979, 1987, 1990, 2006). Alexander's balance/imbalance of power model represents a form of arms race, with both cognition and culture as weaponry, that selects for larger and larger, more and more cooperative groups, with better and better ways to compete, though larger group size may also exacerbate within-group variation and conflicts and dilute the benefits of winning. Such between-group conflicts would have originated in hominins on small scales (indeed, presumably reminiscent of the "warfare" of common chimpanzees; Mitani and Watts, 2001), as represented now in some extant human societies (e.g., Berndt, 1964; Chagnon, 1977; Macfarlan et al., 2014), but escalating as populations increase in size.

Perhaps the most telling evidence in support of Alexander's model is the observation that human history is, in considerable part, the history of human warfare based on groups defined by culture, language, and ultimately, genes (Bowles, 2009; Turchin et al., 2013; Bauer et al., 2016; Turchin, 2016). Warfare may, however, represent only the most extreme, obvious and effective form of between-group human competition, since humans compete, and cooperate to compete, in fluid, dynamic groups at all levels from families to nations, and based on biological kinship, ethnic markers of diffuse long-term ancestry, and cultural differences represented by kinship that can be mainly or purely psychological (Jones, 2003). Groups may also form on the basis of complementary skill sets or interests. In this context, the fluidity of human groupings, with shifting of alliances across time and space as a universality rather than exception, may connect the early evolution of hominids, lost in prehistory, with the recent evolution of modern, historic humans — and all points in between.

The six arenas of social selection described here each generates, given any degree of heritability, social evolution of sets of psychological traits and abilities that have collectively "made us human" (**Table 1**). What is striking about these sets of phenotypes is that they encompass a tremendous range of human-elaborated psychological and social traits, many of which are expected to be reinforcing across arenas (e.g., honesty and morality in partner choice and among-group arms races), transferrable across domains (e.g., finer-scale social discrimination in caregiver choice, partner choice, mate choice), or complementary (e.g., abilities to compromise with, lead, persuade, or control other individuals). The effects of these interacting arenas of social selection echo the emphasis of Laland and Seed (2021) on "dynamical feedbacks between mutually reinforcing aspects of cognition," with human cognitive uniqueness arising from "trait interactions and feedbacks," with the salient traits evolving squarely in the context of complex sociocultural landscapes (see also Dean et al., 2013; Whiten, 2018; Lombard and Högberg, 2021; Spikins et al., 2021). As such, runaway social selection and evolution appear to exhibit the breadth, power and scope to help explain, in principle, how modern humans evolved psychologically from chimp-human ancestors.

DISCUSSION

Uncovering the selective pressures that gave rise to the first hominins, and to modern humans, has been a perpetual challenge ever since Darwin drafted the first clear hypotheses of human origins in 1871. From a broad perspective, it makes sense that the most exceptional human features, large social brains, complex cooperative and competitive interactions, and elaborate culture, should themselves reflect the selective pressures that guided their evolution. The logic of runaway social selection suggests that humans generated and became their own primary selective pressures, through diverse forms of arms races within

TABLE 1 | Phenotypes and abilities postulated to be selected for, in six different arenas of human social selection and evolution.

Arms races within groups	Partner choice	Mate choice	Caregiver-offspring relationship	Cultural traits – social learning	Arms races among groups
Joint attention; Scenario-building; Theory of mind; Leadership; Manipulation of status; Social creativity; Persuasion; Coercion	Loyalty; Honesty; Reputation; Social status; Sustained reciprocity; Fine social discrimination abilities	Fine discrimination of cognitive, emotional, physical traits and abilities; Ability to navigate psyche and behavior of mate Enhanced physical, reproductive and survival abilities	Infant, child eye contact, smiling, laughing, early language development, secure attachment; Social development, maturation in childhood, adolescence Fine discrimination of offspring traits	Enhanced sophistication and efficiency of social learning about cultural norms, including aspects of language, religion, customs, arts, rules and laws, institutions, technology, and resource acquisition methods	Parochial altruism; Ingroup morality; Heroism; Xenophobia; Complex within-group cooperation; Dehumanization of other groups

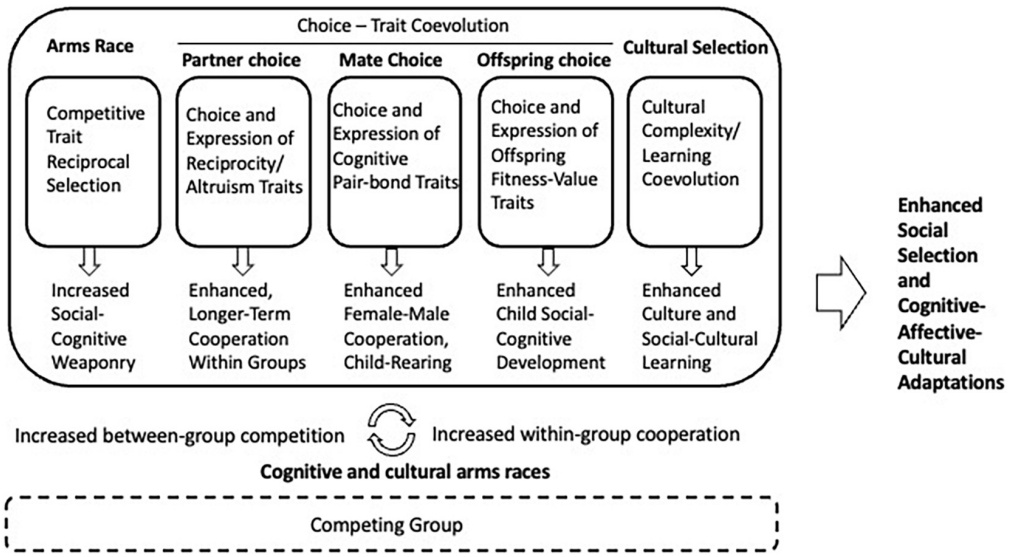

FIGURE 1 | The six arenas (five within groups, one between groups), of human runaway social selection. See **Table 1** for further details on the specific phenotypes selected for in each arena.

and between groups, and through choice-trait coevolutionary-dynamic interactions involving allies, mates, and offspring with caregivers. By the hypotheses presented here, each of these arenas of social selection drove the evolution of different, interacting dimensions of human sociality and culture, that merged to create the humans inhabiting our world today (**Figure 1**). This hypothesis is by no means incompatible with those based on other selective pressures postulated to be important in human evolution, such as alloparental care (Hrdy, 2009; van Schaik and Burkart, 2010) and self-domestication (Wrangham, 2019), but it stresses the importance of runaway social selection as a potential key factor in how and why modern humans evolved.

Tracing the selective history of humans relies on one part evolutionary logic, one part ecology, one part psychology and neuroscience, one part anthropology, and all parts grounded in phylogeny and evidence from archeological remains. An enduring part of the puzzle, the initial divergence of the eventual *Homo* and *Pan* lineages, is addressed here with the hypothesis that the divergent evolution of hominins was "kick-started," in an ape with a small (i.e., 400 cc) brain living at relatively low densities, by ecological conditions that favored increased fluidity, connectivity, tolerance, and especially local cooperation within and between small social groups. At first, such cooperation need not be sophisticated or complex, and need not involve larger brains. But when conditions eventually arose that allowed the evolution of larger and more complex brains (e.g., cooking of foods, and use of more energy-dense foods), and the first manifestations of culture, such early humans would have been poised to enter a socio-ecological niche characterized by increased population densities, larger brain sizes, enhanced competition and cooperation, cumulative culture, and strategic social choices, that collectively encompassed the multiple mechanisms of runaway social selection described above.

Increases in understanding of Darwin's (1871) "insensible grading" from an apelike form to humans requires clear and specific hypotheses that make testable predictions. Indeed, a primary criticism of the runaway social selection model is that it lacks concrete empirical support, in terms of the specific processes involved. The mechanisms that underpin the

hypotheses described here, especially those relating to choice-trait coevolution among allies, mates, and offspring-caregiver interactions, can, however, be evaluated in extant human groups, and ecological benefits from relatively simple primate alliances can be evaluated in field populations using the most relevant taxa. In particular, empirical evaluation of the hypotheses described here regarding social selection in human evolution will require testing for evidence of the operation of each proposed process and link in the causal positive-feedback cycles, especially in small-scale human societies. The hypotheses would thus be falsified by robust findings that the within-generation processes that underpin runaway social selection, in any given arena, do not occur in human societies or, if they occur, do not impact upon variation in inclusive fitness. Neurology and neuroendocrinology may also provide salient evidence of mechanisms for social competition (Dunbar and Shultz, 2007; Rilling, 2014; Shultz and Dunbar, 2014), and the evolutionary transitions of brain evolution (Sherwood et al., 2008; Sherwood and Gómez-Robles, 2017; Stout and Hecht, 2017; Bruner, 2021). Although the challenges inherent in all analyses of the broad scope of human evolution are daunting, the intellectual rewards remain profound, in better comprehension of just what we as a species are, and how we came to be.

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All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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The Evolution of Playfulness, Play and Play-Like Phenomena in Relation to Sexual Selection

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By conceptualizing Sexual Selection, Darwin showed a way to analyze intra-specific individual differences within an evolutionary perspective. Interestingly, Sexual Selection is often used to investigate the origins of sports, arts, humor, religion and other phenomena that, in several languages, are simply called "play." Despite their manifested differences, these phenomena rely on shared psychological processes, including playfulness. Further, in such behaviors there is usually considerable individual variability, including sex differences, and positive relationship with mating success. However, Sexual Selection is rarely applied in the study of play, with exception to what is concerned as infant training behavior for adult sex roles. We offer an integrated grounding of playful phenomena aligning evolutionary propositions based on sexual selection, which might stimulate further exploration of playfulness within evolutionary perspective.

Keywords: play, gaming, playfulness, sexual selection, mental mechanisms, human evolution, ludicity, evolutionary psychology

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INTRODUCTION

When Darwin (1871/1981) concluded that Sexual Selection explains individual variation in bodily and psychobehavioral traits that could not be explained by differences in habits or survival, he kickstarted promising scientific fields (Cronin, 1993; Miller, 2001). Within a single class of evolutionary processes, Darwin explained the existence of extravagant and costly anatomical/physiological and psychosocial behavioral features not directly related to survival, sex differences across species, ontogenetic differences pre and post puberty, intra-specific individual differences, and the rapid divergence within closely related species (Cronin, 1993; Miller, 2001; Luoto, 2019). This Darwinian approach shed light on many human traits considered evolutionary puzzles, including aspects of play (Chick, 2001; Burghardt, 2005), humor (Greengross and Miller, 2011), sports (Manning and Taylor, 2001), arts, and religion (Zahavi and Zahavi, 1997; Miller, 2001; Varella et al., 2011, 2017; Barash, 2012).

Here we explore how Sexual Selection can foster comprehension about the evolutionary facets of playfulness, which is usually called "play," but we suggest it is a broader concept not restricted to children. We argue for the benefits of distinguishing play, playfulness and some of the play-like phenomena and suggest how they might relate to Sexual Selection. Furthermore, we present the

convergent evidence pointing to the evolved nature of psychological tendencies toward playfulness, focusing on the distinction between play and gaming.

DEFINITION AND CONCEPTUAL DISTINCTIONS

Depending on epistemological or linguistic differences, "play" can mean either a behavior or a psychological disposition (Sutton-Smith, 2001; Weisfeld and Weisfeld, 2016; Lebed, 2021). Similarly, it can refer to several playful activities. Consequently, "play" and "playfulness" (and sometimes "game") are used as synonyms. For instance, Huizinga (1938/1980) and Caillois (1958/2001) state that the study of play (or "games" depending on the translation) should include music, theater (role-playing), lottery, philosophy, religion, roller-coaster riding, alcohol drinking, among others. Caillois' French *jeu* and Huizinga's Dutch *spel* are neither equivalent to English *play* nor *game*–neither to the Portuguese *brincar* nor *jogar*, respectively (Lebed, 2021). Some languages have only words for a general concept applicable to anything pleasurable, entertaining and autotelic (e.g., Czech, French, German), what we will call "playfulness" henceforward, while other languages make distinctions about different kinds of "play" (e.g., English, Japanese, Portuguese) (Lebed, 2021).

We argue that, beyond linguistic discussions about how narrow or overlapping is their definitions, we suggest using two insights from Evolutionary Psychology: (1) the idea that the human mind has many evolved psychological specializations, (2) the focus on the constellation of underlying psychological capacities being recruited to perform each class of behaviors (Barrett, 2014; Lewis et al., 2017; Pietraszewski and Wertz, 2022). The distinction between the behavioral dimension in the surface and the underlying psychological dimension (cf. Lopes, 2008; Proyer et al., 2021) and the lack of one-to-one correspondence between behavioral and psychological dimensions are crucial. Although many psychological capacities might jointly contribute to each class of behavior, each class of behavior might have their own evolved core capacity/capacities or set of core capacities. For instance, the evolved core capacity for playing might be Playfulness, which is "a propensity to define (or redefine) an activity in an imaginative, non-serious or metaphoric manner so as to enhance intrinsic enjoyment, involvement, and satisfaction" (Glynn and Webster, 1992, p. 85); "the predisposition to frame (or reframe) a situation in such a way as to provide oneself (and possibly others) with amusement, humor, and/or entertainment" (Barnett, 2007, p. 955); "an inclination to pursue activities with the goal of amusement or fun, with an enthusiastic and in-the-moment attitude" (Van Vleet and Feeney, 2015, p. 637); "an individual differences variable that allows people to frame or reframe everyday situations in a way such that they experience them as entertaining, and/or intellectually stimulating, and/or personally interesting" (Proyer, 2017, p. 114).

Since the terms most often associated to "playfulness" are "play" and "game," **Tables 1**, **2** overview traits used in the literature to, respectively, define them. Definitions of "play" usually focus on behaviors that occur concomitantly to: intrinsic motivation (e.g., "voluntary," "autotelic," "fun"), positive emotions (e.g., "joy." "happiness," "pleasure"), and lack of stressors (e.g., "relaxed field," "play world" or "magic circle"). Authors studying human play define it as "imaginative," while those focusing on non-humans emphasize functionless-like behavioral modifications. Alternatively, definitions of "game" focus on structured rules; conflicts, there are winners and/or losers, and a quantifiable and important/valued outcome. Therefore, a behavior can be considered "play" when is activated the playfulness capacity which generates a playful state of mind. This playfulness state is usually not explicit in definitions of "game," and some argue it is not even necessary (e.g., Lebed, 2021), but the rules and outcomes are reframing the conflicts to turn them interesting, and hopefully fun. That means that playfulness can exist even in non-joyful and serious activities (cf. Huizinga, 1938/1980; Caillois, 1958/2001; Suits, 1978; Proyer, 2017). Gaming playfulness may be qualitatively different from playing playfulness, but both are playful.

Thus, playfulness can be combined with other traits, as shown by Sutton-Smith's (2001) analysis of play(fulness) being depicted as: learning (developmental training), a force or drive (fortune-telling, divine providence, and motivation/necessity), a form of dominance (competitions and games of skill), group identification and belonging (festivals and cultural activities), imagination/creativity (arts and make-believe), self -expression and individualization (hobbies and recreation), and as subversion (jokes and sarcasm). The combination of Playfulness with the tendency for physical activity (i.e., a voluntary movement with energy costs superior to rest levels, Caspersen et al., 1985) might give rise to the class of behavior known as play (cf. Špinka et al., 2001; Burghardt, 2005). Thus, the different subtypes of play (e.g., with object, rough and tumble, roleplaying, rule based) would be further combinations with other psychological capacities (e.g., manipulation, ritualized competition, imagination/representation, normativity). Another example of evolved features in the human mind is artisticality, the autotelic pleasurable capacity for extraordinary ornamentation/aesthetic improvements (Varella et al., 2017; Varella, 2021). The combination between the tendency for physical activity and artisticality gives rise to the different artistic modalities.

Recognizing that behaviors recruit multiple psychological components enables a better understanding of overlapping cases and why many cultures use "play" across different behavioral classes. From a combination of a few psychological invariants one can observe a broad behavioral diversity and overlap of classes. Recruitment of language with playfulness may lead to play on words, jokes, celebrity voice impersonations, or word games, such as crosswords, hangman game, or Wordle. Recruitment of capacities for narrative, exploration, normativity and playfulness may lead to role-playing games (RPGs). Recruitment of language/narrative and artisticality leads to poetry and literary arts. Recruitment of playfulness and artisticality results in colorful domino art, Pictionary, musical jokes and parodies, circus arts, or hobby artists. Recruitment of ritualized competition/cooperation, normativity, self-overcoming and playfulness leads to most sportive games, chase tags, and tabletop games. Recruitment of ritualized competition/cooperation,

TABLE 1 | Traits presented in definitions of "play."

Trait	Author						
	Avedon and Sutton-Smith (1971)	Burghardt (2005)	Chick (2001)	Eberle (2014)	Gray (2009)	Špinka et al. (2001)	Walther (2003)
Autotelic		X		X	X		X
Behavioral modifications		X	X			X	
Ephemeral	X						X
Have rules					X		X
Imaginative				X	X		X
Lack of stressors		X	X		X	X	
Novelty-seeking				X		X	
Open-ended	X						X
Play-signals			X				X
Positive emotion		X	X	X		X	
Purposeless		X					
Self-handicap						X	
Repetition		X				X	

TABLE 2 | Traits presented in definitions of "game."

Trait	Author						
	Avedon and Sutton-Smith (1971)	Juul (2010)	Lever (1978)	Winther-Lindqvist (2019)	Miranda and Stadzisz (2017)	Salen and Zimmerman (2004)	Walther (2003)
Active participation	X	X				X	
Competitive			X	X			
Conflictual	X		X		X	X	X
Clear rules	X	X	X	X	X	X	X
Outcome is emotionally important	X	X		X			
Predefined roles	X		X	X			
Quantifiable outcome		X			X	X	
Unpredicted outcomes	X	X		X	X		

normativity, self-overcoming and artisticality results in rhythmic gymnastics, figure skating, synchronized swimming, slam dunk contest, keepie-uppie competition, dancing contest, capoeira, or rap battles if language is also recruited.

Furthermore, if we consider that most humans are not serious professional sportspeople, gamers, or artists (Moraes, 2021), but nevertheless recruit the universal capacities underlying those tendencies in their leisure time, hobbies and self-entertainment moments, the contribution of playfulness becomes clear and ubiquitous even in adulthood. About 22% individuals consider free-time a time to fun and about 13% consider it a time to dedicate to one's own hobby (Mingo and Montecolle, 2014). Playfulness may lead to many pleasurable activities that can or cannot latter become professionalized.

PLAY AND GAMES AS STEMMING FROM EVOLVED PROPENSITIES

The psychological tendency toward play exhibits many criteria of evolved adaptation. It is present in all human cultures (Huizinga, 1938/1980; Gosso and Otta, 2003; Sandseter and Kennair, 2011) and is typical of mammals (Špinka et al., 2001; Burghardt, 2005), especially regarding large-brained mammal orders (Iwaniuk et al., 2001), suggesting play is at least as antique as the first mammals (Late Triassic), but it might have independently evolved in birds with delayed reproduction (Diamond and Bond, 2003; Kaplan, 2020), fish, turtles and octopuses (Kuba et al., 2003; Burghardt, 2005). Playful phenomena are culturally valued (Sutton-Smith, 2001). Play also has high costs (Harcourt, 1991; Greve et al., 2014; Froehle et al., 2019), is observable very early in ontogeny (Eibl-Eibesfeldt, 2017; Winther-Lindqvist, 2019), provides physical, cognitive and social benefits (Špinka et al., 2001; Bjorklund and Pellegrini, 2002; Sandseter and Kennair, 2011). It results in specific emotional states (Špinka et al., 2001; Burghardt, 2005; Davis and Panksepp, 2011), has a heritable component (in mice, Walker and Byers, 1991; in humans, Olson et al., 2001), and it is at least partly modular, since its content may change, but it does not disappear under any known disorders, regardless if it is an intellectual, personality, endocrinal or mood disorder (cf. Berenbaum and Hines, 1992; Davis and Panksepp, 2011; Papoudi and Kossyvaki, 2019).

Gaming is considered exclusively human (Breuer et al., 2019), arguably because we usually require some spoken acceptance of

explicit rules. Not all animals use violence in competitions, but some of them have non-violent ritualized competitions (Maynard Smith, 1974) that could be called "games" if there was any evidence of mutual agreement. Even rough-and-tumble play and play fighting have some recognizable rules, like controlling own force to avoid harming the play partner, signals of "this is play" ("play face" in primates) and role-reversal (Chick, 2001; Špinka et al., 2001; Burghardt, 2005). Games have also existed for at least 5 or 6 thousand years (Rollefson, 1992), but considering they are universal (Roberts et al., 1959; Chick, 1998; Voogt, 2017), they might have existed for much longer. Indeed, anthropologists have suggested that some archeological artifacts originally considered "works of art" or "religious tools" may be pieces of unknown games (Culin, 1907/2007; Avedon and Sutton-Smith, 1971). Furthermore, gaming is culturally valued (Avedon and Sutton-Smith, 1971; Apostolou et al., 2014; Crist et al., 2016), is associated with physical, cognitive and social benefits (Caillois, 1958/2001; Roberts et al., 1959; Zimmer, 1987; Kaufman et al., 2019). It includes specific mental states (Walther, 2003; McGonical, 2011), and is costly due to self-handicapping rules (Suits, 1978). Gaming develops later than play (Winther-Lindqvist, 2019), and makes individual differences more evident (Caillois, 1958/2001). At least sportive games also have a heritable component (Olson et al., 2001; Tucker and Collins, 2012).

PLAY AS A RESULT OF NATURAL AND SEXUAL SELECTION

Different evolutionary mechanisms can explain different ludic phenomena (cf. Liebold et al., 2019). Play behavior is usually seen as a result of Natural Selection, a way for training hard-to-master skills that would require dangerous conditions if play did not existed (Špinka et al., 2001; Bjorklund and Pellegrini, 2002; Burghardt, 2005). Meanwhile, Sexual Selection is used to explain the evolutionary functions of arts (e.g., Varella et al., 2011, 2017), sports (e.g., Lombardo, 2012; Deaner et al., 2016) and even playfulness as an individual difference trait (e.g., Chick, 2001; Moraes et al., 2021). Play's costs imply play can be a reliable signal of health, and consequently, this might be generalizable to adulthood. The *Signal Theory of Playfulness* (Chick, 2001) postulates a playful attitude not only signals a healthy condition, but other desirable trait, like non-aggressiveness in males and youthfulness in females. Contrarily, theories about the origins of sports, generaly understood as playful competitions of physical skills, postulates sport play signs fighting and hunting skills in controlled conditions to attract mates (intersexual competition), coalitional allies, status and/or resources (intrasexual competition; see Deaner et al., 2016). Moraes et al. (2021) found that in men other-directed playfulness positively predicted the number of long-term and short-term partners, while in women whimsical playfulness positively predicted the number of short-term relationships. Thus, playfulness is possibly being sexually selected in both sexes because playful adults have more partners. Sexual selection also might explain why the adult play (gaming) is, apparently, human-only and why there are robust cross-cultural sex differences (Roberts et al., 1959; Gray, 2004; Deaner and Smith, 2013; Moraes, 2021).

Sexual Selection shapes characteristics that tend to be costly, sometimes even reducing the chances of survival, are highly variable within the same species, they frequently develop in only one of the sexes and/or after puberty, and are species-specific (Zahavi and Zahavi, 1997; Miller, 2001; De Block and Dewitte, 2007; Lange et al., 2019; Petrie, 2021). Sexual Selection can also be roughly divided into Intersexual Selection, which involves adaptations to choose or be chosen as a mate by an opposite-sex individual, and Intrasexual Selection, which involves adaptations to defeat or intimidate same-sex individuals (Apostolou, 2015; Lange et al., 2019; Petrie, 2021).

More playful individuals are preferred as mates (Chick et al., 2012; Proyer and Wagner, 2015), and playfulness is also positively correlated with physical fitness (Proyer et al., 2018), relationship satisfaction (Brauer et al., 2021) and is subject to assortative mating (Chick et al., 2020), which can explain its heritability. Additionally, players of sportive games have more sexual partners (Faurie et al., 2004). However, there is almost no studies about the generalizability to other games and a few exceptions found mixed results (Lange and Schwab, 2019; Moraes, 2021). If neither Natural Selection, nor Intersexual Selection were alone responsible for the evolution of gaming, Intrasexual Selection might also play some role (cf. De Block and Dewitte, 2007). Thus, gaming may be a way to compete for resources that will indirectly increase the fitness, such as status or coalition allies (De Block and Dewitte, 2007, 2009; Balish et al., 2016; Winegard et al., 2018). Importantly, these selective forces may act simultaneously in different degrees. De Block and Dewitte (2009) argue there are so many sportive games because sports act as honest signals of good genes, which must be informative (provide evolutionary relevant information), accurate (hard to falsify, reliable) and transparent (spectators should be able to decode the sign). But there is often a trade-off among these three qualities and different sports target different proportions. Furthermore, there might be redundant and multiple signals display within ornamental signaling (Valentova et al., 2017; Pereira et al., 2019). Additionally, sports that lost their signal value to new ones can continue through exaptation, i.e., acquiring new functions, like when fans try to earn money through bets or try to impress people displaying their knowledge about game-related history and statistics, but the original (distal) function of the sport was to signal players' physical skills.

Some attempts to apply an evolutionary perspective in the study of non-sportive games include Gray's (2004) analysis, showing that men play casino games more often than women as a byproduct of male general higher risk-taking and dependency on resource holding to attract mates. Some researchers study digital games from an evolutionary framework (e.g., Mendenhall et al., 2010; Lange et al., 2019), but it is often not clear if they talk about *digital gaming* or *digital pretense play*. We have no knowledge of attempts to explain the adaptive values of other games through evolutionary mechanisms, but it would surely be interesting. For instance, card games rely on deception and social manipulation (Altice, 2014) and, consequently, they may be the products of

sexual selection processes combining playfulness, cheating and cheater-detection behavioral and mind reading (cf. Varella, 2018).

DISCUSSION

An evolutionary framework has greatly contributed to the study of play, but it has been focused on "repeated, incompletely functional behavior differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed or low-stress setting" (Burghardt, 2005, p. 51). Though it captures what is usually thought when someone says "play," it does not capture all the playful experiences one can get, nor capture the proper psychological level in which evolution operates (Barrett, 2014). Phenomena as "game," "sport," "music-playing," "role-playing," and "fortune-telling" are called "play" in some languages and not in others (Huizinga, 1938/1980). This might reflect a phylogenetic continuity or that similar combinations of psychological mechanisms are being used. We suggest that all of them use in some level the psychological capacity of playfulness. They may have evolved through Natural Selection as mechanisms to actively search for ways of increasing one's own fitness, but also Sexual Selection acted on how they are used to create complex phenomena as gaming and arts (Liebold et al., 2019).

We argue that there is enough robust evidence to support the existence of these mechanisms (Caillois, 1958/2001; Scott and Godbey, 1992; Walther, 2003; Conway, 2010; Argento et al., 2017; Zosh et al., 2018; Lebed, 2021). What is needed is a good theory to avoid the "theory crisis" (Eronen and Bringmann, 2021). Sexual Selection might be this theory. However, researchers should accept some basic principles which make studies richer and less prone to appear contradictory, and avoid misunderstandings (Varella et al., 2013). Some of these principles are already used in other areas, like bio-musicology (Fitch, 2015): recognize that these behavioral phenomena are composed of many interacting psychological components; look for cross-cultural and inter-specific homologies and analogies; avoid elitism and focus on ecological validity; consider the Tinbergen's questions–mechanism, ontogeny, function, phylogeny, plus their updates (e.g., subjective experience, Burghardt, 2005; and sociocultural history as medial explanation between proximal and distal ones, Varella et al., 2012).

Importantly, Darwin's (1871/1981) theory has since been expanded and updated. Different mechanisms of Sexual Selection have been proposed (cf. Puts, 2010; Shuker and Kvarnemo, 2021). For instance, men may play sports more often because women prefer sportive men (Faurie et al., 2004), because sports work as behavioral armaments in intrasexual competition (Lombardo, 2012) or as displays for potential parents-in-law (Apostolou, 2017), besides other bio-socio-cultural functions. Psychological traits can function as both armaments and ornaments (Berglund et al., 1996).

Here we take this sesquicentennial celebration as an opportunity to invite the researchers to get inspired by Darwin's pioneering and courageous move of looking into intra-specific differences and searching the mechanisms that drive them, in order to disentangle some of the most intriguing aspects of human life: How do playful phenomena (games, sports, arts, religion, humor, flirting, etc.) differ among each other? And how they can contribute to individual survival and reproductive success? Future studies should consider the overlapping among playful phenomena, their multiple levels, cultural meaning, interspecies similarities, organism's developmental stage and both Natural and Sexual Selection.

AUTHOR CONTRIBUTIONS

YM: idealization and writing of the manuscript. JV: supervision and revision of the manuscript. MV: manuscript writing and revisions. All authors contributed to the article and approved the submitted version.

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Enhanced Originality of Ideas in Women During Ovulation: A Within-Subject Design Study

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The signaling theory suggests that creativity may have evolved as a signal for mates. Indeed, its aesthetic value might not have been necessary for survival, but it could have helped to attract a mate, fostering childbearing. If we consider creativity as such a signal, we should expect it will be enhanced in the context related to sexual selection. This hypothesis was tested mainly for men. However, both men and women display physical and mental traits that can attract a mate. Previous studies showed that women can be more creative during their peak fertility. We advanced these findings in the present study, applying reliable measures of menstrual cycle phases (examining saliva and urine samples) and the highly recommended within-subject design. We also introduced and tested possible mediators of the effect. We found women's ideas to be more original during ovulation compared to non-fertile phases of the ovulatory cycle. The results are discussed in the context of signaling theory and alternative explanations are considered.

Keywords: ovulatory cycle, sexual selection, creativity, mating behaviors, signaling theory, women

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INTRODUCTION

Men and women both display traits that can attract a mate (Whyte et al., 2021). Men display broad shoulders and facial masculine features. Women display broad hips, breasts, and feminine facial features. Such traits serve as natural ornaments (Miller, 2000a), and as such may indicate the potential partner's ability to cope with parasites, malnutrition, and social competition, foreshadowing the quality of genes that may be passed on to offspring (Zahavi, 1975; Sugiyama, 2005). However, although this utilitarian Neo-Wallacean view of sexual selection is prevalent in the scientific community, there is a possibility that display traits are not indicating anything, but are merely preferred (Prum, 2012; see also Petrie, 2021). In his book "The descent of men, and selection in relation to sex," Darwin (1871) proposed that many secondary sexual ornaments are entirely arbitrary and as such do not provide any particular value or utility. Furthermore, Darwin (1871) argued that elaborate displays being the result of sexual selection may also contribute to behavioral abilities.

Indeed, depending on the short- or long-term context of romantic relation, people value specific attributes in a potential mate (Buss and Schmitt, 1993). Attractive traits can belong to various domains (Miller, 1999, 2000a,b), which has been evidenced for the domain of music (Varella et al., 2010; Charlton, 2014; Kaufman et al., 2016; Madison et al., 2018), humor (Kaufman et al., 2008; Greengross and Miller, 2011; Driebe et al., 2021), creativity (Li et al., 2002),

and art (Clegg et al., 2011). Creativity definitely has its utilitarian value: it has probably allowed for the development of new ways of enabling survival, such as improving hunting methods or building shelters. As Darwin pointed out (1871, p. 74): "The Imagination is one of the highest prerogatives of man. By this faculty he unites former images and ideas, independently of the will, and thus creates brilliant and novel results." However, creativity is also strongly associated with aesthetics (Koestler, 1964), manifesting in painting or dancing, which remains unexplained in terms of the need for survival nor daily habits of life (Darwin, 1871). Beauty is not required for survival, and as Darwin (1871, p. 61) argued: "the taste for the beautiful is confined with the attraction of the opposite sex."

Providing evidence that creativity is an effect of sexual selection is very difficult. However, if we assume such a possibility, we can search for specific consequences. Namely, creativity should be detected and valued by opposite-sex members. Indeed, studies showed that creativity is perceived as sexy by both men and women (Feist, 2001; Li et al., 2002; Kaufman et al., 2016), and is found to be among the top 10 most desired traits worldwide (Buss and Barnes, 1986). Women value creativity in men in the short-term mating context, especially when fertile (Haselton and Miller, 2006; Charlton, 2014). Men prefer females' ornamental and aesthetic creativity (Kaufman et al., 2016).

For bodily and cognitive traits to evolve by natural or sexual selection, some of the individual variation should have a heritable component (Croston et al., 2015). It seems to be the case with creativity. For example, Waller et al. (1993) reviewed studies on twins and concluded that approximately 22% of variation in creativity (namely divergent thinking) is due to the influence of genes. Also, very recently, Zwir et al. (2022) have provided evidence on the genetic networks underlying human creativity. However, studies are inconclusive on the topic of reproductive success that creativity brings (Clegg et al., 2011; Lebuda et al., 2021). For instance, there is evidence that number and quality of creative works among professionals are positively related to the number of their sexual partners (Clegg et al., 2011), and to the interest they evoke in women (Clegg et al., 2008). At the same time, studies by Lebuda et al. (2021) on non-WEIRD population indicated negative correlations between creative potential and number of living children and grandchildren, as well as between creative potential and the number of spouses.

Creativity as a product of sexual selection should also be enhanced in mating contexts. Griskevicius et al. (2006) showed that creative thinking in men can be enhanced in the context of any potential partner, but for women a high-quality and committed partner is needed. The periovulatory time can also provide such a context for women, as it is the only period when sex can result in conception (Gildersleeve et al., 2014). This physiological process involves the release of the dominant ovarian follicle from the ovary into the fallopian tube, where it can be fertilized (Holesh et al., 2021). This moment should activate mechanisms involved in the process of sexual selection not only on a physiological, but also on a psychological and behavioral level. Indeed, throughout the cycle, women are supposed to experience adaptive changes in their subconscious mental and behavioral processes associated with mating (Gangestad and Thornhill, 1998, 2008). They are more sexually aroused (Roney and Simmons, 2013) and interested in mating concerning extra-pair copulation (Gangestad et al., 2005; Pillsworth and Haselton, 2006) or primary partner (Pillsworth et al., 2004). Few studies point to general increase in sexual desire (Jones et al., 2018). Furthermore, arousal seems to manifest itself in domains not associated with sex, such as increased motoric activity (Udry and Morris, 1970), found at the physiological level (Gómez-Amor et al., 1990; Krug et al., 1996).

The elevated self-promotion found in women during increased fertility can be considered a prominent signal manifestation. Women care for their appearance significantly more, trying to attract a potential partner with self-ornamentation, a more fashionable style (Haselton et al., 2007), and revealing clothes (Durante et al., 2008). However, it must be noted that these behaviors can serve not only intersexual selection, but also intrasexual selection (Fisher et al., 2009). Moreover, studies report that women during the fertile window of the ovulatory cycle are more determined to meet potential mates by attending social gatherings (Haselton and Miller, 2006). Some authors suggest that due to such actively realized mating goal, they eat less (Fessler, 2003; Roney and Simmons, 2017) and are more prone to risky behaviors (Šukolová and Sarmány-Schuller, 2011), which is linked to decreased cognitive control found in women during the fertility peak (Hatta and Nagaya, 2009).

It appears that ovulation is a condition dictated by special needs that women signal. Furthermore, their signals are received. Studies show that women are evaluated as more attractive precisely during the fertility peak (Roberts et al., 2004). Men score women's facial appearance as better (Roberts et al., 2004; Puts et al., 2013) and the same goes for their vocal pitch (Pipitone and Gallup Jr., 2008; Puts et al., 2013), and body scent (Singh and Bronstad, 2001; Gildersleeve et al., 2012). As psychological traits can also be attractive, these kinds of signals should be manifested by women as well. However, there is hardly any research to show that. Varella et al. (2017) discuss the role of female ornamentation as overlooked ancestral selective pressure in the evolution of artistic propensities. Previous studies focused mainly on men, investigating how they may change their behavioral manifestation to attract a potential mate (Tifferet et al., 2012; Gao et al., 2017; Bongard et al., 2019). This is probably because, due to parental investment theory (Trivers, 1972), men are supposed to be a less investing sex, and hence, less choosy about a potential partner. In this view, men must court their female partners more, performing more signaling. However, although true in case of many sexually dimorphic species (Janicke et al., 2016), this view does not fit well with quite sexually monomorphic humans (Miller, 2013; Stewart-Williams and Thomas, 2013). Both women and men are highly selective, especially when it comes to long-term relationships (Buss and Barnes, 1986; Lippa, 2007). It has been suggested and shown that mutual ornaments can have a signaling function in both sexes (Kraaijeveld et al., 2007), and as physical attractiveness is highly important for female mate value, it

could be argued that women should prevail not only in the aesthetic domain, but in creative artistic domains in general (Varella et al., 2017). This view has been extensively confirmed by Varella et al. (2017). who reviewed evidence indicating that women are more likely than men to involve artistry in the contexts of inter- and intrasexual selection.

In our studies, we verify hypotheses concerning creativity as a sexually selected trait in women. If we assume that, we should expect it will be enhanced during the fertile phase of the ovulatory cycle, when conception can occur (Gildersleeve et al., 2014). The results of our previous study (Galasinska and Szymkow, 2021) indicate that women's creativity may increase with their fertility. These results are consistent with the signaling theory (Miller, 2000a) and replicate the previous studies conducted by Krug et al. (1994, 1996). We have found that as the probability of conception gets higher, women's thinking becomes more divergent. Divergent thinking leads the individual to numerous and varied responses, being commonly used as an estimate of creative potential (Runco, 2007). This kind of thinking concerns three dimensions: fluency, flexibility, and originality (Guilford, 1968). Among them, it is originality that is the most critical indicator and the primary facet of creativity (Acar et al., 2017). Originality refers to things that are novel and slightly different from others (Lugo et al., 2016). In our study (Galasinska and Szymkow, 2021), two of three dimensions of divergent thinking, namely originality and flexibility, were positively correlated with the probability of conception, and the effect of originality was the strongest.

We also introduced arousal as a mediator, as arousal is found to be increased during peak fertility (Gómez-Amor et al., 1990; Krug et al., 1996; Roney and Simmons, 2013). Arousal is one of the core features of emotional response to environmental challenges with amplified motivation toward the readiness to act (Clore and Storbeck, 2006). It reflects the intensity of behavior, referring to the degree of excitation, activation, and energy mobilization (Duffy, 1962). Activating moods are found to facilitate divergent thinking (Baas et al., 2008). If the mediation of arousal in our study was significant, it would point to an important conclusion that creativity may be promoted as a side effect of increased arousal, which itself can be an adaptation of the way of finding a partner. Such an effect would undermine legitimacy of the signaling role of creativity in this context. However, we found no mediating effect of self-reported arousal. Increased arousal during ovulation may be the effect of increased dopamine release during this phase (Colzato et al., 2010), which is found to improve both divergent thinking and mood (Ashby et al., 1999). Due to this fact, in the present study we decided to additionally test the role of mood, as its facilitating role in creativity is well studied (Fredrickson, 2004; Baas et al., 2008; De Dreu et al., 2008), and cognitive control, associated with flexibility (Isen et al., 1987).

Present Study

This study aimed at replicating the previous one (Galasinska and Szymkow, 2021), in a within-subject design, recommended in studies considering the ovulatory cycle (Gangestad et al., 2016), and importantly, with the use of more reliable measures of cycle phases (examining saliva and urine samples). We hypothesize that ovulating women will be more fluent and flexible in thinking, and more original in ideas comparing to those in non-fertile phases. Furthermore, we hypothesize that they will be more aroused, in a higher mood, and having lower cognitive control comparing to other phases. We will check whether these variables will mediate the effect of enhanced creativity. The original contributions presented in the study are publicly available. This data can be found at https://osf.io/6ypkb/.

MATERIALS AND METHODS

Participants

With the use of Sona system at the SWPS University of Social Sciences and Humanities, we recruited 94 Polish women in reproductive age (19–35), cycling naturally from 21 to 35 days. We excluded 22 participants due to reasons presented in **Supplementary Figure 2**. The final sample comprised 72 women ($M_{age} = 25.53$, $SD_{age} = 5.05$), its size was estimated in accordance with Gangestad et al. (2016) recommendations for within-subject designs. The participants reported not using hormonal contraceptives, not being pregnant, breast feeding, nor having given birth for at least 3 months prior to study participation. The frequency analysis revealed that 39 participants reported being in a relationship lasting from 2 months to 16 years ($M_{years} = 2.72$, $SD_{years} = 3.69$), one participant reported being homosexual, and 10 being bisexual. Also, three participants reported taking antidepressants. We collected the data between July 2020 and April 2021, during the COVID-19 pandemic, a time of relative social isolation. People were predominantly working from home and public social life was suspended due to government sanitary restrictions.

Materials and Procedure

Menstrual Cycle Phase Determination

We studied women during three menstrual cycle phases: early follicular (menstrual), ovulatory, and late luteal (premenstrual), always keeping a minimum of 1-week interval between measurements. The sequence of phases was randomized: the order of the three phases was drawn for each participant before the study began, so each participant had a different order of phases. We present the size of the groups starting the study in each phase in **Supplementary Figure 1**. Following the report by Su et al. (2017), we applied a saliva-based method using ovulatory microscopes (Geratherm) to confirm accuracy of the phases, and urine LH test kits to confirm the results of the microscopy. Study participants were given microscopes and LH tests *via* post and were instructed with a tutorial film on how to use them properly.

Creative Divergent Thinking

Divergent thinking involves fluency (production of ideas), flexibility (their variety), and originality (their uniqueness), which are general factors of creative potential, i.e., can result

in creative products of any kind (Runco, 2007). The most commonly used estimate for such creative potential are open-ended alternate uses tasks (Benedek et al., 2014). In our study, we administered a computerized version of the Alternative Uses Test (AUT; Guilford, 1967). Participants were given a name of a common object and were asked to generate and write different unusual and creative uses for that object in a 5-min period. One of three common objects was applied in each phase, in randomized order: a shoe, a towel, and a bottle. Participants' ideas were scored based on fluency, flexibility, and originality by four trained, independent raters (psychology students), blind to hypothesis, and participants' cycle phases. Raters were tested for inter-rater reliability. *Fluency* scores were the sum of ideas provided. *Flexibility* was assessed by the number of semantic categories applied (Runco, 2007). Each rater had to indicate and collect categories as they saw fit, for example: "art-related," "weapon-related," or "construction related." However, the breadth of categories was determined by each rater's individual characteristics. Averaged *originality* was rated on a 5-point scale (from 1 = *not original* to 5 = *highly original*). The total originality score was divided by the number of ideas to prevent a confounding effect of fluency (Runco and Acar, 2012; Forthmann et al., 2020).

Creative Convergent Thinking

Another paradigm of creativity suggests that it takes distant associative abilities to identify the best matching idea as a solution to a problem (Wu et al., 2020). To test this paradigm of creativity, we applied Remote Associates Test (RAT; Mednick, 1968; Polish version by Sobków et al., 2016), a convergent thinking test (Lee and Therriault, 2013) significantly related to insight problem solving (Chang et al., 2016). It consists of 17 sets of three words that are associated with the fourth word (the solution). We applied 15 items, divided into three phases. Sets of five items per phase were randomly selected for each participant. All item sets are presented in **Supplementary Material**.

Arousal and Its Valence

To examine the general arousal and its pleasantness reported by participants, we applied the Self-Assessment Manikin (SAM; Bradley and Lang, 1994), a picture-oriented survey measuring emotional response. We used the subscale of valence/pleasure (five pictures ranging from the most negative = 1 to the most positive = 5) and arousal (rated from low = 1 to high = 5).[1] The participants were asked to match the picture that corresponded with their state.

[1]This tool also includes the third subscale of dominance. In our study, we focused merely on the potential mediating role of arousal and emotions, and thus, we did not investigate the role of dominance. However, as dominance can be important in the context of mating (Stanton and Schultheiss, 2009), and in the context of creativity (Heinzen et al., 1988), we decided to conduct mediational analyses for the dominance dimension as well. No mediating effect was found.

Mood

We administered the Mood Adjective Checklist (UMACL; Matthews et al., 1990) adapted to Polish by Goryńska (2005), consisting of 29 adjectives describing emotions. Participants used a 4-point scale (from 1 = *definitely not* to 4 = *definitely yes*) to rate if they experienced a particular emotion at the moment of rating. We averaged scores for the three subscales: energetic arousal, tense arousal, and hedonic tone (all $\alpha \geq 0.90$).

Cognitive Control

We administered a color-word Stroop task, with the use of Inquisit Lab programme, drawing from the on-line test library of the Millisecond platform. Participants were asked to install the program on their computer and practice it two times. Contact email address and phone number were provided in case of any questions. The task assesses the ability to inhibit cognitive interference occurring when processing of the stimulus feature affects the simultaneous processing of the other attribute of this stimulus (Stroop, 1935). The instruction was to categorize the color of presented latter strings as either red, green, blue, or black, using the *d*, *f*, *j*, or *k* key, respectively, ignoring the meaning of the word suggesting the color. The background was white. The response mappings (*d*, *f*, *j*, *k*) were continuously displayed. Error responses were followed by a 1,000-ms visual error message (X) and were excluded from further analysis. The task consisted of 84 consecutive trials of randomly presented congruent, incongruent, and control stimuli (28 stimuli per category). Stroop interference was assessed by subtracting the reaction time to incongruent and congruent stimuli. We had to exclude participants with incomplete trials ($N = 15$) from further analysis of results of this task.

Procedure

Continuous email and phone contact with each subject was maintained, as the COVID-19 pandemic has halted laboratory studies. Women were informed they would be participating in a study on mental associations across the menstrual cycle. Qualified participants were given a consent form and indicated the address where study materials were to be sent. They received a tutorial film on the microscope and LH test kits use, and a step-by-step diagram with the images of potential microscope results in each phase. Participants then completed the initial online demographic survey, including the training for the Stroop task. After getting the materials, participants were called and had a chance to ask questions. The instructions were discussed once again to ensure women understood them properly. Participants reported the first day of their last menstruation and previous cycles' length and were instructed to monitor their cycle every morning, using a microscope. They were also asked to provide an index of microscope results for each day, marking it in the calendar together with the first day of the following menstruation. We informed them that they should expect to ovulate between days 10 and 17 after menstruation (Holesh et al., 2021 +/− 4 days' deviation). To read the microscope result, they compared the view with three potential result images provided by the microscope manufacturer.

To test for the follicular phase, women reported the onset of menstruation and appropriate microscope image. They got the

link to the survey on the second or third day, to avoid painful symptoms that may accompany the onset of menstruation (Krug et al., 1994). They were asked to inform the experimenter if painful symptoms were salient. If so, the examination time was to be postponed until the following day. To test for the ovulation phase, women reported the appropriate image from the microscope. To confirm ovulation detected by microscope result, they conducted a urine LH test. They sent a picture of LH test kit result to the experimenter, who verified whether it indicated ovulation or not. If not, from that day, the procedure of testing for ovulation with both types of tests was repeated every day until the experimenter assessed the results of testing as positive. If ovulation was not confirmed by both tests until the 17th day of the cycle (Holesh et al., 2021 +/− 4 days' deviation), the whole procedure was repeated in the following ovulatory cycle. If it was confirmed, women were given a survey link. We did not test for creativity unless two tests positively and consistently indicated ovulation. To test for the luteal phase, women reported the 20th day of the cycle and negative result of the microscope test. Survey link was sent to them within a few days, but not earlier than 1 week after the previous measurement. We present the detailed procedure diagram in **Supplementary Figure 2**.

In each phase of the survey, the participants indicated their subjective feeling of arousal and mood (SAM), they marked on the scale how strongly they felt each emotion at the time (UMACL), they performed the Stroop task, and listed unusual uses of the object named on the screen, within a 5-min period (AUT). The following day they completed another survey, testing creative convergent thinking. The survey consisted of marking arousal and valence (SAM), indicating experienced emotions (UMACL), and performing a creative convergent thinking task (RAT), in which participants were asked to find a word associated with three other words shown on the screen within 30 s.

RESULTS

Using IBM SPSS Statistics 25, we first calculated descriptive statistics for all studied variables, both with the Shapiro–Wilk test. Despite the disturbed normality of all variable distributions, a distribution for the vast majority of variables, specifically for these which were expected to replicate the effect of the previous study, was found to be asymmetric to a small extent, as a skewness of it did not exceed a conventional absolute value of 2. Therefore, we assumed it was reasonable to carry out the analysis based on parametric tests. We administered the Repeated Measures Analysis of Variance ANOVA with post-hoc Scheffe test comparisons for homogenous groups, and Games–Howell test comparisons for others. We applied t-tests for dependent samples to compare combined infertile phases to the fertile phase of ovulation. We calculated partial eta squared to measure the effect size in ANOVA models, and Cohen's d in case of t-test comparisons. To correct for multiple testing, we used the Bonferroni correction. Specifically, we used the value of 0.017 as the critical significance level for the comparisons of three phases, and 0.025 for the comparisons of fertile to non-fertile phases. We calculated Kendall W for the inter-rater reliability of creative divergent thinking assessments. To test the hypothesized role of potential mediators, we applied the MEMORE macro from SPSS, which allowed to infer about indirect effects based on 5,000 bootstrap samples in repeated measures (Montoya and Hayes, 2017).

Creative Divergent Thinking

Kendall W for the inter-rater reliability of the divergent thinking scores for the phase of ovulation was: fluency $W = 0.89$, $p < 0.001$, flexibility $W = 0.65$, $p < 0.001$, originality $W = 0.56$, $p < 0.001$. For the follicular phase: fluency $W = 0.98$, $p < 0.001$, flexibility $W = 0.70$, $p < 0.001$, originality $W = 0.52$, $p < 0.001$. For the luteal phase: fluency $W = 0.77$, $p < 0.001$, flexibility $W = 0.70$, $p < 0.001$, originality $W = 0.63$, $p < 0.001$. These results indicated strong raters' cohesion (Moslem et al., 2019).

As shown in **Figure 1** and **Table 1**, participant's ideas were the most original during the phase of ovulation $F(2, 142) = 8.99$, $p < 0.001$, $\eta_p^2 = 0.11$, and the least original during the late luteal phase. Flexibility of thinking was not differentiated between phases, $F(2, 142) = 1.65$, $p = 0.195$, $\eta_p^2 = 0.02$, nor was the fluency, $F < 1$.

As the literature on the ovulatory cycle often reports fertility as a binary categorical variable, we combined the results of divergent thinking from the infertile phases and compared them to the divergent thinking results from the fertile phase. We found originality to be higher during the fertile ($M = 2.32$, $SD = 0.54$) compared to non-fertile phases ($M = 2.08$, $SD = 0.49$), $t(71) = 3.56$, $p < 0.001$, $d = 0.42$. The mean for flexibility was higher in the fertile phase ($M = 4.73$, $SD = 1.75$), comparing to non-fertile ones ($M = 4.49$, $SD = 1.43$). However, as we corrected for multiple testing, this effect reached significance only for one-tailed test, $t(71) = 1.93$, $p = 0.014$ (one-tailed), $d = 0.23$. No differences in fluency were found, $t(71) = 0.16$, $p = 0.874$. $d = 0.02$.

Creative Convergent Thinking

We found no differences in convergent creative thinking, $F < 1$.

Arousal and Its Valence

Participants' general arousal during ovulation was higher compared to other phases, $F(2, 142) = 4.75$, $p = 0.010$, $\eta_p^2 = 0.06$,

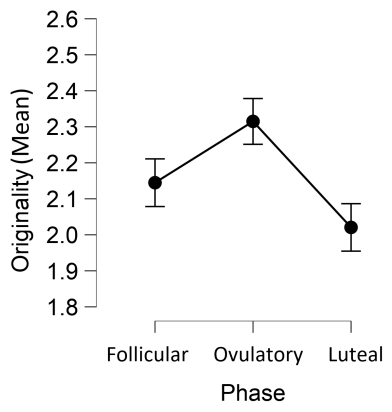

FIGURE 1 | Mean scores of originality of ideas in each phase of the ovulatory cycle.

TABLE 1 | Differences between ovulatory cycle phases in terms of variables studied.

	Follicular		Ovulation		Luteal		*F*	*p*	η^2
	M	*SD*	*M*	*SD*	*M*	*SD*			
Fluency	11.49	6.14	11.57	5.97	11.79	5.56	0.17	0.847	0.00
Flexibility	4.43	1.68	4.73	1.75	4.56	1.57	1.65	0.195	0.02
Originality	2.14	0.56	2.32	0.54	2.02	0.56	8.99	**<0.001**	0.11
Creative convergent thinking	2.01	1.69	2.04	1.61	1.97	1.76	0.04	0.959	0.00
Arousal	2.78	0.98	3.22	0.97	2.79	1.01	4.75	**0.010**	0.06
Valence	3.35	1.14	3.90	0.92	3.68	0.95	5.76	**0.004**	0.08
Energetic arousal	2.67	0.73	3.11	0.68	3.42	0.83	19.07	**<0.001**	0.21
Tense arousal	1.87	0.65	1.71	0.61	2.01	0.36	7.45	**<0.001**	0.10
Hedonic tone	2.79	0.77	3.16	0.65	3.00	0.76	5.56	**0.005**	0.07
Cognitive control	152.97	146.89	170.89	154.18	173.82	152.98	0.33	0.722	0.01

M, mean; SD, standard deviation; F, Anova coefficient; p, level of significance; and η^2, partial eta squared effect size.

with no differences among the other two phases ($p = 0.996$). Its valence was also the most positive during ovulation, $F(2, 142) = 5.76$, $p = 0.004$, $\eta_p^2 = 0.08$ (see **Table 1**).

Mood

Hedonic tone was differentiated between phases, $F(2, 142) = 5.56$, $p = 0.005$, $\eta_p^2 = 0.07$. It was significantly higher during ovulation comparing to the follicular ($p = 0.011$), but not to the luteal phase ($p = 0.424$), with no difference between non-fertile phases ($p = 0.233$). The energetic dimension was also differentiated, $F(2, 142) = 19.07$, $p = 0.001$, $\eta_p^2 = 0.21$. It was higher during luteal compared to follicular phase ($p < 0.001$), but not significantly different compared to ovulation ($p = 0.042$). During ovulation, it was higher compared to follicular phase ($p < 0.001$). Tense dimension was differentiated, $F(2, 142) = 7.45$, $p < 0.001$, $\eta_p^2 = 0.10$. It was similar during the follicular and luteal phases ($p = 0.248$). It was significantly lower during ovulation compared to luteal ($p < 0.001$) but not to follicular phase ($p = 0.297$; see **Table 1**).

Cognitive Control

We found no differences in cognitive control, $F < 1$.

Arousal as a Mediator

To perform mediation analysis, we aggregated data regarding follicular and luteal arousal as infertile phases arousal, and ovulation as fertile phase arousal. Direct effect of originality $b = 0.23$ was significant, as zero fell outside the appropriate 0.95 interval [0.102, 0.363]. Direct effect of arousal was also significant $b = 0.44$, 95% CI[0.169, 0.706]. However, the analysis revealed no indirect (mediating) effect of repeatedly measured arousal, $b = -0.01$, 95% CI[−0.054, 0.040]. Detailed results in **Table 2**.

Positive Mood as a Mediator

We aggregated data on follicular and luteal valence as infertile phases valence, and ovulation as fertile phase valence. Direct effect of valence was significant, $b = 0.27$, 95% CI[0.087, 0.041], however indirect (mediating) effect was not, $b = -0.01$, 95% CI[−0.259, 0.796]. To confirm this effect, we conducted the same analysis using hedonic tone as a mediator. Direct effect of hedonic tone was significant, $b = 0.37$, 95% CI[0.153, 0.583], but the indirect (mediating) effect was not, $b = -0.01$, 95% CI[−0.070, 0.056]. Detailed results in **Table 2**.

DISCUSSION

The aim of the research was to replicate the study investigating enhanced creative potential of fertile women, with the use of more reliable measures of the phases, and more appropriate within-subject design. We tested women during follicular, ovulation, and luteal phases, hypothesizing to find the effect during ovulation. Our hypotheses were based on the signaling theory (Miller, 2000a), which states that creativity may have evolved as a signal for mates. Although we cannot confirm its role as an indicator of fitness, our study suggests that it may be a mental ornament in women, related to the process of sexual selection (Darwin, 1871). Such an ornament should be manifested in the contexts associated with mating, like, for example, during a fertile phase of the ovulatory cycle.

In our study, originality of ideas was enhanced among fertile women. Originality is called an impression stimulator (Runco, 2007), as it affects attention. This sort of saliency starts at the sensory level (Gaspelin and Luck, 2018). As the most captivating feature of creativity, originality is also found to be the strongest predictor of it (Diedrich et al., 2015). There are also various ways to achieve original ideas. Flexibility of thinking can lead to such ideas through breaking patterns (Runco, 2007). In our study, flexibility was not differentiated in the comparison of three phases. But, it was higher during fertile phase, compared to less fertile phases combined. Different processes may also foster originality, for example persistence (Nijstad et al., 2010). Further studies are needed to test this

TABLE 2 | Effect coefficients of the analysis testing arousal and mood as mediators of originality of ideas.

	Arousal				Mood			
			CI 95%*				CI 95%*	
	b	*SE*	*LL*	*UL*	*b*	*SE*	*LL*	*UL*
Ydiff	0.23	0.07	0.102	0.363	0.23	0.07	0.102	0.363
Mdiff	0.44	0.13	0.169	0.706	0.39	0.13	0.136	0.642
Direct	0.24	0.07	0.101	0.382	0.23	0.07	0.092	0.372
Indirect	−0.01	0.02	−0.057	0.039	0.00	0.03	−0.055	0.059

*95% CI is presented as bias-corrected and accelerated 5,000 bootstrapping.

idea. The fluency dimension was not differentiated either. The probability to generate an original idea increases with the number of ideas. However, the number of ideas is not essential, as a creative person may produce only one idea, but it may be an original one (Acar et al., 2017). Women had a similar quantity, but different quality of ideas. Furthermore, this quantity was quite high in each phase (about 11 ideas on average per phase), so we can assume that participants were generally motivated to produce ideas in the study. We cannot exclude the influence of the pandemic, as partial isolation might have affected participants' willingness to engage in any kind of activities related to the outside world, creative activities in particular (Karwowski et al., 2021). This generic increased motivation may have also influenced diversity of their thoughts (flexibility), as this dimension was also not differentiated between phases. However, such motivation was not sufficient to produce similarly original ideas in each phase. Thus, it is difficult to interpret differences in originality between phases in the context of isolation, as it was a fixed condition across the phases. Female's fertility and cycle length are considered to be affected due to illness (Carp-Veliscu et al., 2022) or vaccination (Nguyen et al., 2021). However, the study was conducted in the pre-vaccine (for COVID-19) period. None of the screened participants reported being sick. Morbidity rates during that time were relatively low when we compare them to the following years. However, we cannot exclude asymptomatic cases of COVID-19. We want to emphasize that we did not investigate creativity in participants whose ovulatory cycle was disturbed. The length of all screened cycles was differentiated within a range from 27 to 35 days, so we did not observe notable changes in the cycle length, in the cases when ovulation normally occurred.

Miller (2000a) outlines that creativity, as a subject of selection, concerns a domain associated with aesthetics and fine arts rather than technological innovation. Darwin (1871) pointed to a 'sense of beauty,' suggesting a mechanism for mere aesthetics with no direct benefits. Wallace, on the contrary, pointed to the good-gene, utilitarian model, suggesting signals of vigor and vitality behind the signals of beauty, which started a debate on how exactly the mechanisms of sexual and natural selection interact (Prum, 2012; Hoquet and Levandowsky, 2015). Creative ideas are domain-general and defined as novel and useful (Runco, 2007). However, studies indicate that the effect of novelty is larger than usefulness and the latter is not necessarily predictive of creativity (Diedrich et al., 2015). It is also hard to miss the difference between technology and fine arts. The common variance of creativity and intelligence is found to be moderate, and researchers outline the orthogonality of these two constructs (Runco, 2007). Technological creativity would more likely fit the Wallacean utilitarian view of sexual selection processes (Feist, 2001). As divergent and original thinking is assumed to be independent of IQ (Wallach and Kogan, 1965), in our study we have additionally involved a creative convergent thinking test, reflecting the correlation of creativity and intelligence (Lee et al., 2014), and hence more relevant to survival problem solving. Eventually, we found no differences in these abilities between phases. It leads us to an interesting conclusion, corresponding to the problem of utility or/and beauty aspects of sexual selection. Namely, it is possible that convergent creativity could rather be attributed to natural selection processes, while divergent creativity to sexual selection understood after Darwin (1871) as a non-utilitarian, merely aesthetic mechanism of evolution. Thus, our study suggests that two different types of creativity might have evolved, each one focused on solving problems in different domains, namely survival and reproduction. If so, we should expect divergent creativity, but not the convergent one, to be enhanced in the mating context. This is to be verified in future studies.

The significant role of possible mediators would suggest that creativity may be a by-product of another selection. We tested arousal and positive mood, as they can facilitate creativity (Baas et al., 2008). Men could choose women who were more aroused, or more joyful, not directly creative. Creativity, as facilitated by elevated and activating moods, could have developed in parallel. However, although we found these variables increased during the fertile phase (*vs* infertile phases), we did not detect any mediating effects. Furthermore, both energetic and tense dimensions of mood were the highest during the luteal phase. However, being asked about general arousal, women reported it to be lower comparing to ovulation. We can suppose that during the luteal phase, women experienced mixed emotions. Progesterone may be associated with PMS syndrome (van Wingen et al., 2008), which we did not control unfortunately. But, as estrogen and progesterone act together during the luteal phase, we cannot exclude their

interaction in affecting mood in the way we observed. It is important to note, that we awaited the LH peak during ovulation in our study, which usually co-occurs with a pending decrease of estrogen (Reed and Carr, 2018). Direct hormonal measures are needed to explain the mood effects we obtained.

Fertile phase arousal may manifest differently: as a general arousal on the physiological level, but also as mental, sexual, or motoric stimulation, or even as a motivational boost. It is possible, therefore, that the measures we administered might have not been precise enough and they should be more diversified in future studies. We did not control for premenstrual syndrome, which can also be a confounding variable. Finally, we did not control for typing speed (Forthmann et al., 2017), nor the time of day (Breslin, 2019).[2]

We did not find any differences in cognitive control between the phases; however, this result should be taken with caution. The conditions were not standardized, as the study procedure was conducted *via* the Internet. Participants' PC monitors may differ in size and contrast. Additionally, we were not able to check if all participants did the training as we recommended.

To sum up, the present study replicated the effect of enhanced originality of ideas among women during ovulation (Galasinska and Szymkow, 2021). It suggests that originality in divergent creativity is a plausible candidate for mental ornamentation in women. Being boosted during the fertile phase of the cycle, originality presumably increases mate attraction, potentially leading to conception. Nevertheless, it may also promote intrasexual competition to discourage competitors. More contexts should be studied to confirm the hypothesis on the signaling role of creativity. We presented just one of them, showing that with no other incentives, women may manifest some signals of creativity, which may point to its evolutionary legacy.

[2]Breslin (2019) found that time of day may diversify creative outcomes, with higher effects before noon. Our participants filled out surveys before noon in the vast majority of cases (during the follicular phase, the ratio was 46 women before noon and 25 after noon; during ovulation: 40 before noon, 28 after noon, and during the luteal phase: 44 before noon and 28 after noon). However, the Breslin's effect corresponded particularly with the fluency dimension, which was not differentiated between phases in our study.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/ **Supplementary Material**.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethical Review Board of the Faculty of Psychology in Sopot at SWPS University of Social Sciences and Humanities, Poland. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

KG and AS contributed to the conception of the study and study design. KG conducted the study, organized the database, performed the statistical analysis, and wrote the first draft of the manuscript. AS revised the manuscript critically for important intellectual content. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.859108/full#supplementary-material

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REVIEW
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Sexual Selection and the Treatment of Predecessors' Progeny by Replacement Mates

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Darwin's theory of sexual selection provides a useful framework for understanding the behavior of stepparents. A non-human animal whose new mate has dependent young may kill, ignore, or adopt the predecessor's progeny. The third option has been interpreted as courtship ("mating effort"), and whether selection favors such investment over killing or ignoring the young apparently depends on aspects of the species-typical ecology and demography. The tripartite categorization of responses is a simplification, however, There is variability both within and between species along a continuum from rejection to "full adoption." The average stepparent invests less than the average birth parent, but more than nothing. Human stepparents have often been found to kill young children at higher rates than birth parents, but stepparental infanticide cannot plausibly be interpreted as a human adaptation, both because it is extremely rare and because it is almost certainly more likely to reduce the killer's fitness than to raise it. How sexual selection theory remains relevant to human stepparenting is by suggesting testable hypotheses about predictors of the variability in stepparental investment.

Keywords: Cinderella effects, mating effort, parental investment, sexual selection, stepchild, stepparent

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INTRODUCTION

Darwin's (1871) theory of "sexual selection" initially drew a much cooler response than had been the case with his great treatise on "natural selection" 12 years previously. Even biologists who were totally on board with the earlier theory, including its co-discoverer Alfred Russel Wallace, were skeptical (Richards, 2017). Many thinkers who were prepared to accept the proposition that differential efficacy in coping with extrinsic environmental factors could give direction to the evolution of phenotypes nevertheless balked at the idea that intra-specific interactions could play a similar selective role (Gayon, 2010).

A hundred years later, Darwin's second great theory had still inspired little further theorizing apart from Fisher's (1915, 1930) theory of the "runaway" process, and scarcely more empirical work. Then research on sexual selection suddenly blossomed, and in the 1970s and 1980s, many hundreds of studies of mating competition and mate choice were published (see e.g., Thornhill and Alcock, 1983; Eberhard, 1985; Andersson, 1994), vastly more, in fact, than the number of studies of natural selection by the extra-specific environment (Endler, 1986).

An important stimulus for this belated blossoming was the publication of *Sexual Selection and the Descent of Man, 1871–1971*, an edited volume celebrating the centenary of Darwin's opus (Campbell, 1972). This compendium included chapters by such luminaries as Loren Eiseley, George Gaylord Simpson, Theodosius Dobzhansky, and Ernst Mayr, but in a review in *Science*,

George Williams (1973) proposed that "Parental investment and sexual selection" by the relatively unknown Robert Trivers (1972) was one of two chapters that would turn out to be "the most permanently valuable part of the book" (p. 788). In this prediction, Williams was, as usual, prescient. In the ensuing half century, Trivers's richly detailed argument that differential "parental investment" is the key to understanding the operation and outcomes of sexual selection has undeniably had the greatest influence on both research and further theorizing (Andersson, 1994; Mogilski, 2021).

SEXUALLY SELECTED INFANTICIDE

Sarah Blaffer Hrdy was a graduate student pursuing primatological research in India when the new enthusiasm for sexual selection was sweeping through animal behavior. Trivers was a member of her supervisory committee and visited her at her field site in Abu, Rajasthan. Her first empirical publication (Hrdy, 1974) was about "male-male competition and infanticide" in the Hanuman langurs she studied, and in her acknowledgments, she credited the "inspirational teaching of R.L. Trivers, whose ideas are fundamental to this paper" (p. 55).

A one-male, multi-female troop structure was characteristic of Hrdy's monkey subjects, and bachelor males regularly tried to overthrow current resident breeders. Whenever one of these "political changes" succeeded, Hrdy observed that nursing infants in the troop soon disappeared, and on a few occasions, she or a local informant directly observed a new male's fatal attack. Inferring that such attacks probably caused the unwitnessed deaths as well, Hrdy advanced an explanation in terms of sexual selection: Under conditions like those prevailing at Abu, "infanticide might permit an incoming male to use his short reign over a troop more efficiently. By eliminating an infant unlikely to be his own, a newcomer could hasten the mother's return to sexual receptivity so that she could then bear his own offspring" (p. 46). Although she clearly favored this hypothesis, and bolstered it with an abundance of observational and circumstantial evidence, she also identified areas where further evidence would be needed to conclusively dispose of the alternative possibility that infanticide was just a non-adaptive byproduct of something else.

Early reaction to Hrdy's argument was muted and mixed, but she inspired some researchers (e.g., Bertram, 1975), and she soon captured the attention of a larger audience with an article (Hrdy, 1977) in the *American Scientist*, a semi-popular magazine whose subscribers, in a pre-internet age, included many behavioral biologists. Here, she was no longer so cautious: Her title, in a large bold font, was "Infanticide as a Primate Reproductive Strategy" and a subheading, also in an over-sized font, read "Conflict is basic to all creatures that reproduce sexually, because the genotypes, and hence self-interests, of consorts are necessarily non-identical. Infanticide among langurs illustrates an extreme form of this conflict." She clearly explained the theory while providing engaging accounts of her observations, of relevant langur natural history, and of prior observations, extending back more than a century, which had partially anticipated and now reinforced her insights. Hrdy (1979) followed up with a substantial, scholarly treatment of the theory's applicability to a wider range of animals than just primates.

Some authors (e.g., Curtin and Dolhinow, 1978; Sussman et al., 1994) opposed the sexual selection hypothesis, arguing that infanticide was better interpreted as a maladaptive response to one or another sort of human interference, but in our view, this thesis never fit the facts very well. The timing and selectivity of infanticide, as well as an accumulating body of observational evidence that males of several species systematically stalked and calmly dispatched their victims, seemed clearly to fulfill Williams's (1966) "design" criteria for the identification of an adaptation. In retrospect, the tenacity of those who insisted that infanticide must be pathological seems best interpreted as exemplary of "naturalistic fallacy" thinking whereby only "good" things could be "natural," along with a dollop of the naïve group-level adaptationism that Williams (1966) had demolished, and the equally naïve anti-adaptationism that Mayr (1983) and others eventually sent packing (Alcock, 2003).

Hrdy's sexually selected infanticide hypothesis has been widely vindicated, and no serious controversy remains about its applicability to various species in the natural world (Parmigiani and vom Saal, 1994; Ebensperger, 1998; Packer, 2000; Van Schaik and Janson, 2000; Palombit, 2012; Lukas and Huchard, 2014). Such behavior is by no means ubiquitous, however, and its distribution demands explanation.

KILL, IGNORE, OR ADOPT?

The best documented cases of sexually selected infanticide initially came from studies of mammals, and the perpetrators were always males. Female mammals also kill young who are not their own, but never in order to usurp the parental efforts of the fathers (Lukas and Huchard, 2019). Indeed, Hrdy's original statement of the hypothesis, quoted above, was premised on the idea that the mammalian female's obligate investment of time in gestation and lactation constitutes a contested limiting reproductive resource from the male perspective.

In other vertebrate classes, the situation facing the two sexes is often crucially different. Females usually oviposit shortly after their eggs are fertilized (birds), or even before (many fishes and amphibians), with the effect that major male roles in even the earliest forms of parental care can more readily evolve. One consequence has been the recurrent evolution of what is, from our mammal-centric perspective, "sex role reversal" (Eens and Pinxten, 2000; Janicke et al., 2016). In several species of Charadriiform shorebirds, for example, males incubate the eggs and guard the hatchlings alone, and in some of these, females are bigger and brighter than males, mate polyandrously, and defend a territory that incorporates the smaller territories of two or more males (Jenni, 1974). From the perspective of a female who has ousted a rival territory-holder, any male who is incubating her predecessor's eggs is wasting time and energy, and such females sometimes set about destroying those eggs (Stephens, 1982; Emlen et al., 1989).

This sort of sex role reversal is rather rare even among birds, however (Cockburn, 2006). More than 90% of avian species are socially monogamous, and more often than not, parental care is provided by both mates. In a few such species, replacement mates of both sexes may kill their predecessors' nestlings after pairing up with a widowed or deserted partner (e.g., Freed, 1986; Veiga, 1990; Chek and Robertson, 1991), but providing care to a new partner's dependent young is also a common response, and simply ignoring them is another. What explains the variability? Oddly, although infanticide and "stepparental adoption" present as polar opposites, there is good reason to believe that sexual selection explains both. Does this mean that whatever we might discover can be "explained" *post hoc* by the theory of sexual selection, which is thus predictively empty? Not if the theory directs us to hypotheses about likely correlates and predictors of these alternative responses.

Rohwer (1986) was the first to articulate the problem in these terms. On this basis, he proposed several possible correlates of the alternative responses of avian "stepparents," and then reviewed the available evidence. He began by framing the quest for adaptationist explanations as one of "asking when adoption rather than infanticide will maximize the residual reproductive value (Williams, 1966) of sexually and socially mature adults confronted with unrelated but dependent young who have lost a parent" (Rohwer, 1986: 354). Under what conditions would one response or the other elevate the replacement mate's chances of rearing future broods with the new partner, or perhaps even with other potential partners? In a migratory songbird species with high adult mortality, a low incidence of breeding with the same partner in successive years, and a diminishing chance of successful renesting as the breeding season ticks away, a fitness payoff from stepparental care is unlikely, and such birds commonly kill. In a non-migratory species in which pair bonds may endure for years, by contrast, a widowed parent of unfledged young has more leverage to make stepparental "adoption" the price of re-partnering. More generally, relevant considerations include whether mates and/or territories are scarce, whether renesting in the same season is feasible, how long pair bonds can persist, whether territories and pair bonds are maintained or abandoned after brood failure, whether helping or infanticide or both help maintain the new mate's residual reproductive value, and to what degree providing care to unrelated young entails lost opportunities or other costs. The evidence that Rohwer (1986) was able to muster was spotty and often anecdotal, but in general, it supported his hypothesis that the cross-species variation in the behavior of stepparents is attuned to social and ecological determinants of the fitness consequences of the alternatives.

Rohwer et al. (1999) updated the initial review's arguments and evidence, finding further support for the hypothesis that stepparenting functions as "mating effort" in birds and in other taxa as well, and drew this conclusion: "The principal lesson of this review for students of the human animal is that investing stepparents are neither peculiar to our species nor beyond adaptationist explanation. Although stepparental infanticide occurs in many diverse taxa, it perhaps even more often is the case that non-human stepparents tolerate and care for their wards. And although many puzzling cases remain to be fully explained, it appears that stepparental tolerance and care are best interpreted as acceptable costs of courtship" (p. 386–387).

Although Rohwer (1986) initially drew a categorical distinction between "ignoring" a new partner's offspring and "full adoption," there are intermediate possibilities, and the Rohwer et al. (1999) review describes a number of cases that appear to occupy this middle ground. In both Western and Eastern Bluebirds, for example, stepfathers sometimes feed the young, but they do so at substantially lower rates than fathers (Meek and Robertson, 1992; Dickinson and Weathers, 1999). We suggest that this middle ground is also where the typical behavior of human stepparents falls.

HOMO SAPIENS IS A STEPPARENTING SPECIES

The "mating effort" interpretation of stepparental tolerance and care seems clearly to be applicable to our own species (Anderson, 2000; Gray and Anderson, 2010). The stepparent-stepchild relationship is an ancient and cross-culturally universal element of human societies. The effects of several considerations–our species' lengthy period of childhood and juvenile dependency, the unique degree to which people invest simultaneously in children of different ages, and appreciable incidences of both mortality and divorce during the reproductive years–have long combined to ensure that many single parents re-entered mating markets. A common recourse of widowed or divorced parents is to foster their dependents to trustworthy kin, especially grandmothers, and to then re-enter the mating market unencumbered (Rende Taylor, 2005; Scelza and Silk, 2014; Perry, 2021), but many others retain their children when they "remarry" (in the broad sense, i.e., including *de facto* unions). There is no reason to doubt that these things have been true for hundreds of generations.

The "family studies" literature is potentially misleading in these regards. Focusing solely on trends in the rich world over a few decades, many social scientists have endorsed Cherlin's (1978) proposal that stepparenthood is a "new role" whose tensions derive from the fact that relevant norms are still being worked out. However, the incidence of stepparenthood was actually higher in recent centuries than it is today, mainly because of higher mortality in young adulthood (e.g., Dupâquier et al., 1981). For example, about a third of the female population of two 19th century cities in Netherlands had been widowed at least once by the age of menopause (Van Poppel, 1995). And whereas contemporary infants and toddlers very rarely reside with father and stepmother, this is and was much more prevalent in societies with substantial levels of maternal mortality (Warner, 2018). Perhaps most importantly, studies of contemporary foragers, who provide our best models of deep human history, often indicate that their children were substantially more likely to reside with stepfathers than children in any modern nation state (e.g., Hewlett, 1991; Hill and Hurtado, 1996; Marlowe, 1999). The adaptive problems that stepfamily formation presents have been components of human social life for many millenia, and the psychology of a nuanced response to the demands of children who are not one's own has furthermore evolved in a highly social

context of alloparental care by other interested parties as well as stepparents (Burkart et al., 2009).

There is abundant evidence that the feelings and behavior of human stepparents differ from those of birth parents in ways that are consistent with the view that stepparents are more restrained in their willingness to invest (reviews by Daly and Wilson, 1988, 1994b, 1996, 1998, 2008). Examples include differential expressed affection (e.g., Duberman, 1975), the greater prominence of child support as a source of marital strife in stepfamilies than in birth families (e.g., Messinger, 1976), and differential treatment in domains ranging from hostile interactions (e.g., Flinn, 1988) and vigilance (e.g., Tooley et al., 2006) through ensuring children's medical and dental health (Case and Paxson, 2001) to financial support (e.g., Zvoch, 1999), bequests (e.g., Erixson and Ohlsson, 2019), and various sorts of helping out (e.g., Anderson et al., 1999; Daly and Perry, 2021).

Daly and Wilson (1998) dubbed such manifestations of preference for birth children over stepchildren "Cinderella effects." This label, which has caught on, was perhaps unfortunate because the fairy-tale Cinderella was the victim of a discriminative stepmother whereas most research on the phenomenon has concerned stepfather families (Daly and Wilson, 2008). That said, however, it is clear that stepparents of both sexes discriminate. Studies of US household expenditures have been particularly enlightening in this regard: Princeton economist Anne Case and collaborators have shown that children with stepmothers suffer reduced support, net of family income, in domains that are largely under female control, such as medical checkups and expenditures on food, whereas it is on "big ticket" items such as tuition fees that they are disadvantaged in stepfather households (Case et al., 2000, 2001; Case and Paxson, 2001).

"CINDERELLA EFFECTS" IN VIOLENCE AGAINST CHILDREN

The various Cinderella effects described in the preceding paragraphs were documented in samples of parents that were drawn in such a way as to be representative of their respective populations, and presumably portray average levels of discrimination by parents in general. A less frequent but extremely serious domain of stepchild disadvantage is that of child maltreatment, and it is in the most extreme forms that the largest Cinderella effects have been found. In "baby battering" cases in which shaking and/or blows to the head or abdomen by enraged caretakers were fatal, the case numbers are often indicative of a greater risk at the hands of stepfathers than birth fathers on the order of 100-fold or more. In the first published report exemplifying this contrast, Scott (1973) reported that male perpetrators charged with fatal baby battering in a jurisdiction in the south of England consisted of 14 "putative fathers" and 15 stepfathers, whereas a national survey of a 1970 birth cohort (Wadsworth et al., 1983) indicates that coresiding birth fathers would have outnumbered stepfathers by more than 100 to 1 in a population-at-large sample with the same age distribution as that of the battering victims. The most extreme example of which we are aware comes from Australia: Wallace (1986) reported that the perpetrators of fatal baby battering in New South Wales in 1968–1981 included 17 stepfathers, 11 putative genetic fathers, and one adoptive father. When Australian household survey data are used to estimate living arrangements in the population-at-large, Wallace's data indicate a Cinderella effect of about 300-fold (Daly and Wilson, 2008). For additional examples, see Daly and Wilson (2008) and Daly (2022).

The evidence regarding lethal abuse by stepmothers is much sparser than is the case for stepfathers. Although stepmother cases exist in all large homicide data sets, small children so rarely reside with them that any estimate of a homicide rate must have huge confidence intervals. However, on the basis of analyses of national data from the FBI, Weekes-Shackelford and Shackelford (2004) were able to estimate rates indicating that US stepmothers, like stepfathers, were substantially and significantly more likely to kill young children than birth mothers. This is impressive when one considers that the birth mother cases included neonaticides, a very different sort of killings that often constitutes almost half of all filicides. However, a problem with this FBI data set is that the codes for "stepmothers" and "stepfathers" were not typically applied in cases where the killer's partnership with the birth parent was a *de facto* marriage (Daly, 2022).

Stepmother-stepfather comparisons can be made with more confidence when we turn to non-lethal child abuse. Daly and Wilson (1981) and Creighton and Noyes (1989) analyzed large data sets of mandated abuse reports from the United States and the United Kingdom, respectively. Both data sets contained many stepmother cases, and in both, the rates of validated physical abuse in stepmother and stepfather households were roughly similar and far in excess of those in two-birth-parent households. A different sort of evidence comes from an interview study of South Korean schoolchildren, who reported identical rates of having been beaten at home in stepmother and stepfather households, both rates again far in excess of what children living with both birth parents reported (Kim and Ko, 1990). Finally, stepmother households are sometimes even more extremely overrepresented than stepfather households in the domestic circumstances of adolescent runaways who testify that they are fleeing abusive homes (e.g., Powers et al., 1990).

Oddly, although massive Cinderella effects in child homicide have been well documented in several countries, there have been relentless efforts to promote skepticism about their reality. Detailed rebuttals of some prominent examples are provided by Daly and Wilson (1998, 2001, 2008) and Daly (2022). Perhaps this "disinformation campaign" (Wilson and Daly, 1999) has been motivated by a wish to destigmatize stepparents who are doing their best in emotionally trying circumstances, but it does a disservice to the goal of establishing evidence-based child protection policies and practice (Perry and Daly, in press).

STEPPARENTAL AMBIVALENCE AND RESENTMENT

Can infant-killing by replacement mates be understood as a sexually selected adaptation in human beings, as it is in Hanuman langurs, lions, and many other species? Clearly not! Infanticide

by human stepparents fulfills none of the criteria for identifying adaptation, as laid out by Williams (1966) and further discussed by Mayr (1983) and Andrews et al. (2002). First, in no society or situation is it routine; although the rate at which Canadian preschoolers were beaten to death by coresiding stepfathers in 1974–1990, for example, was more than 120 times the corresponding rate at the hands of coresiding birth fathers, the higher rate by stepfathers still amounts to less than one death per 3000 children at risk per annum (Daly and Wilson, 2001). Furthermore, there are no data supporting the hypothesis that killing stepchildren enhances or ever enhanced the killers' average fitness in any human society; even in traditional societies without formal institutions of law enforcement, self-interested violence is constrained by the threat of vengeance (McCullough, 2008) and those suspected of killing even an infant risk becoming targets of the victim's kin (e.g., Chagnon, 1988). But perhaps the most telling evidence against the hypothesis that killings of stepchildren are the direct expressions of an adaptation is that they are typically performed with spectacular inefficiency: Post-mortem examinations of victims often uncover a prior history of weeks or months of non-fatal assaults (e.g., Scott, 1973), and for every stepparent who kills, there are a great many more who inflict non-lethal damage that raises their own and their partners' investment costs. This is not well-organized, fitness-enhancing behavior! Thus, rather than being an adaptation in its own right, the Cinderella effect in child homicides is best interpreted as a non-adaptive byproduct of discriminative parental solicitude (Daly and Wilson, 1980, 1988), which, like psychological adaptations generally, serves its possessor's interests on average but not in every instance.

We moved to New Zealand in May, 2019, and with long-standing interests in family violence and substitute parenthood, we were curious to see where our new home stood with respect to these problems. Soon after our arrival, a relevant murder trial was in the news (New Zealand Herald, 2019). On June 11, 2018, a 5-month old infant named Lincoln Wakefield had been shaken so violently that he died of the resultant brain injuries. An autopsy revealed that it was not the first time that he had been shaken with sufficient force to damage his brain. The baby's mother had been pregnant with Lincoln when she and William met and began dating, and they had set up house together before the birth. Wakefield could work from home, and he encouraged his new partner to return to her job while he cared for the baby. When interviewed by the police on the day of Lincoln's death, Wakefield eventually confessed to having administered the lethal shaking, explaining his state of mind thus: "I was just gutted he wasn't mine, to be honest. I just wanted to hurt him until he wasn't there," later adding "I was in my own stupid world. I don't know why I did it. He's just not mine. It's hard for me to look at him." Wakefield denied acting with intent to kill, and offered to plead guilty to manslaughter, but on the day that would have been baby Lincoln's first birthday, Wakefield was convicted of murder, and given a life sentence. When pronouncing sentence, Justice Dobson addressed the convicted killer, summarizing the picture that he had gained of Wakefield's mental state in these words: "You tried to deal fondly with Lincoln, but his physical appearance reminded you of his biological father, and increasingly you resented that." Turning to the court, Justice Dobson added "Baby killings by men who are not the biological fathers of their partners' children happen far too often in New Zealand." Sadly, New Zealand is not exceptional in this regard.

Filicides by birth fathers differ from those perpetrated by stepfathers in ways that indicate distinct motives. Daly and Wilson (1994a) reported that over 80% of preschoolers killed by stepfathers in both Canada and Britain died from beatings and/or blunt force trauma, whereas fewer than 50% of the victims of birth fathers were killed in the same way. These results were closely replicated in Weekes-Shackelford and Shackelford's (2004) analyses of United States data, and clearly imply that impulsive rage reactions are involved in a majority of killings by stepfathers, but in far fewer of those by birth fathers. In all data sets, antipathy toward the child is apparently absent in many birth father cases, and at least a few are misguided "mercy killings," but in many more cases, filicidal fathers are more depressed than angry. Daly and Wilson (1994a) found that 44% of Canadian men who killed birth children of preschool age committed suicide at the scene of the crime, compared to just 1.5% of those slew stepchildren; directionally similar but less dramatic contrasts were again evident in the British and United States data, too.

These contrasts between filicides perpetrated by stepfathers and those by birth fathers are readily interpreted as indicative of motivational differences whereby stepfathers more often resent the children and their obligations to them. Killings by birth fathers are sometimes brutal, too, but they are proportionately more likely to involve smothering, gassing, and other less assaultive methods. And even when the cases are brutal, filicidal birth fathers rarely if ever offer explanations for their acts like that of another New Zealander who recently killed his 17-month-old stepson when asked to look after him while the mother went out with a girlfriend: In the agreed statement of facts presented at his trial, the killer explained that he was "tired of being treated as the babysitter" (Stuff, 2020). Parental investment is motivated by parents' intrinsic interest in their children's wellbeing. Stepparental investment, by contrast, is a courtship gesture and a service offered to the new partner, and when stepparents feel that their contributions are insufficiently appreciated and reciprocated, they are apt to become resentful.

There is a large professional literature, and an even larger self-help literature, dealing with reducing tensions in stepfamilies. One point on which there appears to be near unanimity is that it is a mistake to pretend that a stepfamily is a birth family, or to expect that it will, with time, become psychologically indistinguishable from one (e.g., Johnson, 1980; Turnbull and Turnbull, 1983). The Wakefield case provides a poignant example: Registering the baby's birth with the stepfather's surname did not alleviate Wakefield's distress that Lincoln was "not mine" and may even have exacerbated it.

CONCLUSION

It warrants emphasis that stepparent-stepchild relationships need not be toxic, and usually are not. Many children benefit from

the presence and involvement of a stepparent (Booth and Dunn, 1994; Thomson et al., 1994) and only occasionally is the average stepchild found to fare worse on some particular measure than the average child raised by a single parent (e.g., McLanahan and Sandefur, 1994; Adjiwanou et al., 2021). Stepparents make valuable investments in stepchildren, even if those investments are restrained relative to those of "natural" (i.e., birth) parents. It is therefore important to investigate what predicts positive stepparental investment, rather than rejection and exploitation, as well as what predicts its variable magnitude. One clearly relevant variable affecting investment by stepfathers is whether they have birth children residing elsewhere (e.g., Hofferth and Anderson, 2003). We suggest that the degree to which their contributions are appreciatively acknowledged may be another, but a good test of this hypothesis will not be easy.

It is often suggested that if a stepfather had been able to bond with his stepchild from birth, he would feel and act like a birth father. The Wakefield case provides reason to doubt this, and so does the only systematic test of which we are aware: In an observational study of men's interactions with children in a Trinidadian village, Flinn (1988) found not only that stepfathers behaved more "agonistically" toward their partners' children than did the (presumed) genetic fathers, but also that the several stepfathers who had, like Wakefield, begun cohabiting with women who were already pregnant by other men were significantly *more* hostile toward the resultant stepchildren than other stepfathers, despite having resided with them from birth.

That said, there is evidence that ratings of stepparent-stepchild relationship quality, net of the stepchild's current age, increase as a function of the relationship's duration (e.g., Hornstra et al., 2020). To what extent this reflects improvement with time is uncertain, however, since selection (in the sociological rather than Darwinian sense of "selection") will tend to produce the same pattern, for two reasons. The first is that remarriages with stepchildren are much less stable than first marriages or remarriages without children (e.g., White and Booth, 1985) and marital dissolution is surely selective for conflict-proneness. The second sort of selection occurs when adolescents "vote with their feet": Stepchildren leave home at earlier average ages than children living with two birth parents (e.g., Kiernan, 1992; Zhao et al., 1995; Davis and Daly, 1997), are massively over-represented among homeless youth (Kufeldt and Nimmo, 1987; Powers et al., 1990), and increasingly have the option of moving to the other birth parent's home. These selection effects especially challenge interpretation of data from one-off surveys, but they also apply to longitudinal studies with non-negligible drop-out rates since the respondents who are retained may differ systematically from those who drop out.

Rohwer (1986) proposed that the variability among species in their responses to step-offspring ("kill, ignore, or adopt") can be explained as adaptive responses to ecological and demographic variables that affect the alternatives' expected fitness effects. Can these principles help explain variability of response within species, too, even within *Homo sapiens*? We have argued that killing stepchildren has clearly not been selected for in the human animal, but must instead be understood as the maladaptive tail of the "rejection" end of an invest-reject distribution, and that non-lethal abuse of a sort that damages the child and thereby raises investment costs is surely maladaptive, too. However, there is a range of lesser forms of maltreatment that may or may not serve the pertrator's interests, and one might, in principle, propose hypotheses about specific, fine-grained, forms of investment and divestment. We suggest, however, that the adaptations underlying partial investment are probably best characterized at the abstract level of discriminative parental solicitude, and the most promising adaptationist hypotheses for future research are likely to be ones that concern facultative responsiveness to the same ecological and demographic variables that are relevant to the cross-species variability in stepparental response that Rohwer first described and discussed. Candidate variables include cues of local sex ratios and of the local levels of marital stability, mortality, requisite resources (e.g., Willführ and Gagnon, 2013). and environmental predictability, as well as the reproductive values of both mates, child attributes, and whether and to what degree investing in the children will diminish or enhance those values. In short, attention to theory and research on sexual selection promises to inspire and inform future studies of stepfamily dynamics.

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MD wrote the manuscript and GP edited it. Both authors conceived the manuscript together, contributed to the article, and approved the submitted version.

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Women's Estrus and Extended Sexuality: Reflections on Empirical Patterns and Fundamental Theoretical Issues

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How do women's sexual interests change across their ovulatory cycles? This question is one of the most enduring within the human evolutionary behavioral sciences. Yet definitive, agreed-upon answers remain elusive. One empirical pattern appears to be robust: Women experience greater levels of sexual desire and interest when conceptive during their cycles. But this pattern is not straightforward or self-explanatory. We lay out multiple possible, broad explanations for it. Based on selectionist reasoning, we argue that the conditions that give rise to sexual interests during conceptive and non-conceptive phases are likely to differ. Because conceptive and non-conceptive sex have distinct functions, the sexual interests during conceptive and non-conceptive phases are likely to have different strategic ends. We discuss provisional evidence consistent with this perspective. But the exact nature of women's dual sexuality, if it exists, remains unclear. Additional empirical research is needed. But perhaps more crucially, this topic demands additional theory that fruitfully guides and interprets future empirical research.

Keywords: menstrual cycle, fertility, sexual desire, mating, ovulation

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INTRODUCTION

In *The descent of man and selection in relation to sex*, Darwin (1871) introduced the concept of *sexual selection*: "We are, however, here concerned only with that kind of selection, which I have called sexual selection. This depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" [p. 256). Sexual selection received scant attention for a century following this debut (an important exception being Fisher (1930)]. A volume dedicated to the 100-year anniversary of Darwin's book, edited by Campbell (1972), prompted a sea change. In one chapter, Mayr (1972) tackled the important question of what exactly discriminates sexual selection from natural selection, an issue still debated today. In a book review, Williams (1973) offered the prescient observation that Trivers's (1972) chapter on parental investment and sexual selection was among "what may be the most permanently valuable part of the book" (p. 788)—in retrospect, a vast understatement. Its legacy owes more to it promoting adaptationist analysis in *strategic* terms than to particular claims about sexual selection (some of which have been revisited; e.g., Kokko and Jennions, 2008). As Williams summarized, "An organism is represented, in effect, as a player in a game the object of which is to maximize the representation of one's genes … in the population to which one belongs. Sexual reproduction and family life are seen as a complex system of mutual exploitation, conflict, compromise, and cautious coalitions, with each player totally committed to maximizing its own score" (Williams, 1973, p. 788).

As evolutionary psychology sprouted from adaptationist frameworks inspired by Williams, Trivers, Hamilton, and a host of their contemporaries (e.g., Tooby and Cosmides, 1992), it is no wonder that its *functional* analyses of psychological adaptations are very often *strategic* analyses; that is, the functions of psychological adaptations are often understood in terms of how they facilitate individuals' strategic aims.

In this paper, we discuss a long-standing issue in evolutionary behavioral science: How women's sexual interests shift across their menstrual cycles from conceptive to non-conceptive phases, purportedly largely through regulatory effects of ovarian hormones. Conceptive and non-conceptive sexual phases very likely have distinct functions and, hence, ancestrally benefitted women in different ways. A functional analysis therefore leads to a strategic analysis. How do women's sexual interests during different phases of the cycle strategically promote their fitness interests? Though proposals to date have identified some strategic shifts (e.g., increased sexual interests when women are conceptive may "strategically" lead to increased rates of conception), additional strategic analyses (perhaps especially of non-conceptive sexuality) are needed. Our paper is a conceptual one; we do not offer strong claims with respect to empirical patterns. We argue that progress toward understanding human sexual selection and the evolution of human mating could benefit from a more thorough-going commitment to strategic analysis in this domain.

WOMEN'S PURPORTED LOSS OF ESTRUS

> *Estrus is the relatively brief period of proceptivity, receptivity, and attractivity in female mammals that usually, but not invariably, coincides with their brief period of fertility. Human females do not experience estrus. … [E]strus must have been lost at some point in human ancestry.* (Symons, 1979, p. 97).
>
> *Beach goes on to say, "Although human females are not continuously 'sexually receptive,' they are continuously 'copulable'; and their sexual arousability does not depend on ovarian hormones. This relaxation of endocrine control contributes to the occurrence of coitus at any stage of the menstrual cycle" (pp. 357–358). I believe that this is the clearest available statement of what the "loss of estrus" means.* (Symons, 1979, p. 106).

How do women's sexual interests change across their ovulatory cycles? This question is one of the most enduring within the human evolutionary behavioral sciences. Psychological changes across women's cycles have long been thought to embody design features important to inferring the nature of selection pressures that uniquely shaped human sociality. In the two quotes above, from *The Evolution of Human Sexuality*, Symons (1979) states, first, that estrus was lost in women (see also Lancaster and Lee, 1965; Jolly, 1972) and, second, that this loss of estrus effectively amounts to a relaxation of endocrine control over women's sexual arousability. In Symons' view, a key to understanding the evolution of human sexual relations is explaining why women lost estrus and became capable of experiencing sexual arousal across the cycle. Within just a few years following publication of his book, a number of accounts were proposed (Alexander and Noonan, 1979; Benshoof and Thornhill, 1979; Burley, 1979; Symons, 1979).

Nearly four decades later, scores of studies have sought to investigate how women's sexual desire, sexual interests, mating priorities, and mating behavior systematically change across the cycle, as well as the hormonal contributions to these changes (for partial reviews, see Thornhill and Gangestad, 2008; Roney and Simmons, 2013; Gildersleeve et al., 2014a; Gangestad et al., 2021; Roney, 2021; Stern and Penke, 2021; Havlíček and Roberts, in press). A tremendous amount of progress has been made. For instance, the robustness of some empirical patterns that was once questioned is now well-established. On average across women, robust mid-cycle increases in sexual desire has been repeatedly demonstrated (reviewed below in the section, "Change in Sexual Interests Across the Cycle"). Yet there is no clear agreement about these how changes (or lack thereof) should be understood. A variety of theoretical perspectives, which predict different empirical patterns, have been proposed. None is near-universally accepted. Despite some robust empirical patterns, the literature is marked with several large-scale failures to replicate effects once thought to be well-established. Hence, ambiguities about what basic phenomena exist and require explanation persist, a major reason why fundamental questions endure.

This paper reflects on this literature and the key theoretical issues that persist. It consists of four major sections.

First, we begin by discussing some generally well-established empirical patterns. In particular, studies generally support the notion that ovarian hormones affect mean levels of sexual interest. During cycle phases with elevated estradiol and/or diminished progesterone levels, women experience, on average, greater levels of sexual interest.

Second, we describe two broad, alternative perspectives on the nature of female sexual interests and hormonal effects on sexual interests. One perspective argues that hormones affect libido—a generalized state of increased sexual interest. A second perspective views sexual desire as evoked by specific circumstances (sexual "incentives"). In this view, hormones affect the circumstances that evoke sexual interest—that is, hormones moderate the influence that particular conditions and mate features have on sexual interests.

Third, we discuss the evolution of "extended sexuality"—female sexuality during phases when sex cannot lead to conception. Naturally, non-conceptive sex evolved to serve functions other than conception. We illustrate this point with instances of extended sexuality in non-human primates. We argue that, given that extended sexuality *functions* differently from conceptive sexuality, the adaptive *strategies* embodied within extended sexuality should differ from those embodied within conceptive sexuality. Hence, on grounds of *a priori* evolution-inspired theory, the circumstances that evoke sexual interests during extended sexual interests during non-conceptive phases should differ from those that evoke sexual interests when sex is conceptive.

Fourth, we briefly discuss literature in light of these expectations. We describe several patterns consistent with the idea that the conditions that evoke sexual interests when women are conceptive do not perfectly match the conditions that evoke

sexual interests when they are non-conceptive. Nonetheless, much more empirical work is needed in this domain. Indeed, theoretical avenues necessary to make sense of phenomena in this domain have yet to be fully laid out and explored. We also note theoretical implications of the possibility that expected patterns are not realized.

CHANGE IN SEXUAL INTERESTS ACROSS THE CYCLE

In a remarkable study, Roney and Simmons (2013) asked 43 naturally ovulating women to complete a daily diary, which included daily ratings of women's sexual desire, over the course of up to two full cycles. Saliva was collected nearly every day for assays of estradiol, progesterone, and testosterone. In a mixed model regression analysis, within-woman variations in estradiol levels (characteristically high during the conceptive, late follicular phase) positively predicted sexual desire, whereas within-woman variations in progesterone levels (characteristically low during the late follicular phase) negatively predicted it. These associations gave rise to a peri-ovulatory rise in sexual desire.

Other studies have also yielded evidence that women experience heightened sexual interest during the peri-ovulatory phase. In a study of 35 women followed across a cycle, Mass et al. (2009) similarly reported a follicular phase peak in self-reported sexual desire. Women were also video-recorded while viewing a series of erotic pictures of attractive, masculine men and non-sexual control stimuli (kittens and rabbits). During the follicular phase, women exhibited more expressions associated with pleasure when viewing nude men. Rudski et al. (2011) asked women to describe implicitly erotic art (e.g., Georgia O'Keefe's flower paintings). Descriptions written in the follicular phase contained markedly more sexual references than those written during the luteal phase. Near ovulation, women's dreams include greater sexual content (Natale et al., 2003) and, when given a choice of a film to view, they are more likely to choose an erotic one (Zillmann et al., 1994). From a study of 259 naturally cycling women followed over two cycles, Prasad et al. (2014) reported a mid-cycle spike in sexual activity linked with higher same-day estradiol and LH levels (though they did not detect an impact of progesterone levels). Another study that followed several hundred women over five sessions found negative impacts of progesterone on sexual desire (Jones et al., 2018a). A number of studies have reported midcycle increases in women's attraction to men other than primary partners (Gangestad et al., 2002, 2005; Durante and Li, 2009; cf. Jones et al., 2018a; Shirazi et al., 2019b). In large samples of partnered women followed across at least one full cycle, Arslan et al. (2018) found robust increases in both in-pair and extra-pair sexual interest with increased conception risk (see also Shirazi et al., 2019a). And, in a study of ∼3 million women from nearly 150 countries worldwide, Pierson et al. (2021) reported that women were ∼3–5% more likely to engage in sex during the peri-ovulatory phase as compared to the mid-luteal phase. Though some studies have failed to detect similar associations (e.g., Slob et al., 1991; Meuwissen and Over, 1992; Suschinsky et al., 2014), the total body of evidence seems very clear: *On average, women experience greater levels of sexual interest during the late follicular/peri-ovulatory phase than during other phases of the cycle* (especially when compared to the luteal phase; see also Krug et al., 1994, 2000; Van Goozen et al., 1997; Bullivant et al., 2004; Wilcox et al., 2004)[1].

INTERPRETING VARIATION IN SEXUAL DESIRE ACROSS THE CYCLE: LIBIDO VS. INCENTIVE PERSPECTIVES

How do these findings speak to the forms of ancestral selection that shaped women's sexual interests? To our minds, these empirical patterns are not straightforward or self-explanatory. We should ask, what *explains* the observation that, on average, women experience greater levels of sexual interest during the peri-ovulatory phase than during other phases of the cycle?

The Nature and Function of Female Sexual Desire

The motivational priorities perspective seeks to explain shifts in women's sexual desire, based on the argument that the potencies of women's motivations change across the cycle (see Roney and Simmons, 2013, 2016, 2017; Roney, 2018, 2021). When women can potentially conceive, their mating motivations (e.g., sexual interests) assume greater priority. Other motivations (e.g., motivation to eat; Roney and Simmons, 2017) assume less priority. Relative priorities shift during cycle phases when women cannot conceive. Put simply, women should be most motivated to have sex when it has the greatest fitness benefits, and it has the greatest fitness benefits when it can result in conception (For additional discussions of this view, see Jones et al., 2018b; Jünger et al., 2018a).

In contrast to these views, the dual sexuality framework conceptualizes women's estrous and extended sexuality as taking distinct forms—with partly distinct functions arising from different costs and benefits of sex during conceptive versus non-conceptive phases (Thornhill and Gangestad, 2008; for an in-depth discussion of the dual sexuality framework, as well as differential costs and benefits of sex during conceptive and non-conceptive phases, see Gangestad et al., 2021). The circumstances that evoke estrous and extended sexual interests are expected to

[1]Most studies have examined subjective sexual desire or measures of psychological interest, which this generalization pertains to. Few have examined genital arousal, which often does not correspond to psychological motivation, especially in women (Chivers et al., 2010). One exception is Suschinsky et al. (2014), who found a marginally significant increase in genital responses to sexual stimuli during the conceptive phase.

Moreover, consistent with this general theme, some studies have shown an order effect, such that stimuli shown first during a conceptive phase elicit greater sexual interest subsequently, compared to stimuli first shown during the luteal phase (Slob et al., 1991; Wallen and Rupp, 2010; Suschinsky et al., 2014).

We note that empirical exceptions exist. For instance, in a small sample of 33 partnered women, Grebe et al. (2016) reported that progesterone levels positively predict women's sexual interests in their partners. In a study tracking 30 partnered women through 15 consecutive days of a cycle, Righetti et al. (2020) found that estradiol levels negatively predicted women's sexual interests in partners. Though contrary to general trends, these patterns may reflect true effects. Results may reflect moderation effects of relationship qualities not yet fully understood.

differ. Therefore, specific conditions and stimuli likely moderate hormone-associated changes in women's sexual interests. This can produce the small, positive observed associations between conception probability and sexual desire, *on average across women*. We return to further discussion of dual sexuality below.

Sexual-Desire-as-Libido

What does it mean for *sexual desire* to vary across the cycle? Roney and Simmons (2013) introduce their study as one that examines "physiological signals that regulate cyclic patterns of libido" (p. 636). The concept of libido was introduced by Freud (1953): "The fact of the existence of sexual needs in human beings and animals is expressed in biology by the assumption of a 'sexual instinct,' on the analogy of the instinct of nutrition, that is of hunger. Everyday language possesses no counterpart to the word 'hunger,' but science makes use of the word 'libido' for that purpose" (p. 135). Setting aside Freud's psychoanalytic explication of libido, the fundamental premise is that libido is an *internally generated* energy—a "drive"—that motivates sexual activity, and that is satiated by achieving sex. In much the same way that hunger motivates and is satiated by food consumption, the "source [of libido] is a state of excitation in the body, its aim is the removal of that excitation; on its path from its source to its aim the instinct becomes operative psychically. We picture it as a certain quota of energy which presses in a particular direction. It is from this pressing that it derives its name of 'Trieb' (literally 'drive')" (Freud, 1964, p. 96).

An Alternative Perspective on Sexual Desire

An incentive motivational framework offers an alternative conceptualization of sexual motivation (e.g., Both et al., 2007; Toates, 2009). In this perspective, motivational states are *not* internally generated. Rather, organisms are motivated to act in particular ways when presented with *incentive*—a structured environment that promises rewarding outcomes potentially achievable through particular behaviors, which are then motivated. Drive versus incentive perspectives are often distinguished in terms of "push" versus "pull" metaphors: Whereas drive perspectives view motivation as forces that "push" an individual to engage in particular behaviors, incentive perspectives view goal-directed behavior in terms of "pulls" from the environment, which can also be thought of as attractions. Sexual-desire-as-libido arises prior to and independent of *in situ* attraction. By contrast, the incentive motivational framework argues that sexual desire cannot possibly be distinguished from sexual attraction; attraction and desire are inextricably related[2].

That said, internal states, independent of attraction, play highly important roles within an incentive perspective. Rather than directly affect motivation *per se*, however, they *potentiate* (or *de-potentiate*) incentives or attractions—that is, render them more or less potent elicitors of sexual interest. Hence, internal states modulate the activation of motivation, contingent on eliciting conditions. A persistent reduction of sexual desire, then, was not a loss of internal "drive" (libido). Rather, the lack of sexual desire is a result of conditions that do not incentivize experiences of sexual attraction—i.e., an individual's sexual response system was not activated by the circumstances the individual encountered (though other circumstances that were not encountered may or may not prompt sexual responses)[3].

A variety of factors can modulate the potentiation of incentives. In many species, hormones play crucial roles (See Michael, 1993, for an explicit discussion of female hormonal changes as "establishing operations," events that modulate potentiation of reinforcing consequences). In mammalian species in which females exhibit classic estrus—they are sexually receptive or proceptive *only* during a discrete period coinciding with their capacity to conceive—female sexual incentives are potentiated *only* during specific hormonal states. (These often involve multiple hormones, but most consistently the family of estrogens [named, literally, for being the "generators of estrus"; Allen and Doisy, 1923]). Even when female capacity to be sexually attracted to and interested in males is not fully dependent on ovarian hormones, ovarian hormone levels can upregulate or downregulate the sensitivity of females' sexual response system to yield attraction and, hence, desire.

Implications for Understanding the Function of Sexual Desire

A fundamental difference between perspectives on libido and incentive involves how internal states modulating the experience of sexual desire are conceptualized. If sexual desire can be understood as libido, internal states drive sexual motivation, independent of external stimuli. From an incentive perspective, these internal states alter the *potential* for sexual interest; still, sexual interest is contingent on encountering a sexually attractive stimulus, the attractiveness of which depending on the internal state. But what are the implications for viewing sexual desire as solely internally-driven or as responsive to external stimuli?

In fact, implications for understanding the evolved functions of sexual desire run deep. Let us consider a species that exhibits classic estrus—females have evolved to be sexually motivated to mate with male conspecifics only during the estrous phase. The perspective that views sexual desire as internally driven, rather that stimulus-evoked, may imply that the primary function of sexual desire is to obtain sperm (i.e., to conceive). As Fisher (1998) asserted, "The sex drive (the libido, or lust) is characterized by the craving for sexual gratification; [. . .] it evolved primarily to motivate individuals

[2]A full explication of an incentive perspective on sexual motivation and its implications is not possible here, but we note that (a) this view is a broad one, and does not entail specific ideas about the nature of stimuli that are attractive or the processes that affect attraction (e.g., relatively "hard-wired" vs. learned responses); Toates (2009, 2014) explicitly places this view in an evolutionary psychological framework, with the sexual response system involving modular components, (b) in this view, sexual fantasy can give rise to sexual desire through imagined presence of eliciting circumstances, (c) sexual desire is subject to both excitatory and inhibitory processes, understood within a more general hierarchical control system view (see, e.g., Gallistel, 2013); attraction, then, can be inhibited (Finkel, 2014).

[3]In philosophy of science, a dispositional state is one that, given an additional event, will lead to an outcome (e.g., Carnap, 1937; Goodman, 1954). A glass has the disposition to break when dropped on a hard surface. It may never break—but it has the possibility of breaking under specified conditions. In the same way, internal states referred to here are dispositional with respect to sexual desire: An individual under such a state has the possibility of experiencing sexual desire, but actualization of that possibility requires that specific conditions be met.

to seek sexual union with *any* conspecific" (Fisher, 1998, p. 24; cited in Toates, 2009). In his 1979 book, Symons argued that this perspective makes very little sense from modern evolutionary biology. Alternative males differ with respect to genotypic and phenotypic features, which then render them better or worse sires. *Which* male sires a female's offspring has fitness consequences for the female. Hence, selection should shape mechanisms to bias sire choice toward males offering relatively high fitness prospects and away from males offering low fitness prospects. From an incentive perspective, sexual attraction therefore partly functions to affect sire choice (during estrus; below, we discuss other potential functions outside of estrus). Accordingly, discriminatory sexual attraction constitutes a much better *strategy* than does indiscriminant attraction and desire (see also Thornhill and Gangestad, 2008)[4].

Interpreting Variations in Sexual Interests

We now return to the question we posed earlier: What does it mean for women's sexual desire to vary across the cycle? Depending on whether we conceive of sexual desire as libidinous drive or contingent on eliciting conditions, differences in levels of desire across the cycle could arise in a variety of distinct ways.

For one, hormones could affect libido and, hence, affect an internal state of sexual desire, independent of eliciting circumstances (e.g., Roney, 2018, 2021).

Alternatively, hormones could affect the "incentives" that evoke sexual interests—that is, the potency with which circumstances evoke sexual interests, the potency with which male features evoke sexual interests, and/or higher-order contingencies that involve both circumstances and male features. Under particular hormonal conditions, one circumstance may heighten the potency of some male features, whereas another circumstance may heighten the potency of other male features. Under other hormonal conditions, these same contingencies may not exist.

We partially flesh out these separate possibilities with two figures. In **Figure 1**, we illustrate the impact of purported libido on sexual interest. For purposes of the illustration, we consider just two circumstances, both concerning a partnered woman. In one circumstance, she is strongly attached to her partner. In the other circumstance, she is not strongly attached to her partner. We consider one male quality: whether the male is her partner (in-pair) or a non-partner (extra-pair). We represent two hormonal states—the state of high estradiol and/or low progesterone (a conceptive hormonal state); and the state of low estradiol and/or high progesterone (a non-conceptive hormonal state). If hormonal states affect libido, then hormonal states affect sexual interest in all men across all circumstances. Naturally, circumstances may affect sexual interests, male partnership status may affect sexual interests, and circumstances may interact with male features to affect sexual interests (e.g., when women are strongly attached to partners, they may be especially sexually interested in partners as opposed to non-partners). But *hormones* do not *interact with* circumstances or male features to affect interest; hormonal effects on libido are solely main effects, independent of other factors ("inputs") that affect sexual desire (see Roney, 2018, 2021).

Now we consider the possibility that hormonal states affect the circumstances and features that evoke sexual interest. The pattern we illustrate is hypothetical (though see Eastwick, 2009). In **Figure 2A**, panel A, we illustrate one hypothetical pattern for women with high estradiol and low progesterone levels (characteristic of the conceptive periovulatory phase). Here, when women are strongly attached to partners, women are especially sexually interested in partners. When women are not strongly attached to partners, women have no clear preference for partners. In panel B, we illustrate a pattern for women with low estradiol and high progesterone levels (characteristic of the non-conceptive luteal phase). Here, women strongly attached to partners exhibit relatively little interest in partners, but women weakly attached to partners exhibit somewhat more interest. Hormonal state influences the effects of circumstances and male features on sexual interests. In other words, hormones moderate the conditions that elicit sexual interest.

Hormonal Influences on "General" Sexual Desire

Roney and Simmons (2013) and Jones et al. (2018a) asked women to report their "general" sexual desire (sexual desire independent of any target specified). Both found that, on average, women reported greater general sexual desire when estradiol levels were higher and/or progesterone levels were lower within women's cycles—i.e., when hormone levels were characteristic of the periovulatory phase. Arslan et al. (2018) similarly found increases in both in-pair and extra-pair sexual interests when women were conceptive. These main effects have been interpreted as strong, consistent evidence for an increase in "general" sexual desire mid-cycle and, hence, evidence for the view that ovarian hormones affect libido.

In fact, these main effects do not constitute compelling evidence that hormones have effects on libido or "general" sexual desire. Consider **Figures 1**, **2**. In each one, overall (marginal) main effects of hormonal state are represented. In **Figure 1**, which represents hormonal effects on libido, main effects naturally emerge: The main effects of hormones on in-pair and extra-pair sexual interests are identical for both strongly attached and weakly attached women. In **Figure 2**, which represents hormonal effects on what evokes sexual interests, there also exist main effects of hormones—indeed, *main effects of similar magnitude*. What discriminates these figures are not hormonal main effects. Rather, whether there are hormonal *interaction effects discriminates the two*. To rule out the possibility

[4]As Thornhill and Gangestad (2008) also argued, it is not clear that female sexual attraction is essential to insemination. Males should be strongly selected to seek conceptive females to mate with. Female attraction to a male is often not required for a male-female encounter to occur. Females only need to be receptive to male solicitation. Women, in fact, can experience physiological and reflexive changes associated with receptivity without experiencing psychological sexual desire (Laan and Everaerd, 1995). As female sexual attraction and desire are not necessary for indiscriminant insemination, female sexual attraction and desire probably function to influence sire choice and avoid indiscriminant insemination.

We clarify that Roney's (2018, 2021) view is not that sexual interest itself is indiscriminate. It fully recognizes that women have preferences for some potential mates over others. But it argues that the impact of ovarian hormones on sexual desire is *general* and, hence, indiscriminate; estrogens purportedly increase the attractiveness of men in general, whereas progesterone purportedly suppresses their attractiveness in general (e.g., Jünger et al., 2018a).

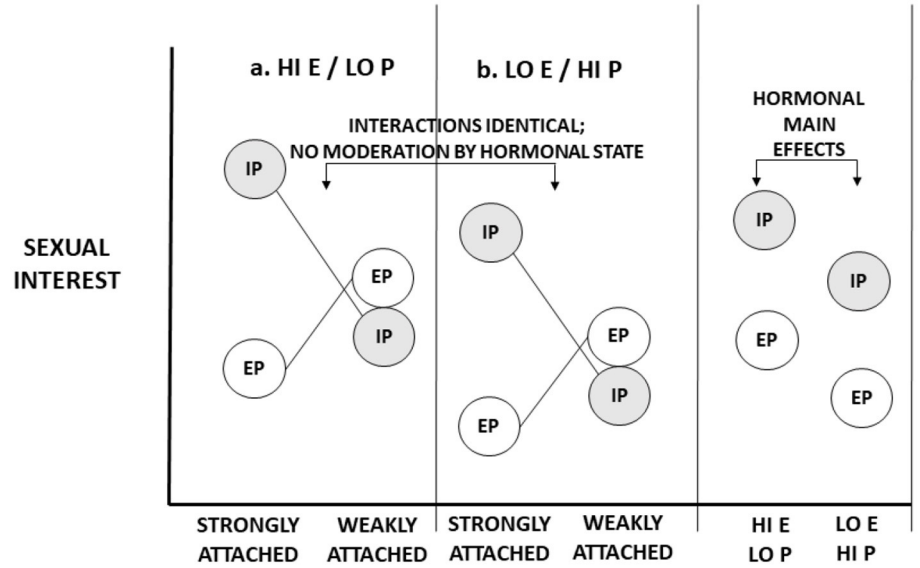

FIGURE 1 | Illustrative representation of the impact of ovarian hormones on "libido"—generalized sexual desire. Two hormonal states are represented: **(a)** High levels of estrogen (E) and/or low levels of progesterone (P), characteristic of the conceptive, peri-ovulatory phase; **(b)** (relatively) low levels of estrogen and high levels of progesterone, characteristic of the non-conceptive, luteal phase of the cycle. Two conditions are represented: Women in relationships in which they are strongly attached and bonded to romantic partners; and women in relationships in which they are weakly attached and bonded with partners. Sexual interests in partners (in-pair [IP] sexual interests) and men other than partners (extra-pair [EP]) sexual interests are considered. Hormonal states have main effects on sexual interests. Values in panel A "add" a constant value to sexual interest. This constant value is reflected in an overall main effect on both IP and EP sexual interests.

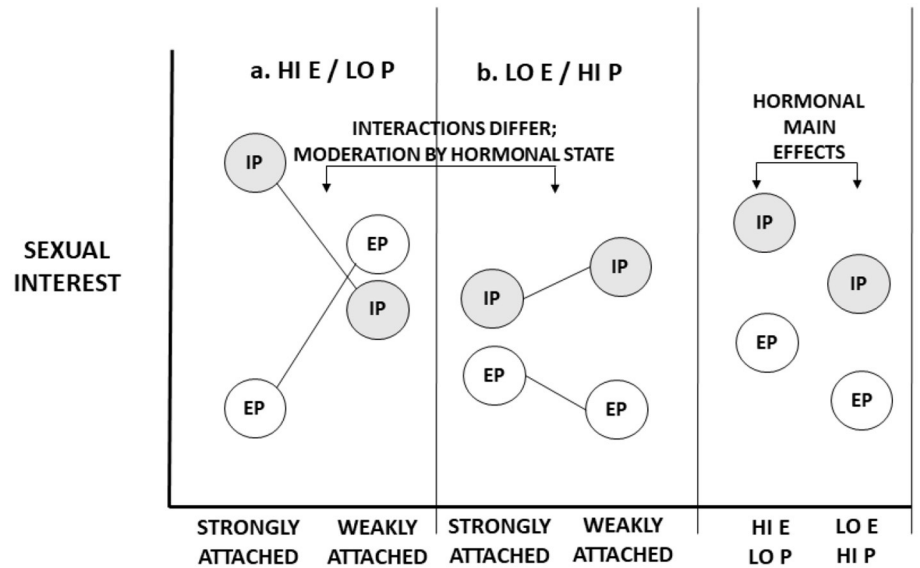

FIGURE 2 | Illustrative representation of the impact of ovarian hormones on the circumstances that evoke sexual interests. Two hormonal states are represented: **(a)** High levels of estrogen (E) and/or low levels of progesterone (P), characteristic of the conceptive, peri-ovulatory phase; **(b)** (relatively) low levels of estrogen and high levels of progesterone, characteristic of the non-conceptive, luteal phase of the cycle. Hormonal states moderate the impact of condition (strength of attachment to partners) on in-pair (IP) and extra-pair (EP) sexual interests. The marginal means of hormonal states for both IP and EP sexual interests are not equal—there is an overall main effect of hormonal state in each—but these main effects are qualified by interaction effects.

of hormonal moderation, we must go beyond main effects and examine whether hormones impact how strongly certain conditions elicit sexual interests.

We offer a parallel example. On average across days, traffic in large metropolitan areas tends to move toward city centers in the morning, and toward suburbs in the afternoons. One explanation is that people have a natural inclination to be in the city during the day, an explanation perfectly consistent with this main effect on direction of traffic flow. We know, however, that there is another explanation. Many people work day shifts. And more people work in the city and live in the suburbs that vice versa. There is no general inclination for people to prefer the city during the day. It is simply a matter of when and in what direction people go to and leave work. The empirical patterns that discriminate these two explanations are not main effects; they are interactions. For people who do work night shifts, the opposite pattern likely holds, inconsistent with the "natural inclination" explanation. The same could be true of sexual interests. Although there exists an overall small mean increase in sexual activity mid-cycle, women in certain circumstances and in the presence of particular targets could have more sexual interest on non-conceptive days.

We now turn to discuss the evolution of non-conceptive sex. We argue that, because non-conceptive sex evolved to serve functions distinct from key functions served by conceptive sex, non-conceptive sexual interests likely evolved to be sensitive to conditions other than the primary conditions that elicit sexual interests when women are conceptive.

EVOLUTIONARY PERSPECTIVES ON THE EVOLUTION OF EXTENDED SEXUALITY

Evolutionary psychology uses theories of selection and phylogenetic considerations to guide hypotheses on proximate psychological processes. Such theories can be used to establish plausibility constraints on psychological theories. In light of an understanding of what ancestral selection would have favored and disfavored, some forms of psychological process are unlikely to have evolved and, hence, are implausible (naturally, some unlikely processes *could* exist. However, their existence should lead us to question our understanding of what ancestral selection would have favored, a point to which we later return). As noted earlier, Symons (1979) applied selectionist reasoning to argue that female sexual attraction and desire are unlikely to be indiscriminating.

Using similar applications of selectionist reasoning, we argue that the conditions that evoke women's sexual interests during the conceptive, peri-ovulatory phase may not exactly match the conditions that evoke sexual interests during non-conceptive (e.g., luteal) phases.

Extended Sexuality: A Phylogenetic Perspective

Sexual receptivity and proceptivity outside of the conceptive phase is referred to as extended sexuality (Rodriguez-Girones and Enquist, 2001)[5]. It is "extended" in two related ways. First, sex during the conceptive phase is a given (even if contingent). Non-conceptive sex, which "extends" outside of the conceptive phase, is found in some species but not others. Second, from a phylogenetic perspective, a state of conceptive *and* non-conceptive sexuality evolved from a prior state of solely conceptive sex (at some point in the lineage, whether evolutionarily distant or recent). Non-conceptive sex evolved as an "extension" of conceptive sex (though influences on extended and conceptive sexuality may differ; see below).

Extended Sexuality in Non-human Primates

"Loss of Estrus"

When Symons (1979) referred to women's "loss of estrus," he effectively referred to the evolution of extended sexuality in human females. At some point in the lineage leading to humans, females possessed classic estrus and were sexually active only when conceptive (like most mammalian species). More recently, females evolved to be sexually active during both conceptive and non-conceptive phases. The evolution of extended sexuality constituted a loss of (classically defined) estrus.

Dixson's Critique

Symons (1979) and others (e.g., Alexander and Noonan, 1979; Benshoof and Thornhill, 1979; Burley, 1979; Spuhler, 1979) generally assumed that, within the human lineage, "loss of estrus" occurred recently in the lineage leading to humans, replaced by "continuous 'copulability.'" That is, these scholars implied that extended sexuality evolved recently in the human lineage. Indeed, they viewed extended sexuality and the resulting outcome of concealed ovulation as distinctly human qualities, having resulted from selection pressures that were distinct to humans.

Alan Dixson (2009, 2012), probably the world's foremost expert on the comparative study of the reproductive biology of primates, claims that the loss of estrus evolved distantly in the human lineage. Prosimian primates exhibit classic estrus, similar to most mammals. By contrast, the vast majority of monkeys and apes possess some degree of extended sexuality; females are sexually active during some non-conceptive parts of their cycles. On this basis, Dixson (2009) argues that loss of estrus evolved approximately 50 million years ago in the lineage leading to humans in an early simian primate, an event shared with lineages leading to virtually all simian primates (even if, in some lineages, extended sexuality has been largely lost; e.g., female gorillas, though sexually active when pregnant, rarely engage in sex during non-conceptive phases of their cycles; Czekala and Sicotte, 2000). Therefore, loss of estrus can tell us little about selection pressures that *distinctly* shaped human reproductive biology.

[5]Sexual receptivity and proceptivity during pregnancy and lactation qualify as extended sexuality (see, e.g., Magganetti and Pillsworth, 2020). Here we focus on sexual receptivity and proceptivity during non-conceptive phases of an ovarian cycle.

The Function of Extended Sexuality in Non-human Primates

Extended sexuality in non-human primates can potentially reveal selection pressures that shaped primate reproductive biology. What benefits led to its evolution?

In his massive compendium on comparative primate biology, Dixson (2012) identifies multiple possible functions, depending on the species. In some species, including in the most studied exemplars of Old World and New World monkeys (rhesus macaques and common marmosets), patterns of female proceptivity and receptivity change markedly across sexually active phases: Compared to conceptive phases, females rarely initiate sex during non-conceptive periods; extended sexual activity largely involves female willingness to copulate with males that initiate sex. Potentially, females in some species gain little from extended sexuality other than cost savings. Within these polygynandrous groups, females may pay fewer costs by engaging in undesired, non-conceptive sex than by repeatedly resisting ardent males.

In other species, however, females initiate sex outside of the conceptive phase. Some researchers argue that females in some of these species gain benefits of paternity confusion (Hrdy, 1979; Van Schaik et al., 2000). Males who have not copulated with a female prior to birth of her offspring can rule out their own paternity. Males may hence benefit from harming, even killing, offspring. By mating with all adult males in the group during each cycle, females may mitigate male-instigated harm to offspring. However, multiple mating potentially compromises female choice. Absent cryptic bias of sireship or male competition for sexual access, females risk drawing a sire at random. Females may have evolved to concentrate efforts to confuse paternity through multiple mating during extended sexuality, while exerting adaptive preferences for sire choice when conceptive, either for genetic quality (e.g., Nunn, 1999) or paternal care and protection (e.g., Alberts and Fitzpatrick, 2012). (For possible examples of this function of primate extended sexuality, see Heistermann et al., 2001 [Hanuman Langurs]; Lu et al., 2012 [Phayre's leaf monkeys]; Knott et al., 2010 [orangutans]; Tiddi et al., 2015 [black capuchins; also Dixson, 2012]; Matsumoto-Oda, 1999; Stumpf and Boesch, 2005; Pieta, 2008 [chimpanzees; but see alternative view in Muller et al., 2011])[6].

How widespread primate extended sexuality for paternity confusion is remains unknown, but exceptions exist. Female Assamese macaques engage in highly extensive extended sexual activity, both during non-conceptive phases of the cycle (characterized by rates of copulation no different from those of conceptive phases) and post-fertilization (Fürtbauer et al., 2011a). Although females are promiscuous and mate with all adult males in a group during a conceptive cycle, males and females frequently form long-term consortships, which account for a substantial portion of all copulations. Males appear unable to detect female conceptive status with certainty, as dominant males do not monopolize conceptive matings; rather, males engage in long-term consortships even during extended sexuality. Synchronous female mating further prevents dominant males from monopolizing matings (Fürtbauer et al., 2011b). Accordingly, male reproductive skew is relatively low (Sukmak et al., 2014). Based on past sexual relations, males infer paternity much better than chance levels and engage in extensive care (largely protection from harassment by other males) of offspring they have sired. This may function as true paternal care, as opposed to mating effort to achieve paternity of future offspring (a function more typical of non-human primates; Minge et al., 2016). Extended sexuality and related adaptations (e.g., suppression of cues of estrus) in this species may have evolved to intensify rates of copulation in consortships, which then translate into direct benefits to females in the form of paternal care (Ostner et al., 2013).

[6]Naturally, for extended sexuality to function effectively in these species, males must not be able to discern when females are conceptive with certainty, even if some predictive but fallible markers of female conceptive status exist.

The Concept of Dual Sexuality

Generally, the conditions that evoke female proceptivity and receptivity during conceptive phases do not perfectly match the conditions that evoke their sexual interests during extended sexuality. This makes sense from a strategy-centered, selectionist perspective. Conceptive sexual interests have been shaped, in part, by selection on outcomes due to the fact that it *is* conceptive. Sex at that time can result in an offspring and, hence, sexual interests have consequences for both fertility scheduling and sire choice. *Conceptive sexuality should embody fitness-enhancing strategies pertaining to regulation of fertility and sire choice*. Non-conceptive sex does not have the same immediate consequences (even if it could have direct benefits and implications for sire choice through pair-bonding). In species with extended sexuality, female proceptivity and receptivity during non-conceptive phases has probably evolved because of functions and benefits other than immediate reproduction. Therefore, *non-conceptive sexuality should embody fitness-enhancing strategies for extracting those benefits (while limiting costs of sex, including the costs of poorly chosen conception)*. Non-conceptive interests could be shaped to look very different or fairly similar to conceptive sexual interests, depending on the nature of benefits of each. But, a priori, these sexual interests are unlikely to be shaped to take *identical* forms.

To capture the idea that conceptive and non-conceptive sexual interests are unlikely to take identical forms, Thornhill and Gangestad (2008) introduced the term, *dual sexuality*. Dual sexuality exists when the psychology underlying conceptive and non-conceptive sexual interests lead them to be differentially evoked by circumstances—i.e., as illustrated in **Figure 2**. Dual sexuality need not imply completely distinct psychologies; some stimuli that evoke conceptive phase interests may also evoke non-conceptive phase interests. As conception probability is graded, dual sexuality may produce changes across the cycle that are similarly graded; psychological shifts are likely influenced by changing hormone levels. In this perspective, black capuchins, Phayre's leaf-eating monkeys, and, likely, Assamese macaques possess dual sexualities, albeit in non-identical ways.

Estrus With Extended Sexuality

Classic estrus, again, exists when females are sexually active only during a restricted period during which they are conceptive. Thornhill and Gangestad (2008) used the term "estrus" to refer to adaptations that characterize female conceptive sexual psychology, even when females also exhibit extended sexuality, to underscore that (a) phylogenetically, extended sexuality evolved as an "add-on" to this conceptive sexual phase, (b) extended sexual interests are likely shaped to be non-identical to conceptive sexual interests, and (c) conceptive sexual interests are likely maintained in species with extended sexuality by some of the same endocrinological mechanisms as in species lacking extended sexuality (i.e., physiological homology exists). In this way, they argued that estrus was not "lost" in simian primates, including humans, despite the evolution of extended sexuality[7].

Additionally, Thornhill and Gangestad argued that human estrus retained not only physiological homology but also conserved function: sire choice (Thornhill and Gangestad, 2008). Upon reflection, we think that they had a useful, valid point but overstated it. While estrous adaptations importantly function to direct sire choice even in species with classic estrus, sire choice can be traded-off against other potential benefits, such as opportunity costs incurred by mate search. Estrous adaptations should function to manage those trade-offs too. As well, estrous sexuality should regulate fertility. Even if sex is potentially conceptive and a suitable partner is available, timing of reproduction may not be opportune (e.g., Dinh et al., 2017, 2021b). Furthermore, species that evolved extended sexuality are not a random set of species. In these species, female sexuality has benefits other than conception. Although those benefits led to the evolution of extended sexuality, they may (depending on the species) also be garnered through conceptive sex, which can lead to adaptive modifications in conceptive sexuality. For example, in Assamese macaques, both non-conceptive and conceptive sex can cement consortships that pay off in currencies of paternal care (contingent on sireship). Adaptations shaped by these benefits may come to be part of estrous sexuality, even if sire choice and fertility regulation adaptations are retained (for an argument along these lines for humans, see Eastwick, 2009; Eastwick and Finkel, 2012).

WOMEN'S EXTENDED SEXUALITY

While most simian primate females are sexually active outside of the conceptive phase, women are extreme exemplars, being sexually active throughout the entire cycle. Evolution-minded thinkers consider the evolution of human extended sexuality a potential key to understanding the forces of selection that forged our mating patterns, patterns of parental investment, and our social nature.

[7]This point of view may seem to contrast with Dixson's (2009, 2012) argument that estrus was lost in an early simian primate. However, the contrast is merely a semantic one. (In Dixson's view, estrus is lost whenever extended sexuality in a cycle evolves – but that of course is not what Thornhill and Gangestad (2008) meant by estrus when claiming it persists).

The Focus on Concealed Ovulation

Early on, Symons, Alexander, and other scholars who portrayed women's extreme extended sexuality in high relief focused on one particular effect—the "concealment" of ovulation. This focus was, in hindsight, both insightful and misleading. Consistent with selection for an "undisclosed" conceptive status[8], women appear to be designed to minimize generalized male access to cues of their conception risk. Yet there could be "leaky cues"—weak cues that are likely not designed to advertise conceptive status to others (Thornhill and Gangestad, 2008; Haselton and Gildersleeve, 2011). However, "concealed ovulation" does not imply that women are incapable of (unconsciously) discriminating their cycle phase. Women likely have mechanisms to discern and functionally respond to changes in conception probability. For instance, even though women are sexually active across the cycle, their sexual psychology and experiences (e.g., the nature of their sexual interests) change.

Furthermore, the idea that women "conceal" ovulation suggests that other female primates fully advertise it, which is not true. Sexual rump swellings have independently evolved at least three times in Old World primates (Pagel and Meade, 2006). Females in these species also exhibit extended sexuality. Sexual swellings arise prior to when females are conceptive in their cycle and persist past ovulation. Although swellings tend to be maximal during the peri-ovulatory phase, the association is far from perfect. Sexual swellings are "graded" signals that, *by design*, are highly imperfect indicators of conception status (Nunn, 1999). Female primates with extended sexuality benefit from it only when males lack access to perfect cues of conceptive status (i.e., female conceptive status is not fully detectable).

Many, if not most, females that display sexual swellings also potentially benefit from extended sexuality through paternity confusion. In some species that did not evolve sexual swellings, females may exhibit other signals. New World female monkeys that may confuse paternity through extended sexuality (e.g., black capuchins) exhibit behavioral displays (e.g., ritualized vocalizations) that may similarly function as imperfect, graded signals (Tiddi et al., 2015). In both Old World and New World species of this sort, females may benefit from attracting maximal male sexual interest during times surrounding ovulation. This way, females can actively or passively (as a result of outcomes of male intrasexual competition) select desired sires when conceptive, while confusing paternity when non-conceptive.

[8]Thornhill and Gangestad (2008) preferred the term, 'undisclosed conceptive status," for several reasons: first, what is important is not that *ovulation* is concealed but, rather, conception risk, which precedes ovulation in the cycle; second, conceptive status is not advertised, yet males generally discern conceptive status via byproducts of other adaptations. Thornhill and Gangestad based this view on modeling by Pagel (1994) showing that costly female signals of conceptive status will not evolve so long as males have access to byproduct cues. Although Thornhill and Gangestad hence argued that sexual swellings likely advertised quality or capacities for successful reproduction, they did permit that females could possibly derive a net benefit from inciting male intrasexual competition through a fallible "fertility signal" (e.g., Nunn, 1999). Based on evidence, we think the latter is likely (though the costliness of sexual swellings remains puzzling, as a cheaper alternative [e.g., the vocalizations of black capuchins] could seemingly derive the same benefit).

The Evolution of Women's Extended Sexuality

Comparatively, the fact that women lack sexual swellings or ritualized behavioral cues overlapping with the conceptive phase is revealing about the potential function of their extended sexuality. It likely has not been shaped to facilitate paternity confusion. Strassmann's (1981) explanation of concealed ovulation, broadened to include extended sexuality, may offer one plausible scenario for the evolution of women's extended sexuality. Strassmann argued that, in a species in which males may potentially engage in true paternal care, males most likely to benefit from caring are non-dominant males. Following successful reproduction, males can choose to invest in care or re-enter the mating market to compete for another fertilization (or some combination of these two). The benefits of engaging in care partly depend on the net benefits (e.g., the rate of success) of competing for mating (e.g., Kokko and Jennions, 2008). Non-dominant males benefit less from competing and, therefore, are most likely to benefit from investment in care. As a result, females evolved to prefer non-dominant males as sires for the benefits of paternal care. Accordingly, concealing their conceptive status prevented dominant males from systematically monopolizing conceptive matings through intrasexual competition against non-dominant males (for a discussion of potential contributions of female-female intrasexual competition to the evolution of undisclosed conceptive status in humans, see Krems et al., 2021).

As Kokko and Jennions (2008) emphasize, male benefits to investment in care also crucially depend on paternity assurance. In Strassmann's scenario, the concealment of ovulation permits non-dominant males to become sires but also limits *their* access to cues to conceptive status. Hence, males do not attain paternity assurance through detection of fertility cues. Rather, paternity assurance is achieved through regular sexual access throughout the cycle of a target female (some portion of which is conceptive), in conjunction with reasonable confidence that other males have not engaged in sex with that female during the cycle[9].

According to this perspective, women's extended sexuality has been shaped to assure paternity of a primary mate to promote male investment in offspring. This view converges with a more general framework for the evolution of pair-bonding and biparental care in humans, supported by modeling (Gavrilets, 2012). In this framework, the evolution of paternal care in humans was led by non-dominant males, who could benefit most from care. Females preferentially mated with such males to obtain care. Ultimately, most dominant males also evolved to care for offspring to attain paternity, given female preferences for males who will invest in offspring (a portion of dominant males will still benefit from substantial mating effort and successful multiple mating outside of pair-bonds; see Gavrilets, 2012, for details).

Regardless of the specifics involved in the evolution of women's extended sexuality and whether these models are correct, we emphasize that extended sexuality evolved for functions other than direct conception. Strassman's explanation offers one possible function of women's extended sexuality, though it has yet to be fully evaluated. (Even if it possesses some truth, it may not fully explain extended sexuality. E.g., unmated women possess extended sexuality too; what functions does extended sexuality serve them? And, for an alternative view that extended sexuality draws male attention and possibly sperm away from other females in polygynous relationships, see Geary et al., 2011). Importantly, because women's extended sexuality evolved for reasons other than the implications of sex for immediate reproduction, the circumstances that evoke sexual interest during extended sexuality are unlikely to be precisely the ones that evoke sexual interest during estrus.

EVALUATIONS OF WOMEN'S DUAL SEXUALITY

We have argued that, based on fundamental conceptualizations regarding functional (and hence strategic) design, women likely possess a dual sexuality. But existing evidence is not yet definitive for answering whether women have dual sexuality. Additional empirical—and, importantly, conceptual—work is needed. Below, we briefly discuss pertinent empirical findings and ideas.

Genetic Benefits for Offspring

The dual sexuality framework is a broad umbrella, with specific theory to be filled in. Generally, conceptive sexuality should be concerned with fertility regulation (timing of reproduction) and sire choice (choosing a right male as a father). One prominent theory along these lines asserts that, when women are conceptive, they have increased preference for male features that may have ancestrally been indicators of genetic quality—indirect benefits that sires pass to offspring. Researchers have examined preferences for candidate features of genetic quality, some of which are directly involved in regulating male-male competition: the body scents of symmetrical men (Gangestad and Thornhill, 1998; Rikowski and Grammer, 1999; Thornhill and Gangestad, 1999; Thornhill et al., 2003); facial masculinity (e.g., Penton-Voak et al., 1999); vocal masculinity (Puts, 2005; Feinberg et al., 2006; Pisanski et al., 2014); facial symmetry (though findings were largely negative; e.g., Koehler et al., 2002); body masculinity (e.g., Little et al., 2007); facial features associated with testosterone (Roney et al., 2011); behavioral indicators associated with dominance, confidence, and "social presence" (Gangestad et al., 2004, 2007; Flowe et al., 2012; Giebel et al., 2013; Cantú et al., 2014).

A meta-analysis and *p*-curve analysis suggested that non-zero true effects in targeted preferences exist (Gildersleeve et al., 2014a,b; cf. Wood et al., 2014). At the same time, recent large-scale replication studies and studies examining hormonal

[9]As discussed earlier, Assamese macaques exhibit forms of mating that are rare for an Old World monkey. Although females mate promiscuously, males and females form prolonged consortships and copulate throughout female cycles. Unlike most macaques, females evidence little sexual swelling. Fathers may engage in true paternal care, largely in the form of protection from other males. Although paternal care is hardly as extensive as that found in most human societies, its evolution may be supported by similar kinds of sexual adaptations, independently evolved in the lineage: relatively undisclosed conceptive status, extreme extended sexuality, greater paternity assurance to consorts through repeated copulation throughout the cycle (and, indeed, after conception).

influences have not been encouraging (e.g., Dixson et al., 2018; Jones et al., 2018c,d; Jünger et al., 2018a,b; Marcinkowska et al., 2018; Stern et al., 2019, 2020, 2021). Most effects appear to be in predicted directions. Some have been suggestive of true effects (e.g., on estradiol-vocal masculinity preference links: Jones et al., 2018c; on progesterone-body muscularity links: see Dinh et al., 2021a, on Stern et al.'s, 2021, study). However, effects have typically been small and non-significant. Small true effects cannot be ruled out. (We think small true effects are consistent with the overall findings. Conversely, an across-the-board null hypothesis does not explain the *p*-curve results or why predicted effects are sometimes significant, whereas significant effects in the direction opposite that predicted have not been reported). Large, robust effects that early work suggested are not consistent with findings. We return later to briefly comment on these findings.

Pair-Bonding and Estrous Sexual Psychology

The dual sexuality framework is broad and encompass multiple distinct theories. Even if one theory is wrong, others may be right. Above, we described how females often benefit from choosing non-dominant males as sires because these males are more likely to care for offspring, which may have led to the evolution of human extended sexuality. Undisclosed conceptive status prevents dominant males from monopolizing conceptive matings, permitting females to choose non-dominant males willing to invest in care as sires (Strassmann, 1981). At first blush, these statements may appear to be incompatible with the idea that women retain estrous preferences for dominant and intrasexually competitive males.

However, women's preferences for sire choice may be conditional. Women may act on estrous preferences for dominant males very selectively and only under certain conditions. Perhaps most of the time, a woman in a valuable relationship with a highly-investing partner would have benefitted most from conceiving with her partner. Thornhill and Gangestad (2008) made this point:

> We have characterized estrous sexuality in terms of adaptations designed to garner good genes for offspring. Much evidence speaks to the existence of those adaptations in women (see Chapters 9 and 10). . . . [More broadly, however], estrous sexuality should generally function to enhance adaptive sire choice by females. One component of adaptive sire choice is choice of a partner who can deliver genetic benefits to offspring. But *in pair-bonded species, in many instances the best sire for a woman's offspring is in fact the pair-bond mate*, and not merely in instances in which the mate has good genes; the primary partner delivers non-genetic material benefits in a variety of currencies (Chapter 4) and loss of those benefits could have a drastic negative impact on a female's fitness. [pp. 307-308; emphasis added]

A year after, Eastwick (2009) proposed his adaptive workaround hypothesis. Because of the value of strongly bonded relationships, he conjectured, women evolved adaptations that function to strengthen highly valued relationships when conceptive in their cycles. Eastwick and Finkel (2012) found that women in strong pair-bonds experienced more intimate sex with partners when conceptive and were less likely to say they would act on extra-pair attraction. Eastwick proposed that the function of these changes is to solidify pair-bonds, as a counterforce to estrous adaptations that might weaken bonds. Alternatively, results could also be consistent with Thornhill and Gangestad's (2008) claim that women may have evolved to select highly investing partners as sires.

Recently, we and some colleagues sought to assess whether partnered women's bond strength (or, as we refer to it, "loving attachment" to partners) moderates the impact of ovarian hormones on their in-pair and/or extra-pair sexual interests. We assessed urinary estrogen and progesterone levels in 181 women who participated in up to 4 sessions, across a period of about a month. In an initial session, women completed extensive questionnaires assessing their relationship qualities (both from their perspective and the perspective of their partners). Loving attachment strongly interacted with within-woman progesterone levels to predict in-pair versus extra-pair sexual interests. Simple main effect analyses showed that, when women were strongly attached to partners (1*s* above the mean), low progesterone levels (characteristic of the follicular and peri-ovulatory phases) were associated with low levels of extra-pair interests relative to in-pair sexual interests. Furthermore, low progesterone levels were associated with greater rates of initiation of sex with partners for these women. For women relatively unattached to partners (1*s* below the mean), a contrasting pattern held: When progesterone levels were low, their extra-pair interests tended to be greater compared to when their progesterone levels were high (Dinh et al., 2022b), potentially consistent with the view that, for these women, mid-cycle increases in extra-pair attraction partly reflect interest in indicators of genetic quality (e.g., Durante et al., 2016).

These empirical patterns illustrate the same point made by **Figure 2**: an ovarian hormone moderates the impact of a circumstance—the level of relationship attachment—on in-pair versus extra-pair sexual interests. It does not fit the pattern in **Figure 1**.

Relationship Features and Extended Sexuality

To offer predictions about changes in women's sexual interests across the cycle, we must have some understanding of both estrus and extended sexuality. Women's extended sexuality should have been shaped to enhance the benefits that led to its evolution.

Based on the notion that women's extended sexuality has been selected to foster investment by primary partners, Grebe et al. (2013) argued that women's sexual interests during non-conceptive phases should be particularly sensitive to relationship features. Specifically, Grebe et al. (2013) suggested that women should be particularly interested in bolstering investment from primary partners—and hence initiate sex with partners more during extended sexuality—when women are highly invested in their relationships but their partners' investment lags behind their own. A within-woman study of very modest sample size (50) yielded support for these ideas (see also Sheldon et al., 2006; Grøntvedt et al., 2017).

In the study of 181 women mentioned above, we conducted analyses that further tested these notions. We did not find support for the prediction that women's overall relationship investment, relative to their partners' investment, predicts in-pair versus extra-pair sexual interests when hormone levels are characteristic of the non-conceptive luteal phase (high progesterone levels relative to estrogen levels). In preregistered exploratory analyses, however, we found that estrogen levels moderated the impact of discrepancies in women's versus their partner's levels of romantic passion. When women were more passionate about their partners than their partners were about them, women experienced greater in-pair sexual interests, relative to extra-pair interests, when their estradiol levels were relatively low—i.e., characteristic of extended sexuality (Dinh et al., 2022b).

The function of romantic passion is purportedly distinct from that of loving attachment. Strong pair-bonding—a state of interdependence in which both partners regard the interests of their partners to be their own interests—purportedly facilitates efficient biparental care of offspring (e.g., Fletcher et al., 2015). Romantic passion (also referred to as romantic love, passionate love, or limerence; Tennov, 1999) functions in the context of pair-bond formation. It promotes pair-bonding through motivational impacts and/or signaling-of-commitment (e.g., Fisher, 1998; Galperin and Haselton, 2010). Romantic passion may ultimately lead to loving attachment, after which romantic passion may wane, its function fulfilled. When women express greater levels of romantic passion than their partners, they signal that they are more interested in developing a strong pair-bond than their partners are. If extended sexuality evolved in part to foster male interest in greater investment, female-male discrepancies in levels of romantic passion plausibly predict women's extended sexual interest in partners, relative to other men.

The Impact of Male Attractiveness

Although hormonal moderation of the impact of various relationship qualities on in-pair versus extra-pair sexual interests has not received a lot of attention to date, one moderation effect has received a good deal of attention. As might be expected, male partners' sexual attractiveness negatively associates with women's interests in extra-pair men; women with "sexy" partners express less interest in other men, compared to women with relatively "unsexy" partners. Multiple studies have found that this effect is stronger when women are conceptive in their cycles (e.g., Pillsworth and Haselton, 2006; Larson et al., 2012; Dinh et al., 2022a; see Gangestad and Dinh, 2021, for a review). The purported explanation is that women place greater value on sexually attractive male features when conceptive in their cycles, presumably because these features were associated with genetic benefits to offspring ancestrally. Recently, Arslan et al. (2018) claimed to find no support for this moderation effect. In fact, however, two coding errors distorted results. When these coding errors were corrected, analyses on Arslan et al.'s sample using their most powerful method of assessing conception risk (a continuous measure; Gangestad et al., 2016) yielded considerable support for this moderation effect (Gangestad and Dinh, 2021; but see also response by Arslan et al., 2021).

In our recently collected dataset of 181 women, we examined moderating impacts of ovarian hormone levels on the association between male partners' attractiveness and women's extra-pair sexual interests (Dinh et al., 2022a). Analyses found that when women's progesterone levels were low—characteristic of the follicular and peri-ovulatory phase—partner attractiveness more strongly predicted extra-pair interest in a negative direction, consistent with previous effects. However, some preregistered effects examined were near-zero. All in all, the null hypothesis that there exist no effects is a very poor explanation of the overall pattern of results, even if we currently do not fully understand the reasons for variable effects (Dinh et al., 2022a,b)[10].

This moderation effect, if robust, begs a question. This effect assumes that women differentially value sexually attractive features across conceptive versus non-conceptive phases. Yet, as we discussed above, large-scale replication studies have not found strong, compelling evidence for hormonal moderation of mate preferences (e.g., for muscular bodies). Durante et al. (2016) suggested one possible resolution. Perhaps mate preference shifts are moderated. For instance, women who are strongly attached to partners may express relatively little interest in extra-pair men when conceptive. It may make sense that these women also show little evidence of increased interest in, say, muscular men when conceptive. The same may apply for women with attractive partners—or, more generally, women who show relatively little interest in extra-pair men during conceptive phases for other reasons. By contrast, when women do express interest in extra-pair men when conceptive, they may be particularly interested in muscular men. This may be one reason why preference shifts are weak overall and not consistently detected. It also remains untested to date.

Clarifications

Based on a priori ideas about how selection has shaped women's estrous sexuality and extended sexuality, we have argued that it is unlikely that women's conceptive and non-conceptive sexual interests are evoked by precisely the same conditions. This possibility has not been extensively explored. We have briefly discussed evidence arising from recent empirical work, guided by general notions about dual sexuality, that are consistent with hormonal moderation effects on the conditions that evoke women's in-pair and/or extra-pair sexual interests.

We emphasize two points. First, the findings we discuss are provisional. We have not discussed findings in detail, as the papers that present these results must still undergo peer review and evaluation. Furthermore, some findings arose from analyses that were not preregistered or were preregistered as exploratory. Future research may further evaluate the robustness of these findings.

Second, we present these results as illustrative of findings consistent with dual sexuality. The framework is compatible

[10]Outcome measures that yielded effects tapped *absolute* levels of *intensity* of extra-pair sexual interest. Ones that did not tapped *frequency* of sexual interests *relative* to that of typical days. Perhaps one of these features explain variability in findings, though this possibility remains speculative.

TABLE 1 | Illustrative effects that distinguish the motivational priorities perspective and the dual sexuality framework.

Perspective	Expectations regarding hormonal interactions with condition
Motivational priorities	Few, if any, hormonal interactions on sexual desires are expected. For women in romantic relationships, estradiol should be positively associated with and/or progesterone levels should be negatively associated with sexual interests in both in-pair and extra-pair partners. Conditions (such as loving attachment) may have independent effects on in-pair and extra-pair sexual interest, but these effects should not generally be moderated by estradiol and/or progesterone levels.
Dual sexuality	Some hormonal interactions with condition should exist, though different views of estrous and extended sexuality offer different predictions about the nature of these interactions. *Sire choice and fertility regulation favoring partners women are strongly attached to*. When women are strongly attached to romantic partners, women's sexual interests should be especially focused on in-pair partners, relative to extra-pair partners, when estradiol levels are high and/or progesterone levels are low (i.e., during estrous sexuality). See Dinh et al. (2022b). *Pair-bond extended sexuality theory*. When women are more involved in their relationships than partners are, women's sexual interests should be especially focused on in-pair partners relative to extra-pair partners, when estradiol levels low and/or progesterone levels are high (i.e., during extended sexuality). See Dinh et al. (2022b).

with a number of distinct theories about the contrasting functions of estrus and extended sexuality. We encourage further development of selection-based theories that propose differences in what conditions elicit sexual interests during estrus versus extended sexuality.

To illustrate different predictions made by the motivational priorities perspective and certain theoretical variations that fall under the dual sexuality framework, we include **Table 1**. It focuses specifically on predictions made about moderating effects of relationship qualities (see the above sections, "Pair-bonding and estrous sexual psychology" and "Relationship features and extended sexuality").

WHAT IF THE CONDITIONS THAT EVOKE CONCEPTIVE AND NON-CONCEPTIVE SEXUAL INTERESTS DO NOT DIFFER?

Multiple lines of research suggest that women's estrus and extended sexuality are distinct sexualities. However, existing evidence has not convincingly demonstrated through repeated replication that distinct conditions differentially evoke conceptive and non-conceptive sexual interests. What if it turns out there are no differences between the conditions that evoke conceptive and non-conceptive sexual interests?

Such a state of affairs should have clear consequences for theory, as it should lead us to question the a priori basis for expecting differences. *A priori*, if the functions of conceptive and non-conceptive sexual interests differ, conceptive and non-conceptive sexualities were shaped by selection to strategically garner the benefits (and limit the costs) of each; this implies that conceptive and non-conceptive sexual interests should be elicited by different circumstances.

Are there scenarios in which these expectations would be wrong? We are not sure. If these expectations are wrong, evolution-minded scholars should attempt to explicate the selection pressures that would have shaped women's sexual interests to yield the empirical patterns observed. Perhaps alternative understandings of what selection would have favored are needed. But for theoretical progress to be made, those alternatives must be spelled out.

SUMMARY REMARKS

The current literature on shifts in women's sexual interests across the cycle is rife with conflicting findings. No one theoretical perspective is widely accepted. We have discussed what is known and what is not known and reflected on key issues.

First, despite conflicting findings, one general empirical pattern appears to be firmly established: On average, women experience greater sexual desire and interest when conceptive in their cycles than when non-conceptive. Hormonal changes likely are a proximate process accounting for these shifts (Roney and Simmons, 2013).

Second, the ultimate reasons underlying these empirical patterns on changes in sexual interests are not straightforward or self-explanatory. One perspective views hormonal signals as directly influencing "general" sexual desire, or libido. We argue that, alternatively, hormones potentiate or de-potentiate the effect of conditions on target-specific sexual interests. The existence of main-effect associations between hormone levels and sexual desires are compatible with both perspectives. The perspectives differ with respect to whether they expect distinct conditions to differentially evoke sexual interests as a function of conceptive status.

Third, we make the key point that extended sexuality evolved to serve functions distinct from the functions of estrous sexuality. We discussed the evolution of extended sexuality, provided evidence from non-human primate examples, and addressed possible functions of women's extended sexuality. Different functions demand different strategies to attain benefits. *A priori*, based on evolutionary logic, we argued that the conditions that evoke sexual interest across conceptive and non-conceptive phases likely differ.

Fourth, our understanding of women's sexuality, including possible differences between estrous and extended sexuality, is not well established. We discussed illustrative lines of research that examine hormonal moderation of conditions that affect sexual interests. More work is needed along these lines. Unless potential moderation is explored, we cannot conclude that important moderation effects do not exist.

Patterns of change and stasis in women's psychology across the cycle likely reveal important truths about selection, which has shaped many features distinct to humans. After four decades of rather intense theoretical and empirical

scrutiny, consensual understanding of these patterns remain elusive. Tremendous progress has been made, though firm conclusions cannot yet be drawn regarding cyclic shifts in women's psychology and behavior. Much more empirical research and theoretical developments are necessary for a thorough and nuanced understanding of human mating and sexuality.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because the article presents preliminary results. However, this article is primarily a conceptual paper and not an empirical research paper. All preliminary findings will ultimately be reported in papers that will give access to all pertinent data uploaded to a publicly accessible repository. All data will be de-identified. Requests to access the datasets should be directed to Steven Gangestad sgangest@unm.edu.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of New Mexico, Main Campus IRB. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

Both authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Vocal Cues to Male Physical Formidability

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Animal vocalizations convey important information about the emitter, including sex, age, biological quality, and emotional state. Early on, Darwin proposed that sex differences in auditory signals and vocalizations were driven by sexual selection mechanisms. In humans, studies on the association between male voice attributes and physical formidability have thus far reported mixed results. Hence, with a view to furthering our understanding of the role of human voice in advertising physical formidability, we sought to identify acoustic attributes of male voices associated with physical formidability proxies. Mean fundamental frequency (F_0), formant dispersion (D_f), formant position (P_f), and vocal tract length (*VTL*) data from a sample of 101 male voices was analyzed for potential associations with height, weight, and maximal handgrip strength (*HGS*). F_0 correlated negatively with *HGS*; P_f showed negative correlations with *HGS*, height and weight, whereas *VTL* positively correlated with *HGS*, height and weight. All zero-order correlations remained significant after controlling for false discovery rate (*FDR*) with the Benjamini–Hochberg method. After controlling for height and weight—and controlling for FDR—the correlation between F_0 and *HGS* remained significant. In addition, to evaluate the ability of human male voices to advertise physical formidability to potential mates, 151 heterosexual female participants rated the voices of the 10 strongest and the 10 weakest males from the original sample for perceived physical strength, and given that physical strength is a desirable attribute in male partners, perceived attractiveness. Generalized linear mixed model analyses—which allow for generalization of inferences to other samples of both raters and targets—failed to support a significant association of perceived strength or attractiveness from voices alone and actual physical strength. These results add to the growing body of work on the role of human voices in conveying relevant biological information.

Keywords: voice pitch, physical formidability, fundamental frequency, handgrip strength, sexual selection

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INTRODUCTION

Different sensory channels — e g., chemical, acoustic, visual, and tactile — are used by animals to broadcast and assess opportunity and risk in agonistic and sexual interactions. Vocalizations conveying relevant information about the bearer, e.g., sex, age, biological quality, emotional states, and attitudes, can be broadcast over long distances, in the dark, or when lines of sight are interrupted.

Animal acoustic signals often exhibit some degree of sexual dimorphism. The occurrence of anatomical and behavioral sex differences had long puzzled naturalists, and it was not until Darwin published his seminal book "The Descent of Man, and Selection in Relation to Sex" (Darwin, 1872/1981) that a plausible mechanism for such differences had been proposed. It should be noted though, that Wallace seemed to favor the action of natural selection in promoting sex-specific differences (Wallace, 1889). More recently, additional mechanisms to account for the origin of sexually dimorphic characters have been proposed, e.g., sex-specific ecological niches and sexual food competition (Slatkin, 1984); the causes of sexual dimorphism seem multiple and might interact in complex manners (for a review of the causes of sex dimorphism in primates, see Plavcan, 2001). In many primates, including humans, vocalizations are markedly sexually dimorphic and both sexual selection mechanisms originally proposed by Darwin (1872/1981)—i.e., mate selection and intrasexual competition—are thought to be a major influence in voice attributes dimorphism (Pisanski et al., 2014, 2018; Puts et al., 2016).

Body size and strength are key determinants of animal physical formidability (Fessler et al., 2012) – i.e., fighting ability or resource-holding potential – and therefore play a major role in social interactions. In normal circumstances, larger individuals have better chances of winning agonistic contests with conspecific competitors over limited resources, however, because resources are seldom worth the risk of open combat, most animal species rely on social hierarchies and dominance cues to avoid physical injury (Fitch and Hauser, 2003). In this direction, body size also serves as a visual cue to physical prowess and dominance in different animal species. This is also true for male humans — i.e., taller men are perceived as more leader-like (Blaker et al., 2013) and stronger (Sell et al., 2009) than shorter men. Likewise, in naturalistic environments, the former are granted higher social dominance (Stulp et al., 2015), and in cooperative groups, stronger men are readily granted a higher social status and are perceived as stronger leaders by others (Lukaszewski et al., 2016).

Given the physiological and anatomical constraints acting upon sound production, some acoustic attributes of animal vocalizations serve as cues to body size and physical strength in different animal species. In terrestrial mammals, vocal signals are produced in a two-step process. First, air from the lungs is pushed through the larynx causing the vibration of the laryngeal vocal folds, then the laryngeal vibrations are propagated into the air within the supralaryngeal structures where they are modified by the resonances of these elements (for a review, see Taylor et al., 2016).

Because larger animals — having larger, heavier vocal folds — are predicted to produce vocalizations with a lower F_0, a negative correlation between F_0 and body size has been proposed (Titze, 2000). Along these lines, Bowling et al. (2017) found a negative correlation between "head + body size" and vocalization frequencies across a range of carnivore and primate species. Similarly, Martin et al. (2017) showed that body weight — another operationalization of body size — is an important determinant of minimum vocalization frequency in different terrestrial and aquatic mammal species. Analogous results were also reported by Riede and Brown (2013) based on their analysis of F_0 vs. body weight in different mammal species, and more recently, Aung et al. (2021a) also reported negative associations of F_0 and P_f with both height and weight.

However, because larynx development is not constrained by overall body size in humans and a few other mammalian species, and vocal folds can grow out of proportion in males in response to increased levels of testosterone during puberty, it has been suggested that vocalization frequencies do not reliably correlate with body size in those species (Fitch, 2000). Indeed, previous studies on the relationship between human F_0 and body size have reported mixed results. A recent meta-analysis on the relationship between height and diverse acoustic attributes of human voice found that several *VTL* estimates based on formant frequencies accounted for up to 10% of the height and weight variance, while F_0 accounted for less than 2% of those variances (Pisanski et al., 2016).

Thus far, relatively few studies have focused on the association between directly measured physical strength and voice attributes. While some studies reported a significant negative correlation of male physical strength with F_0 (Hodges-Simeon et al., 2014), P_f (Puts et al., 2012; Hodges-Simeon et al., 2014), and the standard deviation of the fundamental frequency (F_0SD; Puts et al., 2012), other studies, failed to find a significant relationship between physical strength and F_0 (Sell et al., 2010; Atkinson et al., 2012; Smith et al., 2017; Han et al., 2018) or an association of physical strength with F_0SD, D_f, P_f, or *VTL* (Han et al., 2018).

Similarly, research into the relationship between strength ratings from male voice stimuli and actual strength has also thus far provided mixed results. Puts et al. (2012) found a relationship between F_0 and strength perceived from male voices, while Sell et al. (2010) observed a relationship between strength ratings from male voices and actual handgrip strength, suggesting the existence of vocal cues to physical strength, strength proxies, or covariates. In turn, Rosenfield et al. (2020) found that experimentally lowering the F_0 of men voices increased the perception of fighting ability from voices alone in the Tsimané, a small-scale Amazonian society. Along these lines, in a recent meta-analysis of previous studies, Aung and Puts (2019) concluded that F_0 showed a marginal negative correlation with upper-body strength ($\bar{r} = -0.07$, $p = 0.028$).

The mixed results of those studies which explored the association between F_0 and physical formidability (see above), and the low magnitude of this association whenever found, led some authors (Han et al., 2018; Armstrong et al., 2019; and notably Feinberg et al., 2019) to propose that F_0 does not signal formidability. Because a trend to associate F_0 and formidability has been reported in many studies, these authors suggest that this tendency reflects a general bias to associate lower frequency sounds with larger sound sources. Puts and Aung (2019), on the other side of the debate, claim that regardless of the way an association between low voice pitch and formidability might have originated, such an association would only be maintained if it were an honest signal. Furthermore, it has recently been shown that F_0 mediates the relationship between objective and perceived dominance, that is that listeners perceive formidable

men as being more formidable in part because of their voice pitch (Aung et al., 2021b).

In relation to the apparent association of listeners' perceptions of physical formidability and actual biological attributes, in absence of evident associations of acoustic attributes and formidability proxies, Kleisner et al. (2021), have also suggested that physical strength—and most likely other biological attributes—cannot be predicted solely by one acoustic variable, but rather by a combination of multiple interacting acoustic parameters.

Interestingly, in recent years researchers have begun to explore the association of non-verbal vocalizations in humans (e.g., roars, screams, grunts, and laughs) and their role in signaling different biological qualities. Listeners seem to be able to accurately judge inter-individual differences in strength from roars, while no single acoustic attribute seem to be associated with actual strength (Raine et al., 2019; Šebesta et al., 2019; Kleisner et al., 2021). In addition, roars seem to better predict strength than aggressive or normal speech (Raine et al., 2019; Šebesta et al., 2019; Kleisner et al., 2021). Non-linear phenomena appear to play an important part in the communication role of non-verbal vocalizations (Anikin et al., 2021; Kleisner et al., 2021) by means of lowering perceived voice pitch, and causing vocalizers to sound larger, more formidable and more aggressive (Anikin et al., 2021).

This study is aimed at expanding on previous findings on the association of different sexually dimorphic attributes of male voices — F_0, D_f, P_f, and *VTL* — with height, weight and physical strength, three key determinants of physical formidability, and thus, contributing to the current debate. Here, we also explore whether perceptual adaptations may have enabled the assessment of physical formidability by females based on male voices alone. The latter study was designed to test the hypothesis of a positive association between male speakers' strength and strength perception from their voices by female raters.

MATERIALS AND METHODS

Anthropometry and Acoustic Attributes

Anthropometric Measurements and Voice Recordings

One hundred one self-reported heterosexual male students from a mid-sized Spanish university [median age = 20.48 years, interquartile range (*IQR*) = 2.36 years] participated in this study in exchange for course credit. The procedure was approved by the Local Research Ethics Board, and all participants gave written informed consent. Height was measured using a Seca 217 stadiometer and weight was measured on an electronic scale (Rowenta Bodymaster) using standard procedures. Handgrip strength was measured in both hands using a hydraulic dynamometer (Saehan SH5001), taking three measurements for each hand, alternating sides. Because 50% of left-handed people and 9% of right-handed people are weaker in their dominant hand than in their non-dominant hand (Crosby and Wehbé, 1994), here, maximal handgrip strength, i.e., regardless of hand and handedness, was used for the analysis.

The male participants provided voice recordings by reading the following text: "Hace unos días te llamaron para tener una entrevista de trabajo en una importante empresa internacional" (A few days ago you were called in for a job interview at a major international company). All participants were native speakers of Spanish. Recordings were made with an AKG D3700S cardioid microphone and a Fostex FR-2LE recorder at a sampling rate of 44,100 Hz and 16-bit quantization. All recordings were made by the same researcher keeping all conditions unchanged in a quiet, non-soundproofed room, locating the microphone 8 cm away from the speaker's mouth at an angle of 45° to avoid aerodynamic noise. Recordings were saved as uncompressed .wav files.

Spectrographic Analysis of Male Voices

Each recording was analyzed using Praat version 5.2.27 software (Boersma and Weenink, 2017). The fundamental frequency was calculated using acoustic periodicity detection based on autocorrelations, i.e., correlating of a time-domain signal with itself; this technique is more accurate, noise-independent, and robust than alternative methods like those based on cepstrum or combs (Boersma and Weenink, 2017). A floor of 75 Hz and a ceiling of 300 Hz, with a Hanning window length of 0.01 s, were used following programmer's recommendations (Boersma and Weenink, 2017). F_0 was calculated according to programmer's instructions; F1 through F4 were measured using Praat as described by Valentova et al. (2019), while D_f, P_f, and *VTL* were calculated as described by Fitch (1997), Reby and McComb (2003), and Puts et al. (2012), respectively.

Voice Ratings

Vocal Stimuli for Physical Strength, and Attractive Ratings

Voice recordings from the 10 weakest and 10 strongest males from the same sample were used as stimuli in the voice assessment study. Groups do differ significantly in height, weight, *HGS* and *VTL*, while they do not present significant differences in age, F_0, D_f, and P_f (see **Table 1**).

Female Raters

One hundred fifty-one self-reported heterosexual female students from a mid-sized Spanish university (median age = 20.16 years, IQR = 2.11) who reported no chronic or acute hearing impairment participated in the study in exchange for course credit. Voice recordings were presented in random order by means of headphones, and participants were asked to rate each

TABLE 1 | Mann–Whitney *U*-test results.

	Weakest males mean rank	Strongest males mean rank	U	Z	*P*
Age	11.8	9.20	37.00	−0.982	0.326
Height	7.35	13.65	18.50	−2.381	0.017
Weight	7.80	13.20	23.00	−2.041	0.041
HGS	5.50	15.50	0.00	−3.779	<0.001
F_0	12.10	8.90	34.00	−1.209	0.226
D_f	12.50	8.50	30.00	−1.512	0.130
P_f	12.60	8.40	29.00	−1.587	0.112
VTL	7.70	13.3	22.00	−2.117	0.034

TABLE 2 | Descriptive statistics for the male sample.

	Min	Max	Mean	SD	Median	MAD	IQR
Age (yrs)	17.98	26.11	20.77	1.77	20.52	1.85	2.36
Height (cm)	161.00	192.20	176.55	6.97	176.45	6.75	8.93
Weight (Kg)	53.50	114.40	73.36	11.68	72.35	10.08	13.28
HGS (Kg)	24.50	63.00	44.49	8.61	44.40	8.01	10.90
F_0 (HZ)	94.28	167.23	120.51	14.88	121.00	18.25	22.50
D_f (Hz)	855.30	1284.39	1054.27	75.47	1057.92	67.32	92.62
P_f	−1.29	1.28	0.00	0.63	−0.06	0.71	1.01
VTL (cm)	15.63	19.22	17.32	0.85	17.32	0.92	1.24

SD, Standard deviation; MAD, median absolute deviation; IQR, interquartile range.

voice for perceived physical strength and perceived attractiveness on a 4-point ordinal scale (1 = physically weak, 4 = physically strong; 1 = unattractive, 4 = attractive). All raters gave written informed consent and assessed all voice stimuli.

Statistical Analyses

All data analyses were conducted with R software (v4.1.0; R Core Team, 2021). Shapiro–Wilk tests of normality indicated that males' age, anthropometric variables (except body weight) and voice variables were non-normally distributed. Associations between anthropometric variables and acoustic attributes were explored by means of Spearman rank correlation analysis. All tests were two-tailed, and the significance level was set to $\alpha = 0.05$. In order to avoid false positive findings, the Benjamini and Hochberg (1995) false discovery rate (FDR) was used to correct multiple comparisons with FDR < 0.05 considered as statistically significant.

Given that previous studies in this field have shown inconsistent results, it was expected that if any association was to be observed, they would range from low to moderate in magnitude. In this study, the association of voice attributes with different proxies of physical formidability in a sample of 101 men was analyzed. While this study might be slightly underpowered, our sample size would allow to detect a correlation of 0.275 with a 0.80 statistical power. Bootstrapping provides an alternative to relying on underpowered samples. Thus, the significance of the correlations was also assessed through this method with 5,000 simulation iterations.

In the voice ratings study, to avoid random effects in raters and targets, linear mixed models were used to assess the relationship of measured handgrip strength with perceived physical strength and attractiveness from voices alone.

Data were analyzed using R statistical package version v4.1.0 (R Core Team, 2021) using the ordinal package (Christensen, 2019). Model parameters were estimated according to maximum likelihood using Laplace's approximation (clmm function).

RESULTS

Anthropometric Measurements and Vocal Frequencies

Descriptive statistics of the speakers' anthropometric and acoustic variables used in this study are shown in **Table 2** (see also **Supplementary Tables 1, 2**).

In order to analyze the relationship between anthropometric measurements and the different acoustic attributes, Spearman rank correlation coefficients were calculated. Height showed a significant negative correlation with P_f and a positive correlation with *VTL* but did not significantly correlate with F_0 or D_f. Similarly, weight — another operationalization of body size — showed significant negative correlations with D_f and P_f, and a positive correlation with *VTL*, but did not show a significant correlation with F_0. *HGS* showed significant negative correlations with F_0, P_f and a positive correlation with the estimated *VTL*, but did not correlate with D_f.

None of the acoustic attributes of male voices, nor the anthropometric speaker variables showed any significant correlations with age. As expected, height, weight and *HGS* were significantly correlated with each other, as were some of the acoustic attributes of male voices among themselves. The complete correlation matrix is shown in **Table 3**.

TABLE 3 | Zero order Spearman correlations of anthropometric correlates of physical formidability and acoustic variables.

	Age	Height	Weight	HGS	F_0	D_f	P_f	VTL
Age	–	−0.03 ($p = 0.787$)	0.07 ($p = 0.502$)	−0.07 ($p = 0.5$)	0.04 ($p = 0.729$)	−0.09 ($p = 0.355$)	−0.06 ($p = 0.534$)	0.11 ($p = 0.787$)
Height		–	0.57 ($p < 0.001$)	0.34 ($p < 0.001$)	−0.1 ($p = 0.329$)	−0.18 ($p = 0.078$)	−0.27 ($p = 0.006$)	0.27 ($p = 0.006$)
Weight			–	0.33 ($p < 0.001$)	−0.03 ($p = 0.769$)	−0.25 ($p = 0.013$)	−0.36 ($p < 0.001$)	0.31 ($p = 0.002$)
HGS				–	−0.26 ($p = 0.009$)	−0.23 ($p = 0.018$)	−0.28 ($p = 0.004$)	0.28 ($p = 0.004$)
F_0					–	0.02 ($p = 0.835$)	0.05 ($p = 0.612$)	−0.02 ($p = 0.865$)
D_f						–	0.56 ($p < 0.001$)	−0.88 ($p < 0.001$)
P_f							–	−0.84 ($p < 0.001$)
VTL								–

After correcting for false discovery rate using the Benjamini–Hochberg method, all significant zero-order correlations remained significant (see **Supplementary Table 3**). In addition, because our study was slightly underpowered (see section "Materials and Methods"), the confidence intervals of all correlations were calculated through bootstrapping. All significant correlations were supported by this analysis (see **Supplementary Table 4**).

To control for any effect of body size (i.e., height and weight) on the correlation of *HGS* with the acoustic variables, and vice versa, partial Spearman rank correlations were calculated. After controlling for height and weight, the correlation of *HGS* with F_0 and *VTL* remained significant, with very little variation in the correlation coefficients and *p*-values (see **Table 4**), while the correlation between *HGS* and P_f bordered significance [$r_{(101)} = -0.29$, $p = 0.052$] when controlling for the aforementioned variables. In turn, when the effects of *HGS* and weight are controlled for, the correlations of height with P_f and *VTL* become non-significant; and when the effects of *HGS* and height are partialled out, only the correlation between weight and P_f remained significant (see **Table 4**). However, only the partial correlation between F_0 and *HGS*—controlling for height and weight—remained significant after adjusting for the false discovery rate using the Benjamini–Hochberg method (see **Supplementary Table 5**).

Physical Strength and Attractiveness Assessments From Male Voices

Table 5 summarizes the descriptive statistics of physical strength and attractiveness ratings for male voices provided by female raters.

Linear mixed model analyses were used to identify a possible relationship between speakers' handgrip strength and physical strength perceived from male voices. These models contribute to avoiding false-positives by accounting for random variance between raters and targets, and allow the generalization of inferences to other raters and targets (e.g., Durkee, 2019). Given that strength ratings can take values between 1 and 4 (4 ordinal levels), a mixed multilevel logistic regression with cumulative logit link function was used to model handgrip strength.

Three models were considered, as follows: Model 1—the maximal model for our design—which allowed random intercepts for both raters and targets and random slopes for raters, while Model 2 allowed random intercepts for both raters and targets and fixed slopes, and Model 3 allowed random intercepts and slopes for raters only, but not for targets, that is, by considering targets as fixed effects, thus Model 3 only allowed to evaluate the ability of raters to accurately appraise strength based on this particular set of voice stimuli. Random effects were significant for all three models (see **Table 6**).

Models 1, 2, and 3 were assessed using the corrected Akaike's Information Criterion (*AICc*), Δ*AICc*—the difference between the test model *AICc* and the *AICc* of best fitting model— and *AICc* weights [$w_i(AIC)$]—the conditional probabilities for each model being the best model (Wagenmakers and Farrell, 2004). Based on these criteria, Model 1 appears to be the most plausible model (see **Table 7**).

For Model 1, the group (weakest vs. strongest men) coefficient did not reach statistical significance ($b = 0.93$, $p = 0.126$), therefore perceived strength from voices only is not significantly associated with actual strength.

TABLE 4 | Partial Spearman correlations of anthropometric correlates of physical formidability with acoustic attributes of male voices.

	F_0	D_f	P_f	VTL
HGS	−0.25	−0.19	−0.20	0.21
(controlling for height and weight)	(p = 0.012)	(p = 0.068)	(p = 0.052)	(p = 0.038)
Height	−0.05	−0.01	−0.05	0.08
(controlling for strength and weight)	(p = 0.633)	(p = 0.939)	(p = 0.597)	(p = 0.410)
Weight	0.08	−0.15	−0.22	0.16
(controlling for strength and height)	(p = 0.442)	(p = 0.140)	(p = 0.029)	(p = 0.127)

TABLE 5 | Female ratings of male voices.

	Weakest males		Strongest males	
	Mean	SD	Mean	SD
Strength ratings	2.28	0.39	2.59	0.35
Attractiveness ratings	2.12	0.40	2.42	0.42

SD, standard deviation.

TABLE 6 | Standard deviation of raters' and targets' random effects.

		Group-level effects	SD
Strength ratings	Model 1	Rater (Intercept)	1.01
		Rater (Group slope)	0.49
		Target (Intercept)	1.35
	Model 2	Rater (Intercept)	0.88
		Target (Intercept)	1.33
	Model 3	Rater (Intercept)	0.70
		Rater (Group slope)	0.11
Attractiveness ratings	Model 1	Rater (Intercept)	0.91
		Rater (Group slope)	0.15
		Target (Intercept)	1.28
	Model 2	Rater (Intercept)	0.95
		Target (Intercept)	1.28
	Model 3	Rater (Intercept)	0.70

SD, Random effect standard deviation using ordinal cumulative mixed models.

TABLE 7 | Information criteria for the general linear mixed models.

	AICc	ΔAICc	Df	wi(AICc)
Strength ratings				
Model 1	6256.43	0.00	8.00	0.93
Model 2	6261.62	5.19	6.00	0.07
Model 3	7308.61	1052.18	5.00	0.00
Attractiveness ratings				
Model 2	6607.76	0.00	6.00	0.86
Model 1	6611.41	3.66	8.00	0.14
Model 3	7602.35	994.59	5.00	0.00

Following the same approach, using attractiveness ratings based on male voices alone the analysis showed that random effects were significant for all three models (see **Table 6**). Given that the $\Delta AICc$ between Models 2 and 1 is 3.66, both models could be considered, however, *wi(AICc)* for model 2 is far larger than *wi(AICc)* (0.86 vs. 0.14), thus, Model 2 is the most plausible model (see **Table 7**).

The group (weakest vs. strongest men) coefficient for Model 2 did not reach significance ($b = 0.78$, $p = 0.176$). Thus, target strength group — i.e., weakest vs. strongest males — does not have a significant effect on the attractiveness ratings by female raters.

DISCUSSION

Here, we found that F_0, one of the most noticeable attributes of human voice, is negatively correlated with handgrip strength in males, and that this correlation remains significant after controlling for false discovery rate by Benjamini–Hochberg and potential confounders (height and weight). This finding is in line with the observations of Hodges-Simeon et al. (2014), who reported a negative association between F_0 and upper-body strength in a sample of peripubertal Tsimane males, but seems to contradict other studies which failed to find an association of voice pitch and physical strength (Sell et al., 2010; Atkinson et al., 2012; Smith et al., 2017; Han et al., 2018). Our results are also consistent with the conclusions of a recent meta-analysis. While the zero-order correlation between F_0 and physical strength in our study was moderate in size ($r = -0.26$, $p = 0.009$), this association appeared to be stronger than the correlation reported in the meta-analysis conducted by Aung and Puts (2019) in which the authors found a marginal association between male F_0 and upper-body strength ($\bar{r} = -0.07$, $p = 0.028$). It should be noted that, whereas the studies included in Aung and Puts' meta-analysis used a composite measurement of upper-body strength, in our study direct measurements of handgrip strength alone were used. Such a methodological difference may have contributed to apparent differences over the correlation between F_0 and physical strength. In addition, the studies included in Aung and Puts' meta-analysis may not have been statistically robust enough to assert a moderate correlation; 9 of the 11 male samples included in that meta-analysis ranged from 8 to 63 participants only, and/or exhibited substantial age heterogeneity. For instance, an Andean sample consisted of men aged between 15 and 71 ($N = 20$, $M = 34.8$, $SD = 19.10$), while, in another study, the age of Tsimane participants ranged between 19 and 68 years ($N = 49$, $M = 35.8$, $SD = 13.5$) — compared to a low age dispersion in the sample used in the current study (median age = 20.48 years, $IQR = 2.36$).

Thus, with regard to the debate as to whether F_0 actually signals formidability or simply reflects a general tendency to associate lower frequency sounds with larger bodies, our results seem to favor the former position, in that F_0 correlates negatively with physical strength, one of the key components of physical formidability.

While we found a significant positive a zero-order correlation between *VTL* and *HGS* that remains significant after we control for height and weight ($r = 0.21$, $p = 0.038$), our results fail to show an association between *VTL* and *height* when we control for the contribution of *strength* and *weight* ($r = 0.08$, $p = 0.410$). It should be noted that previous associations between *VTL* and *height* were based on zero-order correlations (Pisanski et al., 2016), while in this study we controlled for potentially confounding variables. However, only the correlation between F_0 and *HGS* remains significant after controlling for false discovery rate and potential confounders.

In order to assess the non-verbal communicational value of male voices, the voices of the 10 weakest and 10 strongest males were rated by the female subjects for perceived strength and attractiveness. Here, actual physical strength failed to show a significant effect on perceived strength or attractiveness ratings from male voices given by heterosexual female subjects. This negative result seems to contradict previous studies, where the authors found that listeners could assess physical strength from voices (Sell et al., 2010; Raine et al., 2018, 2019) or roars (Raine et al., 2018, 2019). However, our results are in line with other studies which found no association between physical strength—a key determinant of fighting ability—and perceived fighting ability (Šebesta et al., 2019), between actual threat potential—derived from the measures of their upper-body strength, height, and weight—and perceived threat potential (Han et al., 2017), or an association between self-reported fighting ability and perceived fighting ability (Doll et al., 2014)—which could be assumed to be related, at least in part, to physical strength.

The different outcomes of the studies above might reflect differences in fitness variables used in the various studies (handgrip strength, composite measures of fighting ability or threat potential), and/or procedure differences (ratings of perceived fighting ability, threat potential or strength). Thus, it is clear that the true nature of the association of actual and perceived strength—or its proxies—is still unclear; and a standardized approach to this issue will help comparison among different studies.

Unlike previous studies, here the effect of actual speaker strength on perceived strength ratings elicited by male voice stimuli was assessed by ordinal linear mixed models so as to avoid inflated false-positives due to random variance between raters and stimuli. The treatment of raters and stimuli as random effects increases the accurateness of extrapolating statistical inferences to other samples of raters and stimuli (Judd et al., 2012; Durkee, 2019). While this approach allows for the generalization of the results to other samples, it is also more strict than fixed effects models; therefore, this might contribute to explain the differences observed in different studies.

Intersexual selection and intrasexual competition—the two original mechanisms of sexual selection proposed by Darwin (1872/1981)—may both act upon the same sexually dimorphic characters (Berglund et al., 1996), that is, secondary sex characters may play a role both in intrasexual competition, and also serve as cues in mate selection. While in this study we analyzed the potential of male voices in advertising physical strength to female raters—a desirable attribute and a potential indicator of biological

quality—it will of interest to analyze whether there are sex-specific differences in assessing physical strength from auditory cues, e.g., if males are better in assessing physical strength from voices only; if so, this might be indicative of a greater role of male voices in intrasexual competition mechanisms.

Our research has some potential limitations and shortcomings. A larger sample would have been needed to provide sufficient statistical power to detect a low-to-moderate correlation between vocal frequency and body size (Pisanski et al., 2014). In the same vein, physical strength and attractiveness ratings from male voices provided by male raters – together with female ratings – would have helped to further understand the role of intrasexual competition and intersexual selection in the evolution of voice sexual dimorphism. Further, only a few acoustic attributes of human voice were studied here. In this regard, the analysis of prosodic attributes of human voice may prove essential to effectively understanding the role of human voice in non-verbal communication.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Comité de Ética de Investigación, Facultad de Psicología, Universidad de Murcia, Spain. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

AM and FM proposed and designed the study. AM, FM, DE-C, CG, and NK collected the data. ML conducted the data analysis. AM, FM, and ML wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.879102/full#supplementary-material

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BRIEF RESEARCH REPORT
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Evolution of Artistic and Athletic Propensities: Testing of Intersexual Selection and Intrasexual Competition

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Since Darwin proposed that human musicality evolved through sexual selection, empirical evidence has supported intersexual selection as one of the adaptive functions of artistic propensities. However, intrasexual competition has been overlooked. We tested their relative importance by investigating the relationship between the self-perceived talent/expertise in 16 artistic and 2 sports modalities and proxies of intersexual selection (i.e., mate value, mating and parenting efforts, sociosexuality, and number of sexual partners) and intrasexual competition (i.e., aggressiveness, intrasexual competitiveness) in heterosexuals. Participants were 82 Brazilian men, 166 Brazilian women, 146 Czech men, and 458 Czech women (Mage = 26.48, SD = 7.12). Factor analysis revealed five factors: Literary-arts (creative writing, humor, acting/theater/film, poetry, storytelling), Visual-arts (painting/drawing, sculpting, handcrafting, culinary arts, architecture design), Musical-arts (playing/instruments, singing, dance, whistling), Circus-arts (juggling, acrobatics), and Sports (individual, collective). Multivariate General Linear Model (GLM) showed more associations of the arts to intersexual selection in women and to intrasexual selection in men, and overall more relationships in women than in men. In women, literary and musical-arts were related to elevated inter- and intrasexual selections proxies, visual and circus-arts were related to elevated intersexual selection proxies, and sports were related to intrasexual selection proxies. In men, literary-arts and sports were related to elevated inter- and intrasexual selection proxies, musical-arts were related to intrasexual proxies, and circus-arts were related to intersexual proxies; visual-arts did not have predictors. Although present in both sexes, each sexual selection component has different relative importance in each sex. Artisticality functions to attract and maintain long/short-term partners, and to compete with mating rivals.

Keywords: arts, aesthetic behavior, sexual selection, aggression, mating, creativity, sport, ornament

INTRODUCTION

Recently, an increasing number of theoretical propositions and empirical studies have developed to explain the evolved aspects of artistic propensities. Some researchers support the hypothesis that artistic activities result from non-artistic pre-existing psychological capacities recently co-opted as a non-specialized by-product to generate human artistic output (e.g., Pinker, 2004; Souza, 2004; Hodgson and Verpooten, 2015). Others argue for the existence of a set of ancestral psychological capacities that are specialized in processing artistic information (e.g., Eibl-Eibesfeldt, 1989; Zahavi and Zahavi, 1999; Martindale et al., 2007; Dutton, 2009; Davies, 2012; Sütterlin et al., 2014; Hogh-Olesen, 2018; Richards, 2019; Varella, 2021). The main proposed ancestral adaptive values are related to survival benefits (e.g., in-group cohesion, parental bonding, cognition and health improvement) and to reproductive advantages (e.g., mate selection, intrasexual competition) (Dissanayake, 2008; Varella et al., 2010, 2011, 2017; Menninghaus, 2019; De Tiège et al., 2021; Kalinowski et al., 2021). The different evolutionary perspectives are not mutually exclusive (Menninghaus, 2019), so dismissing one perspective does not necessarily support another (Varella et al., 2017). Not every behavioral tendency has adaptive value, not every ancestral adaptation is currently adaptive, and ancestral adaptive value does not need to be consciously represented in one's mind for one to behave adaptively (Varella et al., 2012, 2013). Only corroborative and cumulative empirical evidence can strengthen the case for exaptationist and adaptationist propositions (cf. Andrews et al., 2002; Schmitt and Pilcher, 2004).

Roughly 150 years ago, Darwin (1871) proposed that animal, including human, body and psychobehavioral ornaments evolved mostly through sexual selection by female mate choice. He integrated various sources of evidence and argued that the pleasures, the universality, the prehistoric antiquity, the emotions evoked, and the adaptive convergence of musical and dancing behaviors "become intelligible to a certain extent, if we may assume that musical tones and rhythm were used by our half-human ancestors, during the season of courtship, when animals of all kinds are excited not only by love, but by the strong passions of jealousy, rivalry, and triumph" (p. 572). By stressing jealousy, rivalry, and triumph alongside love, Darwin suggested a plurality of evolutionary mechanisms that includes both inter and intrasexual selection.

Intersexual Selection

Artistic propensities could have evolved as an ornament. Converging evidence has mostly corroborated intersexual selection as one of the possible processes influencing the evolution of human aesthetic creativity and artistic propensities (Low, 1979; Karamihalev, 2013). The mere listening of enjoyable background music leads to: increased testosterone levels in women (Fukui, 2001), women's increased attractiveness ratings of male photographs (May and Hamilton, 1980; Marin et al., 2017), and women's increased desire to go on a romantic date with the individuals in the photographs; no such effects were found in men (Marin et al., 2017). Groovy background music increases women's desire to meet again a speed dating partner, and the synchronization of their body sway predicts their interest in a long-term relationship beyond perceived attractiveness (Chang et al., 2021). Even seeing a guitar impacts on women's mating decisions: women tend to reply positively to a friendship request on social network when the profile picture shows a man holding a guitar (Tifferet et al., 2012). Further, activated mating motivations increase creative displays in men and women; both short-term and long-term contexts increase men's creativity, but only a high-quality mate and a long-term context increase creativity in women (Griskevicius et al., 2006).

Regarding mate preferences, "artistic-intelligent" is the third most preferred factor among married couples and explains 4.5% of the variance behind "kind and considerate" (16%) and "socially exciting" (6.9%). In an unmarried sample, "creative" is ranked the 7th most important mate preference trait (Buss and Barnes, 1986). Across 37 cultures, men and women rank "artistic" and "creative" as the 6th and 7th most important characteristics in a romantic partner, respectively (Buss et al., 1990). In a 25-year follow up study in India, the preferences for "creative and artistic" increased in both sexes (Kamble et al., 2014), and 30 years later in Brazil, the preference for "creative and artistic" increased in men and decreased in women (Souza et al., 2016). Both sexes prefer more ornamental and aesthetic types of creativity (e.g., writing music, poetry, drawing) in a prospective sexual partner than "applied/technological" and "everyday/domestic" forms of creativity; although women prefer relatively more the first type, while men prefer more the third type of creativity (Kaufman et al., 2016). Women's preferences are even influenced by their fertility status: those in their maximally fertile phase prefer "creativity" over "wealth" for a short-term relationship, but not for a long-term one (Haselton and Miller, 2006), and they prefer composers of complex musical pieces for short-term relationships (Charlton, 2014). Further, women in their peak fertility exhibit increased creativity (Galasinska and Szymkow, 2021) and more attractive dance movements (Miller et al., 2007; Fink et al., 2012).

Importantly, after satisfying mate preference necessities (e.g., intelligence, income, attractiveness), men and women prefer creativity in a romantic partner (Li et al., 2002; Thomas et al., 2020). Men's creativity increases women's rating of attractiveness and mate appeal (Prokosch et al., 2009; Watkins, 2017), independently of intelligence (Prokosch et al., 2009), and even compensates for low facial attractiveness (Watkins, 2017). The reverse also may be supported, as men also perceived creative women as more attractive (Watkins, 2017). Women appreciate funny men, while men value women who appreciate their jokes (Bressler and Balshine, 2006; Bressler et al., 2006; Hone et al., 2015). Men and women prefer mates who privately sing or play musical instruments (Bongard et al., 2019). Individuals who like to sing more, who sing with higher pitch modulation, and higher-pitched singing in women are perceived as more attractive (Valentova et al., 2019). In men, physical size positively predicts speech and singing attractiveness (Valentova et al., 2019). Last, for dance, good male dancers receive more attention and are rated by women as more attractive and masculine than bad dancers (Weege et al., 2012). Dancing women who are rated as more

attractive and feminine receive more visual attention (Röder et al., 2016). Dance movements of physically stronger men are evaluated as more attractive by women (Hugill et al., 2009; Weege et al., 2015).

Regarding the connection of creativity and artistic propensities with sexual strategies and mating outcomes, men with higher-pitched singing have higher sociosexuality (i.e., variety of casual sex) (Valentova et al., 2019). Men and women with greater humor production have more short-term uncommitted sex, and the ability to produce humor in both sexes mediates the positive effects of intelligence and mating success (Greengross and Miller, 2011). Poets and artists of both sexes tend to have more sexual partners than control groups, and higher levels of creative engagement correlate with higher numbers of sexual partners (Nettle and Clegg, 2006). Men exhibiting a stronger tendency to engage in everyday forms of creative activity tend to report more sexual partners in the last year, but no corresponding result is found for women (Beaussart et al., 2012). Successful male visual artists have more sexual partners and have a more long-term oriented sexual strategy than less successful visual artists, with no effect found in female visual artists (Clegg et al., 2011). High music achievement in men relates to higher number of children, and, in both sexes, music aptitude and achievement relate to a long-term mating orientation, i.e., low number of sex-partners, older age of first intercourse, and restricted sociosexuality (Mosing et al., 2015).

Despite the inter-sexual selection hypothesis being well corroborated empirically, some predictions have not been supported. These conflicting findings indicate the necessity for further research. For instance, visually creative individuals in a non-industrialized semi-nomadic Kenyan tribe with natural fertility tend to have fewer children (Lebuda et al., 2021). Further, individuals with greater musical ability have lower mating success (Mosing et al., 2015). Others report no effect of women's conception risk on their short-term preferences for male creativity (Prokosch et al., 2009). Last, the attractiveness of one's singing voice is not related to their sexual strategies (Valentova et al., 2019), and musicians and non-musicians do not differ in the number of sex partners (Harrison and Hughes, 2017).

Intrasexual Competition

The maintenance of long-term relationships, parental effort, and intrasexual competition are central, although understudied, domains of sexual selection (Andersson, 1994; Puts, 2010; Varella et al., 2017). Artistic propensities could have evolved as an armament in the prestige competition (De Block and Dewitte, 2007; Varella et al., 2017; Winegard et al., 2018). Both sexes should compete intrasexually using the traits that the other sex finds desirable, and "artistic" and "creative" are among the desired traits in a mate (Buss and Barnes, 1986; Buss et al., 1990). Indeed, the same women's vocal parameters that men find attractive (i.e., femininity) are used by other women to track the threat of potential rivals (Puts et al., 2011). Self-promotion *via* aesthetics and beauty can be both an intersexual ornament and an intrasexual armament in both sexes, although mostly in women (Varella et al., 2017; Mafra et al., 2020). Fisher and Candea (2012) showed that popular women musicians include in their song lyrics topics of intrasexual competition such as mate manipulation, self-promotion, and competitor derogation/manipulation. Nevertheless, little effort has been made to empirically explore intrasexual selection hypotheses, and to contrast the effects of inter and intrasexual components.

Comparing Intersexual and Intrasexual Selection

Chen and Chang (2015) found that, in men, creativity (i.e., general originality) increases in an intersexual vs. intrasexual situational condition, but in women, creativity is the same in both situations. Moreover, creative males exhibit a mating strategy bias toward intersexual courtship compared to intrasexual competition. Even beyond the arts, there has been minimal work that compares the two components of sexual selection. Sports, like the arts, can be seen as play/leisure and profession, dependent on specific motivation, talent, skill, and as sexually selected cultural displays and honest fitness indicators (Zahavi and Zahavi, 1999; Miller, 2000; De Block and Dewitte, 2007; Lombardo, 2012; Hsu and Valentova, 2020; Moraes et al., 2021; Hsu et al., 2022). There also have been theoretical propositions suggesting that both intersexual and intrasexual selection might have influenced the evolution of athletic propensities (e.g., Lombardo, 2012; Apostolou, 2015), however, no direct empirical tests have been conducted beyond sex differences (e.g., Apostolou, 2015).

The few studies comparing the strength of inter- and intrasexual selection were performed for sexually dimorphic male-biased traits. Concerning bodily traits, there is a higher relevance of intrasexual competition than intersexual selection; physical dominance leads to mating success (Kordsmeyer et al., 2018). For the evolution of human voice characteristic, although the low fundamental frequency predicts attractiveness and dominance ratings, the intrasexual component *via* physical dominance exhibit a stronger role than mate selection (Puts, 2010; Hodges-Simeon et al., 2011; Puts et al., 2016). Therefore, the relative importance of inter- and intrasexual selection in the case of artistic and athletic propensities requires empirical investigation.

Aims

We investigated associations of proxies of intersexual selection and intrasexual competition with individual variation in artistic and athletic tendencies in a cross-cultural sample (Brazil and the Czechia). Based on the available evidence, we hypothesized that in both sexes artistic and athletic propensities would be more associated with traits related to intersexual selection (e.g., mate value, number of partners) than intrasexual selection (e.g., competitiveness, aggressiveness).

METHOD

Participants

Participants were 82 Brazilian men (Mage = 28.35, SD = 5.91), 166 Brazilian women (Mage = 26.05, SD = 6.43), 146 Czech

men (Mage = 26.74, SD = 7.45), and 458 Czech women (Mage = 26.52, SD = 7.60), all of whom identified as heterosexuals (18–69 years old). Unfinished participation (n = 472), and non-heterosexual participants (n = 104) were excluded from this study. Intrasexual and intersexual selections work in different ways in non-heterosexual individuals (cf. Semenyna et al., 2020).

Procedures

Participants were recruited between April 2013 and April 2014 through social media. Upon informed consent, they voluntarily answered the anonymous online questionnaires in Qualtrics (Provo, UT). This study was a part of a bigger project (cf. Valentova et al., 2020), thus only information relevant to the present study is provided. The procedure took about 50 min; there was no payment for participation. The procedure was the same in both countries.

Materials

All questionnaires were back-translated and adjusted to Brazilian-Portuguese and Czech language. Participants provided basic socio-demographic data: age, sex, and relationship status.

Inspired by the Creative Achievement Questionnaire (Carson et al., 2005), we asked participants to indicate their self-perceived level of talent/experience in 18 artistic leisure activities (i.e., 16 artistic and 2 sports modalities) using a scale from 0 (no talent/experience) to 10 (very much talent/experience). Principal component analysis with Varimax rotation grouped the leisure activities according to eigenvalues > 0.1 (see **Table 1**). The solution yielded 5 factors named as follows: (PC1) Literary-arts (creative writing, humor, acting in theater/film, poetry, storytelling), (PC2) Visual-arts (painting/drawing, sculpting, handcrafting, culinary arts, architecture design), (PC3) Musical-arts (playing instruments, singing, dance, whistling), (PC4) Sports (individual and collective sports), (PC5) Circus-arts (juggling, doing acrobatics).

The Self-Perceived Mate Value questionnaire was inspired by previous measures testing this concept (see Fernandez et al., 2014). The participants reported how easy it would be (1 = *extremely difficult*; 7 = *extremely easy*) to find a short-term (i.e., "If you were single, how easy would it be for you to find a short-term mate for romance?" and "If you were single, how easy would it be for you to find a short-term mate for only sex?") and a long-term mate (i.e., "If you were single, how easy would it be for you to find a potential long-term mate?" and "If you were single, how easy would it be for you to find a long-term relationship potentially leading to marriage?"). Using the same scale, they also answered a more general question "How easy would it be to find a potential partner at this moment, in the city where you live if you were single." Finally, the participants self-rated their physical attractiveness on a scale from 1 (*Not at all attractive*) to 7 (*Very attractive*). Factor analysis with varimax rotation yielded a 2-factor solution with eigenvalues > 1. (3.008; 1.220) accounting for 70.465% of the total variance. The factors were named Short-term mate value and Long-term mate-value and their regression scores entered into further analyses.

The Sociosexual Orientation Inventory-Revised (SOI-R; Penke and Asendorpf, 2008) measures the propensity toward uncommitted sexual variety using 9 items completed *via* 9-point scales. The SOI-R is divided into sociosexual behavior (α = 0.790), attitudes (α = 0.777), and desires (α = 0.828).

The Brief Life-History Scale (Kruger, 2017) has 4 items for each dimension: mating effort (α = 0.687; e.g., "sleep with a large number of people in your lifetime") and parenting effort (α = 0.574; e.g., "caring and emotionally supportive in a long-term relationship"), measured on a 7-point scale (1 = *not at all*; 7 = *very much*) for how each item describe the participants.

The Intrasexual Competition Scale (Buunk and Fisher, 2009) has 12 sex-specific items (e.g., "I want to be just a little better than other men/women.") measuring intrasexual competitiveness on a 7-point scale (1 = *not at all applicable*; 7 = *completely applicable*). Factor analysis with varimax rotation yielded a 3-factor solution with eigenvalues > 1. (4.862; 1.474; 1.061) accounting for 61.644% of the total variance. The factors were named as Attractiveness envy, Superiority, and Status protection. Their regression scores entered into further analyses.

The Brazilian adaptation of the Buss-Perry Aggression Questionnaire (Gouveia et al., 2008) has 26 items answered on 5-point scales (1 = *extremely uncharacteristic of me*; 5 = *extremely characteristic of me*) loading onto 4 subscales: anger (α = 0.834; e.g., "Some of my friends think I'm a hothead"), hostility (α = 0.688; e.g., "I am suspicious of overly friendly strangers"), physical aggression (α = 0.813; e.g., "If somebody hits me, I hit back"), and verbal aggression (α = 0.603; e.g., "I often find myself disagreeing with people"). The Czech translation kept the same items as the Brazilian version. The average of the items per subscale entered further analyses.

TABLE 1 | Factor loadings of the 18 leisure activities after principal component analysis.

	Component loadings					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**Uniqueness**
Creative writing	0.804					0.320
Storytelling	0.732					0.398
Humor	0.679					0.412
Poetry	0.650					0.439
Acting theater film	0.512					0.620
Handcrafting		0.756				0.391
Painting and drawing		0.712				0.437
Architectural design		0.702				0.457
Sculpting		0.666				0.341
Culinary arts		0.550				0.566
Singing			0.848			0.221
Musical instrument playing			0.767			0.322
Dance			0.502			0.528
Whistling			0.459			0.682
Individual sport				0.752		0.364
Collective sport				0.751		0.379
Juggling					0.768	0.319
Acrobatics					0.705	0.340

Applied rotation method is varimax.

Analyses

Analyses were run using SPSS 26.0 (IBM Corp., Armonk, NY, United States). To test for a potential effect of sex, we performed a multivariate General Linear Model (GLM) with the 5 leisure activities factors (viz., literary, musical, visual, and circus arts, and sports) as dependent variables, sex as a factor, and age as a covariate.

To test the influence of indicators of inter- and intrasexual selection on artistic talent/experience factors, we ran a multivariate GLM for each sex separately with artistic talent/experience factors as dependent variables, while two mate value subscales (short-term and long-term), life history sub-scales (mating and parenting efforts), sociosexuality (behavior, desires and attitudes), numbers of long-term and short-term partners, four aggressiveness subscales (anger, hostility, physical, and verbal aggression), three intrasexual competitiveness subscales (attractiveness envy, superiority, and status protection), and age entered as predictors. We report partial Eta-squared (ηp2) and Observed power as effect size estimators.

RESULTS

Influence of Sex and Age on Leisure Activities

We created a multivariate GLM with the five leisure activities factors as dependent variables, sex as factor, and age as a covariate. Age had significant negative effect on Musical arts (F = 10.15, df = 1, p = 0.001, η_p^2 = 0.012), and Circus arts (F = 5.26, df = 1, p = 0.022, η_p^2 = 0.006), and no significant effect on Literary arts (F = 3.18, df = 1, p = 0.075, η_p^2 = 0.004), Visual arts (F = 3.55, df = 1, p = 0.060, η_p^2 = 0.004), or Sports (F = 1.78, df = 1, p = 0.183, η_p^2 = 0.002). Sex had a significant effect on all the leisure activities, namely, Literary arts (F = 24.92, df = 1, p < 0.001, η_p^2 = 0.030), Visual arts (F = 52.34, df = 1, p < 0.001, η_p^2 = 0.060), Musical arts (F = 17.05, df = 1, p < 0.001, η_p^2 = 0.020), Sport (F = 7.29, df = 1, p = 0.007, η_p^2 = 0.009), and Circus arts (F = 68.43, df = 1, p < 0.001, η_p^2 = 0.077). Specifically, women showed higher score in Visual arts and Musical arts, while men scored higher in Literary arts, Sport, and Circus arts. Due to these differences, we performed analyses separately for men and women, controlling for age.

Influence of Intrasexual Competition and Intersexual Selection Indicators on Leisure Activities

We constructed two multivariate GLMs separately for men and women, with the five leisure activities as dependent variables, and indicators of intersexual selection and intrasexual competition as predictors.

In women (N = 541), the model (Pillai's Trace = 0.039, F = 4,213, p = 0.001, η_p^2 = 0.039, Observed power = 0.960) showed that Literary arts were predicted positively by Short-term mate value, SOI-R Desire, IC-Superiority, and negatively by SOI-R Attitude. Visual arts were predicted positively by parenting effort, and negatively by anger and IC-Attractiveness envy. Musical arts were predicted positively by Short-term mate value and IC-Attractiveness envy, and negatively by hostility and SOI-R Attitude. Circus arts were predicted positively by the number of long-term partners, and negatively by Parenting effort and SOI-R Attitude. Sport was predicted positively by verbal aggression, and negatively by anger. See **Table 2**.

In men (N = 209), the model (Pillai's Trace = 0.064, F = 2,571, p = 0.028, η_p^2 = 0.064, Observed power = 0.787) showed that Literary arts were predicted positively by Long-term mate value, IC-Superiority and verbal aggression, and negatively by hostility. Musical arts were predicted positively by IC-Status protection. Circus arts were positively predicted by Short-term mate value. There was no significant predictor for Visual arts. Sports were predicted positively by Short-term mate value, IC-Superiority and physical aggression, and negatively by anger. See **Table 3**.

DISCUSSION

We investigated the relative importance of intersexual and intrasexual selection as possible evolutionary mechanisms maintaining human artistic and athletic propensities. We tested whether individual differences in artistic and athletic propensities covary with traits related to inter- or intrasexual selection in both sexes in Brazilian and Czech samples. We found that although inter- and intrasexual selections are present to a certain degree in both sexes, each sexual selection component has different relative importance in each sex. This finding is aligned with the "beauty and the beast" model (Puts, 2010), in which intrasexual competition is argued to be more relevant in men and intersexual selection more relevant in women throughout human evolution. Moreover, in line with the empirical review pointing to a slight superiority of women in the aesthetic and artistic domains (Varella et al., 2017), we found higher overall effect sizes and more significant relationships between the artistic propensities and the sexual selection processes in women than in men. In women, literary and musical arts were related to both elevated inter- and intrasexual selection proxies; visual and circus arts were related to elevated intersexual selection proxies; while sports were only related to intrasexual selection proxies. In men, literary arts and sports were related to both elevated inter- and intrasexual selections proxies; musical arts were related to a single elevated intrasexual proxy, and circus arts were related to a single elevated intersexual proxy. Thus, in accordance to the Mutual Mate Choice model (Stewart-Williams and Thomas, 2013), as for other physical and vocal traits (Puts, 2010; Puts et al., 2016; Saxton et al., 2016; Kordsmeyer et al., 2018), both components of sexual selection might have been among the influential selective pressures acting upon the ancestral evolution of human artisticality (De Block and Dewitte, 2007; Varella et al., 2017) and athleticism (Lombardo, 2012; Apostolou, 2015; Deaner et al., 2016).

In women, artistic tendencies were associated with nine proxies of intersexual selection (five positive and four negative) and seven proxies of intrasexual competition (four negative and three positive). For literary arts, despite the negative association

TABLE 2 | Parameter estimates of the multivariate general linear model (GLM) model indicating the effect of the independent variables on artisticality in women.

Dependent variable	Parameter	B	SE	*t*	*p*	95% CI		Partial eta^2	Observed power
						Lower bound	Upper bound		
Literary arts	Intercept	–0.866	0.394	–2.299	0.028	–1.640	–0.092	0.009	0.593
	Age	0.022	0.006	3.445	0.001	0.010	0.035	0.022	0.930
	LH parenting effort	0.028	0.044	0.631	0.528	–0.059	0.115	0.001	0.097
	LH mating effort	0.060	0.048	1.249	0.212	–0.034	0.154	0.003	0.239
	SOI-R behavior	–0.007	0.034	–0.217	0.828	–0.073	0.059	0.000	0.055
	SOI-R attitude	–0.054	0.023	–2.309	0.021	–0.100	–0.008	0.010	0.635
	SOI-R desire	0.074	0.029	2.570	0.010	0.017	0.130	0.012	0.728
	N of long-term relationships	–0.075	0.043	–1.740	0.082	–0.159	0.010	0.006	0.412
	N of short-term relationships	0.009	0.007	1.387	0.166	–0.004	0.022	0.004	0.283
	Mate value–Long term	0.090	0.046	1.957	0.051	0.000	0.180	0.007	0.497
	Mate value–Short term	0.194	0.050	3.883	0.000	0.096	0.292	0.028	0.972
	BPA anger	–0.095	0.061	–1.568	0.118	–0.214	0.024	0.005	0.347
	BPA physical aggression	0.050	0.078	0.645	0.519	–0.103	0.203	0.001	0.099
	BPA verbal aggression	0.128	0.069	1.850	0.065	–0.008	0.264	0.006	0.455
	BPA hostility	–0.063	0.066	–0.959	0.338	–0.191	0.066	0.002	0.160
	IC attractiveness envy	–0.027	0.047	–0.571	0.568	–0.118	0.065	0.001	0.088
	IC superiority	0.150	0.045	3.358	0.001	0.062	0.238	0.021	0.918
	IC status protection	–0.065	0.043	–1.509	0.132	–0.150	0.020	0.004	0.325
Visual arts	Intercept	–0.603	0.413	–1.461	0.145	–1.414	0.208	0.004	0.308
	Age	–0.001	0.007	–0.163	0.871	–0.014	0.012	0.000	0.053
	LH parenting effort	0.130	0.046	2.807	0.005	0.039	0.221	0.015	0.800
	LH mating effort	0.070	0.050	1.397	0.163	–0.029	0.169	0.004	0.286
	SOI-R behavior	–0.035	0.035	–1.008	0.314	–0.105	0.034	0.002	0.172
	SOI-R attitude	–0.015	0.025	–0.618	0.537	–0.063	0.033	0.001	0.095
	SOI-R desire	0.002	0.030	0.065	0.949	–0.057	0.061	0.000	0.050
	N of long-term relationships	0.042	0.045	0.941	0.347	–0.046	0.131	0.002	0.156
	N of short-term relationships	–0.010	0.007	–1.379	0.169	–0.023	0.004	0.004	0.280
	Mate value–Long term	0.034	0.048	0.711	0.477	–0.060	0.129	0.001	0.109
	Mate value–Short term	0.060	0.052	1.142	0.254	–0.043	0.163	0.002	0.207
	BPA anger	–0.150	0.064	–2.356	0.019	–0.275	–0.025	0.011	0.652
	BPA physical aggression	0.093	0.082	1.145	0.253	–0.067	0.254	0.003	0.208
	BPA Verbal aggression	0.091	0.073	1.254	0.210	–0.052	0.234	0.003	0.240
	BPA hostility	0.025	0.069	0.357	0.721	–0.110	0.159	0.000	0.065
	IC attractiveness envy	–0.096	0.049	–1.965	0.050	–0.192	–1.517E-5	0.007	0.501
	IC superiority	0.092	0.047	1.953	0.051	–0.001	0.184	0.007	0.496
	IC status protection	0.055	0.045	1.213	0.226	–0.034	0.143	0.003	0.228
Musical arts	Intercept	1.042	0.408	2.554	0.011	0.241	1.844	0.012	0.722
	Age	–0.016	0.007	–2.400	0.017	–0.029	–0.003	0.011	0.669
	LH parenting effort	0.025	0.046	0.549	0.584	–0.065	0.115	0.001	0.085
	LH mating effort	0.060	0.050	1.204	0.229	–0.038	0.158	0.003	0.225
	SOI-R behavior	–0.025	0.035	–0.728	0.467	–0.094	0.043	0.001	0.112
	SOI-R attitude	–0.075	0.024	–3.073	0.002	–0.122	–0.027	0.018	0.866
	SOI-R desire	0.013	0.030	0.425	0.671	–0.046	0.071	0.000	0.071
	N of long-term relationships	0.004	0.044	0.095	0.924	–0.083	0.092	0.000	0.051
	N of short-term relationships	–0.008	0.007	–1.223	0.222	–0.022	0.005	0.003	0.231
	Mate value–Long term	0.019	0.048	0.394	0.694	–0.075	0.112	0.000	0.068
	Mate value–Short term	0.119	0.052	2.305	0.022	0.018	0.221	0.010	0.634
	BPA anger	0.002	0.063	0.039	0.969	–0.121	0.126	0.000	0.050
	BPA physical aggression	0.044	0.081	0.541	0.588	–0.115	0.202	0.001	0.084
	BPA verbal aggression	–0.020	0.072	–0.281	0.779	–0.161	0.121	0.000	0.059
	BPA hostility	–0.154	0.068	–2.264	0.024	–0.287	–0.020	0.010	0.618
	IC attractiveness envy	0.116	0.048	2.410	0.016	0.021	0.211	0.011	0.672
	IC superiority	0.025	0.046	0.547	0.584	–0.066	0.116	0.001	0.085
	IC status protection	0.000	0.045	–0.006	0.995	–0.088	0.087	0.000	0.050
Sports	Intercept	–1.067	0.399	–2.671	0.008	–1.852	–0.282	0.013	0.760
	Age	0.002	0.007	0.268	0.789	–0.011	0.015	0.000	0.058
	LH parenting effort	0.080	0.045	1.795	0.073	–0.008	0.168	0.006	0.433

(Continued)

TABLE 2 | (Continued)

Dependent variable	Parameter	B	SE	*t*	*p*	95% CI		Partial eta^2	Observed power
						Lower bound	Upper bound		
	LH mating effort	0.028	0.049	0.567	0.571	–0.068	0.123	0.001	0.087
	SOI-R behavior	0.023	0.034	0.664	0.507	–0.044	0.089	0.001	0.102
	SOI-R attitude	0.000	0.024	0.018	0.986	–0.046	0.047	0.000	0.050
	SOI-R desire	–0.007	0.029	–0.238	0.812	–0.064	0.050	0.000	0.056
	N of long-term relationships	–0.011	0.044	–0.244	0.808	–0.096	0.075	0.000	0.057
	N of short-term relationships	0.000	0.007	–0.040	0.968	–0.014	0.013	0.000	0.050
	Mate value–Long term	0.085	0.047	1.821	0.069	–0.007	0.176	0.006	0.443
	Mate value–Short term	0.042	0.051	0.835	0.404	–0.057	0.142	0.001	0.133
	BPA anger	–0.133	0.062	–2.164	0.031	–0.254	–0.012	0.009	0.579
	BPA physical aggression	0.153	0.079	1.941	0.053	–0.002	0.308	0.007	0.491
	BPA verbal aggression	0.237	0.070	3.379	0.001	0.099	0.375	0.021	0.921
	BPA hostility	–0.064	0.066	–0.960	0.337	–0.194	0.067	0.002	0.160
	IC attractiveness envy	–0.047	0.047	–0.986	0.324	–0.139	0.046	0.002	0.166
	IC superiority	0.065	0.045	1.435	0.152	–0.024	0.154	0.004	0.299
	IC status protection	0.010	0.044	0.237	0.813	–0.075	0.096	0.000	0.056
Circus arts	Intercept	0.249	0.377	0.660	0.510	–0.492	0.989	0.001	0.101
	Age	–0.008	0.006	–1.234	0.218	–0.020	0.004	0.003	0.234
	LH parenting effort	–0.112	0.042	–2.660	0.008	–0.195	–0.029	0.013	0.756
	LH mating effort	0.071	0.046	1.536	0.125	–0.020	0.161	0.004	0.335
	SOI-R behavior	–0.011	0.032	–0.358	0.721	–0.075	0.052	0.000	0.065
	SOI-R attitude	–0.056	0.022	–2.478	0.014	–0.100	–0.012	0.012	0.696
	SOI-R desire	0.008	0.027	0.279	0.780	–0.046	0.062	0.000	0.059
	N of long-term relationships	0.088	0.041	2.135	0.033	0.007	0.168	0.009	0.568
	N of short-term relationships	0.000	0.006	0.069	0.945	–0.012	0.013	0.000	0.051
	Mate value–Long term	0.065	0.044	1.487	0.138	–0.021	0.152	0.004	0.317
	Mate value–Short term	0.009	0.048	0.196	0.844	–0.085	0.103	0.000	0.054
	BPA anger	–0.008	0.058	–0.135	0.893	–0.122	0.106	0.000	0.052
	BPA physical aggression	0.039	0.075	0.521	0.603	–0.108	0.185	0.001	0.081
	BPA verbal aggression	–0.006	0.066	–0.087	0.930	–0.136	0.124	0.000	0.051
	BPA hostility	0.097	0.063	1.550	0.122	–0.026	0.220	0.005	0.340
	IC attractiveness envy	–0.016	0.045	–0.369	0.712	–0.104	0.071	0.000	0.066
	IC superiority	–0.020	0.043	–0.459	0.646	–0.104	0.064	0.000	0.074
	IC status protection	0.071	0.041	1.719	0.086	–0.010	0.152	0.006	0.404

LH, life history; SOI-R, the sociosexual orientation inventory-revised; BPA, Buss-Perry Aggression questionnaire; IC, intrasexual competition.

with SOI-R Attitude, we found a positive association between short-term mate value and sociosexual desire, conceptually, replicating the relationship between humor and casual sex (Greengross and Miller, 2011), and that poets have more sexual partners (Nettle and Clegg, 2006). Moreover, literary arts were also positively related to the superiority dimension of Intrasexual Competition (i.e., IC-superiority) indicating an ornamental competition facet in asserting superiority over rivals (Varella et al., 2017). In visual arts, we found a positive association with parenting effort and negative associations with IC-Attractiveness envy and anger which indicates a clear intersexual selection pattern focused on maintaining a long-term bond, collaboration, and reducing conflict. In musical arts, we found positive associations with short-term mate value and IC-Attractiveness envy and negative associations with SOI-R Attitude and hostility, indicating a specific combination of intra- and intersexual selection. This pattern supports the finding of explicit intrasexual competitive strategies in the song lyrics of female pop musicians (Fisher and Candea, 2012). Importantly, our musical arts factor was composed of singing, playing musical instruments, and dancing. Dancing was more distant from the two previous items, and future studies might focus on specific differences between auditory and body movement music modalities. For circus arts, we showed that the tendencies to aesthetically enhance bodily movements are positively related to the number of long-term partners and negatively to parenting effort and SOI-R Attitude, indicating a higher serial monogamy pattern, although it leads to higher reproductive success in men than in women (Jokela et al., 2010).

In men, seven proxies of intrasexual competition (five positive and two negative), and three proxies of intersexual selection were (positively) associated with artistic tendencies. In literary arts, we found a positive association with long-term mate value which disagree but mirrors previous findings in which humor and poetry relates to short-term mating (Nettle and Clegg, 2006; Greengross and Miller, 2011). Poetry, humor, and creative writing might have slightly different effects, and some of them might be more related to short-term, while others to long-term, sexual strategies. Moreover, literary arts were positively related to the IC-superiority and verbal aggression (although negatively

TABLE 3 | Parameter estimates of the general linear model (GLM) model indicating the effect of the independent variables on artisticality in men.

Dependent variable	Parameter	B	SE	*t*	*p*	95% CI		Partial eta^2	Observed power
						Lower bound	Upper bound		
Literary arts	Intercept	0.091	0.636	0.144	0.886	–1.162	1.345	0.000	0.052
	Age	0.001	0.010	0.125	0.900	–0.019	0.022	0.000	0.052
	LH parenting effort	–0.022	0.067	–0.326	0.745	–0.155	0.111	0.001	0.062
	LH mating effort	–0.073	0.066	–1.109	0.269	–0.203	0.057	0.006	0.197
	SOI-R behavior	–0.002	0.051	–0.049	0.961	–0.102	0.097	0.000	0.050
	SOI-R attitude	–0.020	0.035	–0.570	0.569	–0.088	0.049	0.002	0.088
	SOI-R Desire	0.052	0.043	1.225	0.222	–0.032	0.136	0.008	0.230
	N of long-term relationships	0.036	0.049	0.733	0.465	–0.061	0.134	0.003	0.113
	N of short-term relationships	–0.004	0.009	–0.395	0.693	–0.022	0.014	0.001	0.068
	Mate value–Long term	0.189	0.064	2.952	0.004	0.063	0.315	0.044	0.836
	Mate value–Short term	0.049	0.071	0.693	0.489	–0.091	0.189	0.003	0.106
	BPA anger	0.100	0.096	1.035	0.302	–0.090	0.289	0.006	0.178
	BPA physical aggression	0.052	0.099	0.523	0.602	–0.143	0.246	0.001	0.081
	BPA verbal aggression	0.260	0.101	2.574	0.011	0.061	0.460	0.034	0.726
	BPA hostility	–0.334	0.104	–3.205	0.002	–0.539	–0.128	0.051	0.890
	IC attractiveness envy	0.007	0.084	0.083	0.934	–0.158	0.172	0.000	0.051
	IC superiority	0.157	0.070	2.241	0.026	0.019	0.296	0.026	0.606
	IC status protection	–0.062	0.067	–0.920	0.359	–0.194	0.071	0.004	0.150
Visual arts	Intercept	–1.995	0.653	–3.057	0.003	–3.282	–0.708	0.047	0.860
	Age	0.028	0.011	2.638	0.009	0.007	0.050	0.035	0.747
	LH parenting effort	0.069	0.069	0.997	0.320	–0.067	0.205	0.005	0.168
	LH mating effort	–0.044	0.068	–0.654	0.514	–0.178	0.089	0.002	0.100
	SOI-R behavior	–0.032	0.052	–0.610	0.543	–0.134	0.071	0.002	0.093
	SOI-R attitude	–0.046	0.036	–1.284	0.201	–0.116	0.025	0.009	0.248
	SOI-R desire	0.064	0.044	1.461	0.146	–0.022	0.150	0.011	0.307
	N of long-term relationships	0.008	0.051	0.159	0.874	–0.092	0.108	0.000	0.053
	N of short-term relationships	0.007	0.009	0.789	0.431	–0.011	0.026	0.003	0.123
	Mate value–Long term	0.047	0.066	0.708	0.480	–0.083	0.176	0.003	0.108
	Mate value–Short term	0.099	0.073	1.356	0.177	–0.045	0.242	0.010	0.271
	BPA anger	0.043	0.099	0.430	0.667	–0.152	0.237	0.001	0.071
	BPA physical aggression	–0.096	0.101	–0.951	0.343	–0.296	0.103	0.005	0.157
	BPA verbal aggression	0.172	0.104	1.658	0.099	–0.033	0.377	0.014	0.378
	BPA hostility	0.085	0.107	0.794	0.428	–0.126	0.296	0.003	0.124
	IC attractiveness envy	–0.062	0.086	–0.717	0.474	–0.231	0.108	0.003	0.110
	IC superiority	0.001	0.072	0.012	0.990	–0.141	0.143	0.000	0.050
	IC status protection	0.004	0.069	0.054	0.957	–0.132	0.140	0.000	0.050
Musical arts	Intercept	0.967	0.714	1.354	0.177	–0.441	2.374	0.010	0.271
	Age	–0.018	0.012	–1.499	0.135	–0.041	0.006	0.012	0.320
	LH parenting effort	0.073	0.076	0.961	0.338	–0.076	0.222	0.005	0.160
	LH mating effort	0.043	0.074	0.574	0.566	–0.104	0.189	0.002	0.088
	SOI-R behavior	0.091	0.057	1.611	0.109	–0.021	0.203	0.013	0.361
	SOI-R attitude	–0.027	0.039	–0.689	0.492	–0.104	0.050	0.002	0.105
	SOI-R desire	0.017	0.048	0.358	0.720	–0.077	0.112	0.001	0.065
	N of long-term relationships	0.002	0.055	0.035	0.972	–0.107	0.111	0.000	0.050
	N of short-term relationships	–0.001	0.010	–0.086	0.932	–0.021	0.019	0.000	0.051
	Mate value–Long term	0.081	0.072	1.130	0.260	–0.061	0.223	0.007	0.203
	Mate value–Short term	–0.106	0.080	–1.327	0.186	–0.263	0.051	0.009	0.262
	BPA anger	0.078	0.108	0.724	0.470	–0.135	0.291	0.003	0.111
	BPA physical aggression	–0.188	0.111	–1.698	0.091	–0.407	0.030	0.015	0.394
	BPA verbal aggression	–0.203	0.114	–1.791	0.075	–0.427	0.021	0.017	0.429
	BPA hostility	–0.208	0.117	–1.780	0.077	–0.439	0.023	0.016	0.425
	IC attractiveness envy	0.150	0.094	1.600	0.111	–0.035	0.335	0.013	0.357
	IC superiority	0.044	0.079	0.555	0.579	–0.112	0.199	0.002	0.086
	IC status protection	0.155	0.075	2.058	0.041	0.006	0.304	0.022	0.535

(Continued)

TABLE 3 | (Continued)

Dependent variable	Parameter	B	SE	*t*	*p*	95% CI		Partial eta^2	Observed power
						Lower bound	Upper bound		
Sports	Intercept	0.607	0.681	0.892	0.374	–0.736	1.950	0.004	0.144
	Age	–0.024	0.011	–2.146	0.033	–0.046	–0.002	0.024	0.570
	LH parenting effort	0.099	0.072	1.376	0.170	–0.043	0.241	0.010	0.278
	LH mating effort	0.002	0.071	0.033	0.974	–0.137	0.142	0.000	0.050
	SOI-R behavior	0.034	0.054	0.633	0.527	–0.072	0.141	0.002	0.097
	SOI-R attitude	0.052	0.037	1.392	0.166	–0.022	0.125	0.010	0.283
	SOI-R desire	–0.084	0.046	–1.850	0.066	–0.174	0.006	0.018	0.453
	N of long-term relationships	0.019	0.053	0.366	0.715	–0.085	0.124	0.001	0.065
	N of short-term relationships	7.382E-5	0.010	0.008	0.994	–0.019	0.019	0.000	0.050
	Mate value–Long term	0.071	0.069	1.042	0.299	–0.064	0.207	0.006	0.179
	Mate value–Short term	0.279	0.076	3.673	0.000	0.129	0.428	0.066	0.955
	BPA anger	–0.263	0.103	–2.555	0.011	–0.467	–0.060	0.033	0.720
	BPA physical aggression	0.238	0.106	2.256	0.025	0.030	0.447	0.026	0.612
	BPA verbal aggression	–0.053	0.108	–0.486	0.628	–0.266	0.161	0.001	0.077
	BPA hostility	0.016	0.112	0.142	0.888	–0.204	0.236	0.000	0.052
	IC attractiveness envy	0.007	0.089	0.082	0.935	–0.169	0.184	0.000	0.051
	IC superiority	0.235	0.075	3.122	0.002	0.087	0.383	0.049	0.874
	IC status protection	0.046	0.072	0.639	0.524	–0.096	0.188	0.002	0.097
Circus arts	Intercept	0.412	0.792	0.521	0.603	–1.150	1.974	0.001	0.081
	Age	–0.002	0.013	–0.143	0.886	–0.028	0.024	0.000	0.052
	LH parenting effort	0.052	0.084	0.616	0.539	–0.114	0.217	0.002	0.094
	LH mating effort	–0.071	0.082	–0.861	0.390	–0.233	0.091	0.004	0.137
	SOI-R behavior	–0.059	0.063	–0.931	0.353	–0.183	0.066	0.005	0.153
	SOI-R attitude	–0.012	0.043	–0.270	0.787	–0.097	0.074	0.000	0.058
	SOI-R desire	0.034	0.053	0.637	0.525	–0.071	0.139	0.002	0.097
	N of long-term relationships	–0.054	0.062	–0.879	0.380	–0.175	0.067	0.004	0.141
	N of short-term relationships	0.008	0.011	0.707	0.481	–0.014	0.031	0.003	0.108
	Mate value–Long term	0.108	0.080	1.358	0.176	–0.049	0.266	0.010	0.272
	Mate value–Short term	0.188	0.088	2.135	0.034	0.014	0.363	0.023	0.565
	BPA anger	–0.011	0.120	–0.092	0.927	–0.248	0.225	0.000	0.051
	BPA physical aggression	0.113	0.123	0.919	0.359	–0.129	0.355	0.004	0.150
	BPA verbal aggression	–0.119	0.126	–0.942	0.347	–0.367	0.130	0.005	0.155
	BPA hostility	0.129	0.130	0.994	0.322	–0.127	0.385	0.005	0.167
	IC attractiveness envy	–0.020	0.104	–0.194	0.846	–0.225	0.185	0.000	0.054
	IC superiority	0.090	0.088	1.025	0.306	–0.083	0.262	0.005	0.175
	IC status protection	0.052	0.084	0.627	0.532	–0.113	0.218	0.002	0.096

LH, life history; SOI-R, the sociosexual orientation inventory-revised; BPA, Buss-Perry Aggression questionnaire; IC, intrasexual competition.

related to hostility), which are possibly useful tendencies in gaining prestige against competitors within this highly language-mediated modality. The general pattern of associations in literary arts was the only similarity for both sexes. In musical arts, we found a positive connection with the IC-protection of status, which is in accordance with findings that the hierarchy of musical ability within the orcherstra is associated to a more masculine digit lenght ratio (Sluming and Manning, 2000), male physical size positively predicts speech and singing attractiveness (Valentova et al., 2019), male physical strength predicts dance attractiveness (Hugill et al., 2009; Weege et al., 2015), and "good" male dances are rated as more masculine (Weege et al., 2012). Although we did not capture the intersexual component, our results shed some light on the reason why cues and perceptions of masculinity are aligned with attractiveness ratings. Women might be detecting indications of men's ability to win intrasexual competition and consequently viewing these men as attractive (Weege et al., 2012, 2015). We did not replicate the positive relationship with sociosexuality (Valentova et al., 2019), although in that study that finding was restricted to higher-pitched male singing and not to the entire musical arts factor. In visual arts, we had no significant predictor, which does not corroborate the finding that successful male visual artists had more sexual partners and a long-term oriented sexual strategy (Clegg et al., 2011). Finally, we showed that the tendencies to aesthetically enhance bodily movements (circus arts) are positively related to mate value for short-term relationships, which supports the proposal that male bodily strength is the best predictor of mating and reproductive success (Lidborg et al., 2022).

Artisticality is not the only route to compete for, create and/or maintain sexual relationships potentially leading to differential reproductive success. Athleticism was related

to intrasexual competition in both sexes (i.e., less anger in both sexes and more verbal aggression in women, and more physical aggression and intrasexual competition superiority in men) corroborating Graves (2010), Lombardo (2012), and Longman et al. (2020), and expanding their logic to include women. Moreover, athleticism was associated to high short-term mate value in men, corroborating Zahavi and Zahavi (1999) and Miller (2000). Although we did not include all dimensions of physical activities, such as exercises or body practice which might have different motivations than sports (Hsu and Valentova, 2020), we corroborate studies proposing that sexual selection could have influenced athleticism and sports activities (De Block and Dewitte, 2009; Graves, 2010; Lombardo, 2012; Apostolou, 2015; Deaner et al., 2016; Longman et al., 2020).

We relied on a convenience sample of heterosexual individuals in our correlational study, and thus we cannot propose any unidirectional causal links. However, our samples were from two disparate cultures which improves generalizability. Importantly, the biggest difference between our and some previous studies is that we sampled the "common" population, not professional artists or athletes which may explain the relatively weak or no associations in our study. However, even weak associations among a general population show the potential of art-related behavior in sexual selection. We did not control for public versus private artistic display, or for success and professional arts, which are factors important in sexual selection, and should be the focus of future studies. Our study does not allow for an in-depth examination within each artistic/sport factor. Future studies should explore the specific intra/intersexual correlates for each leisure activity because they might differ in the level of skill or aggressiveness involved which could translate into being used more as an ornament or an armament. For example, boxing is quite different from golf, and likewise, the status of lead guitarists is dissimilar from those playing a keyboard in the background.

This cross-cultural study indicated that sports and each artistic modality exhibit their own sexual selection pattern and each could possibly yield different individual qualities (cf. Sluming and Manning, 2000; Candolin, 2003; Valentova et al., 2017; Pereira et al., 2019). In general, artistic propensity is influenced by both intra- and intersexual selection for both sexes, however, we found more intrasexual competition proxies in men and slightly more intersexual proxies in women. Further, there were more relationships between artistic propensities and sexual selection in women, and between athletic propensities and sexual selection in men. Thus, artistic tendencies in humans can serve the dual function of attracting/maintaining short- or long-term partners, and as tactics for competing with rivals. Athletic tendencies were related to intrasexual competition proxies in both sexes and intersexual proxy only in men, indicating that they might serve a dual function in men while serving more as an armament in women. Therefore, we expanded the scope of sexual section processes to show their relative and simultaneous influences. Future studies should explore different sexual selection processes and also survival values to test their relative importance across a higher cultural diversity.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Open Science Framework https://osf.io/59cjb/.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MV, MF, and JV conceived and designed the study. MV searched the literature and drafted the manuscript. MV, JV, ZŠ, and KB gathered the data. JV organized and analyzed the data and wrote the results. All authors wrote, revised, and approved the final manuscript.

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Darwin's sexual selection hypothesis revisited: Musicality increases sexual attraction in both sexes

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A number of theories about the origins of musicality have incorporated biological and social perspectives. Darwin argued that musicality evolved by sexual selection, functioning as a courtship display in reproductive partner choice. Darwin did not regard musicality as a sexually dimorphic trait, paralleling evidence that both sexes produce and enjoy music. A novel research strand examines the effect of musicality on sexual attraction by acknowledging the importance of facial attractiveness. We previously demonstrated that music varying in emotional content increases the perceived attractiveness and dating desirability of opposite-sex faces only in females, compared to a silent control condition. Here, we built upon this approach by presenting the person depicted (target) as the performer of the music (prime), thus establishing a direct link. We hypothesized that musical priming would increase sexual attraction, with high-arousing music inducing the largest effect. Musical primes (25s, piano solo music) varied in arousal and pleasantness, and targets were photos of other-sex faces of average attractiveness and with neutral expressions (2s). Participants were 35 females and 23 males (heterosexual psychology students, single, and no hormonal contraception use) matched for musical background, mood, and liking for the music used in the experiment. After musical priming, females' ratings of attractiveness and dating desirability increased significantly. In males, only dating desirability was significantly increased by musical priming. No specific effects of music-induced pleasantness and arousal were observed. Our results, together with other recent empirical evidence, corroborate the sexual selection hypothesis for the evolution of human musicality.

KEYWORDS

origins of music, cross-modal priming, sexual selection, face perception, romantic attraction, mate choice, evolutionary musicology

Introduction

Although music, like language, is a universal phenomenon (Blacking, 1973; Brown, 1991), its origins remain unclear, especially because musical behavior has no apparent immediate survival value (Darwin, 1871). Fitch (2015, 1) has argued that the debate about the origins of music can only move forward fruitfully if the object of study is clearly defined. He suggests

differentiating between *musicality* (i.e., "the set of capacities and proclivities that allows our species to generate and enjoy music in all of its diverse forms") and *music* (i.e., "the product of human musicality"). For example, studying humans' ability to sing may offer insights into the basis of human musicality, whereas studying the diverse forms and social functions of songs across cultures may be an endeavor followed by ethnomusicologists. Both approaches can mutually support each other. Musicality as a stable human trait can be discussed within a bio-musicological framework (Wallin, 1991) and studied from cognitive, developmental, neural, comparative (Fitch, 2015) as well as evolutionary (Wallin, 1991) perspectives. Varella et al. (2017, 758) define the broader term of *artisticality* as "the instinctive propensities to develop psychological faculties that underlie a whole array of multimodal and extraordinary aesthetically enhancing activities," which encompasses musicality among other things.

Sexual selection and the evolution of musicality

The current debate about the origins of music involves a wide range of theories, which can be broadly categorized into adaptationist (Huron, 2001; Honing and Ploeger, 2012) and non-adaptationist (James, 1890; Sperber, 1996; Pinker, 1997). Darwin's sexual selection hypothesis of the evolution of musicality (Darwin, 1871) is one of the three frequently discussed (e.g., Zahavi and Zahavi, 1999; Miller, 2000; Varella et al., 2017; Verpooten, 2021) – and not mutually exclusive – adaptationist theories of the origins of musicality, alongside proposals for a prominent role of music in social cohesion (e.g., Roederer, 1984; Dunbar, 2004; Brown, 2007; Savage et al., 2020), parental care and infant communication (e.g., Dissanayake, 2000, 2008; Falk, 2004; Mehr et al., 2020; Leongómez et al., 2021) and territorial antipredatory and territorial defense (e.g., Hagen and Hammerstein, 2009) through natural selection. The present study aims to further elucidate the role of sexual selection in the evolution of musicality from a psychological perspective.

Falsification, and not speculation, is at the core of any theory building (Popper, 1935), which will ultimately be the only way to shed light on the complexity of human musicality and its origins. Here, we thus aim to empirically test Darwin's sexual selection hypothesis of music (Darwin, 1871; Miller, 2000, see also Bannan, 2017). Darwin, comparing music to reproductive behavior in animals (such as in birds, insects, amphibians, fish, reptiles and gibbons), argued that music acts as a courtship display in reproductive partner choice. As a costly and "honest" signal of fine motor skills (Miller, 2000) and advanced cognitive abilities (Charlton, 2014) musicality may be indicative of biological fitness and good genes and thus the result of selection pressure in the social environment (for a review see Karamihalev, 2013; Ravignani, 2018).

Darwin did not regard musicality as a sexually dimorphic trait, which is in consonance with both males and females producing and enjoying music. However, sex differences regarding musicality in adulthood have been documented (e.g., Sluming and Manning, 2000; Varella et al., 2010; Miles et al., 2016). Darwin wrote (1871, 572), "I conclude that musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex." This does not preclude the possibility of sex differences in musicality and mating behavior, such as those observed related to the human voice (e.g., Evans et al., 2008; Valentova et al., 2017, 2019; Pisanski et al., 2018), which Darwin (1871, 573) already noted: "Women are generally thought to possess sweeter voices than men, and as far as this serves as any guide, we may infer that they first acquired musical powers in order to attract the other sex." Darwin also proposed a common origin of music and language, known as the musical protolanguage hypothesis, for which some empirical evidence has emerged (Thompson et al., 2012). This theory argues for a common ancestor of music and speech.

Some evidence for a genetic basis for musicality, a necessary prerequisite for adaptation (Croston et al., 2015), has accumulated (Gingras et al., 2015; Mosing et al., 2015; Järvelä, 2018; Beccacece et al., 2021). In general, heritability depends on the specific aspect of musicality under consideration. For example, heritability estimates seem to be larger for pitch perception than for rhythm perception abilities (Pulli et al., 2008; Seesjärvi et al., 2015). Musical development (i.e., the enculturation into a musical system) appears to follow a standard developmental schedule as well (Hannon and Trainor, 2007). However, although musicality has a moderate genetic basis, musical ability and mating success were negatively associated in a twin study (Mosing et al., 2015). Further evidence against the sexual selection hypothesis of music includes the finding that musicians and non-musicians reported similar sexual activity (Harrison and Hughes, 2017).

From a psychological perspective, it is a challenging task to develop experimental paradigms that can offer insights into musicality's evolutionary roots. Several experiments have provided mixed empirical support for Darwin's assertion so far. For example, visually displaying a musical instrument may increase male attractiveness in social media (Tifferet et al., 2012), whereas attractiveness ratings do not differ for fictitious verbal profiles of musicians and non-musicians, neither in males nor females (Bongard et al., 2019). These studies did not directly examine the effect of music experience (i.e., musical sounds) on sexual attraction and courtship (Darwin, 1871), which seems to be more relevant in the context of Darwin's theory. Two studies by Charlton et al. (2012) and Charlton (2014) involving actual music examined the effect of fertility cycle phase on mate choice in groups of females. First, it was shown that complex music was preferred to simple music, but there was no effect of cycle phase (Charlton et al., 2012). In a follow-up two-alternative forced-choice task (Charlton, 2014), females were told that the two musical excerpts were composed by male composers. Females in the fertile phase of their cycle preferred complex excerpts to simple ones, but only when the composers were potential short-term – and not long-term – sexual partners. This is in line with Darwin's theory that

females may gain genetic benefits for offspring by selecting partners that show musical proficiency.

Multiple cues in mate choice

Another line of research has started to investigate the effect of music on sexual attraction by considering other relevant biological cues in mate choice, such as the human face (May and Hamilton, 1980; Marin et al., 2017; Madison et al., 2018). It is very likely that in evolutionary history multiple cues of various modalities have played a role in romantic attraction (Valentova et al., 2017, 2019), especially in a small-group social setting, in which music and dance were probably performed and enjoyed (Morley, 2013; Killin, 2018; for a review of human dance and evolution see Fink et al., 2021). The human face is the main factor determining physical attractiveness regarding short- and long-term relationships because it indicates genetic fitness (Currie and Little, 2009), but cognitive factors such as creativity and intelligence may also play a significant role (Boogert et al., 2011). This research approach is backed up by previous findings from the crossmodal priming and multimodal interaction literature, suggesting that sound and music can alter the perception of various types of visual stimuli, including facial expressions (Logeswaran and Bhattacharya, 2009, for a review see Gerdes et al., 2014). Likewise, music performance research has shown that visual information related to the performer can also alter the appreciation of music (Platz and Kopiez, 2012). In short, combining multiple cues in an experimental design enhances ecological validity because music was, until the last century, always perceived live in a multimodal setting, with the performer being present.

Watkins (2017) demonstrated that overall ratings of males, and females' attractiveness depend on facial attractiveness and creative story-telling ability. A follow-up study involving a divergent thinking measure showed that males' overall attractiveness was similarly rated when less attractive faces were paired with creative texts and attractive faces with less creative texts, suggesting a compensating interplay between physical and cognitive factors. This effect was not observed for ratings of female attractiveness, for which facial attractiveness was the main determinant of their overall perceived attractiveness. Madison et al. (2018) conducted a similar study by combining displays of three levels of musical creativity (i.e., improvisations of different quality) with three levels of facial attractiveness. Male and female participants, while listening to the music, rated four mate value scales (intelligence, health status and parenting skill) and four mate preference scales (date, intercourse, and short-and long-term relationship) for each combination as well as facial attractiveness. In line with the sexual selection theory of music, an increase in musical performance quality was associated with higher ratings on the respective scales (with a few exceptions) for both sexes. However, the effects of facial attractiveness on the set of ratings were found to be much larger than the effect of musical performance quality. Moreover, music performance quality affected females' ratings more than males' ratings, whereas the latter were more influenced by facial attractiveness than the former. Taken together, the studies by Watkins (2017) and Madison et al. (2018) involving language and music skills indicate that for both sexes, cognitive and biological factors play a role in romantic attraction, and that females are more influenced by factors such as cognitive intelligence and creativity than males, for whom facial attractiveness appears to be the more relevant cue in mate choice.

Marin et al. (2017) studied the psychological mechanisms underlying the contingent effect of music on facial attractiveness and dating desirability ratings in males and females. In a crossmodal priming paradigm, excerpts of piano solo music were used as primes and other-sex faces as targets. Musical arousal and pleasantness were manipulated to test whether misattribution of arousal may underlie priming effects. Indeed, compared to a silent control condition, females reported higher facial attractiveness and dating desirability ratings after musical priming, with the highest ratings associated with high-arousing music, supporting the idea of misattributed arousal (White et al., 1981). These effects were not present among males, and the study could not reveal any significant effects of females' cycle phase. Since high-arousing music is also more complex than low-arousing music (Marin and Leder, 2013), these results can also be interpreted within the context of Darwin's sexual selection theory of music (see also Charlton, 2014), suggesting that cognitive and affective music-induced effects on face perception cannot be easily disentangled. Furthermore, participants were not told that the presented music had a direct relation with the target face to be rated.

The present study

As in Marin et al. (2017), we examined in the present study the role of musicality in sexual attraction, but this time presenting the person depicted (target) as the performer of the music (prime), thus establishing a direct link. We used the same stimulus sets as in Marin et al. (2017) (i.e., piano solo music and faces of average attractiveness) and also collected facial attractiveness and dating desirability ratings as two common measures of sexual attraction. Moreover, we decided to invite only participants who reported being single to enhance ecological validity and to be more stringent than in our previous study. Since the role of the fertility cycle is difficult to evaluate in a laboratory study because of limited resources to test large samples to demonstrate small effects, we decided not to address this question in the present study. We thus considered females who were not taking hormonal contraception, were not breast-feeding and who were not having their period on the day of the experiment. Due to the fact that males and females rated other-sex faces (and thus different target faces) we decided to conduct the statistical analyses separately for each group (see Madison et al., 2018, for a similar approach). Moreover, to enable a valid comparison of results, male and female participants were carefully matched on a range of background

variables, such as musical training, mood prior to the experiment and liking of the music heard in the experiment. We consider this as a strength of our study, which will allow for a clearer interpretation of our results and comparison with Marin et al. (2017).

Based on Darwin's theory and on the results of Marin et al. (2017), we predicted that musical priming should lead to higher ratings of facial attractiveness (H1) and dating desirability (H2) in comparison to a silent control condition in females (but see Madison et al., 2018). We further predicted, for the group of females, that high-arousing (i.e., more complex music) will lead to the largest effects for both ratings (H3–H4), and that pleasantness induced by music should not play a role (H5 (main effect) and H6 (interaction between arousal and pleasantness)), based on the results of Charlton (2014), Marin et al. (2017), and White et al. (1981). For males, assuming that music is not a sexually dimorphic trait (Darwin, 1871, but see Marin et al., 2017), we generally predicted similar, but weaker, effects of musical priming on sexual attraction (H7–H12). However, in comparison to ratings given by females, female facial attractiveness should not be strongly influenced by musical priming in males (H13) (Marin et al., 2017; Madison et al., 2018).

Materials and methods

Participants

Based on the results reported in Marin et al. (2017), an *a priori* statistical power analysis using G*Power 3.1.9.4 was performed. The main analysis was conducted separately for males and females because the target faces differed between the two groups (see also Madison et al., 2018). Therefore, the power analysis was also conducted for each group separately. To make the present results comparable to Marin et al. (2017), our hypotheses were also tested within the framework of repeated-measures ANOVA (analysis of variance). Thus, a set of four orthogonal contrasts following our hypotheses were computed, and the power analyses were conducted for each contrast. In Marin et al.'s (2017) group of females, the average within-subject correlation across all possible correlations between the five conditions (i.e., control and four musical priming) was $r(62) = 0.930$ for attractiveness ratings and $r(62) = 0.944$ for dating desirability ratings. In the group of males, the average within-subject correlation across the five conditions was $r(30) = 0.955$ for attractiveness ratings and $r(30) = 0.964$ for dating desirability ratings.

For the current group of females, a medium effect size of 0.274 (Cohen's *f*, directly computed from partial eta-squared reported in Marin et al., 2017), with an alpha of 0.05, a desired power of 0.80 and a correlation among repeated measure of $r = 0.93$ were used to obtain a minimum sample size for attractiveness ratings of contrast 1. The results yielded a sample size of six with an actual power of 0.82. If the within-subject correlation was lowered to $r = 0.80$, to be more conservative, the sample size increased to 13 with an actual power of 0.82. For dating desirability ratings and contrast 1, we predicted a large effect (Cohen's $f = 0.593$), and a within-subject correlation of $r = 0.944$, which yielded a sample size of three and an actual power of 0.85. With a lower correlation of $r = 0.80$, the sample size increased to five with an actual power of 0.87. Sample sizes for contrast 2 were similarly determined by basing the computation on the exact results reported in Marin et al. (2017). For attractiveness ratings, a minimum sample size of four participants was required to reach an actual power of 0.84. For dating desirability ratings, the determined sample size was six, with an actual power of 0.89. For attractiveness ratings of contrasts 3 and 4, no significant effects ($\eta_p^2 < 0.001$) were expected. For dating desirability ratings and contrasts 3 and 4, the effect sizes were also negligible. For the group of males, we did not predict any significant effects on attractiveness ratings. For dating desirability ratings a marginally significant effect was observed in Marin et al. (2017) for contrast 1, and a power analysis for contrast 1 yielded a sample size of four with an actual power of 0.921.

It was decided to test a similar number of participants as in Marin et al. (2017), although the power analysis revealed that such a large sample was not necessary for testing our hypotheses. Another reason for testing larger samples was that we did not control for whether a woman was in the fertile or infertile phase of the reproductive cycle, thus to obtain an unbiased sample a larger number of participants was considered as more appropriate. The same holds true for the background variables of musical training and music preference, which are unlikely to be similar across small samples. Last, although the stimuli of the current study were the same as those used in Marin et al. (2017), this study is not a direct replication, and the criterion regarding the relationship status of the participants and the instructions were different, which further justifies testing two larger samples of participants.

Fifty-seven female heterosexual participants (mostly German and Austrian psychology students) were tested, out of which 22 were excluded prior to the exploratory data analysis. Eleven students were excluded due to technical problems (during the experiment it was discovered that one version of the computer program used to conduct the experiment had the wrong rating order in one of the two blocks). Two participants were excluded because they were using hormonal contraception, and seven were excluded because they had their menstruation on the day of the experiment. Two female participants reported more than 3 years of musical training and were thus also excluded.

Thirty heterosexual male participants were tested, and one person had to be excluded because he previously participated in a similar experiment. Three male participants reported more than 3 years of musical training, and one participant was not wearing the headphones in an appropriate way during the experiment. One male participant reported mild hearing loss in one ear, but was not excluded because the experiment was not measuring fine-grained music perception skills.

After an exploratory data analysis of the background variables, two other male participants were excluded: in order to balance the number of participants of the experimental conditions, one male participant was excluded because he reported extreme tiredness.

Another male participant reported very low liking ratings of Romantic piano music (not at all comparable with ratings by female participants), and was thus excluded. It is important to note that all exclusions were made prior to the main analysis of the experimental data.

Our final two groups of 35 females and 23 males were matched across several background variables (Tables 1, 2). All participants reported being single and not in a relationship. Females were not taking hormonal contraception, not pregnant and not breast-feeding. The two groups of male and female participants did not statistically differ with respect to age, the three subscales of the multidimensional mood questionnaire, years of musical training, role of music in their life, and liking for the piano music played in the experiment (Table 1). Moreover, participant groups were similar regarding their music listening behavior and preference for classical music (Table 2). Additionally, the two groups also reported on their wish to have children in the future (5 missing values), which was similar in females (21 yes, 14 no or not sure) and males (13 yes, 5 no or not sure), $\chi^2(1) = 0.77$, $p = 0.38$.

Materials and measures

The same materials as reported in Marin et al. (2017) were employed. For the two versions of the experiment (i.e., one for males and one for females), we used 20 male and 20 female faces of average attractiveness (Europeans with light complexion) as targets, respectively. Targets were always other-sex faces, and 17 same-sex faces were used in distractor trials. All faces were presented in frontal view, with direct gaze and neutral facial expression on a gray background (Schacht et al., 2008). Musical primes were 80 excerpts of 19th-century Romantic piano solo music (available on OSF). Since these piano excerpts were played by a solo performer, the choice of this musical style increased the credibility of the task. These excerpts had a length of 25 s and varied in their emotional contents (low vs. high arousal, unpleasant vs. pleasant), and were selected from stimuli rated in Marin and Leder (2013). Seventeen additional excerpts were used in distractor trials. Compressed file sizes, a measure of musical complexity, varied significantly between low-and high-arousing excerpts (see Marin et al., 2017, for further details on the stimuli). Facial attractiveness

TABLE 1 Participant characteristics I.

Group	Age	Mood pos.-neg.	Alertness/fatigue	Quietude/ disquietude	Yrs. musical training	Role of music in life	Liking of solo piano music
Females							
M	22.2	17.66	14.51	16.17	0.88	5.20	4.77
SD	2.8	1.94	3.50	2.43	1.07	1.68	1.66
Males							
M	23.4	17.35	15.48	15.70	1.13	5.96	4.96
SD	2.9	2.27	2.91	2.67	1.20	1.22	1.15
Mann–Whitney-U							
U	304.50	380.00	341.50	357.00	339.50	299.50	399.00
p	0.117	0.717	0.329	0.465	0.361	0.091	0.955

Summary in terms of groups' mean age, the three MDBF scores, years of musical training, role of music in life, and liking of 19th-century solo piano music. *M*, mean; *SD*, standard deviation; *U*, test statistic of the Mann–Whitney-U test; *p*, calculated probability; Yrs., years; pos., positive; neg., negative; MDBF, Mehrdimensionale Befindlichkeitsfragebogen – multidimensional mood state questionnaire. $N_{women} = 35$, $N_{men} = 23$. All degrees of freedom are 2. Role of music in life and liking of piano music were assessed on 7-point scales. All variables were used to match groups.

TABLE 2 Participant characteristics II.

Group	Listening to classical music	Active music listening	Passive music listening	Going to concerts*	One-night stand	Long-term relationship
Females						
M	2.63	4.14	5.89	3.41	3.97	3.49
SD	1.42	1.94	1.53	1.78	2.12	1.76
Males						
M	2.74	4.57	6.09	3.68	2.96	3.39
SD	1.32	1.59	0.90	1.49	1.92	1.64
Mann–Whitney-U						
U	375.50	349.00	392.00	332.00	288.00	396.50
p	0.657	0.388	0.859	0.474	0.065	0.922

Summary of groups' musical listening behavior and the reported interest in a one-night stand and long-term relationship. *M*, mean; *SD*, standard deviation; *U*, test statistic of the Mann–Whitney-U test; *p*, calculated probability. $N_{females} = 35$, $N_{males} = 23$. All degrees of freedom are 2. All ratings were given on 7-point scales with low numbers indicating a lower frequency. For the variables "one-night stand" and "long-term relationship" lower numbers indicate high willingness. All variables, except for "one-night stand" and "long-term relationship", were used to match groups. *$N_{females} = 34$, $N_{males} = 22$.

was assessed on a 7-point scale, ranging from (1) *very unattractive* to (7) *very attractive*, and the instructions were: *"Please report the perceived sexual attractiveness of the face."* Dating desirability was also assessed on a 7-point scale, ranging from (1) *no, by no means* to (7) *yes, by all means*, with the following instruction: "*Please report whether you would like to date this person.*"

We used the short form A of the three-dimensional mood questionnaire [MDBF A] by Steyer et al. (1994) to assess mood, alertness and quietude prior to the experiment. In a short self-developed questionnaire after the experiment, participants reported on their socio-demographic and musical background (musical preference, listening behavior, and musical training), and their liking of the music played in the experiment (i.e., 19th-century piano solo music). Furthermore, participants were asked to report on their willingness to have a one-night stand or to enter a long-term relationship with the most attractive people shown in the experiment. Females were asked to provide information regarding their menstrual cycle and hormonal contraceptive use. To be specific, we asked the following questions: *Did you like the music heard in the experiment?* (1) not at all … (7) very much; *What role does music play in your life?* (1) no role … (7) a very large role; *How often do you listen to classical music?* (1) never … (7) very often; *Have you ever received musical training (university, music school, private lessons)?* Report of years of musical training and when it was finished; *How often and how do you listen to music? Passive, while doing other things:* (1) never … (7) very often; *Active, while not doing other things:* (1) never … (7) very often; *Active in a concert:* (1) never … (7) very often; *Please think of the faces that you regarded as particularly attractive. Report on your wish to have a one-night stand or a long-term relationship with these persons*. For each part: (1) very much … (7) not at all. They also reported on how difficult it was for them to judge facial attractiveness on a scale ranging from (1) very easy to (7) very difficult. Using open questions, participants were asked to report on their thoughts about the research question/hypothesis underlying the experiment. In addition, three standardized questionnaires on emotional intelligence, empathy and personality were administered but not evaluated for this study.

Procedure

The study was approved by the local ethics committee of the University of Innsbruck, Austria (approval number 16/2019). Participants were recruited from a pool of (mostly undergraduate) psychology students. The study was advertised to investigate the perception of facial attractiveness. There was no reference to music to avoid selection bias. Students either received course credits or a monetary compensation of 12 Euro.

Participants were tested in a quiet room with constant lighting conditions and no window. The experiment was run in Matlab R2017a (The MathWorks Inc., Natick, United States) and the music was played through Sennheiser HD 380 Pro headphones at a fixed loudness level (70 dB as measured with a dB meter). Instructions and faces were presented on a 24 inch screen (Acer 24 inch, TFT display monitor) placed approximately 70 cm away from the sitting participant. After having signed the informed consent form, participants were asked to report on their mood prior to the experiment, then the actual experiment started.

The experiment consisted of two blocks (priming and control), which were counterbalanced across participants. Moreover, there were two rating scales (facial attractiveness and dating desirability), whose order was also counterbalanced across participants of the two block orders. For each participant the rating order was the same in both blocks. After a practice trial, participants began the experiment. To avoid fatigue, participants were encouraged to take a self-paced break after half of the trials were completed in the priming block.

In the (silent) control condition, participants were asked to rate 37 faces (20 targets and 17 same-sex distractor faces to prevent demand characteristics) of potential partners on facial attractiveness and dating desirability. Each trial was announced with a statement shown on the screen for 5 s ("*The next trial will follow soon*"), then the photograph followed for 2 s on a black background. After the photograph had disappeared, one of the two rating scales was shown on the screen and participants answered by mouse click. Then the other scale was shown. All faces were randomly presented.

In the priming block, the same types of ratings were obtained for each target. Each of the 20 target faces was shown for four times and randomly combined with one of the 20 musical excerpts of each emotion quadrant (spanned by arousal and pleasantness). These 80 trials were intermingled with 17 distractor trials. All trials were randomly presented and announced for 5 s with a statement saying *"The next trial will follow soon."* While participants were listening to the music, a small white cross was shown in the middle of the screen. Participants were asked to look at it in order not to miss the onset of the visual target. Then both ratings were given before the next trial began.

The only difference between the procedure described in Marin et al. (2017) and the one used in the current experiment is a statement in the general instructions, namely that the musical excerpts were presented as played by the people shown on the photographs which followed the musical excerpts: "Dear Participant, you will now be asked to provide ratings on a series of participants who could be potential partners. In each trial you will first listen to music, which was played on the piano by the respective person. Then you will see their face. You will be asked to rate the sexual attractiveness and your willingness to have a date with this person. While listening to the music, please look at the fixation cross. Please provide spontaneous ratings."

When the experiment was completed, participants were asked to fill in a short self-developed questionnaire. In total, the experimental session lasted around 90 min. Participants were either paid or assigned course credits, thanked and debriefed.

Statistical analysis

All analyses were conducted using IBM Statistics SPSS 26. In the case of violations of sphericity (i.e., a significant Mauchly Test),

Greenhouse–Geisser corrections were performed. Effect sizes for eta or partial eta squared were interpreted by following Cohen's (1988) suggestions (small = 0.01, medium = 0.06, and large = 0.14, but see Lakens (2013) for limitations of this interpretation for within-subject comparisons). Within-subject error bars were computed using the *superb* package in R.[1] When interpreting the results of orthogonal, planned contrasts, it is not necessary to observe significant main effects or interactions in the ANOVA (Gonzales, 2009).

Results

Distractor trials (i.e., trials with same-sex faces) were not analyzed and removed from the data set. Males and females were analyzed separately because the target faces differed between groups (Marin et al., 2017). A set of four orthogonal contrasts within the framework of repeated-measures analysis of variance (ANOVA) were computed to test our hypotheses regarding attractiveness and dating desirability ratings, respectively. Contrast 1 compared the silent control condition with the average across the four musical priming conditions. Contrast 2 tested the effect of music-induced arousal and compared differences between musical primes with low-and high-arousing music. Contrast 3 compared the effect of primes with unpleasant music to those with pleasant music. Contrast 4 tested the interaction between music-induced arousal and pleasantness.

We first tested whether attractiveness ratings were affected by musical priming in females (Figure 1A). A repeated-measures ANOVA with condition as within-subject factor (control and 4 music conditions) revealed a marginal effect of condition, F (2.15, 72.96) = 2.90, $p = 0.058$, $\eta_p^2 = 0.08$ (medium effect). The planned contrast analyses revealed that attractiveness ratings were significantly higher in the music conditions ($M = 3.54$, 95% CI [3.23, 3.85]) than in the control condition ($M = 3.36$, 95% CI [3.05, 3.67]), $F(1, 34) = 4.44$, $p = 0.043$, $\eta_p^2 = 0.12$ (medium effect). Ratings did not significantly differ between low-arousing ($M = 3.53$, 95% CI [3.21, 3.84]) and high-arousing music ($M = 3.56$, 95% CI [3.24, 3.87]), $F(1, 34) = 0.53$, $p = 0.470$, $\eta_p^2 = 0.02$ (small effect). Music-induced pleasantness did not affect attractiveness ratings, $F(1, 34) = 0.01$, $p = 0.916$, $\eta_p^2 < 0.001$ (no effect). There was no significant interaction between music-induced arousal and pleasantness on attractiveness ratings, $F(1, 34) = 0.001$, $p = 0.981$, $\eta_p^2 < 0.001$ (no effect).

Next, we analyzed dating desirability ratings and how they were affected by musical priming in females (Figure 1A). A repeated-measures ANOVA with condition as within-subject factor (control and 4 music conditions) revealed a significant effect of condition, $F(1.78, 60.38) = 4.81$, $p = 0.014$, $\eta_p^2 = 0.12$ (medium effect). Contrast 1 comparing the control condition to the four music conditions was significant, $F(1, 34) = 6.45$, $p = 0.016$, $\eta_p^2 = 0.16$ (large effect), with lower dating desirability ratings for the control condition ($M = 2.99$, 95% CI [2.63, 3.35]) than for the music conditions ($M = 3.27$, 95% CI [2.89, 3.64]). There was no significant difference between the conditions of low-and high-arousing music, $F(1, 34) = 0.04$, $p = 0.848$, $\eta_p^2 = 0.001$ (no effect). Similarly, there was no significant effect of musical pleasantness, $F(1, 34) = 1.73$, $p = 0.196$, $\eta_p^2 = 0.05$ (small effect). The interaction between music-induced arousal and pleasantness was not significant, $F(1, 34) = 0.12$, $p = 0.733$, $\eta_p^2 = 0.003$ (no effect).

In males, facial attractiveness ratings were not affected by musical priming (Figure 2A). A repeated-measures ANOVA with condition as within-subject factor (control and four music conditions) revealed no significant effect of condition, $F(2.07, 45.62) = 0.67$, $p = 0.521$, $\eta_p^2 = 0.03$ (small effect). Contrast 1 showed no significant difference between the silent control and the four music conditions, $F(1, 22) = 0.57$, $p = 0.458$, $\eta_p^2 = 0.03$ (small effect). Contrast 2 revealed that there was no difference between the low-and high-arousing conditions, $F(1, 22) = 0.09$, $p = 0.771$, $\eta_p^2 = 0.004$ (no effect). Contrast 3 showed no significant difference between the unpleasant and pleasant primes, $F(1, 22) = 2.52$, $p = 0.127$, $\eta_p^2 = 0.10$ (medium effect). Contrast 4 tested the interaction between music-induced arousal and pleasantness, which was not significant either, $F(1, 22) = 0.16$, $p = 0.695$, $\eta_p^2 = 0.007$ (no effect).

Finally, we examined the effects of musical priming on dating desirability in males (Figure 2B). A repeated-measures ANOVA with condition as within-subject factor revealed a marginal effect of condition, $F(2.07, 45.45) = 2.84$, $p = 0.067$, $\eta_p^2 = 0.11$ (medium effect). Contrast 1 was significant, $F(1, 22) = 6.88$, $p = 0.016$, $\eta_p^2 = 0.24$ (large effect), with higher ratings of dating desirability for the music conditions ($M = 3.41$, 95% CI [2.94, 3.88]) than for the control condition ($M = 3.22$, 95% CI [2.74, 3.71]). Contrast 2 testing for the effects of music-induced arousal was not significant, $F(1, 22) = 0.08$, $p = 0.784$, $\eta_p^2 = 0.003$ (no effect). Contrast 3 testing for the effects of pleasantness was not significant, $F(1, 22) = 1.49$, $p = 0.235$, $\eta_p^2 = 0.06$ (medium effect). Last, the interaction between music-induced arousal and pleasantness was not significant, $F(1, 22) = 0.16$, $p = 0.697$, $\eta_p^2 = 0.007$ (no effect).

Since the group of male participants was smaller than the group of female participants, we repeated the analysis with 25 participants including the two outliers that were removed after the exploratory data analysis. The pattern of results was very similar for both attractiveness and dating desirability ratings (see Supplementary material).

Table 2 shows that there was a marginal effect indicating that females ($M = 3.97$, $SD = 2.12$) reported to a larger degree than males ($M = 2.96$, $SD = 1.92$) that they would be willing to have a one-night stand with the most attractive persons shown in the experiment, $U = 288.00$, $p = 0.065$, $\eta^2 = 0.06$ (medium effect). There was no significant difference between females ($M = 3.49$, $SD = 1.76$) and males ($M = 3.39$, $SD = 1.64$) reporting on their desire to have a long-term relationship with the most attractive persons shown in the experiment, $U = 396.50$, $p = 0.922$, $\eta^2 < 0.001$ (no effect).

Participants were invited to report on their thoughts about the purpose of the experiment. All except two participants reported

1 https://CRAN.R-project.org/package=superb

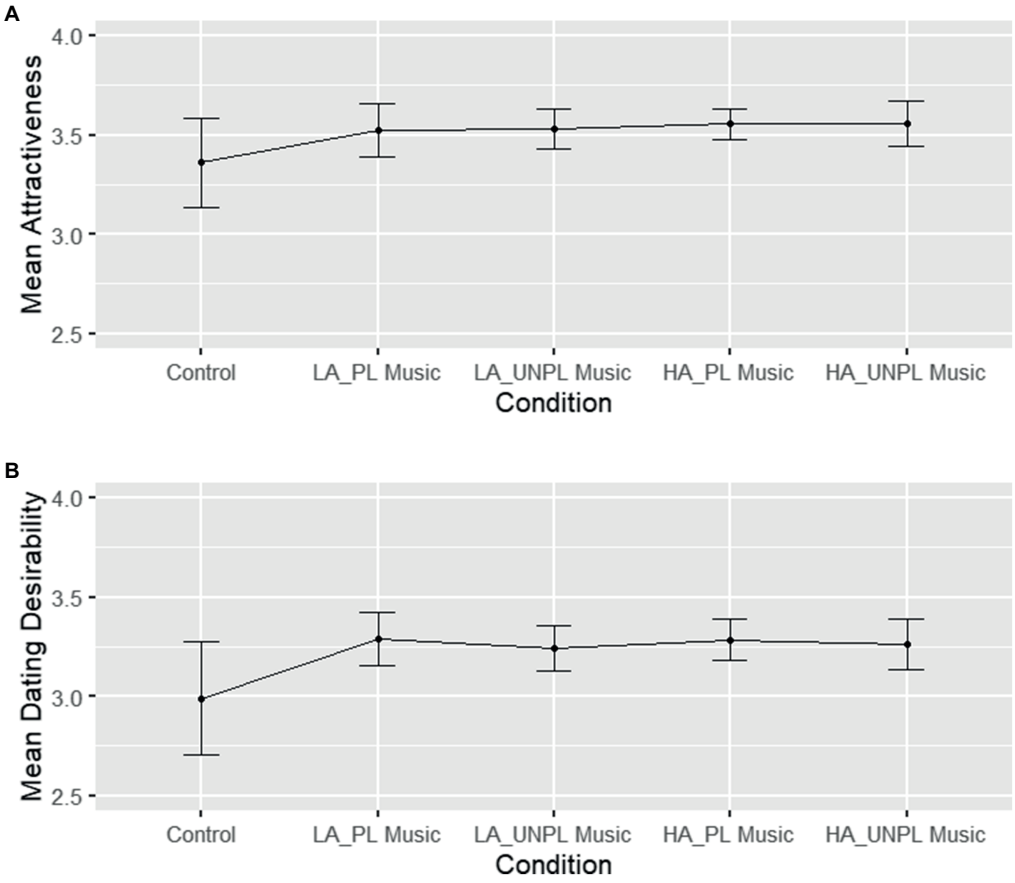

FIGURE 1
Females' average facial attractiveness ratings of males given for each experimental condition. **(A)** Average facial attractiveness ratings. **(B)** Average dating desirability ratings. Error bars represent correlation-and difference-adjusted 95% confidence intervals. LA, low-arousing; HA, high-arousing; PL, pleasant; UNPL, unpleasant. Scales range from 1 to 7, with one indicating very low attractiveness/dating desirability.

that the study is about the effect of music (i.e., not musicality but music experienced as sound) on attractiveness. One male and one female participant referred to the effect of musical talent (musicality) on attractiveness. Speculations about the role of music in the experiment mostly comprised mood induction (positive vs. negative) and references to effects of musical parameters such as tempo and loudness. Males and females did not differ regarding their reported difficulty in judging the facial attractiveness of faces, $U = 398.00$, $p = 0.921$, $\eta^2 < 0.001$ (no effect), which was generally rated as of intermediate difficulty, $M = 4.78$, 95% CI [4.34, 5.17] on a 7-point scale.

Discussion

Darwin's (1871) sexual selection hypothesis for the evolution of musicality has gained recent attention in the field, partly due to its clear predictions and slowly growing empirical support (e.g., Charlton, 2014; Marin et al., 2017; Madison et al., 2018; Chang et al., 2021; for a review see Ravignani, 2018; Fink et al., 2021). Musicality can be embedded into the wider context of human artisticality and creativity, for which empirical evidence for sexual selection has also accumulated (e.g., Karamihalev, 2013; Galasinska and Szymkow, 2022; Varella et al., 2022). Here, we tested Darwin's assertion in relation to one aspect of musicality, namely instrumental music.

People use multiple cues in partner choice (Regan et al., 2000), and thus combining cues from several modalities may enable researchers to assess the effect of musicality on partner choice in a more ecologically valid setting. Here, we followed our previous approach by combining musical primes with facial targets (Marin et al., 2017). In the current study, the people shown on the photographs were presented as performers of the musical excerpts. Two groups of male and female participants, matched on several background variables, rated other-sex faces on facial attractiveness and dating desirability (two common measures of sexual attraction) after having listened to musical excerpts varying in emotional contents. The general picture emerging from our analysis is that musicality related to instrumental music may be a potential cue in mate choice in both sexes, with stronger effects in females than in males. In the group of females, H1 and H2 were supported by the data, indicating that both attractiveness and

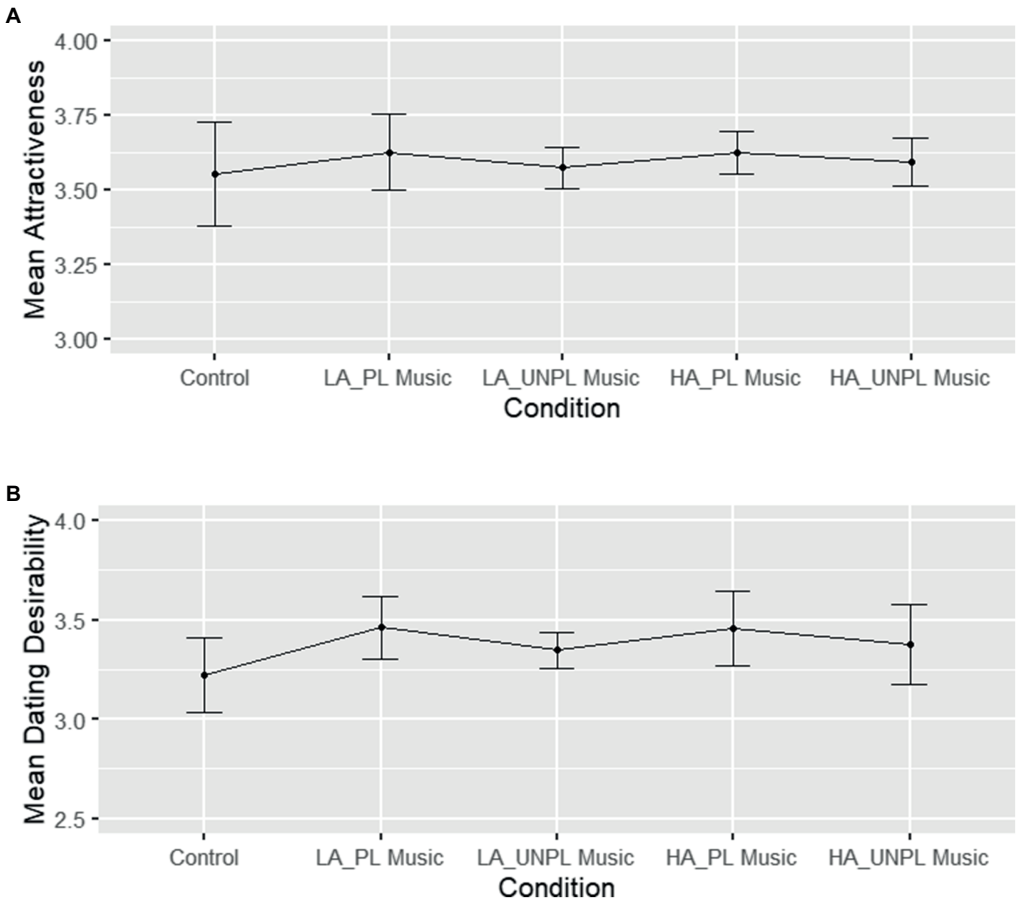

FIGURE 2
Males' average facial attractiveness and dating desirability ratings of females given for each experimental condition. **(A)** Average facial attractiveness ratings. **(B)** Average dating desirability ratings. Error bars represent correlation- and difference-adjusted 95% confidence intervals. LA, low-arousing; HA, high-arousing; PL, pleasant; UNPL, unpleasant. Scales range from 1 to 7, with one indicating very low attractiveness/dating desirability.

dating desirability ratings increased after music exposure compared to a silent control condition. However, there was no supporting evidence for H3 and H4 because both ratings were similar after low-and high-arousing music. H5 and H6 were supported by the data, suggesting that there was no significant main effect of music-induced pleasantness and no interaction between pleasantness and arousal. In the group of males, the results for attractiveness and dating desirability ratings differed. There were no significant effects whatsoever for attractiveness ratings (refuting H7 and H9, supporting H11), but musical priming led to higher dating desirability ratings in comparison to the silent control condition (supporting H8 and H12, refuting H10). In line with our prediction (H13), the contrasts on attractiveness ratings revealed that males' ratings of facial attractiveness were not as strongly influenced (non-significant small effect) as those of females (significant medium effect). Females also reported to a larger degree than males to be willing to have a one-night stand with the most attractive persons seen in the experiment (marginal effect), and the sexes did not differ in their desire to have a long-term relationship with these persons.

In agreement with Darwin's theory (1871), our data suggests that having listened to short, high-quality excerpts of solo piano music increases male facial attractiveness and dating desirability in females, and dating desirability in males when rating female faces. Therefore, we found further evidence that the experience of music can alter the perception of the human face in a romantic scenario, and moreover, that music has a positive effect on a behavioral measure of sexual attraction, namely dating desirability (Marin et al., 2017; Chang et al., 2021).

Our findings are consistent with Darwin's (1871) view that music plays a role in romantic attraction in both sexes (Madison et al., 2018), not just among females as previously reported (May and Hamilton, 1980; Charlton, 2014; Marin et al., 2017). However, our findings indicate that female facial attractiveness is impervious to musical priming in males (Watkins, 2017; Madison et al., 2018), which is probably due to its biological significance in being a marker of fecundity (Johnston, 2006). At the same time, males' behavior may still be affected by indicators of musicality (see also Madison et al., 2018), which clearly warrants further experiments on sex differences regarding how different cues affect various

measures of partner choice (Jonason et al., 2012; Walter et al., 2020). More generally, our results can be interpreted within the context of the mutual mate choice (MMC) model, which accommodates both the fact that sexual dimorphism is relatively low among humans and that there are still some evolved sex differences (Miller, 2013; Stewart-Williams and Thomas, 2013). Both sexes have artistic motivations, capacities for appreciation and production of music, but there are still some differences in the degree and circumstances under which these tendencies are expressed (Varella et al., 2017). Mutual mate choice is necessary because in humans there is high paternal investment and alloparental care (e.g., grandmother effect), so both sexes compete for partners and both sexes select mates.

Contrary to our expectations, and not in line with Darwin's theory, high-arousing, more complex music did not yield the largest effects on sexual attraction (but see Charlton, 2014; Marin et al., 2017; Madison et al., 2018). This discrepancy between research findings may be attributed to differences in experimental designs and research questions. First, the within-subject design of the present study clearly differs from a design in which a face is only paired once with a musical excerpt varying in affect and complexity (Madison et al., 2018) or from a two-alternative forced-choice task in which two musical excerpts varying in complexity are presented without any visual stimuli (Charlton, 2014). There are advantages and disadvantages to these designs, but ours enabled us to show that music has an effect on face perception and dating desirability in the first place because we employed a silent control condition (which was not present in the designs of Charlton, 2014, and Madison et al., 2018). Future studies may also add other types of control conditions besides silence. Second, in Marin et al. (2017), misattribution of arousal, as an unconscious mechanism explaining the effect of music-induced affect on face perception, was the focus of interest. Considering that only the instructions differed between Marin et al.'s (2017) and the present study, it is likely that by establishing a cognitive, conscious link between musical primes and faces, the participants' attention was guided to different aspects of the musical excerpts than in Marin et al. (2017). In the current within-subject design, all musical excerpts were generally of a high standard (CD recordings of world-class performers) and allegedly stemmed from the same performer in the four music conditions. Thus, the general positive impression associated with the performer may have overruled the likely, more subtle, role of the varying affective and compositional contents across these excerpts.

Interestingly, Figures 1B, 2 show that music-induced pleasantness, and not arousal, plays a non-significant role in determining sexual attraction, especially in males and for ratings of dating desirability. We interpret this observation by suggesting that induced pleasantness in a mating context may be perceived as rewarding and thus elicit approach behavior, which would be in line with Darwin's argument that "the progenitors of man, either the males or females or both sexes, before acquiring the power of expressing their mutual love inarticulate language, endeavored to charm each other with musical notes and rhythm" (1871, p. 880). Throughout his book *The descent of man* Darwin stresses the charming character of sounds during mate choice in animals and humans, which spurs the discussion about the mutual role of affective and cognitive cues in musical signals. Musical complexity as a signal of advanced motor skills, intelligence, and creativity may not be the only way through which music affects romantic attraction (Marin et al., 2017). There may also be an additional (or alternative) route, possibly including both affective and aesthetic responses, as suggested by Darwin. To be specific, Darwin explained the evolution of ornaments by their inherent aesthetic quality and not necessarily by which fitness quality they could indicate. There has been an ongoing theoretical debate about the exact mechanisms underlying sexual selection (Miller, 1998; Davis and Arnocky, 2022). Thus, future behavioral studies should be more carefully designed to be able to differentiate between such mechanisms.

At present the role of individual differences in musical priming effects on sexual attraction was not examined. Previous research has shown that subjective experience of music-induced complexity and arousal depends on person-related factors such as personality traits and musical background in females (Marin and Leder, 2018). Although the current sample of non-musicians and the one of Marin et al. (2017) did not differ regarding a wide range of background variables including musical training, age and mood, the sample of the current study listened less frequently to classical music and liked the piano solo music of the experiment less than the sample of Marin et al. (2017). This may explain why the effects of music-induced arousal and pleasantness were less differentiated in the current study than expected. Interpersonal attraction is partly determined by the similarity-attraction effect (Caspi and Herbener, 1990; Tidwell et al., 2013), thus future studies will have to shed light on the extent to which individual differences regarding musical sophistication and one's self-perception of musicality may impact on the mechanisms determining the power of musicality in mate choice.

There are several limitations of the present research that need to be addressed. At the moment, our findings are not generalizable beyond the Western population studied in the experiment (Henrich et al., 2010), thus cross-cultural studies should be conducted as a next step. The current study focused on sexual attraction in the context of short-term mating. However, as Charlton (2014) found, we may expect differential effects of musicality on short- vs. long-term mating strategies in females. In this regard, it may also be worthwhile to include a wider range of person-related rating scales (see Madison et al., 2018). Another limitation concerns the present focus on motoric (performance) skills as an indicator of musicality. The role of mental fitness indicators in partner choice, such as creative intelligence as seen in musical improvisations (Madison et al., 2018), may also be studied in combination with biological cues in the future. Given that we studied music pertaining to a single musical style, our findings should not be over-interpreted but taken as a motivation to extend this research program to other musical styles and listener groups.

Our empirical findings have important implications for a better understanding of mating behavior observed in real-life

settings in which music and dancing plays a role. For example, nightclubs have been identified as human mating grounds (Mannion et al., 2009) in which background music might be one factor influencing the sexual appeal of others. The positive effect of background music on dating desirability has recently been demonstrated by a speed dating paradigm (Chang et al., 2021). Moreover, the socio-cultural phenomenon of groupies searching for sexual attention of rock stars (Barres, 2005; Larsen, 2017) as well as the phenomenon of adolescent girls seeking platonic romantic passions with male musicians and other celebrities (Engle and Kasser, 2005) may be partly based on perceptual crossmodal interactions.

In conclusion, crossmodal priming paradigms may be useful to study the evolution of music from a psychological and behavioral perspective. We show that being exposed to music may increase sexual attraction in both sexes when rating faces of average attractiveness. In light of growing evidence for Darwin's sexual selection theory, we will need to discuss whether his theory should stand on its own, or whether it should be integrated into broader, adaptationist theories which include other aspects of social bonding, such as singing to infants and social grooming (Savage et al., 2020; Leongómez et al., 2021).

Data availability statement

The dataset and musical stimuli presented in the study can be found at: OSF: https://osf.io/dp3es/?view_only=6a3d15fad004479bae839dc8c9efcf79.

Ethics statement

The studies involving human participants were reviewed and approved by the Board for Ethical Questions in Science of the University of Innsbruck. The patients/participants provided their written informed consent to participate in this study.

Author contributions

MM developed the study concept and the study design. Testing and data collection were performed by IR and MM. IR performed the data analysis and interpretation under the supervision of MM, and provided critical revisions. MM drafted the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.971988/full#supplementary-material

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Assortative mate preferences for height across short-term and long-term relationship contexts in a cross-cultural sample

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Height preferences reflecting positive assortative mating for height—wherein an individual's own height positively predicts the preferred height of their mate—have been observed in several distinct human populations and are thought to increase reproductive fitness. However, the extent to which assortative preferences for height differ strategically for short-term versus long-term relationship partners, as they do for numerous other indices of mate quality, remains unclear. We explore this possibility in a large representative sample of over 500 men and women aged 15–77 from Canada, Cuba, Norway and the United States. Participants' own heights were measured, and they indicated their height preferences for a long-term and short-term mate using graphic stimuli containing metric indices. Replicating the "male-taller norm," participants on average preferred taller-than-average male mates, and shorter-than-average female mates. Positive assortative preferences for height were observed across sexes and samples, however the strength of these height preferences varied with relationship context for men, and not for women. Taller men preferred relatively shorter women for short-term relationships than for long-term relationships, indicating stronger assortative preferences for height in a long-term context. These results provide preliminary evidence that, in addition to mate preferences for other physical traits related to mate quality such as masculinity in the body, face, and voice, assortative preferences for height do vary as a function of expected relationship length, but this was surprisingly only observed in preferences for female height.

KEYWORDS

assortative mating, body size, relationship context, relationship length, cross-cultural, mate choice, mate preferences, sexual selection

Introduction

One hundred and fifty years ago, Darwin published his now remarkably influential theory on sexual selection, emphasizing the role of phenotypic qualities in mate choice decisions (Darwin, 1871). Since then, a vast body of literature offers converging evidence that mate choice decisions are critical for the reproductive success of humans and all other sexually reproducing organisms, and as such mate preferences have been largely shaped by sexual selection to maximize fitness (Andersson, 1994; Conroy-Beam et al., 2019a). Mate preferences in humans are intensively studied and shown to range from preferences for specific character or personality traits, such as kindness and honesty, to preferences for physical traits, such as age or physical attractiveness, that ostensibly function to target mates of high genetic quality, resource holding potential, and/or reproductive potential (Shackelford et al., 2005; Roberts and Little, 2008; Walter et al., 2020).

Mate preferences for physical height in humans are observed in both sexes and across diverse cultures (Courtiol et al., 2010; Pisanski and Feinberg, 2013; Yancey and Emerson, 2014; Stulp et al., 2017). This is perhaps not surprising given that height predicts a range of life-history and fitness-related factors including health, socioeconomic status, dominance, and reproductive maturity (Pisanski and Feinberg, 2013; Stulp and Barrett, 2016 for reviews). Body size in humans, like in many other animals (Andersson, 1994), is a sexually dimorphic trait under natural and sexual selection that is both highly heritable and susceptible to environmental influences. For instance, there is evidence that taller men and women have, on average, a lower risk of mortality than do relatively shorter individuals (Wormser et al., 2012). Shorter-than-average men in turn exhibit the lowest rates of both social and reproductive success (Stulp and Barrett, 2016), particularly in industrialized or western populations where stature predicts substantial variance in social status (Judge and Cable, 2004). Among women, a basic principle of allocation underscores a trade-off between skeletal growth and reproduction, with shorter women typically reaching sexual menarche, and thus reproductive maturity, sooner than taller women, and as a consequence giving birth to their first child relatively earlier (Stearns, 2000; Stulp and Barrett, 2016). At the same time, short mothers experience more complications during pregnancy and parturition (in part due to their small pelvis size) and higher rates of child morbidity and mortality in both developing and industrialized countries (Stearns, 2000; Stulp and Barrett, 2016).

The mate height preferences of both sexes are likely to reflect adaptive mate choice decisions (Kuijper et al., 2012; Buss and Schmitt, 2019), however it remains unclear exactly which aspects of mate quality that are linked to height can explain the most variance in height preferences (Kowal et al., 2021). Height preferences have been studied using a range of methodologies including numerical self-report, judgments of figure drawings, and mate-choice relevant tasks (e.g., outcomes of speed dates or dating advertisements; see Courtiol et al., 2010 for review). These studies offer converging evidence for a "male-taller-norm" among young heterosexual western adults: women generally indicate preferences for men taller than themselves, whereas men indicate preferences for relatively shorter women (for reviews, see Pisanski and Feinberg, 2013; Stulp and Barrett, 2016). A similar pattern emerges in actual mated pairs at a rate much higher than expected by chance (Gillis and Avis, 1980; Stulp et al., 2013b). Western women generally prefer men who are taller than the average man in their given population, for example, men that are around 180 cm tall (Beigel, 1954; Salska et al., 2008; Courtiol et al., 2010). However, women's preferences for above-average height in men appear to asymptote within one or two standard deviations of the average (Beigel, 1954; Pawlowski, 2003; Fink et al., 2007; Salska et al., 2008; Courtiol et al., 2010; Stulp et al., 2013a, 2013b; i.e., the "male-not-too-tall norm"). This aligns with evidence that, although taller men are generally healthier than average-height or short men, very tall men have relatively higher rates of health complications (Stulp et al., 2014; Stulp and Barrett, 2016).

Men's preferences for women's heights have consistently been shown to be weaker, less consistent, and less robust than women's preferences for men's heights (Pierce, 1996; Salska et al., 2008; Courtiol et al., 2010; Stulp et al., 2013a). This may reflect evolved and/or sociocultural sex differences in mate preferences (Walter et al., 2020), wherein, for example, body size in men can index dominance and resource holding potential—traits that are more likely to have been sexually selected among men than women. Among women, indices of youth and fertility are more likely to have been selected for, and indeed are reflected in the general mate preferences of men (Buss and Schmitt, 1993; Shackelford et al., 2005; Walter et al., 2020). Nevertheless, female height can still index health and fecundity to potential mates. The limited existing research on preferences for women's heights suggests that western heterosexual men prefer average or shorter-than-average women, however others report the opposite or no preference at all (Courtiol et al., 2010 for review). Studies examining the preferences of men who identify as non-heterosexual also show mixed findings, with support both for and against a general tendency to prefer a partner taller than oneself (Valentova et al., 2014, 2016). In addition, such preferences appear to be moderated by a number of factors, including the height of the rater (Valentova et al., 2014).

Indeed, an individual's own height is known to predict their preferred height in a mate. Beyond absolute height preferences, several studies have found evidence for positive assortative preferences for height, such that taller individuals tend to prefer taller mates and vice versa (Pawlowski, 2003; Kurzban and Weeden, 2005; Fink et al., 2007; Courtiol et al., 2010; Stulp et al., 2013b). Assortative mating in humans and other animals is most often positive, that is, occurs between two individuals that share a given phenotypical quality (Thiessen and Gregg, 1980; Conroy-Beam et al., 2019b). Such a preference can be adaptive if it increases genetic homology while avoiding inbreeding (Thiessen and Gregg, 1980). Researchers have posited that positive assortative preferences for height may increase the likelihood that height differences between mated pairs are not extreme. Indeed, preferences for relative height in humans typically do not exceed

a difference of 25 cm between heterosexual mates (Pawlowski, 2003; Fink et al., 2007; Salska et al., 2008). Positive assortative preferences for height may thus function to increase one's pool of potential partners (Pawlowski, 2003) or the quality of resultant offspring. Height is highly hereditable ($h = 0.80$; Stulp and Barrett, 2016), hence the offspring of two tall individuals will likely be tall as well. There is also some evidence that extreme height differences between mated pairs predict a higher likelihood of birth complications (Stulp et al., 2011).

While mate preferences can differ somewhat from actual mate choices due to conflicts of interest between the sexes and numerous factors that limit the extent to which certain individuals can attain a preferred or high-quality mate (Jiang et al., 2013; Stulp et al., 2013b), a recent meta-analysis indicates weak positive assortative mating for height in heterosexual couples across 43 western ($r = 0.25$) and non-western ($r = 0.21$) countries (Stulp et al., 2017), with no cross-cultural differences (Stulp et al., 2017). Notably, assortative preferences for height have not been consistently replicated, for example, in non-traditional societies such as several tribes on the African continent including the Hadza, Himba, Datoga and Tsimane' (Sear and Marlowe, 2009; Sorokowski et al., 2011, 2015; Sorokowski and Butovskaya, 2012).

The present study tests whether preferences for mate height differ for committed long-term compared to uncommitted short-term relationships in a large cross-cultural sample of adults. While most human societies practice marriage, short-term liaisons among single people or through serial monogamy and extra-pair affairs are even more common in our species (Buss and Schmitt, 1993 for review). Many studies have shown that mate preferences for traits linked to mate quality can differ for short- versus long-term relationships (Buss and Schmitt, 1993, 2019). Much of this research has focused on female preferences for male androgen-mediated traits, such as facial, vocal and bodily masculinity. In general, women show relatively stronger preferences for androgen-mediated male traits in the context of a short-term versus long-term relationship (Little et al., 2011), presumably because the potential benefits of choosing a male mate with relatively high androgen levels (e.g., higher immunocompetence that may be passed to offspring) outweigh the potential costs (e.g., higher risk of infidelity and decreased investment) in a short-term but not long-term relationship (Puts et al., 2012 for review; e.g., Buss and Schmitt, 1993, 2019). However, mate preferences have also been shown to vary by relationship context for traits that may not be directly linked to androgen-levels, but that nevertheless predict characteristics relevant in a potential long-term versus short-term mate. This may include, for example, relatively stronger preferences for intelligence and honesty in long-term mates, and for sex drive or athleticism in short-term mates (Buss et al., 1990; Regan et al., 2000; Muggleton and Fincher, 2017).

Despite being a sexually dimorphic trait in humans, height does not appear strongly and consistently related to circulating testosterone levels in adult men (Kowal et al., 2021). Thus, while female preferences for male height may not vary by relationship context as a function of variable androgen-linked immunity benefits *per se*, as they do for androgen-mediated traits, other benefits could be gained from such a preference when expressed by either sex. Indeed, this is because height is linked more broadly to mate quality and health benefits in both sexes, and to fecundity in women. To our knowledge, only one previous study examined height preferences for short-term versus long-term mates, and that study focused only on heterosexual women's preferences for sexual dimorphism in hypothetical mate pairs. Testing a sample of nearly 150 Polish women, Pawlowski and Jasienska (2005) found that women preferred relatively taller male mates in a short-term than long-term mating context. However, the effect of relationship length was small, as more than half of the women showed the same height preference regardless of relationship context (Pawlowski and Jasienska, 2005). No previous study has tested whether preferences for women's heights differ by relationship context.

Here, we test the prediction that positive assortative preferences for height will be observed across four human populations and further explore whether these preferences differ by hypothetical relationship context for both men's and women's heights. This exploratory study included a diverse sample of over 500 male and female raters aged 15 to 77. To address the overabundance of studies on the height preferences of predominantly western undergraduate students (Courtiol et al., 2010 for review; Pisanski and Feinberg, 2013), participants were recruited from both rural and urban regions in Canada, Cuba, Norway and the United States. While some researchers have suggested that population-level height differences may influence height preferences (Pawlowski, 2003; Stulp and Barrett, 2016), evidence is lacking for cross-cultural differences in assortative mating for height (Pawlowski, 2003; Fink et al., 2007; Stulp et al., 2017). Indeed, if height preferences reflect long-standing evolved mechanisms in our species, they are likely to be relatively stable across cultures (Shackelford et al., 2005). Moreover, differences in height among same-sex individuals *within* each of the sampled countries (up to 50 cm) far outweighed the average differences in height between countries (Cubans were on average 6 cm shorter than same-sexed Norwegians, with North Americans falling in between these two extremes). We thus had no *a priori* predictions that country would explain significant variance in assortative preferences for mate height above and beyond individual differences in height. As a result, we did not test for differences between countries, but instead modeled the variation in height preferences across these countries, using country as a random-intercept term. Our analyses hence focus on testing for an effect of relationship context on assortative preferences for height in both men and women.

Materials and methods

Participants

Descriptive statistics for the ages, heights, and weights of men and women in each country are given in Table 1. Five-hundred and

thirty-six participants took part (333 women, 203 men), aged 15–77 (mean age 25.8 ± 11.4 years). Participants were recruited from the general population (rural and urban) and from local universities in four countries: Canada ($n = 143$), Cuba ($n = 187$), Norway ($n = 95$) and the United States ($n = 111$), using a combination of recruitment methods ranging from online advertisements to word-of-mouth (self-reported nationalities are given in Supplementary Table S1).

Overall, 93.3% of participants reported the opposite-sex as their preferred sex for a romantic relationship, 3.4% reported a preference for the same-sex, 2.8% for either sex, and 0.6% did not report their sexual orientation. While height preferences can differ between heterosexual and non-heterosexual samples (Valentova et al., 2014, 2016), our sample size of non-heterosexual participants was not large enough to test for group differences. Thus, all participants regardless of their sexual orientation or age were included in the statistical analyses reported in this paper. However, models including only heterosexual participants who self-reported as preferring the opposite-sex, and models including only participants aged 17 to 40 (i.e., spanning the most reproductively relevant years of the human lifespan), can be found in the Supplementary Materials. Excluding participants on the basis of their sexual orientation and/or age from analyses did not change any significance levels. Participants provided written informed consent. Depending on the country sample, they received course credit for taking part (Canada, United States), or a small gift (Cuba, Norway). The study was conducted according to the Declaration of Helsinki on Biomedical Studies Involving Human Subjects.

Stimuli

Minimalistic graphic representations of back-facing male (Figure 1A) and female (Figure 1B) bodies were first generated by hand, scanned, and then digitally edited using Adobe Photoshop CS6. We controlled for body symmetry by inverse mirroring the left side of the body to the right (following Courtiol et al., 2010). In addition, aspect ratios between body width and height, and between the hips, shoulders and waist, were

TABLE 1 Descriptive statistics for age, height, and weight of each sample by sex and country.

Sex of rater	Country		*N*	Mean	SD	Min	Max
Men	All	Age	203	26	11.3	15.0	75.0
		Height (cm)		178.3	7.8	152.4	200.7
		Weight (kg)		76.5	16.9	47.8	149.7
	Canada	Age	46	18.5	1.7	17.0	28.0
		Height (cm)		179.2	7.2	160.1	190.5
		Weight (kg)		71.4	12.2	47.8	99.8
	Cuba	Age	86	23.1	3.2	19.0	32.0
		Height (cm)		176.0	6.9	160.0	190.0
		Weight (kg)		69.9	11.6	50.0	110.0
	Norway	Age	42	33.8	14.8	15.0	75.0
		Height (cm)		181.2	7.2	165.0	200.0
		Weight (kg)		85.6	18.1	54.0	125.0
	United States	Age	29	35.4	16.4	19.0	70.0
		Height (cm)		179.8	10.0	152.4	200.7
		Weight (kg)		90	21	61.2	149.7
Women	All	Age	333	25.7	11.4	15.0	77.0
		Height (cm)		164.9	7.5	130.0	190.5
		Weight (kg)		62.9	15.4	28.6	149.7
	Canada	Age	97	19.1	2.3	17.0	29.0
		Height (cm)		165.1	7.9	149.9	190.5
		Weight (kg)		60.6	12	38.6	98.9
	Cuba	Age	101	21.2	3.4	18.0	32.0
		Height (cm)		163	7.7	130.0	180.0
		Weight (kg)		56.4	8.2	40.0	84.0
	Norway	Age	53	28.9	13.5	15.0	67.0
		Height (cm)		167.6	5.7	154.0	177.0
		Weight (kg)		63.8	12.1	46.0	100.0
	United States	Age	82	37.1	13.5	20.0	77.0
		Height (cm)		165	7.3	144.8	188.0
		Weight (kg)		72.9	21.2	28.6	149.7

standardized across the scale. Bodies were positioned from shortest to tallest and labeled A to E, with heights given in both metric (cm) and imperial (feet, inches) units. The central figure marked "C" on the graphic represents average height for each sex, with adjacent bodies representing ±5 cm and ± 10 cm deviations from the mean for a range of 20 cm. Scale values derive from population statistics obtained for North American adults (Shields et al., 2008; NCD Risk Factor Collaboration, 2016), as this approximates height distributions for Central and Northern global populations (NCD Risk Factor Collaboration, 2016). Height scale values were selected so as to avoid extremes at either end of the average distribution of heights, and the same standardized scale was used for all participants in all four countries to allow for direct cross-cultural comparisons. Adding numerical labels representing absolute heights to our scale, rather than using a wholly visual representation of relative height differences between hypothetical pairs such as the sexual dimorphism in stature (SDS) scale (Pawlowski, 2003; Fink et al., 2007; Sorokowski et al., 2011), allowed for more precise numerical calculation of absolute height preferences and of the strength of the relationship between own and preferred height, in real units.

Procedure

Participants were simultaneously presented with the graphic representations of men and women (Figures 1A,B), on two separate laminated pages of A4 paper (Canada, Cuba, Norway) or as two digital images scaled to the same size (United States). They were then asked to indicate their height preference for a mate of their preferred sex in the context of a stable long-term relationship (for example, marriage) and a short-term relationship (for example, a one-night stand) following previous work (Little et al., 2002; Feinberg et al., 2012; O'Connor et al., 2014). The order in which long-term or short-term preferences were tested was randomized. Participants were instructed that they could select more than one preferred height only if they strongly felt that they equally prefer multiple height options. However, multiple preferred heights were selected on only 2.6% of trials (28 of 1,072) and were thus averaged together to obtain a single preferred height value. Participants also reported their sex, age, and sexual orientation. Canadian, Cuban, and Norwegian samples (80% of participants) completed the study using pen and paper; their heights and weights were measured using metric tape and a digital scale. American participants completed the study online using

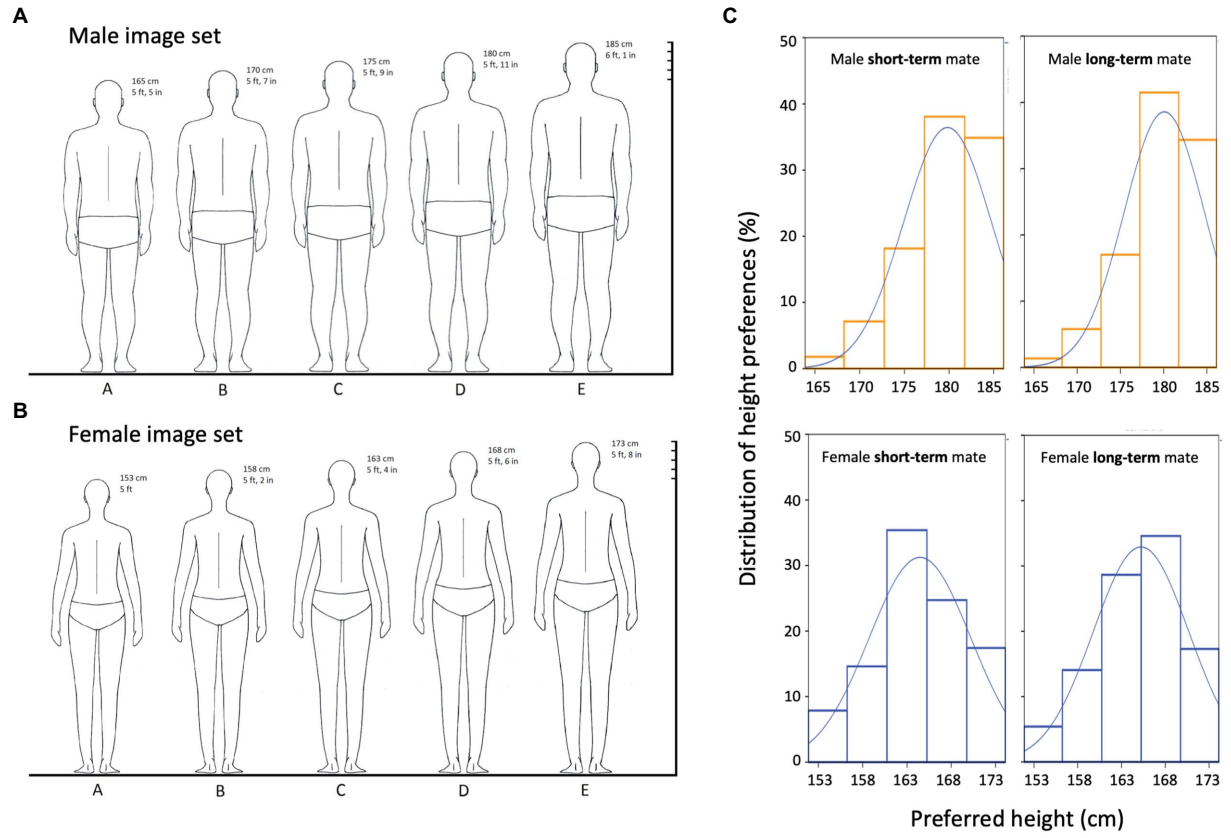

FIGURE 1
(A,B) Stimulus image set featuring back-facing silhouettes of men (panel **A**) and women (panel **B**) used to measure mate height preferences. See *Stimuli* for detailed descriptions of stimulus creation and parameters. **(C)** Distributions of raw absolute height preferences for male heights (top row) and female heights (bottom row) in short-term versus long-term relationship contexts.

survey software (Research Core, 2017, Qualtrics, Provo, Utah, United States); their heights and weights were self-reported.

Models and results

For full statistical models, data, R code and output, and research stimuli see Supplementary Materials and online materials (Open Science Framework, https://osf.io/ah97w/).

We coded the response variable (Height Preference) in centimeters. Figure 1C shows the distribution of absolute height preferences for female and male mates in either relationship context. Table 2 reports absolute height preferences across countries. These absolute preference values (and their general distributions; Figure 1C) are notably based on rater's raw responses and are largely given here for comparisons with previous studies. The values do not account for variance tied to individual raters or groups, including variance as a function of the rater's own height, as we explore in our linear mixed effects models.

To test our key hypothesis regarding assortative preferences for height by relationship context, we ran a series of linear mixed effects models using the R package lmerTest (Kuznetsova et al., 2017). In all models, we set REML to false, and fit with Maximum Likelihood to facilitate model comparison. We centered the response variable (Height Preference) on the sample mean (such that the intercept effects approximate a *t*-test, and the intercept itself is not 0 cm, an impossible value) and z-scored the Own Height variable. We then created models specifying random slopes and intercepts maximally with correlations between random effects and binary variables sum-to-zero coded (−0,5, 0.5) to reduce false positives and to create a full-factorial ANCOVA-like analysis (Barr, 2013). We entered all fixed-effects as random slopes at each participant's random intercept (i.e., all main effects and all two-way and three-way interactions among own height, sex, and relationship context). When grouping data by self-reported free-response nationality or by country, we nested each participant within their nationality or country. We also fit random intercepts for age as a control. Because we had no formal predictions regarding the age or country/nationality of raters, we did not enter these as a fixed-effects terms and the factors are instead treated as nuisance variables.

Twenty-two participants chose not to indicate a height preference for either a long-term or short-term relationship partner, and their data were thus excluded from these models. For analyses we thus included the short-term and long-term preferences of 514 participants, totaling 1,028 observations, however this varies slightly depending on the analysis as some participants did not complete all demographic questions. The number of observations per analysis are noted in the Supplementary Materials in each model's output.

The R code for Model 1 nesting participants by country is:

lmer(height_preference ~ height_z_scored × Sex × Relationship_context + (1 + height_z_scored × Sex × Relationship_context || ID_NUMBER:Country) + (1 | Age), data = data, REML = FALSE).

TABLE 2 Absolute (raw) height preferences by sex, country, and relationship context. These raw values do not account for variance due to individual or sample differences.

	Country	Relationship context	Preferred height (cm)	
			Mean	SEM
Preferred Heights for Women	Canada	Long-term	167.178	0.8792
		Short-term	165.565	0.9177
	Cuba	Long-term	164.802	0.6294
		Short-term	164.018	0.6824
	Norway	Long-term	165.976	0.7536
		Short-term	166.077	0.8289
	United States	Long-term	165.552	1.2353
		Short-term	164.517	1.3230
Preferred Heights for Men	Canada	Long-term	180.402	0.5046
		Short-term	179.629	0.5550
	Cuba	Long-term	179.208	0.4532
		Short-term	178.943	0.4470
	Norway	Long-term	179.971	0.7674
		Short-term	180.181	0.7814
	United States	Long-term	179.691	0.6629
		Short-term	179.962	0.6979

SEM = standard error of the mean.

To facilitate interpretation of results, we subsequently split the data by sex of rater and re-ran the models. Table 3 displays fixed effects for the country-level model, for both sexes combined and for each sex separately. Full model results including random effects are given in Supplementary Table S2 in the Supplementary Materials; Models excluding participants on the basis of their reported sexual orientation and/or age are given in Supplementary Tables S3, S4, and show the same pattern of results.

The results of Model 1 show that, in general, men preferred shorter women whereas women preferred taller men, relative to their own body heights (Table 3). Examining these effects for each sex separately while controlling for country-level variance shows that, on average, women prefer men 2.3 cm (or almost 1 inch) taller than the average men in their country, and men prefer women 2.5 cm (or about 1 inch) shorter than the average women in their country. Own height therefore positively predicted preferences for mate height, confirming positive assortative preferences for height in both sexes and across countries (Figure 2). However, this was qualified by relationship context in preferences for women's heights. Indeed, taller men preferred relatively shorter women for short-term relationships than they did for long-term relationships (Table 3; Figure 2).

We then tested the same model again, replacing country with the self-reported free-response nationality ($k = 39$) of each participant, rather than their country of residence (see Supplementary Table S1 for a break-down of reported nationalities).

The R code for Model 2 nesting participants by nationality is:

TABLE 3 Model 1: Linear mixed effects model testing for differences in assortative preferences for mate height as a function of a short-term versus long-term relationship context, nesting participants by country.

	Women and Men	Women only	Men only
(Intercept)	−0.103 [−0.678, 0.472]	1.167*** [0.612, 1.722]	−1.244* [−2.318, −0.169]
Own height (of rater, z-scored)	1.892*** [1.304, 2.479]	2.461*** [1.700, 3.222]	1.453** [0.519, 2.388]
Sex (of rater)	−2.374*** [−3.524, −1.224]		
Relationship context	0.112 [−0.462, 0.686]	0.392 [−0.169, 0.953]	−0.140 [−1.249, 0.969]
Own height × Sex	−0.681 [−1.856, 0.494]		
Own height × Relationship context	0.735* [0.172, 1.299]	0.381 [−0.265, 1.027]	1.076* [0.114, 2.038]
Sex × Relationship context	−0.558 [−1.707, 0.590]		
Own height × Sex × Relationship context	0.690 [−0.437, 1.816]		

Own height of rater is coded in models as "height_z_scored"; Sex of rater is coded as "Sex"; Relationship context has two levels: short-term, long-term; [Lower 95% CI, Upper 95% CI]. See Supplementary Table S2 for full model with random effects.
***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

lmer(height_preference ~ height_z_scored × Sex × Relationship_context + (1 + height_z_scored × Sex Relationship_context || ID_NUMBER,Nationality_selfreport,Country) + (1 | Age), data = data, REML = FALSE).

Table 4 displays fixed-effects for the nationality-level model, comparing men and women together and separately. Full model results including random effects are given in Supplementary Table S5 in the Supplementary Materials. Models excluding participants on the basis of their reported sexual orientation and/or age are given in Supplementary Tables S6, S7, and show the same pattern of results.

In Model 2, own height again significantly and positively predicted preferences for height. As found in the country-level model, there was a main effect of relationship context, specific to preferences for women's heights. This was qualified by an interaction with the rater's own height, revealing again that for short-term relationships taller men preferred relatively shorter women than they did for long-term relationships (Table 4; Figure 2).

Discussion

Our results partially corroborate previous findings, namely that women generally prefer taller men, and men generally prefer shorter women, relative to their own heights (Beigel, 1954; Salska et al., 2008; Courtiol et al., 2010; Stulp et al., 2013a). This result extends the "male taller norm" to four industrialized countries. Our results further corroborate a positive relationship between participants' own heights and their mate height preferences, that is, positive assortative preferences for height (Stulp et al., 2017). However, assortative height preferences were qualified by relationship-context. Surprisingly, and in contrast to research on individual differences in preferences for facial and vocal masculinity in the context of a short-term versus long-term relationship (Little et al., 2011), our effects were specific to preferences for women's heights. Taller men preferred relatively shorter women for short-term relationships than for long-term relationships.

Few studies have examined men's preferences for women's heights, and those studies have typically produced smaller effect sizes and less consistent results than have studies examining women's preferences for men's heights (Pierce, 1996; Salska et al., 2008; Courtiol et al., 2010; Stulp et al., 2013a). In addition, no previous study, to the authors knowledge, has tested for differences in men's preferences for women's heights across relationship contexts, despite the important trade-off between female height and reproduction (Stearns, 2000; Stulp and Barrett, 2016). However, our finding that women's preferences for men's heights did not differ (while men's did) is unexpected, as predictions regarding context-specific mating strategies have traditionally focused on variation in women's preferences (Buss and Schmitt, 1993, 2019). Moreover, one previous study found that women do prefer a larger sexual dimorphism in stature (SDS) for hypothetical short-term than long-term relationships (i.e., they prefer silhouette drawings representing a relatively larger difference in height between a male–female pair; Pawlowski and Jasienska, 2005). However, that study used the SDS scale (Pawlowski, 2003), aimed at measuring preferences for relative height between heterosexual pairs, that is not directly comparable to our scales. While our sample size of female raters was more than double that of Pawlowski and Jasienska (2005), suggesting that a lack of statistical power in our study is unlikely to explain the contrasting results, their study controlled for phase of menstrual cycle in their female raters whereas our study did not. Regrettably, neither study examined the potential influence of the current relationship status of participants on height preferences. More research is clearly needed to understand context-specific mating strategies in height preferences, particularly for women's heights, using comparable methods to discern the robustness of these effects.

The absolute height preferences of each sex observed here support a general tendency for raters to prefer taller-than-average men and shorter-than-average women and, most consistently, to dis-prefer mates of either sex that exhibit a very short or very tall stature (Courtiol et al., 2010; Stulp and Barrett, 2016 for reviews). These observed absolute preferences corroborate studies

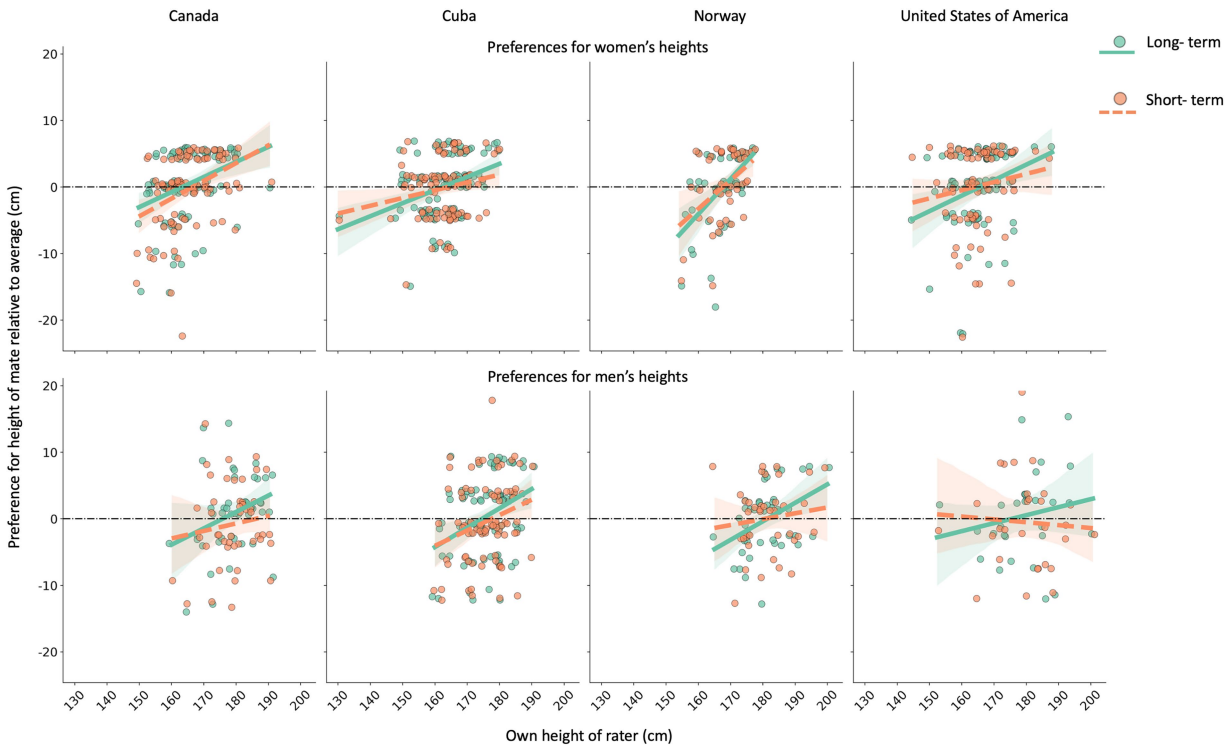

FIGURE 2
Assortative preferences for the heights of potential female mates (top row) and male mates (bottom row) in all four countries. The heights of raters positively predict how much taller-than-average or shorter-than-average they prefer their mates to be, with similar effects observed across countries. Men's preferences for women's heights are relatively stronger for a long-term (solid lines and green coloration) than short-term (dashed lines and orange coloration) relationship context. 95% confidence intervals are represented by shaded regions surrounding each regression line.

suggesting that the costs of shortness outweigh the benefits of tallness, particularly for men (Stulp et al., 2014), wherein both men and women of average to somewhat above-average height appear to enjoy the highest reproductive success, at least in western societies, though this relationship varies widely across studies (Stulp and Barrett, 2016).

Despite modest cross-cultural differences in the population-level height distributions of Cubans, North Americans, and Norwegians, raters from all countries sampled in this study showed a similar pattern of height preferences. A recent meta-analysis comparing the heights of actual mated heterosexual couples also found no significant cultural differences (Stulp et al., 2017), suggesting that individual height differences may trump population-level height differences, as the variation in heights within countries is typically several times greater than between countries. Fink et al. (2007) also found no cross-cultural differences in preferences for sexual dimorphism in stature among participants from Austria, Germany and the United Kingdom, and no differences when comparing these samples to a Polish sample (Pawlowski, 2003).

While previous studies have shown relatively stronger preferences for various physical traits in hypothetical short-term compared to long-term relationship contexts, particularly for androgen-mediated masculinity in the face, body and voice (Little et al., 2011; Puts et al., 2012), our results suggest that this ostensibly adaptive mechanism may not robustly or consistently generalize to women's preferences for all sexually dimorphic male traits, including physical height. However, while height is not closely linked to androgen levels in men (Kowal et al., 2021), preferences for indices of mate quality that are not directly hormonally mediated (such as height) may nevertheless differ for short-term versus long-term mates (Buss et al., 1990; Regan et al., 2000; Muggleton and Fincher, 2017). We did not find evidence of this for preferences of men's heights.

Like the SDS scale (Pawlowski, 2003; Pawlowski and Jasienska, 2005), the scale used in the present study represented a normal distribution of heights for the sampled populations, omitting extremes, and importantly, did not elicit floor or ceiling effects. However, a limitation of such a scale is that it constrains the extent to which very short or very tall respondents can choose partners who are much shorter or taller than themselves. Thus, a broader representation of heights would allow for a correspondingly broader range of preference responses, and potentially a stronger mapping between own and preferred height. Incorporating a broader range of height preference options would also allow researchers to more readily use a single standardized height preference scale when comparing responses across human populations whose height distributions vary considerably from one another. Another potential limitation of

TABLE 4 Model 2: Linear mixed effects model testing for differences in assortative preferences for mate height as a function of a short-term versus long-term relationship context, nesting participants by self-reported nationality.

	Women and Men	Women only	Men only
(Intercept)	−0.020 [−0.571, 0.530]	1.041*** [0.498, 1.584]	−1.015 [−2.046, 0.015]
Own height (of rater, z-scored)	1.649*** [1.095, 2.202]	2.207*** [1.502, 2.912]	1.189* [0.293, 2.086]
Sex (of rater)	−2.033*** [−3.133, −0.932]		
Relationship context	0.111 [−0.463, 0.685]	0.386 [−0.176, 0.947]	−0.138 [−1.247, 0.970]
Own height × Sex	−0.815 [−1.921, 0.291]		
Own height × Relationship context	0.743* [0.180, 1.305]	0.390 [−0.256, 1.035]	1.076* [0.115, 2.038]
Sex × Relationship context	−0.551 [−1.699, 0.597]		
Own height × Sex × Relationship context	0.675 [−0.451, 1.800]		

Own height of rater is coded as "height_z_scored"; Sex of rater is coded as "Sex"; Relationship context has two levels: short-term, long-term; [Lower 95% CI, Upper 95% CI]. See Supplementary Table S5 for full model with random effects.
***$p < 0.001$; and *$p < 0.05$.

the scale employed here is that visual representations of bodies were given alongside a numeric metric representing each figure's height. While this allowed us to quantify height preferences in objective units, it prevents conclusions about whether participants were basing their judgments on the illustration, the metric, or both. The commonly used SDS scale does not contain metrics (Pawlowski and Jasienska, 2005; Fink et al., 2007; Sorokowski et al., 2011; Valentova et al., 2014), and that approach may indeed increase the implicit nature of the preference task and reduce conscious cognitive biases. Finally, while physical height and weight measurements were taken from our Canadian, Cuban and Norwegian participants (80% of our study sample), American respondents self-reported their body size. Self-reports of height can be biased, particularly among men (Merrill and Richardson, 2009), and thus have the potential to weaken the true association between own and preferred height, as may have been the case for our sample of American men.

Despite the cross-cultural nature of this study, the countries sampled here all score high on the World Health Organization's Global Health Statistics, with comparably low rates of disease and childhood mortality (World Health Statistics, 2016). It is possible that cross-cultural differences in mate height preferences across relationship contexts may differ in countries with a high versus low health index. For example, selection may favor earlier sexual maturation (and thus shorter stature) in countries with high childhood mortality and low life expectancy (Sear, 2010). Indeed, assortative preferences for height have not been consistently replicated in non-traditional African societies namely among the Hadza, Himba, Datoga and Tsimane' tribes (Sear and Marlowe, 2009; Sorokowski et al., 2011, 2015; Sorokowski and Butovskaya, 2012). Replication studies may therefore include participants from countries representing a wider range of ecological conditions. In future work, researchers may also test whether the preferences observed here translate into real-life mate choices, that is, whether or not stronger assortative mating in height is observed in actual committed (e.g., married) couples compared to shorter-term (casual) partnerships. Finally, it is important to emphasize that human relationships are complex and that mating contexts extend beyond a binary division of short-term and long-term partners. Integrating this complexity in study designs will undoubtedly help to illuminate and advance our understanding of human mate preferences.

Data availability statement

The datasets analyzed for this study, full statistical models, R code and output, and research stimuli can be found in the online Supplementary materials and the Open Science Framework (https://osf.io/ah97w/).

Ethics statement

The studies involving human participants were reviewed and approved by the McMaster Research Ethics Board and methods were carried out in accordance with the approved guidelines. The participants provided their written informed consent to participate in this study.

Author contributions

KP and DF designed the research. KP, MF-A, ND-S, AO, AS, and RP collected the data. KP, AO, and RP coded and analyzed the data. DF performed statistical modeling. KP created stimuli and figures. KP, AO, and DF wrote the paper. KP, NE, EM, CL, and DF supervised the project. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.937146/full#supplementary-material

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Sex differences in emotional perception: Evidence from population of Tuvans (Southern Siberia)

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Prior studies have reported that women outperform men in nonverbal communication, including the recognition of emotions through static facial expressions. In this experimental study, we investigated sex differences in the estimation of states of happiness, anger, fear, and disgust through static photographs using a two-culture approach. This study was conducted among the Tuvans and Mongolian people from Southern Siberia. The respondents were presented with a set of photographs of men and women of European and Tuvan origin and were asked to interpret each of them. They were asked: "What does the person in the photo feel?" We found that the Tuvans easily identified happiness and anger; however, the level of accuracy of fear and disgust recognition was low. No sex differences in the recognition of happiness, disgust, and fear were observed. However, anger recognition was significantly moderated by the perceiver's sex and the origin of the model. Compared to Tuvan men, Tuvan women were significantly less accurate in identifying anger in male Tuvans. Furthermore, the age effect was found in recognition of fear: older Tuvans were more accurate while recognizing the fearful faces of Tuvan, but not the European models.

KEYWORDS

emotion recognition, facial expressions, sex differences, anger, Tuvans

Introduction

The theoretical basis for studies of human emotions and related facial expressions dates back to Darwin's book, *The Expression of the Emotions in Man and Animals* (Darwin, 1872). Earlier, he discussed the evolutionary foundations of emotions and their expressions in his book *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871). So far, the questions of the universality of expression and recognition of basic human emotions remain one of the most popular topics for evolutionary psychologists and human ethologists.

Previous studies that examined various populations found that women were more accurate than men in judging basic emotional states from static facial images by means of forced choice (see the meta-analyses of Thompson and Voyer, 2014). The effect sizes in this study were approximately Cohen's $d = 0.4$. Same conclusions were drawn from the most recent study of facial emotion recognition through videos, where the results demonstrated robust sex differences favoring women (Cohen's $d = 0.54$, Wingenbach et al., 2018). Sex differences, where women outperform men in non-verbal communication abilities, have been found across different age cohorts, including infants, children, and adults, with the largest age effects on anger, fear, sadness, and no effect on disgust (see meta-analysis: Hayes et al., 2020). Interestingly, the largest effect size for sex differences has been found in infants, favoring girls in their ability to recognize emotional facial expressions according to a meta-analysis (McClure, 2000). However, the forced-choice approach has apparent limitations, as it suggests solutions by offering a ready-made option (Lorette, 2021). Recently, an increasing number of studies have adopted a different approach in which observers are offered to freely label emotional facial expressions (Gendron et al., 2018). In this study, we used this method in particular. To the best of our knowledge, this is the first study that tests sex differences in emotional recognition using free-labelling approach.

Despite an abundance of studies, the factors that moderate human emotion recognition remain poorly understood to this date. Recently, it has been pointed out that the type of emotion is one of the factors that moderate recognition of human emotions. For instance, Thompson and Voyer's (2014) meta-analytic research showed that sex differences in recognition of basic emotions from stimuli of various modalities (visual, auditory, and mixed) reach the largest effect sizes when identifying angry, fearful, and disgusted states (around $d = 0.2$), with anger having the largest effect compared to other emotions combined. However, Wingenbach et al. (2018) reported no significant interaction between observers' sex and the type of recognized emotion. From an evolutionary perspective, the foundations of female hypersensitivity to negative emotions may be rooted in the psychological differences between males and females related to maternal behavior. Such differences could also occur partly because of women's inherent role as a primary caretaker ("primary caretaker hypothesis," Babchuk et al., 1985), suggesting that women are capable of recognizing infant emotional cues more accurately. It concerns the ability to recognize potential threats to the infant's survival by detecting and analyzing negative emotions (see also "fitness threat hypothesis," Hampson et al., 2006). Numerous studies have shown the impact of the model's sex on the perception of emotions. Some of them demonstrated that women perceive emotions more accurately in male models, whereas the model's sex did not affect recognition of emotions in men (Rahman et al., 2004). Other studies reported that the sex of model influenced neither the female nor the male ability to recognize emotions (Thayer and Johnsen, 2000). Older adults were generally reported to have poorer recognition of facial expressions (see meta-analyses: $N = 10{,}526$; Hayes et al., 2020).

The current study investigated facial emotion recognition among non-WEIRD (western, educated, industrialized, rich, and democratic) populations of traditional Mongolian origin nomadic pastoralists, Tuvans, who are settled in one of the most inaccessible regions of Russia (and most recently joined) in Southern Siberia, and thereby have limited contact with the Western culture. Special interest in studying the Tuvan population concerns their social environment as until recently, they remained a highly monoethnic, patriarchal society, predominantly speaking the Tuvan language and following cultural traditions in daily life (e.g., sex-based division of labor; Lindquist, 2008). Relevant communication studies in Mongolian cultures suggest that Tuvans are more predisposed to expressing emotions through gestures than through facial expressions (Sereedar, 2011). In this study, we suggested that such a specific cultural environment could moderate their ability to recognize emotional states through facial expressions. Thus, this study investigated whether facial emotion recognition differed as a function of participant's sex, stimuli sex and ethnicity origin of facial stimuli (European vs. Mongolian). We predicted that women would be better at recognizing anger, fear, and disgust than men, whereas no sex differences would be observed in the recognition of happiness. While exploratory in nature, we also predicted that Tuvans would evaluate facial emotion expressions differently between Caucasian and Mongolian faces.

Materials and methods

Data collection and participants

The participants of our study were Tuvans, a nomadic pastoralist population of Mongolian origin from Southern Siberia (Hooper, 2020), who speak the Siberian Tuvan language, Tuvan. Today, most of the Tuvans live in the territory of the Tuva Republic (approximately 260,000 people), one of the most culturally isolated regions of Russia bordering Mongolia in the south. Traditionally, the Tuvan society was organized as patrilineal clans, which formed the primary identity of people and determined their legal rights (Lindquist, 2008). They consider themselves Buddhists (Lamaism); however, a fraction of the Tuvans define themselves as shamanists. It is noteworthy that the Tuva Republic joined Russia (USSR) only in 1944. This population speaks in the Tuvan language for everyday communication (most of them know only a few Russian words) and remains predominantly monoethnic to date. We conducted our research in a rural settlement, Erzin, located in a natural conservation area, Ubsunur Hollow. To date, Erzin residents have had limited contact with the European population and limited exposure to the Western culture. We collected data from 67 individuals aged 18–45 years (35 men and 32 women, mean age 29.5 years, SD = 9.29) in August 2021.

According to Tuvans, the age group considered for this study had similar cultural norms and social status.

Stimuli

This study used color photographs of four Caucasians (two men and two women) and four Tuvan models (two men and two women) exhibiting emotional facial expressions (happiness, anger, fear, and disgust) as stimuli. When selecting models, we considered the age range of the research cohort (18–45 years); consequently, we selected photos of middle-aged men and women of the similar age range. Images of Caucasians were obtained from the FACES database (Ebner et al., 2010). Due to their rarity, stimuli of Siberian Mongolian origin, Tuvans, were created by us particularly for this project. For this purpose, four Tuvan models (actors recruited on a voluntary basis from the capital of Tuva) were invited to display the target facial expressions in front of the camera. To ensure that the stimuli data were reliable, we conducted a pilot forced-choice research using an online form, in which 120 Moscow residents, aged 18–45 years, participated. According to the results, stimulus images were considered sufficiently reliable to be used in the study (for more details, see Supplementary Table 1). The final set of stimuli contained 32 cards (eight faces × four facial expressions). A neutral facial expression of the same model was displayed on each card along with one facial emotional expression each.

Design and procedure: free-labelling facial configuration

Each participant was presented with 32 stimulus cards: (European: 2 men + 2 women + Tuvan: 2 men + 2 women) × four emotional expressions: *anger*, *disgust*, *fear*, and *happiness*. Stimulus cards were displayed randomly on a laptop screen with no time limit for viewing. During the evaluation of each emotion, the experimenter asked the respondent to describe what was shown in the image. The respondent was asked: "What does the person in the image feel?" Next, the participants' answers were noted by the experimenter's assistant (Tuvan representative). Before this, each participant was asked whether they knew the model in person. The assistant provided the translation (Russian-Tuvan and vice versa) and necessary explanations when required. The last response was fixed as the final answer, which was accepted after clarifying all questions of the interviewee (for more details, see Supplementary Table 2).

Coding

The participants' responses were coded into a binary variable: 1 (able to guess) was assigned to the cases when the intended emotional facial expression from the stimulus card corresponded to an emotional label (or synonyms) stated by a participant (for synonyms, see Supplementary Table 2). In cases where there was a mismatch, 0 (not able to guess) was assigned. To test the intercoder reliability, we engaged two observers who recorded answers from 10 randomly selected participants' interviews (five Tuvan men and five Tuvan women) independently. The inter-observer agreement was found to be almost perfect (Cohen's kappa, $\kappa = 0.92$, $p < 0.0001$). Finally, a rough clarifying approach was applied to the resulting answers, and it was believed that an expert understood an emotional facial expression only if he/she correctly and accurately recognized the corresponding emotion on two similar stimuli (models of the same sex and origin). Same sex models and their origin were factors necessary to remove possible effects related to the individual facial features of the models. Same sex models and their origin were factors necessary to remove possible effects related to the individual facial features of the models that could influence emotion recognition.

Statistical analysis

We used a binomial test to assess the consistency of the Tuvans when they labelled four given emotional expressions (anger, happiness, disgust, and fear), with 0.16 set as an expected chance level consistency [based on the number of available and known basic emotional states (six)]. The binomial model included participants' answers received for each emotional category. The ability to correctly guess a facial expression was set as the binary response variable, which was calculated by averaging the results from similar stimuli (models of the same sex and origin). Only in the cases where the perceiver was able to correctly guess the facial expression from both similar stimuli, the response variable was set to 1 (able to guess); in other cases, it was set to 0 (not able to guess).

To assess the impact of the models' sex and origin, and that of the perceivers on the ability to correctly distinguish between emotional facial expressions, we used generalized estimating equations (GEE), a binary logistic model with repeated measures, conducted for each emotional expression separately. Here, we used the encoding technique described above. There were four measurements per subject (for each emotional expression). The statistical model assessed both the main effects and the interactions between the independent variables. We conducted a detailed analysis, where binary variables (sex and ability to guess emotions) were matched using the chi-squared criterion to focus on the obtained significant effects.

Results

According to the binomial test, the easiest emotion to identify for the participants was happiness [95% of participants ($p < 0.000$) correctly labelled the smiling configuration] followed by anger [66% of Tuvans ($p < 0.000$) correctly labelled the crowing facial configuration]. However, Tuvans tended to show a low accuracy rate for identifying fear (25% identified, $p < 0.000$) and disgust

(22% identified, $p < 0.006$). All results were statistically significant, with an expected chance level consistency of 0.16.

The frequency of correct guesses of emotional facial expressions is shown in Figure 1. It was slightly easier for the Tuvans to identify happiness, anger, and disgust through facial expressions of same-sex Tuvans, implying that Tuvan men were slightly better at recognizing these emotions on the faces of Tuvan men and women on the faces of Tuvan women (Figures 1A–C). Fear was better recognized on female faces by both male and female perceivers, independent of the model's origin (Figures 1D,D1). Although there were almost no sex differences in the perception of happiness through faces of European models (Figure 1A1), both male and female Tuvans better recognized anger on male, but not female, European faces (Figure 1B1).

To test the significance of these results, we applied binary logistic models with repeated measurements to assess the impacts of the models' and perceivers' sex, model origin, and perceiver's age.

According to the results of the statistical analysis, the ability to correctly guess disgust and happiness was affected neither by the model's sex and origin nor by the sex and age of the perceivers (for detailed statistics, see Supplementary Tables 3, 4). Similarly, the recognition of anger and fear was significantly affected by several independent factors. The sex and origin of the models as well as the sex of the perceiver had a significant impact on correctly identifying anger (Table 1), whereas recognition of fear was affected by the model's origin and the perceiver's age (Table 2).

We conducted additional analyses to address the independent factors that affected recognition of anger and fear while focusing on the obtained significant effects. The analyses revealed that all Tuvan women, compared to Tuvan men, were less frequently correct in guessing anger through facial expressions in male Tuvan models (chi-squared test for independence: $N = 67$, $\chi^2 = 6.2$, $df = 1$, $p = 0.02$). However, all other effects of sex on the perception of anger stimuli were insignificant, and there were no sex differences in recognition of anger in female models of Tuvan origin ($N = 67$, $\chi^2 = 0.6$, $df = 1$, $p = 0.568$), as well as in female ($N = 67$, $\chi^2 = 0.998$, $df = 1$, $p = 0.430$) and male ($N = 67$, $\chi^2 = 0.17$, $df = 1$, $p = 1.0$) models of European origin.

According to the binary logistic model, the recognition of fear was affected by the model's origin and age (Table 2). This effect was visualized in Figure 2. Relying on the visualization, the older the perceivers, the more accurate they were in recognizing fear in Tuvan models of both sexes.

Discussion

The study was conducted in an infrastructurally and geographically isolated settlement in Southern Siberia, among Tuvans. Until now, it has remained a strongly patriarchal culture. Here, we studied whether the accuracy of estimations of emotional statuses differed between sexes and other moderating factors.

Our data revealed that the easiest emotions to identify for the Tuvans (both men and women) were happiness and anger; however, they tended to show low accuracy rates for fear and disgust. Similar results have been reported in many other East Asian populations before (Matsumoto and Ekman, 1989). It can be argued that East Asians, compared to representatives of Western culture, process faces differently; they pay more attention to the eye region. Thus, the lack of focus on the mouth may contribute to the systematic misclassification of facial expressions: disgust as anger and fear as surprise (Tan et al., 2015).

Contrary to what was expected, we found no effect of the ethnic origin of stimuli (European vs. Mongolian) on emotional recognition. The Tuvans did not evaluate facial emotional expressions between European and Mongolian faces differently (there was no lack of recognition of emotions on European faces).

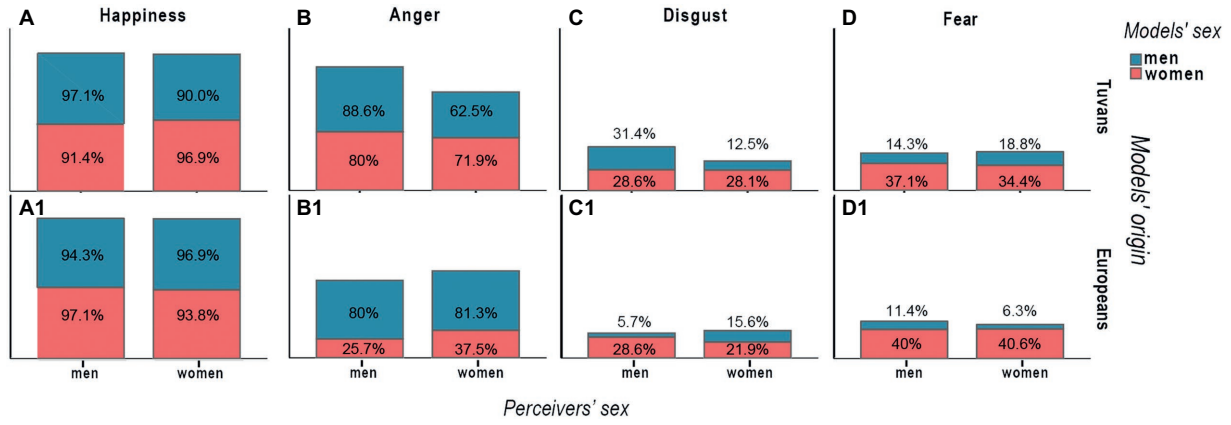

FIGURE 1
Relative frequencies of right guesses, where general number of perceivers of the same sex estimating models of the same sex and origin are taken as 100%.

TABLE 1 Effects of models' sex and origin, and sex and age of perceivers on ability to guess anger.

Dependent var.: Guess anger

Predictors	*B*	Wald chi-squared	*p* (sig.)
Models' sex	−0.501	0.378	0.539
Models' origin	−1.431	2.681	0.102
Perceivers' sex	1.181	0.822	0.364
Perceivers' age	0.014	0.170	0.680
Models' sex × Models' origin	**2.142**	**18.533**	**<0.001**
Models' sex × Perceivers' sex	0.749	1.708	0.191
Models' sex × Perceivers' age	0.007	0.065	0.799
Models' origin × Perceivers' sex	**−1.274**	**4.946**	**0.026**
Models' origin × Perceivers' age	0.004	0.016	0.898
Perceivers' sex × Perceivers' age	−0.020	0.253	0.615

GEE, binary logistic model with repeated measures. The amount of measurements taken per subjects is 4. The amount of subjects is 67. The significant predictors are shown in bold.

TABLE 2 Effects of models' sex and origin, and sex and age of perceivers on ability to guess fear.

Dependent var.: Guess fear

Predictors	*B*	Wald chi-squared	*p* (sig.)
Models' sex	0.207	0.022	0.883
Models' origin	**1.742**	**4.378**	**0.036**
Perceivers' sex	1.360	0.698	0.403
Perceivers' age	**0.096**	**6.943**	**0.008**
Models' sex × Models' origin	−0.934	2.351	0.125
Models' sex × Perceivers' sex	0.015	0.001	0.981
Models' sex × Perceivers' age	−0.042	1.257	0.262
Models' origin × Perceivers' sex	0.146	0.085	0.770
Models' origin × Perceivers' age	**−0.053**	**4.220**	**0.040**
Perceivers' sex × Perceivers' age	−0.047	0.900	0.343

GEE, binary logistic model with repeated measures. The amount of measurements taken per subjects is 4. The amount of subjects is 67. The significant predictors are shown in bold.

Similar conclusions were drawn in one of the previous studies, where no differences in the perception of facial features of Buryats (Mongolian people of Southern Siberia) were found between Caucasian and Mongolian raters (Russians and Buryats; Rostovtseva et al., 2022). We believe that these results can be explained by the impact of global international media (Internet, television, and cinema), which provides an opportunity for audiences from different parts of the world to become acquainted with different types of human appearances.

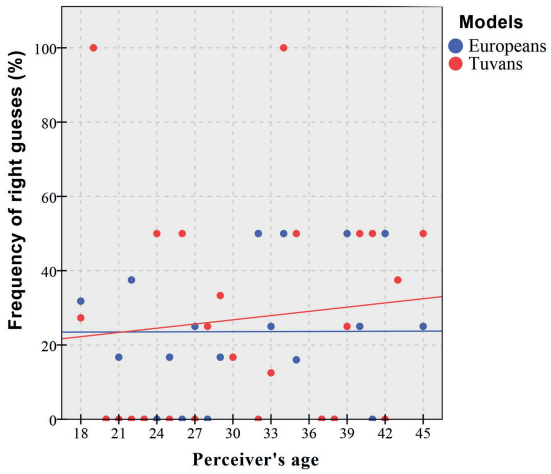

FIGURE 2
Impact of perceivers' age on fear recognition in models of European and Tuvan origin.

We found an age effect in fear recognition: older Tuvans were better at recognizing fearful faces of Tuvan, but not European models. Despite the fact that previous studies reported that older adults were typically worse at fear recognition due to general aging processes (reviewing Isaacowitz and Stanley, 2011), in our case, the upper margin of participants' age was only 45 years. Thus, we suppose that older individuals are more experienced in communicating with representatives of their own population and, thus, may be more sensitive to some aspects of emotional recognition.

Unlike most previous studies, which used a forced-choice format, we found no sex differences in the recognition of happiness, disgust, and fear. Moreover, independent factor analyses revealed that all Tuvan women were less successful in recognizing anger than Tuvan men, in the case of Tuvans' male models. However, to our knowledge, a pattern in which women were inferior to men in the perception of negative, threat-signaling emotional status has not been discovered. One possible explanation for this is women's poor communication abilities, a result of cultural conditioning. Even today, Mongolian cultural traditions encourage gender division of labor, where women's occupation and social environment are limited to the household (Anzhiganova and Ak-Lama, 2016; Natsak, 2022), and prescribe limited contact with strangers of opposite sexes. Nevertheless, the reasons for Tuvan women's particular insensitivity to men's angry facial expressions remain poorly understood and require further research.

Our study had certain limitations. The significance level of the sex-based difference in anger recognition did not survive the Bonferroni correction for multiple comparisons. One possible reason for this could be the small sample size, which, in turn, was due to the nature of the small-scale population that was studied. Another limitation was that we used posed emotional expressions as stimuli rather than genuine ones. However, this is a general limitation of such studies.

Data availability statement

The datasets presented in this study are available upon reasonable request from the corresponding author.

Ethics statement

The study was approved by the Ethical Committee of the Institute of Ethnology and Anthropology of the Russian Academy of Sciences. All subjects and models signed informed consents prior to the experiment.

Author contributions

AM, MB, and VR contributed to conception and design of the study and drafted the manuscript. AM, VR, AD, and KA collected the data. AM processed the raw data and organized the database. VR and AM performed the statistical analysis. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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The mediating role of sexually selected traits in the association of androgynous tendencies with lower sexual activeness among Chinese youths

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Androgynous tendencies and persistently low fertility rates have been observed in many countries, causing major social concerns. The theory of sexual selection suggests a possible mechanism between androgyny and decreased sexual activeness, as masculinity and femininity constitute an important aspect of reproductive strategies. This theory has also been proven by evolutionary and societal evidence. Therefore, we investigate the association between masculinity and femininity with sexual activeness, as well as the influence of gender-role conformity on the frequency of sexual intercourse through sexually selected traits among 42,492 Chinese youths. Sexual activeness was measured using sexual attitudes, experience, behaviors, and pleasure. Mediation analysis was employed to investigate the effects of sexually selected traits on the association between masculinity and femininity with sexual activeness, and gender-role conformity with the frequency of sexual intercourse. Low sexual activeness was found to be associated with low gender-role conformity. Our findings also suggest that physical attractiveness, sexual motivation, and interpersonal relationships may mediate the association between sexual activeness and gender-role conformity, supporting the males-compete/females-choose model.

KEYWORDS

sexual selection, gender-role conformity, androgynous tendencies, sexual activeness, low fertility rate

Introduction

Sexual selection was defined in the book by Charles Darwin, the Descent of Man (1871), as "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction"(Darwin, 2008). Based on the theory of sexual selection, ecological traits including masculinity and femininity (also referred to as gender roles), are considered to constitute a portion of human reproductive strategies (Cornwell et al., 2006; Kruger, 2006). The theory that high masculinity and femininity traits serve as indicators of

high sexual activeness is supported by a series of studies on evolution, anthropology, physiology, and sociology. Masculinity in males was observed to shape physical characteristics such as jaw size, muscularity, and midface robustness (Marcinkowska et al., 2019), to reflect certain traits such as mate quality, paternal investment, and competitiveness (Bribiescas et al., 2012), while facial femininity in females was also observed to be associated with fecundability (Little et al., 2014). Studies have demonstrated that prenatal exposure to high levels of testosterone plays a significant role in the construction of adult masculinity (Imperato-McGinley et al., 1979) and increases sexual activeness in males (Halpern et al., 1998). However, high levels of testosterone in females result in decreased sexual activeness (Law Smith et al., 2012; Das and Sawin, 2016; Niu and Zheng, 2020). Additionally, certain moral and quasi-moral traits relevant to femininity in females, including kindness and agreeableness (Eisenberg et al., 2001), have been sociologically and biologically demonstrated to increase sexual attractiveness (Zietsch et al., 2008).

Interestingly, an increasing trend of androgynous tendencies has been observed among Chinese youths over the past few decades. A survey of Chinese college students conducted in 1998 reported that while 32.3% of male students viewed themselves as masculine and 69.6% female students viewed themselves as feminine, 23.1% and 15.4% of male and female students, respectively, viewed themselves as androgynous (Shaomei, 1998). However, a more recent survey on 5,286 Chinese college students in 2011 reported that the proportion of male and female students who viewed themselves as masculine and feminine has decreased to 25.0% and 27.3%, respectively, while the proportion of male and female students who viewed themselves as androgynous has increased to 33.01% and 29.58%, respectively (Dianzhi, 2011). During the same period, the total fertility rate (TFR) in China declined below replacement levels from 2.7 in 1988 (Abbafati et al., 2020) to 1.7 in 2021 (Searchinger et al., 2013; Shen, 2021), leading to major economic and social concerns. As androgyny may impact sexual behaviors which correlates with fertility, it is therefore of great social significance to evaluate the potential roles of androgynous tendency on sexual activeness among youths of reproductive age.

At present, population-based studies on the relationship between gender-role conformity and sexual activeness or fertility decline are limited. Theories on the declination of fertility suggest that higher education, welfare institutions (Freedman, 1979), and greater stress of living (Liu and Raftery, 2020) contribute to fewer births. However, these studies often draw largely on various sociological theories, while disregarding the biological nature of human sexuality (Duckworth and Trautner, 2019). Furthermore, these studies typically focus on sexual minorities or individuals with sexually transmitted infections and tend to focus only on masculinity and not femininity (Little et al., 2011). Therefore, the present study aims to investigate the association between gender-role conformity and sexual activeness among male and female heterosexual Chinese youths. Mediation analysis was also employed to investigate the effect of sexually selected traits in the associations.

Materials and methods

Data source and participants

Our study utilized data from the 2019 National College Student Survey on Sexual and Reproductive Health, an internet-based self-administered survey conducted from November 2019 to February 2020. The study which aims to assess the sexual and reproductive health (SRH) of Chinese students, was commissioned by the China Family Planning Association (CFPA). The development of the questionnaire and study design has been previously described in detail (Zou et al., 2021). The questionnaire contained 92 questions categorized into four sections: SRH knowledge and attitudes, intimacy and sexual experience, individual health status, and socioeconomic and demographic characteristics.

A multistage sampling approach was utilized, and 1,764 higher education institutions, including key universities, ordinary universities, and vocational colleges, were selected after balancing the types of educational institutes. A total of 55,757 students responded. For the purposes of this study, only respondents who (1) provided informed consent, (2) answered all questions and passed the consistency checks and logic verification, (3) were aged between 15 and 25 years old, and (4) were undergraduate students who self-reported their gender orientation as heterosexual, were included. A total of 42,492 university or vocational college students were included in the final analyses. This study has been approved by the Institutional Review Board of Tsinghua University (IRB No. 20190083).

Exposure

The main exposure of interest was participants' self-rated conformity to their gender roles (masculinity for males and femininity for females), which was assessed using the question "I consider myself as conforming to traditional gender roles" adopted from the traditional masculinity-femininity (TMF) scale (Kachel et al., 2016). Response options ranged from 1 (strongly disagree) to 7 (strongly agree). Self-rated gender-role conformity scores were standardized by subtraction of the mean value and division by the standard deviation (SD). Gender-role conformity scores were categorized into low and high using the median value as a cutoff point (six for males and five for females).

Outcomes

The main outcome of interest was sexual activeness measured using sexual attitudes, experience, behaviors, and satisfaction. Attitudes toward sexual behaviors were assessed using the following questions: "If one has premarital sex, he or she will have a more satisfied marriage," and "You have ever felt guilty for being sexually active." Response options were "strongly disagree," "disagree," "not sure," "agree," and "strongly agree." The options "agree" and "strongly

agree" were categorized as positive attitudes, while the other options were categorized as neutral/negative attitudes.

Sexual experience was assessed by two aspects: having had intimate partners (i.e., girlfriends for males and boyfriends for females) and the age of first penetrative sexual intercourse. The age of first penetrative sexual intercourse was dichotomized into two categories: before and after 16 years of age. First penetrative sexual intercourse before 16 years of age was considered to be early first penetrative sexual intercourse.

Sexual behaviors were assessed by two aspects: having ever had penetrative sexual intercourse (anal or vaginal) and the frequency of sexual intercourse in the past year. The frequency of sexual intercourse was measured based on how frequently the participants had sexual intercourse. Response options were "never had sexual intercourse," "have not had sexual intercourse in recent years," "have sexual intercourse several times per year," "have sexual intercourse several times per month," "have sexual intercourse three to five times per week," "have sexual intercourse one to two times a week," and "have sexual intercourse nearly every day." Those who selected "have sexual intercourse three to five times per week," "have sexual intercourse one to two times per week," and "have sexual intercourse nearly every day" were categorized as having frequent sexual intercourse.

Sexual satisfaction was assessed using the following questions: "Have you ever had an orgasm?" and "Do you feel satisfied with the sex you are having currently?." Responses "have ever" to the first question were considered to indicate sexual satisfaction, while responses "have never" or "I do not know what an orgasm is" were considered to indicate no sexual satisfaction. Responses "very satisfied" or "satisfied" to the second question were considered to indicate sexual satisfaction, while responses "neutral," "not satisfied," or "strongly not satisfied" were considered to indicate no sexual satisfaction.

Other covariates

Data on sex, age, ethnicity, hometown region, school type, average monthly expenditure, having had received sexual education at school, self-rated parent–child relationship, parental highest educational attainments, having had parent–child discussions relevant to sexual behaviors, and tobacco/alcohol consumption were also collected. Age and self-rated parent–child relationship scores were analyzed as continuous variables, while the remaining variables were analyzed as categorical variables. Self-rated parent–child relationship scores ranged from 0 (terrible) to 10 (good).

Statistical analysis

Continuous variables were reported as mean ± SD, while categorical variables were described as proportions (percentages). Categorical variables were compared using Pearson's χ^2 test, and continuous variables were compared using *t*-test. Multivariable logistic regression was used to assess the association between gender-role conformity scores and sexual attitudes, experience, behaviors, and satisfaction. The results were reported as odds ratio (OR) and 95% confidence intervals (95% CIs). The models were adjusted for age, ethnicity, school type, average monthly expenditure, self-rated parent–child relationship, having had received sexual education at school, parents' highest educational attainments, and tobacco and alcohol assumption. Analyses for "early age of first penetrative sexual intercourse," "having had an orgasm," and "current sexual satisfaction" were limited to respondents who reported having had sexual intercourse.

Mediation analysis

Mediator variables were classified into individual-and interpersonal-level factors. Individual-level factors included self-perceived physical attractiveness and sexual motivation, while interpersonal-level factors included self-rated interpersonal relationships. Self-perceived physical attractiveness was assessed using a 10 point scale ranging from 0 (terrible) to 10 (excellent), with higher scores implying higher satisfaction with appearance. Sexual motivation was assessed using the following question: "Do you want to have a girlfriend/boyfriend?" Response options included "I really want a girlfriend/boyfriend," "I want a girlfriend/boyfriend," "I am unsure," "I do not want a girlfriend/boyfriend," and "I really do not want a girlfriend/boyfriend." Responses "I really want a girlfriend/boyfriend" or "I want a girlfriend/boyfriend" were considered to indicate high sexual motivation. Self-rated interpersonal relationships were assessed using the following question: "Do you have many friends?" Response options ranged from 1 (nearly have no friend) to 10 (have many friends).

First, logistic regression was used to investigate the association between individual- and interpersonal-level mediators with frequent sexual intercourse (Supplementary Table S1). Second, mediation modeling frameworks were constructed (Figure 1), with A representing exposure, M representing mediators, Y representing outcome, and C representing a set of confounders. The total effect (TE) of gender roles on frequent sexual intercourse could be present through two separate pathways: (1) directly between gender roles and frequent sexual intercourse, measured using the average direct effect (ADE), or (2) through biological and societal mediators, measured using the average causal mediation effect (ACME).

In the framework, T_i denoted continuous exposure representing the different SDs of the gender-role conformity score. $Y_i(t)$ was used to characterize the binary outcome variable under exposure status t, which was equal to 1 if respondent i reported frequent sexual intercourse (i.e., $Y_i(1)$ estimated respondent i s sexual intercourse status, whose gender-role conformity score was 1 SD). In addition, $M_i(t)$ was used to measure mediators under exposure status t, and X_i denoted the abovementioned set of confounders. If the mediator was a continuous variable

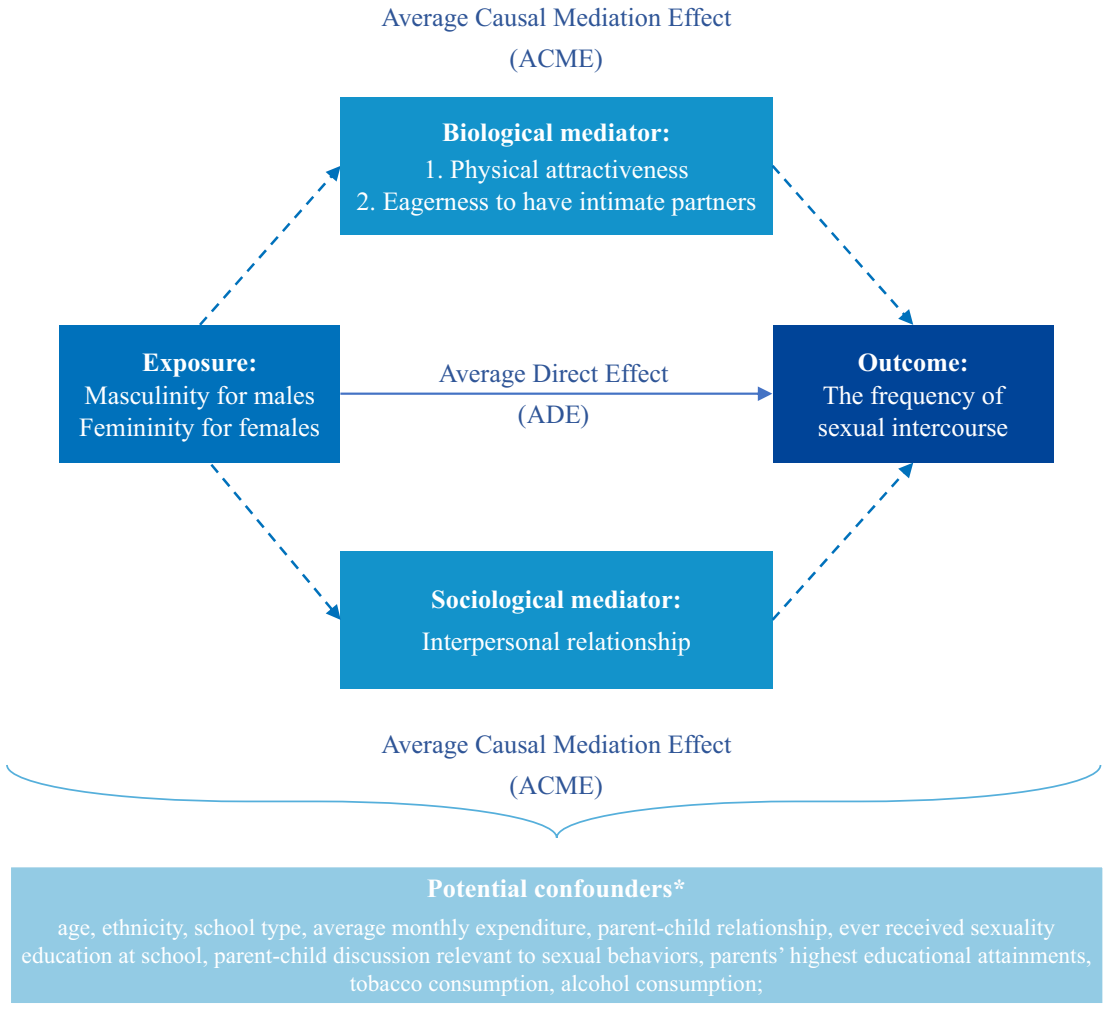

FIGURE 1
Conceptual diagram.

(self-perceived physical attractiveness and self-rated interpersonal relationship), we used formula (1) to measure the association between mediators and exposure and formula (2) to characterize the relationship between outcome and exposure, considering the mediator effect:

$$M_i = \alpha_2 + \beta_2 T_i + \xi_2^{\intercal} X_i + \epsilon_{2i} \tag{1}$$

$$Y_i = 1\left\{Y_i^* > 0\right\} \text{ where } Y_i^* = \alpha_3 + \beta_3 T_i + \gamma M_i + \xi_3^{\intercal} X_i + \epsilon_{3i} \tag{2}$$

Considering that there might have been an exposure-mediator interaction, formula (2) was rewritten as formula (3):

$$\begin{aligned} Y_i &= 1\left\{Y_i^* > 0\right\} \\ \text{where } Y_i^* &= \alpha_3 + \beta_3 T_i + \gamma M_i + \kappa T_i M_i + \xi_3^{\intercal} X_i + \epsilon_{3i} \end{aligned} \tag{3}$$

ACME (δ_i) was defined as the difference between the potential outcome when the exposure value was fixed and the mediator level intervening from $M_i(t_0)$ to $M_i(t_1)$. ADE (ζ_i) estimated the difference between potential outcome when the value of mediator was fixed and the exposure level intervening from t_0 to t_1. TE (τ_i) was the sum of the ACME and ADE:

$$\delta_i(t) \equiv Y_i\left(t, M_i(t_1)\right) - Y_i\left(t, M_i(t_0)\right) \tag{4}$$

$$\zeta_i(t) \equiv Y_i\left(t_1, M_i(t)\right) - Y_i\left(t_0, M_i(t)\right) \tag{5}$$

$$\begin{aligned} \tau_i &\equiv Y_i\left(t_1, M_i(t_1)\right) - Y_i\left(t_0, M_i(t_0)\right) \\ &= \frac{1}{2}\sum_{t=t_0}^{t=t_1}\left\{\delta_i(t) + \zeta_i(t)\right\} \end{aligned} \tag{6}$$

The PM was defined as follows:

$$PM = \delta_i(t) / \zeta_i(t) \quad (7)$$

Point estimates for the ACME, ADE, TE, and proportion of mediation (PM), as well as their respective 95% CIs, were estimated with 1,000 bootstrap resamples. The estimated coefficients are linked to the probability scale, rather than to that obtained from the logistic regression model, with its exponentiation obtaining the OR. The formulas were adjusted for binary variables. All formulas were deduced mathematically by Dustin Tingley (Imai et al., 2010).

Main analyses were performed using Stata SE™ version 15.1 (College Station, Texas, United States). Causal analyses were performed using R version 4.1.1.

Results

Differences in sample characteristics between high gender-role conformity and androgyny groups

The sociodemographic characteristics of male and female students are presented in Table 1. A total of 14,316 males and 28,176 females were included in the study. Among males with high gender-role conformity, 78.88% resided in urban areas (androgyny: 74.88%), 28.90% have an average monthly expenditure above 2,000 yuan (androgyny: 23.71%), 26.92% have had parent–child discussions on sexual behaviors (low: 22.93%), and 54.87% have received sexual education at school (androgyny: 50.38%). Males with high gender-role conformity also reported better father–child relationship (high: 8.01 ± 2.11 vs. androgyny: 7.32 ± 2.17, $p < 0.0001$) and mother–child relationship (high: 8.49 ± 1.76 vs. androgyny: 7.83 ± 2.00, $p < 0.0001$) compared to males with low gender-role conformity.

Among females with high gender-role conformity, 77.92% resided in urban areas (androgyny: 73.95%), 25.89% have an average monthly expenditure above 2,000 yuan (androgyny: 23.99%), 30.77% have had parent–child discussions on sexual behaviors (androgyny: 26.99%), and 60.92% have received sexual education at school (androgyny: 58.12%). Females with high gender-role conformity also reported better father–child relationship (high: 7.39 ± 2.23 vs. androgyny: 6.86 ± 2.39, $p < 0.0001$) and mother–child relationship (high: 7.99 ± 1.92 vs. androgyny: 7.47 ± 2.17, $p < 0.0001$) compared to females with low gender-role conformity.

Males with high gender-role conformity report significantly higher tobacco use (high: 27.23% vs. androgyny: 23.11%, $p < 0.0001$) and alcohol consumption (high: 57.49% vs. androgyny: 51.29%, $p < 0.0001$), while females with high gender-role conformity report significantly lower tobacco use (high: 5.43% vs. androgyny: 6.96%) and alcohol consumption (high: 27.71% vs. androgyny: 29.83%, $p < 0.0001$), compared to males and females with low gender-role conformity.

Distribution of gender-role conformity among males and females

The distribution of gender-role conformity among males and females is presented in Figure 2. Males on average have a gender-role conformity score of 5.55 ± 1.28 on a scale of 7. There was a skewed distribution of gender-role conformity scores among males, with the majority reporting high masculinity conformity (56.25% reported scores of 6 points and above). On average, the gender-role conformity score was 6.49 ± 0.50 in the high masculinity group and 4.35 ± 0.94 in the androgynous group.

Females on average have a gender-role conformity score of 4.87 ± 1.36 on a scale of 7. In contrast to males, there was a normal distribution of gender-role conformity scores among females, with the majority reporting moderate femininity conformity score (53.91% reporting a score between 4 and 5), showing greater androgynous characteristics. On average, the gender-role conformity score was 5.73 ± 0.78 in the high femininity group and 3.28 ± 0.82 in the androgynous group.

Association between androgynous tendency and sexual activeness

The association between gender-role conformity score and sexual activeness is presented in Table 2. Participants with high gender-role conformity were found to have more liberal attitudes toward sexual intercourse, were more likely to have intimate partners, were more likely to be sexually satisfied, and were more likely to exhibit more frequent sexual behaviors, compared to androgynous participants. Both males and females with high gender-role conformity were significantly more likely to agree with premarital sexual intercourse (male: OR 1.05, 95% CI 1.01–1.09, female: OR 1.06, 95% CI 1.03–1.09), have an intimate heterosexual partner (male: OR 1.18, 95% CI 1.13–1.22, female: OR 1.21, 95% CI 1.18–1.24), have had penetrative sexual intercourse (male: OR 1.12, 95% CI 1.07–1.17, female: OR 1.23, 95% CI 1.18–1.27), have more frequent sexual intercourse (male: OR 1.10, 95% CI 1.05–1.15, female: OR 1.20, 95% CI 1.15–1.24), and be sexually satisfied (male: OR 1.38, 95% CI 1.23–1.54, female: OR 1.15, 95% CI 1.08–1.23). Both males and females with high gender-role conformity scores were also significantly less likely to feel guilty for being sexually active (male: OR 0.85, 95% CI 0.82–0.89, female: OR 0.95, 95% CI 0.92–0.98), while males with high masculinity conformity scores were significantly more likely to have had an orgasm (OR 1.19, 95% CI 1.08–1.30). However, this was not significant in females with high femininity conformity scores (OR 1.05, 95% CI 0.99–1.11).

Roles of individual- and interpersonal-level mediators

The TE, ADE, ACME, and PM of the association between gender-role conformity and frequent sexual intercourse are

TABLE 1 Sociodemographic characteristics of male and female students stratified by level of gender-role conformity.

Characteristics	Male			Female		
	N = 14,316			*N* = 28,176		
	Low gender-role conformity (androgyny)	High gender-role conformity	Value of *p*	Low gender-role conformity (androgyny)	High gender-role conformity	Value of *p*
	N = 6,262	*N* = 8,054		*N* = 10,782	*N* = 17,394	
	n (%)	*n* (%)		*n* (%)	*n* (%)	
Age (in years)*, mean ± standard deviation (SD)	19.70 ± 1.50	19.81 ± 1.50	<0.0001	19.69 ± 1.53	19.82 ± 1.52	<0.0001
Ethnicity			0.728			0.619
Han	5,735 (91.58)	7,363 (91.42)		9,708 (90.04)	15,693 (90.22)	
Minority	527 (8.42)	691 (8.58)		1,074 (9.96)	1,701 (9.78)	
Hometown region			<0.0001			<0.0001
Rural	1,573 (25.12)	1,701 (21.12)		2,809 (26.05)	3,841 (22.08)	
Urban/suburban	4,689 (74.88)	6,353 (78.88)		7,973 (73.95)	13,553 (77.92)	
School type			<0.0001			<0.0001
College	2,504 (39.99)	2,871 (35.65)		3,463 (32.12)	4,892 (28.12)	
University	3,758 (60.01)	5,183 (64.35)		7,319 (67.88)	12,502 (71.88)	
Average monthly expenditure (RMB)			<0.0001			<0.0001
0–999	1,020 (16.29)	1,012 (12.57)		1,860 (17.25)	2,681 (15.41)	
1,000–1,999	3,757 (60.00)	4,714 (58.53)		6,335 (58.76)	10,209 (58.69)	
≥2,000	1,485 (23.71)	2,328 (28.90)		2,587 (23.99)	4,504 (25.89)	
Ever received sexual education at school	3,155 (50.38)	4,419 (54.87)	<0.0001	6,266 (58.12)	10.597 (60.92)	<0.0001
Self-rated parent–child relationship score (0–10)*, mean ± SD						
Paternal	7.32 ± 2.17	8.01 ± 2.11	<0.0001	6.86 ± 2.39	7.39 ± 2.23	<0.0001
Maternal	7.83 ± 2.00	8.49 ± 1.76	<0.0001	7.47 ± 2.17	7.99 ± 1.92	<0.0001
Parental highest educational attainment			<0.0001			<0.0001
Primary school and below	834 (13.32)	886 (11.00)		1,486 (13.78)	2,128 (12.23)	
Middle school	2,461 (39.30)	2,904 (36.06)		4,342 (40.27)	6,697 (38.50)	
High school	1,593 (25.44)	2,219 (27.55)		2,715 (25.18)	4,619 (26.56)	
College and above	1,374 (21.94)	2,045 (25.39)		2,239 (20.77)	3,950 (22.71)	
Parent–child discussion relevant to sexual behaviors		<0.0001			<0.0001	
Never	4,826 (77.07)	5,886 (73.08)		7,872 (73.01)	12,042 (69.23)	
Ever	1,436 (22.93)	2,168 (26.92)		2,910 (26.99)	5,352 (30.77)	
Tobacco use			<0.0001			<0.0001
Ever	1,447 (23.11)	2,193 (27.23)		750 (6.96)	945 (5.43)	
Never	4,815 (76.89)	5,816 (72.77)		10,032 (93.04)	16,449 (94.57)	
Alcohol consumption			<0.0001			<0.0001
Ever	3,212 (51.29)	4,630 (57.49)		3,216 (29.83)	4,820 (27.71)	
Never	3,050 (48.71)	3,424 (42.51)		7,566 (70.17)	12,574 (72.29)	
Self-rated masculinity/femininity score (1–7)*, mean ± SD	4.35 ± 0.94	6.49 ± 0.50	<0.0001	3.28 ± 0.82	5.73 ± 0.78	<0.0001

*Uses *t*-test; others use $\chi 2$ analyses. SD, standard deviation.

presented in Table 3. The ACME and ADE of individual- and interpersonal-level factors were significant, indicating mediating effects of physical attractiveness, sexual motivation, and interpersonal relationships on the association between gender-role conformity and sexual activeness, regardless of sex. Exposure-mediator interactions were observed between physical attractiveness, sexual motivation, and interpersonal relationships with gender-role conformity scores in females, as well as between physical attractiveness with gender-role conformity scores in males (Supplementary Table S2).

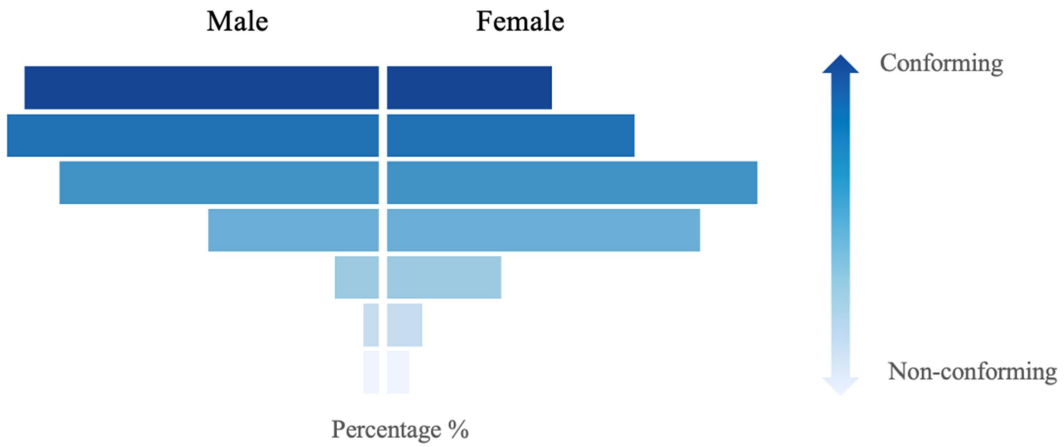

FIGURE 2
The distribution of gender-role conformity among male and female youths.

TABLE 2 The association between androgynous tendency and sexual activeness among males and females.

Variables	Sex[a]	
	Male	Female
Openness toward sexual behaviors		
Agree with premarital sex	1.05 (1.01–1.09)*	1.06 (1.03–1.09)***
Ever feel guilty for being sexually active	0.85 (0.82–0.89)*	0.95 (0.92–0.98)**
Sexual experience		
Have had a girlfriend/boyfriend	1.18 (1.13–1.22)***	1.21 (1.18–1.24)***
Early age of first penetrative sexual intercourse (before 16 years of age)[b]	1.09 (0.97–1.20)	1.05 (0.95–1.15)
Sexual behaviors		
Have had penetrative sexual intercourse (anal/vaginal)	1.12 (1.07–1.17)***	1.23 (1.18–1.27)***
Frequent sexual intercourse (more than once per week)	1.10 (1.05–1.15)***	1.20 (1.15–1.24)***
Sexual pleasure		
Have experienced an orgasm[b]	1.19 (1.08–1.30)***	1.05 (0.99–1.11)
Current sexual satisfaction[b]	1.38 (1.23–1.54)***	1.15 (1.08–1.23)***

The standardized gender-role conformity score is considered a continuous variable in all analyses, and the estimated odds ratio (OR) represents the change in odds followed by a 1-unit decrease in SD.
[a]Adjusted for age, region, ethnicity, school type, average monthly expenditure, self-rated parent–child relationship, if he or she has ever received sexual education at school, if he or she has ever had parent–child discussions relevant to sexual behaviors, parents' highest educational attainments, tobacco consumption, and alcohol consumption.
[b]Analyze for individuals who have had sexual intercourse. n = 3,703 for males, and n = 5,046 for females.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Among males, the PM by sexual motivation was 13.83% (95% CI: 0.45%–33.77%), by physical attractiveness, 42.48% (95% CI: 27.04%–58.89%), and by interpersonal relationship, 41.66% (95% CI: 23.71%–89.54%). Among females, the PM by sexual motivation was 47.99% (95% CI: 36.73%–65.04%), by physical attractiveness, 28.55% (95% CI: 21.67%–35.07%), and by interpersonal relationships, 17.23% (95% CI: 10.74%–23.20%).

Discussion

Our findings suggest that heterosexual youths with low gender-role conformity, or androgyny, were less sexually active, and among those who had penetrative sexual intercourse, androgynous tendency was significantly associated with decreased sexual satisfaction. Our findings also suggest that physical attractiveness, sexual motivation, and interpersonal relationships may play a mediating role, indicating that sexually selected traits may be an important underlying mechanism in this pathway.

Our finding of a positive association between gender-role conformity and high sexual activeness is consistent with existing evidence. Previous studies showed that males with more masculine traits, such as certain facial characteristics, were more sexually active (Lidborg et al., 2022), while females with more feminine traits have more sexual partners. According to the theory of sexual selection, masculinity and femininity are regarded as part of

TABLE 3 The mediation effect of sexually selected traits between gender-role conformity score and sexual activeness.

	TE	ACME (average)	ADE (average)	PM (average)
Individual-level factors				
Self-perceived physical attractiveness (0–10)				
Male	0.0197 (0.0111, 0.0268)**	0.0084 (0.0039, 0.0128)**	0.0113 (0.0055, 0.0159)***	42.48% (27.04, 58.89%)**
Female	0.0200 (0.0171, 0.0223)***	0.0057 (0.0039, 0.0074)***	0.0143 (0.0122, 0.0162)***	28.55% (21.67, 35.07%)***
Sexual motivation				
Male	0.0112 (0.0060, 0.0156)**	0.0016 (0.0001, 0.0031)*	0.0096 (0.0046, 0.0141)**	13.83% (0.45, 33.77%)*
Female	0.0126 (0.0096, 0.0155)***	0.0061 (0.0044, 0.0044)***	0.0065 (0.0034, 0.0090)***	47.99% (36.73, 65.04%)***
Interpersonal-level factors				
Self-rated interpersonal relationship (0–10)				
Male	0.0114 (0.0063, 0.0160)***	0.0048 (0.0031, 0.0067)***	0.0066 (0.0007, 0.0116)*	41.66% (23.71, 89.54%)***
Female	0.0196 (0.0174, 0.0216)***	0.0034 (0.0020, 0.0048)***	0.0162 (0.0143, 0.0178)***	17.23% (10.74, 23.20%)***

The standardized gender-role conformity score is considered a continuous variable in all analyses. All models are adjusted for age, region, ethnicity, school type, average monthly expenditure, self-rated parent–child relationship, if he or she has ever received sexual education at school, if he or she has had parent–child discussions relevant to sexual behaviors, parents' highest educational attainments, tobacco consumption, and alcohol consumption. *ACME = average causal mediation effect,* ADE, average direct effect; PM, proportion of mediation.

[a]Analyze for individuals who have never had sexual intercourse. $n = 10{,}613$ for males, and $n = 23{,}130$ for females.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

human reproductive strategies. Hence, individuals with high masculinity and femininity are considered more "prepared" for reproduction. These factors may contribute to more liberal sexual attitudes and more aggressive sexual behaviors, resulting in higher frequencies of sexual intercourse (Rahman et al., 2005; Manning and Fink, 2008). These sexually selected traits are also often linked to higher levels of sex hormones such as testosterone and estradiol, which have been associated with increased sexual desire (van Anders, 2012; Cappelletti and Wallen, 2016) and higher sexual attractiveness (Giagulli et al., 2011; Haupt et al., 2020). Additionally, more masculine males and more feminine females reported higher levels of sexual satisfaction, consistent with previous studies (Pedersen and Blekesaune, 2003; Daniel and Bridges, 2013). Higher masculinity and femininity in males and females, respectively, may correlate with higher self-esteem and more positive body image, resulting in greater confidence and consequently, higher sexual satisfaction (Sánchez-Fuentes et al., 2014).

Findings from our study suggest that physical attractiveness and interpersonal relationships mediate the association between gender role conformity and sexual activity in males. As masculinity often correlates with physical attractiveness, men with more masculine appearances may tend to have better reproductive success. These results support the males-compete/females-choose (MCFC) model proposed by Darwin, suggesting that different sexes play different roles in reproduction, and that men typically compete for sexual attraction from females (Darwin, 2008; Dixson, 2020). Many other studies have also demonstrated that males have a stronger sense of intrasexual selection compared to females (Puts, 2010; Lassek and Gaulin, 2022). Physical attractiveness and interpersonal relationships constitute a part of the reproductive strategies of males; the former is utilized for short-term attractiveness (Buss et al., 2017; Buss and Schmitt, 2019), while the latter is utilized for long-term sexual relationships (Dixson et al., 2016). Studies have reported a female preference for more masculine craniofacial traits for short-term relationships than for long-term relationships (Little et al., 2011; Dixson et al., 2016). However, in long-term relationships, females prefer males with good moral or quasi-moral characteristics, such as intelligence, honesty, and warmth required for better interpersonal relationships (Regan et al., 2000). In addition, higher physical attractiveness and the ability to navigate interpersonal relationships are useful during courtship, crucial for reproductive success (Wong and Candolin, 2005; Eikenaar et al., 2012).

Another important finding was that sexual motivation had a greater mediating effect on females than on males. This is consistent with earlier observations. And the males-compete/females-choose model that females invest more in their offspring than their male counterparts became, in essence, a scarce resource, driving male–male competition to attract and retain mates. As mentioned above, females usually play the role of choosers in the mating process and have stronger internal motivation for intersexual selection (Eibl-Eibesfeldt, 1979; Stewart-Williams and Thomas, 2013).

Overall, this study has several strengths. First, it investigated the association between gender-role conformity and sexual activeness from a broader perspective by measuring not only sexual attitudes and experiences but also sexual behaviors and pleasure, allowing for a more precise evaluation of sexual activeness. Both masculinity and femininity were also accounted for. Second, mediation analysis was employed to investigate the associations of various factors with gender-role conformity through both biological and sociological pathways. This approach enabled us to better understand the gender-role patterns as they relate to sexual activeness between different sexes, increasing our understanding of sexual selection theory. Third, our study was based on a large-scale population-based survey in China. The large sample size

ensured the statistical power of the modeling process, providing robust results with higher precision. More importantly, this study addresses the current knowledge gap concerning gender-role distribution among Chinese youths.

This study also has several limitations. First, as the measurement of gender-role conformity was self-reported, measurement bias may be present. However, as there has yet to be a robust gender-role measurement scale with high reliability and validity, this approach has the highest feasibility. Second, as the frequency of sexual intercourse was also self-reported, recall bias may be present. However, attempts were made to mitigate the severity of biasness by cross-checking survey questions and performing logic verification. Third, as this is a cross-sectional study, causal inference cannot be drawn. Fourth, the question "Do you want to have a girlfriend/boyfriend?" may not the best measure of sexual motivation. Intimate partnership establishment refers to both sexual and emotional intimacy, and someone who is highly motivated to have sex may prefer short-term relationship (i.e., casual sex, one-night stands) to avoid emotional intimacy. Finally, although we adjusted for possible confounders, we were unable to adjust for confounding from cultural and psychosocial factors, which may result in residual confounding. Future studies should consider these additional factors related to masculinity, femininity, and sexual activeness.

In conclusion, among heterosexual Chinese youths of reproductive age, high gender-role conformity (i.e., high masculinity in males and high femininity in females) was associated with a significantly higher level of sexual activeness, implying that androgynous tendencies may contribute to a decrease in population fertility. We also found that such an association between gender-role conformity and sexual activeness was mediated through physical attractiveness, sexual motivation, and interpersonal relationships.

Data availability statement

The datasets presented in this article are not readily available because the data have not been made available on a permanent third-party archive because the Institution Review Board of Tsinghua University ruled that we could not post the data. Requests to access the datasets should be directed to the corresponding author (tangk@mail.tsinghua.edu.cn).

Ethics statement

The study was reviewed and approved by the Institution Review Board of Tsinghua University (IRB no. 20190083). Written informed consent to participate in this study was provided by the participants.

Author contributions

SZ and KT conceived of the presented idea. SZ and FG planned and carried out the simulations. SZ took the lead in writing the manuscript with the support from FG, JH, and KT. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.1011467/full#supplementary-material

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Effects of sex and sex-related facial traits on trust and trustworthiness: An experimental study

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The ability to trust others, including strangers, is a prerequisite for human cooperation. Economically it is not rational to trust strangers, as trust can be easily exploited. Still, generally, the level of trust toward strangers is relatively high. Trust is closely related to trustworthiness: when trusting others, one expects them to reciprocate. Some individuals elicit more trust than others. Apparently, humans use subtle cues for judging the trustworthiness of their interaction partners. Here, we report on an experiment that investigates trust and trustworthiness in a population of 176 mainly Dutch students. The aims of our study were: (1) to investigate how the sex of interaction partners and their facial appearance (femininity/masculinity) affect the degree of trust and trustworthiness, compared to fully anonymous conditions; (2) to test whether individuals who elicit trust in their interaction partners are trustworthy themselves. Each subject of our experiment played five one-shot Trust Games: one with an anonymous interaction partner, and four "personalized" games after seeing a 20s silent video of their interaction partner (twice same-sex, and twice opposite-sex). The degree of facial sexual dimorphism was investigated with geometric morphometrics based on full-face photographs. Our results revealed that, despite the already high level of trust in the anonymous setting, the personalization of interactions had a clear effect on behavior. Females elicited more trust in partners of both sexes. Interestingly, females with more feminine faces elicited less trust in both male and female partners, while males with more masculine facial shape were more trusted by females, but less trusted by males. Neither sex nor facial femininity/masculinity predicted trustworthiness. Our results demonstrate that (1) sex and sex-related facial traits of interaction partners have a clear effect on eliciting trust in strangers. However, (2) these cues are not reliable predictors of actual trustworthiness.

KEYWORDS

trust, trustworthiness, trust game, sex differences, facial femininity, facial masculinity, sexual dimorphism, geometric morphometrics

Introduction

A large part of Darwin's (1871) *The Descent of Man* is devoted to the question whether and how humans differ from "lower animals" regarding their "social instincts" and their "moral sense," and how and when these differences might have arisen in human evolution. The extensive cooperation between unrelated individuals, and even complete strangers who are not likely to meet again, is a striking feature of human societies, which distinguishes humans from all other organisms (Melis and Semmann, 2010). The ability to trust other individuals, including strangers, is perhaps the most important prerequisite for such large-scale cooperation. Trying to understand the nature of human trust and trustworthiness is therefore a research goal in the Darwinian tradition.

Trust as a phenomenon is being studied in various disciplines, including the social sciences, psychology, and economics (Bateson, 1988; Hardin, 2002; Uslaner, 2018; Kumar et al., 2020; Liu and Chen, 2022). The definitions of trust vary from field to field. Generally defined as "the intention to accept vulnerability based on positive expectations of the intentions or behavior of another" (Rousseau et al., 1998, p. 395), trust may also refer to such aspects as risk-taking (Luhmann, 1988), compatible interests of trustor and trustee (Hardin, 2002), and is even defined by some authors as "a bias in the processing of imperfect information about the partner's intentions" (Yamagishi and Yamagishi, 1994, p. 136). Trust may also be manifested in sharing private information with a person, without any direct return expectations.

Here, we adopt a commonly used definition in the behavioral sciences and refer to trust as the willingness to put oneself in a vulnerable position with expectation of mutual benefits. Trust is closely related to trustworthiness: when trusting others, one expects them to reciprocate (be trustworthy; Hardin, 2002). However, trust does not imply any mechanisms of control of reciprocation, and thus can be easily exploited. This is the main reason why trusting strangers in short-term interactions is considered irrational from an economic perspective (Mas-Colell et al., 1995; Kacelnik, 2006).

Although trust is frequently manifested in human everyday life (Weiss et al., 2020), the evolutionary emergence and stability of trust is not well understood: as trust can be exploited, it should easily break down. Results of experimental studies based on the Trust Game (Kreps, 1990; Berg et al., 1995) show that humans are generally predisposed to trust other individuals (Berg et al., 1995; Ostrom and Walker, 2003; Johnson and Mislin, 2011; Wilson and Eckel, 2011; Wilson, 2018; Gómez-Miñambres et al., 2021), and that repeated interactions with the same partner are able to sustain and even reinforce trust (Anderhub et al., 2002; Bornhorst et al., 2004; Cochard et al., 2004). Interestingly, in one-shot interactions, under "all-or-nothing" condition, the fact of being trusted does not systematically induce reciprocation (Kiyonari et al., 2006), whereas in continuous versions of the game, with the option to vary the trust investment, insufficient demonstration of trust reduces reciprocal trustworthiness (Gómez-Miñambres et al., 2021).

Despite the abundance of empirical evidence that humans are generally prone to trust others, recent studies also suggest that there are considerable differences in the level of between-individual trust and trustworthiness across cultures (Thanetsunthorn and Wuthisatian, 2019; Kwantes and Kuo, 2021). And even within the same culture human trust is not indiscriminate. Studies demonstrate that social proximity has a strong effect on trust and trustworthiness (relatives, friends, and in-group members are generally trusted more than unfamiliar individuals; Dinesen et al., 2020; Porto and Pilati, 2021). The establishment of a reputation of trustworthiness in longer-term interactions or in a community is an efficient way to grow trust, but this requires the availability of reliable information about the long-term behavioral tendencies of others. Entering new social environments and interacting with strangers (which is especially common under modern urban conditions of big cities), most people do not trust indiscriminately: under such conditions, they use all kinds of information that may indicate the trustworthiness of their interaction partners. Several studies have shown that some individuals elicit more trust than others, even if the trusting person has never interacted with these individuals before (Wilson and Eckel, 2006; Rezlescu et al., 2012; Brustkern et al., 2021; Rostovtseva et al., 2022a). Apparently, humans use subtle cues to judge whether an interaction partner is trustworthy or not. A number of studies revealed that the shape of a neutral face contributes to perceived trustworthiness (Todorov et al., 2008; Stirrat and Perrett, 2010; Rezlescu et al., 2012; Kleisner et al., 2013; see also the meta-analysis of Siddique et al., 2022 and references therein). Most studies converge to the point that trustworthy-looking faces have elevated brow ridges, prominent cheekbones, lower upper facial width-to-height ratio, and wider chin. Besides this, perceived trustworthiness was reported to be positively related to facial self-resemblance (DeBruine, 2002; Farmer et al., 2014) and facial typicality (Sofer et al., 2015). Results on the association between facial attractiveness and perceived trustworthiness are contradictive (Wilson and Eckel, 2006; Sofer et al., 2015).

Here, we report on an experiment that sheds some light on the determinants of trust between strangers. The subjects in our experiment played a one-shot Trust Game (Kreps, 1990; Berg et al., 1995; Jaeger et al., 2022), which tests both their degree of trust and trustworthiness, with several other subjects. We compare the behavior of individuals in "anonymous" and "personalized" interactions. Under "anonymous" condition, they did not receive any information on their interaction partner; while under "personalized" condition they were shown a brief silent video of their partner, whom they never met before. To allude to the second half of Darwin's (1871) book (*Selection in Relation to Sex*), we were particularly interested in sex differences regarding trust and trustworthiness. According to numerous studies, there is a persistent stereotype of women being perceived as more trustworthy than men in various aspects, such as honesty, telling

the truth, and reciprocation (see the review by Schniter and Shields, 2020). Quite a number of studies examine sex differences in trust and trustworthiness under anonymous conditions of the "investment" variant of the Trust Game. Most of them indicate that without information about the sex of a partner, males are more predisposed to trust strangers than females, but there are no sex differences in trustworthiness (see the meta-analysis by Van den Akker et al., 2020). Our study was designed to address the following questions: (a) To what extent does trust and trustworthiness occur under anonymized conditions? (b) To what extent does trust and trustworthiness of individuals differ in relation to own sex and the sex of one's interaction partner? (c) What happens if these conditions are personalized: does seeing a partner affect the behavior? (d) Are there particular facial cues that elicit trust and/or trustworthiness? and (e) Are individuals who tend to elicit trust in their interaction partners actually more trustworthy?

For the assessment of particular facial features that may contribute to eliciting trust and/or trustworthiness, we focused on facial femininity and masculinity. The literature provides some fragmental evidence that discrete facial traits hypothetically associated with sex-specific facial appearance may predict perceived and actual trustworthiness (Stirrat and Perrett, 2010; Sanchez-Pages et al., 2014). To our knowledge, the present study is the first to test whether and how facial femininity/masculinity, measured directly from the facial morphology of the studied subjects by means of geometric morphometrics, may contribute to human trust and trustworthiness.

Materials and methods

Overview of the experiment

The experiment we will report on is part of a larger study that was conducted in 2017 at the University of Groningen in Netherlands (Rostovtseva et al., in preparation). The participants of the study had to show up on two different experimental days. On the first day, all subjects completed general demographic questionnaires providing information on their age, ethnicity, sex (male or female), and sexual orientation (heterosexual, homosexual, or bisexual). Individual photographs and videos were taken on the first day of the experiment as well. On the second day, the participants had to take decisions in ten situations that correspond to well-known games from game theory (e.g., Dictator Game, Prisoner's Dilemma Game, Trust Game, Stag Hunt Game, and Coordination Game). Here, we focus on the Trust Game that investigates trust and trustworthiness (see below). Each participant played five editions of the Trust Game against five different interaction partners. The first edition took place in an anonymous setting (without any information about the interaction partner); the other four took place under 'personalized' conditions (after having seen a 20 s silent video of the interaction partner). The interaction partners in the first two personalized editions were of the same sex, while they were of the opposite sex in the other two personalized editions. In each edition of the Trust Game, the subjects had to take a decision in two different roles: the role of a trustor and the role of a trustee (see below).

The Trust Game

The Trust Game (TG) is a one-shot two-player game, where one of the players is in the role of trustor, while the other is in the role of trustee. Many variants of the TG have been studied in the literature (Kreps, 1990; Berg et al., 1995; Breuer et al., 2016; Andreozzi et al., 2020); here, we applied the variant of the TG where the trustor makes a binary choice, while the trustee has a range of options (Jaeger et al., 2022). In our study, the trustor was endowed with a fixed budget (50 points) and was asked to make the binary choice of either keeping the endowment or entrusting it to the other player. In the latter case, the endowment was tripled (to 150 points). Subsequently, the second player (the trustee) was endowed with these 150 points and had to decide how much to return to the trustor (options were: 100, 75, 50, or 0 points) and how much to keep for themselves (50, 75, 100, or 150 points). Returning 100 points may be viewed as the most "fair" outcome, since then the profit of 100 points is equally shared between the trustor and the trustee. However, the decision on how much to return was entirely at the discretion of the trustee, who could not be punished in any way for "unfair" behavior.

In our experiment, the Trust Game was embedded in a real-life story. The trustor was asked to imagine to be a farmer with some goods for sale (worth 50 points on the local village market), who meets a stranger on their way to the city market. The stranger offers to take the goods to the city market, expecting to sell them there for thrice the local value. The farmer then had to decide whether to accept or to decline the offer, knowing that it is solely the stranger's decision whether to return any money (and how much). Conversely, the trustee was asked to imagine to be a seller on the city market, who was entrusted goods that could be sold for thrice the local price in the city. The decision then was whether to return any money to the farmer, and if so, how much (see Supplementary Materials for the instructions we gave to the participants).

To prevent learning effects, the participants did not get any feedback on the outcome of the interactions in the Trust Game. In particular, they did not receive any "immediate" payoffs but rather a cumulative payoff at the end of the whole experiment. The games were not real-time interactive. Instead, we first recorded the decisions of all participants in the various decision situations. Only at the end of the experiment, payoffs were assigned to these decisions, by matching each decision of a participant with a decision of the participant's partner. In the anonymous setting, the partner was chosen at random, while in the personalized setting the partner was the person shown on the video. The partner's decision was a decision that the partner had made in the anonymous setting, as we assumed that these decisions best reflect

the behavioral predispositions of the partner. Subsequently, the payoffs were calculated according to the game rules and summed up with the payoffs from all other experimental games. The participants did not receive any information about the exchange rate between the currency used in the experimental games (points) and their final payoff in Euros; they were only informed about their overall payoffs (in Euros) at the end of the experiment. At the stage of recruitment, the subjects were told that the average *per capita* payoff for the whole experiment would be around 40 €, but that the actual payoff would strongly depend on individual performance. Therefore, participants were highly motivated in optimizing their decisions.

Experimental procedure

Our study involved 176 subjects (87 females, 89 males). The participants were recruited by distributing flyers among the students of various BSc programs (mainly in the life sciences) of the University of Groningen and by posting a call for participants at the "Subjects Portal" of the Faculty of Behavioral and Social Sciences of the University of Groningen. All of them were 18–30 years old, with male subjects being slightly older (median = 22 years) than female (median = 21 years). Most participants (93%) were of Dutch, German, and Belgian origin (with 88% being Dutch). Five percent of male participants and 2% of female participants indicated that they were homosexual. This could have affected their behavior in same- vs. opposite-sex settings. However, the numbers were so small that it was impossible to run separate analyses on non-heterosexual participants. Excluding these participants did not affect our conclusions.

The experiment took place in computer rooms, with 15–21 same-sex participants per session. The experimental games (including the Trust Game) were implemented in the Survey Monkey Audience online form, where participants had to make their decisions by choosing options on a computer screen. Each participant was seated at a personal computer, separated from neighbors by vertical desk dividers to provide privacy. They were informed that all decisions would be treated anonymously, and others would not know their decisions at any step of the experiment. Participants were not allowed to communicate with each other during the experiment, and were asked to address all questions only to the experimenter. Each participant was asked whether they knew the partner shown in the video in person. When the answer was affirmative, the experiment continued but the case was excluded from further analysis.

Pictures and videos

Prior to the experimental games, a silent video of each participant was recorded (20 s neutral talk to the camera), and face photographs were taken. The duration of each video was restricted to 20 s, since, according to an earlier study by other authors, 20 s is sufficient for making judgments about prosocial behavioral predispositions (Fetchenhauer et al., 2010). Videos and photographs were made under daylight condition. Each participant was seated on a fixed chair facing the window. The camera was set at the eyes' height and at the fixed distance from an object (0.5 m for videotaping, 1.7 m for photographs). For videotaping, participants were asked to look into the camera and tell how they spent the morning. The videos were subsequently muted since voice parameters would have interfered with the effects of visual cues. Facial photographs were taken in full-face perspective with neutral facial expression, and head visually set to a natural position. Each participant was also asked to complete a general questionnaire providing information on sex, nationality, and age.

Twenty videos (10 male and 10 female) were used in the "personalised" edition of the Trust Game. These 20 videos were randomly selected from the videos of subjects of Dutch, German, and Belgian origin. According to the design of the experiment, each video was planned to be shown 40 times (20 in a same-sex, 20 in an opposite-sex setting). However, actual participation was somewhat lower; as a result, each video was displayed 31–40 times (nearly a half in the same-sex, and a half in the opposite-sex setting). Each subject played four personalized editions of the Trust Game, each with a different interaction partner, whom the subject had never met before. In general, there were 704 displays of the videos in the experiment. After the exclusion of five interactions due to personal acquaintance between the partners, 699 unique personalized interactions remained in the analysis.

Facial morphometry

Facial shape was analyzed using geometric morphometrics (Bookstein, 1997). Photographs of individuals with beard and with considerable deviation from a natural head position were excluded from this part of the analysis, along with 13 individuals who were not of Dutch, Belgian, or German origin. Thereafter, 145 individuals (72 males, 73 females) were included in the facial shape analysis. The 20 subjects from the videos, representing interaction partners in the Trust Game, were all part of this subsample. For the analysis of associations between facial shape and behavior in the Trust Game, there remained 141 individuals, as four subjects did not show up on the second experimental day. The number of unique personalized interactions for this part was 560, as four more cases were excluded because of personal acquaintance with an interaction partner.

Seventy landmarks and semi-landmarks were manually placed on each photograph using tpsDig2 2.17 (Rohlf, 2015). For the configuration of landmarks, we followed Windhager et al. (2011), excluding the vertex landmark that has an imprecise position when assessed from a frontal perspective. The final configuration included 36 landmarks linked to the classical anthropometric approximations to cranio-facial and soft-tissue

facial shape determinants (Bunak, 1941; Alexeev and Debets, 1964; Stirrat and Perrett, 2010; Windhager et al., 2011; Tanikawa et al., 2016; Rostovtseva et al., 2021), as well as 34 semi-landmarks, which were used for covering facial outline and eyebrows shapes (Figure 1).

To test for reliability of the manual digitalization of landmarks, two independent observers placed all 70 landmarks and semi-landmarks on randomly selected photographs of 20 males and 20 females. The inter-observer agreement was assessed by means of geometric morphometrics as the ratio of among-individual variance component to the sum of among-individual and measurement error components (Zelditch et al., 2012), using the "vegan" package for R (adonis() function with Euclidian method; Oksanen et al., 2020). The inter-observer agreement was 0.96. We considered the method reliable enough to use the landmark coordinates obtained by one of the observers.

All individual facial configurations were standardized for the position, orientation, and scale by Generalized Procrustes superimposition across the general sample of 145 subjects (see Zelditch et al., 2012, for an explanation and justification of the method). Superimposition was held together with sliding semi-landmarks using minimum bending energy criterion in "geomorph" package for R (Adams et al., 2021).

Visualization of the sex differences was implemented by (i) thin-plate deformation grids, which were made in R using functions developed by Claude (2008) and adjusted by the authors according to the purpose of the present study; (ii) geometric morphometric morphs, which were created by unwarping and averaging individual photographs in tpsSuper 2.04 (Rohlf, 2015).

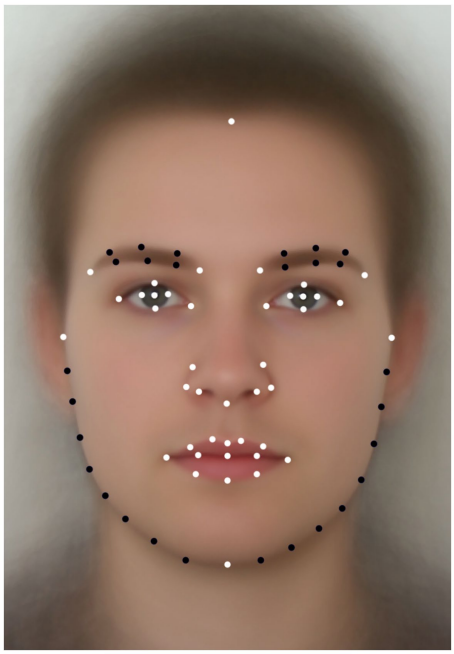

FIGURE 1
Landmarks and semi-landmarks configuration. Averaged portrait with configuration of landmarks (white) and semi-landmarks (black) is presented. For detailed description of the used anthropometric approximations see Rostovtseva et al. (2021).

Individual femininity/masculinity shape scores were obtained using linear discriminant analysis for two groups (males and females) conducted on the Procrustes coordinates of the facial landmarks and semi-landmarks. The procedure was held using "MASS" package for R (Venables and Ripley, 2002).

Statistical analysis

Statistical analysis was performed using a wide range of methods. Group differences in categorical (or binary) variables were assessed using a Chi-squared test for independence, and Fisher's exact test (in case of small sample sizes). For estimating effects occurring under personalized condition, which implied repeated interactions with different partners, we applied generalized estimating equations (GEE) analysis with repeated measures (binary logistic and linear models with multiple predictors). Associations between two continuous variables were assessed with linear regression models, and with major axis regression using "lmodel2" package for R (Legendre, 2018). Facial shape score standardization (within each sex) was conducted using z-score transformation. A Mann–Whitney *U*-test was used to assess differences between two groups in case of asymmetrical distributions of continuously scaled variables. Most of the statistical analyses were conducted in SPSS ver. 26.0 (IBM Corp., Armonk, NY, United States). Details of the analysis are discussed in the Results section, where the statistical conclusions are presented.

Statistical analysis related to geometric morphometrics was conducted in R. Sex differences in facial shape were assessed by multivariate analysis of variance using the "vegan" package for R (adonis function with Euclidian method; Oksanen et al., 2020). Statistical significance was revealed within this function by a permutation test (with 10,000 permutations; Good, 2000).

Results

Behavior in the Trust Game

The participants in our experiment had to make two types of decisions: (1) in the role of trustor, they had to make the binary choice of whether or not to entrust their goods (worth 50 points on the local market) to their interaction partner; (2) in the role of trustee, who had sold the entrusted goods for 150 points elsewhere, they had to decide whether to return 100, 75, 50, or 0 points to the trustor. We consider returning 100 points a "fair" outcome, as in this case both the trustor and the trustee have a revenue of 50 points. From a purely economic perspective, the trustee should not return anything, as the interaction partners will not meet again in the future, and there is no way to punish "unfair" behavior. This, in turn, implies that, from a

purely economic perspective, trustors should never entrust their goods, as these goods will be lost and no revenue will be obtained (Mas-Colell et al., 1995; Kacelnik, 2006). In contrast to this expectation, experiments based on the Trust Game typically find that human subjects have a relatively high tendency to entrust goods to their interaction partner when in the position of trustor and a relatively high tendency to return at least part of the revenue to the trustor when in the position of trustee (Berg et al., 1995; Cochard et al., 2004; Wilson and Eckel, 2011; Wilson, 2018; Andreozzi et al., 2020; see "Discussion" for more details).

Moreover, the participants had to make both types of decisions (as trustor and trustee) five times: first in an anonymous setting, where they had no information on their interaction partner; twice in a same-sex personalized setting, where they were sequentially shown two silent videos of their two different interaction partners (who were of the same sex); and twice in an opposite-sex personalized setting, where they were sequentially shown two silent videos of two other interaction partners (who were of the opposite sex).

Figure 2 gives an overview of the behavioral decisions in our experiment. Figure 2A shows that participants of both sexes had generally a high level of trust: in the position of trustor: 70% of all subjects entrusted their commodities to their interaction partner, despite of the risk that their partner might not return anything, leaving the trustor with a loss of 50 points. Figure 2B shows that, irrespective of sex, the participants were generally trustworthy: in the position of trustee, 46% of all subjects returned the "fair share" of their revenue to the trustor (= 100 points, the maximal amount that could be returned in the experiment). As shown in Figure A1 (Statistical Appendix A), only a minority of males (17%) and females (10%) did not return anything in the role of trustee.

In cooperation experiments, one often observes a decline in cooperation tendency with the number of repetitions of a cooperation game (Andreozzi et al., 2020). In our experiment, anonymous interactions always preceded personalized interactions, and same-sex interactions always preceded opposite-sex interactions. We did not observe a systematic sequence effect on trust decisions (Figure 2A), but the frequency of fair returns, our measure of trustworthiness, slightly declined (Figure 2B).

Generally, trust and trustworthiness decisions did not differ much between anonymous and personalized conditions. In about 80% of the personalized interactions (557 out of 699) subjects made the same trust decision as in their previous anonymous interaction. Only in 142 out of 699 cases a switch occurred, either from distrust [anonymous] to trust [personalized] ($N = 79$) or from trust [anonymous] to distrust [personalized] ($N = 63$). Similarly, in about 80% of the personalized interactions (563 out of 699) subjects returned the same amount in the trustworthiness part of the game as in their previous anonymous interaction. Only in 136 out of 699 cases personalization induced a shift, either in the positive (increase in the number of points returned; $N = 37$) or the negative (decrease in the points returned; $N = 99$) direction. Within-individual consistency in the five trust- and trustworthiness-related choices can also be quantified by Fleiss' kappa (Landis and Koch, 1977). This yields a value of $\kappa = 0.451$ ($p < 0.001$) for the consistency of the five trust decisions and a value of $\kappa = 0.833$ ($p < 0.001$) for the consistency of the five trustworthiness decisions (which were categorized on the binary scale "fair" versus "non-fair" returns to trustor, as in Figure 2B). According to the classification of Landis and Koch (1977), which is debated in the literature (Gwet, 2014), the κ-value for trust indicates a "moderate" level of consistency, while the κ-value for trustworthiness indicates "almost perfect" intra-individual consistency. These results suggest that individuals were quite consistent in their decisions, indicating that the effect of

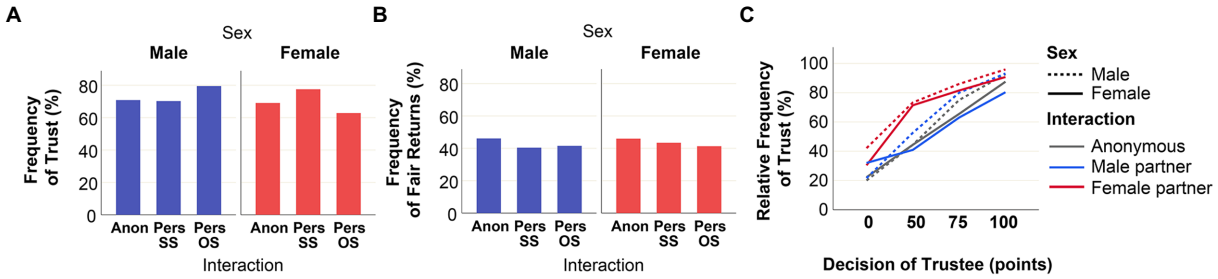

FIGURE 2
Overview of behavior in the Trust Game. **(A)** Percentage of cases where individuals in the role of trustor entrusted commodities to their interaction partner (the trustee). **(B)** Percentage of cases where individuals in the role of trustee returned a fair share of the revenue (=100 points) to the trustor. **(C)** Association between trust (vertical axis) and trustworthiness (horizontal axis; expressed as the number of points returned to the trustee). The percentages in **(A)** and **(B)** are shown separately for males (blue) and females (red), and according to whether the decisions were taken in an anonymous setting ("Anon"), a personalized same-sex setting ("Pers SS"), and a personalized opposite-sex setting ("Pers OS"). The six curves in (C) represent the association between trust and trustworthiness for male (dashed lines) and female (solid lines) participants, dependent on whether they interacted with an anonymous partner (grey), a male partner (blue), or a female partner (red). Data from 176 subjects (89 males, 87 females) are shown, who subsequently participated in one anonymous interaction, two same-sex personalized interactions, and two opposite-sex personalized interactions. Only 699 of the 704 personalized interactions were included in the analysis (see Materials and methods).

personalization on trust and especially on trustworthiness was relatively weak.

Figure 2C displays to what extent trust and trustworthiness were associated. The six curves depict the percentage of "trust" decisions in relation to the individuals' "trustworthiness," which is represented by the number of points returned to the trustor (0, 50, 75, 100, where 100 corresponds to a "fair" return). The curves show the associations between trust and trustworthiness separately for males and females, in each case under three experimental settings: anonymous, same-sex personalized, and opposite-sex personalized. All six curves clearly indicate a positive association between the propensity to trust and the level of trustworthiness. In other words, participants who were more predisposed to trust their interaction partners were also more trustworthy.

Sex-related differences in trust and trustworthiness

Under anonymous conditions, male and female subjects do not seem to differ in their level of trust (Figure 2A) and trustworthiness (Figure 2B). This is confirmed by Chi-squared tests for independence that did not reveal significant sex differences in either trust ($X^2 = 0.069$, $df = 1$, $p = 0.792$) or trustworthiness ($X^2 = 1.962$, $df = 3$, $p = 0.580$). In contrast, a clear sex effect was observed under personalized conditions: the highest levels of trust were observed in males interacting with female partners (male opposite-sex interactions), and in females interacting with female partners (female same-sex interactions; Figure 2A). This suggests that female interaction partners elicit a higher level of trust (in both male and female subjects) than male interaction partners.

Figure 3 investigates the effect of particular types of interaction partners on the behavior of male and female subjects in more detail. In the personalized setting, we made use of 20 videos (10 males: M1–M10, and 10 females: F1–F10). Each of these videos was shown to 17 ± 2 male and 17 ± 2 female subjects. The design of our study allowed us to compare, for each subpopulation of participants that had seen a given video, the frequency of "trust" decisions after having seen the video with the frequency of "trust" decisions in the anonymous setting (see Supplementary Figure 1). Figure 3A displays the shifts in trust frequency that each of the 20 videos elicited in the male and female interaction partners. A clear pattern emerges: the female videos generally led to an increase in the level of trust in both male and female participants, while the male videos led to a reduction in the trust level, especially in females.

To assess the statistical significance of the observed differences, we considered all those personalized interactions where the "trust" decision after showing the video differed from the earlier decision in the anonymous setting. Figure 3B shows how often such a switch from distrust to trust and from trust to distrust occurred for male (top graph) and female (bottom graph) participants, depending on the sex of the interaction partner (males: blue bars, females: red bars). To test for differences, we applied a binary logistic model, where a switch in the positive or negative direction was set as a response variable, where the participant's sex, the sex of the interaction partner, and the interaction of sexes were set as independent factors. Since each decision-maker was included in the analysis four times, generalized estimating equations (GEE) with repeated measures were used. The statistical analysis (Table 1) confirms that the sex of the interaction partner is a highly significant ($p < 0.001$) predictor of shifts in trust; the negative B-value indicates that

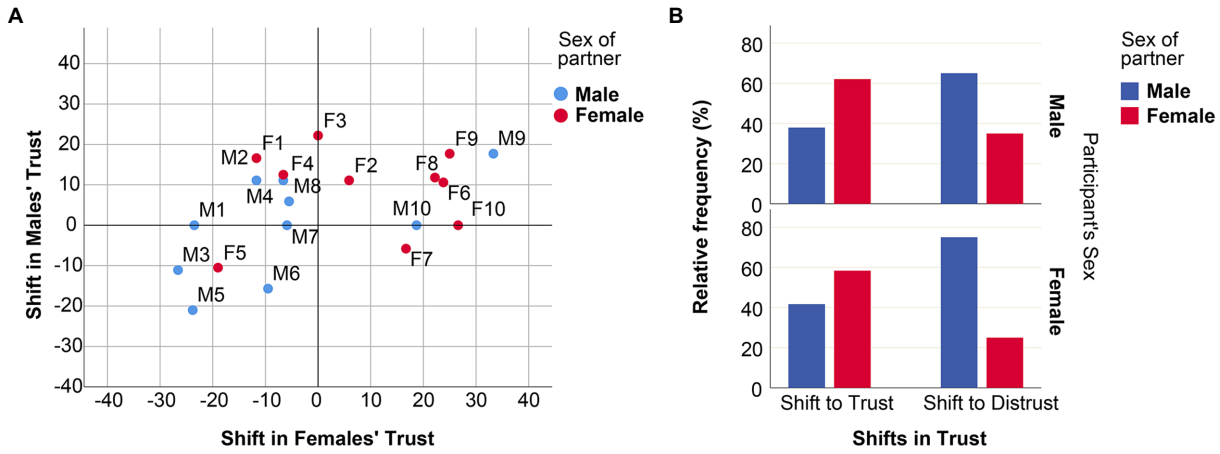

FIGURE 3
Shifts in trust decisions elicited by the 20 videos of interaction partners. **(A)** The graph depicts the average shift in trust in female (horizontal axis) and male (vertical axis) subjects elicited by each of the 20 videos of interaction partners (10 males, M1–M10, and 10 females: F1–F10). Negative scores indicate that showing the corresponding video reduced trust on average (in comparison to the trust level in the anonymous setting); positive scores indicate an increase in trust. **(B)** Relative frequency distributions of individual switches in (the binary) trust decision, in relation to the sex of the interaction partners in the Trust Game. N=142.

male interaction partners induce a decrease in trust (in comparison to the anonymous setting), while female interaction partners induce an increase in trust, both in male and female participants.

We followed the same general procedure to investigate whether and how trustworthiness was affected by the sex of the interaction partner. Supplementary Figure 2 presents for each of the 20 videos shown the distributions of trustworthiness decisions in the personalized and the anonymous setting—for that subpopulation of subjects that was shown the video under scrutiny. Shifts in trustworthiness elicited by a certain partner video were quantified in two different ways: (a) by the average difference in the number of returned points between the personalized and the anonymous setting, and (b) by the difference in the frequency of "zero returns" between the personalized and the anonymous setting—where in the two methods, the average and the frequency refer to that subset of participants that was shown a given video. Again, switches in behavior were calculated separately for male and female subjects.

Figure 4 displays for both measures the shift in trustworthiness induced by each of the 20 videos (males: M1–M10, females: F1–F10). Both panels confirm our previous observation (Figure 2B) that the level of trustworthiness was generally lower in the personalized setting than in the anonymous setting. In fact, not a single video enhanced trustworthiness (as measured by the number of points returned to the trustor; Figure 4A) in both sexes, and only 3 videos enhanced trustworthiness (as measured by the percentage of zero returns; Figure 4B) in at least one sex (females). The negative shift in trustworthiness occurred both in male and female participants, and was independent of the sex of the interaction partner. For detailed statistics see Table A1 in the Statistical Appendix A.

TABLE 1 Sex-related shifts in trust.

Dependent variable: Shift to trust			
Predictors	*B*	Wald X^2	*p*
Sex of decision-maker (male)	0.043	0.005	0.945
Sex of interaction partner (male)	−1.472	14.152	<0.001***
Sex of decision-maker * Partner's sex	0427	0.278	0.430

Results of the GEE with repeated measures, based on a binary logistic model with two predictors and their interaction. *N*[interactions] = 142. B, coefficients; Wald X^2—statistics, and associated *p* value.

Figure 5 depicts the associations between the shift in trust and the shift in trustworthiness that was elicited by each of the 20 videos (see the figure caption for detailed statistics). The top panels (Figures 5A,B) suggest that in male participants, there is no association between the "trust response" and the "trustworthiness response" that is elicited by male and female videos. This means that interaction partners who elicited an increase in trust in male subjects did not necessarily elicit an increase in trustworthiness in the same subjects. The outcome was very different for female participants: there was a strong and significant positive association between the trust response and the trustworthiness response that is elicited by male and female interaction partners (Figures 5C,D). Those partners from the videos who induced positive shifts in female trust also received more points from them in the trustworthiness part of the Trust Game.

Effect of sex-related facial traits on trust and trustworthiness

One of potential factors influencing the perception of partners' appearance is the degree of facial masculinity/femininity. To test

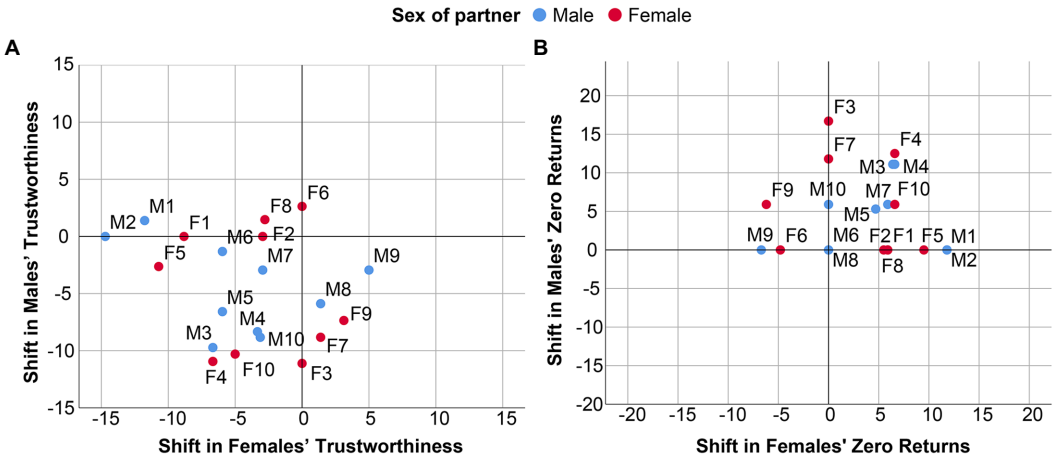

FIGURE 4
Shifts in trustworthiness elicited by the 20 videos of interaction partners. The graphs depict the average shift in trustworthiness in female (horizontal axis) and male (vertical axis) subjects elicited by each of the 20 videos of interaction partners (10 males: M1-M10 and 10 females: F1-F10). The two panels correspond to two different ways to quantify a shift in trustworthiness. **(A)** Average difference in returns in the personalized and the anonymous setting; **(B)** difference in the frequency of zero returns in the personalized and the anonymous setting. Notice that a positive value in **(B)** indicates a negative effect on trustworthiness.

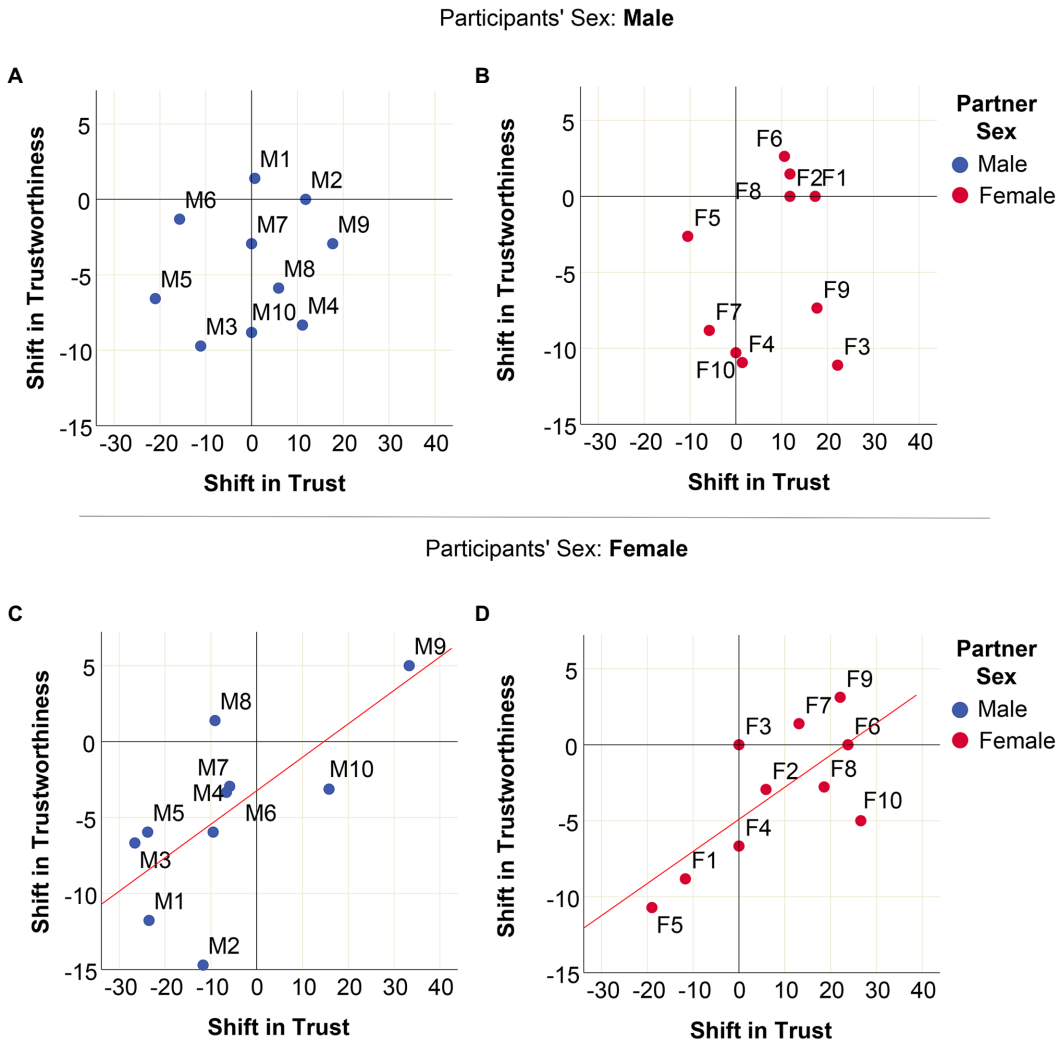

FIGURE 5
Associations between trust and trustworthiness as elicited by 10 male and 10 female videos. Major axis regression analysis of the association between shifts in trust (*x*-axis) and shifts in trustworthiness (*y*-axis) elicited by 20 videos (males: M1–M10, 10 females: F1–F10). **(A)** Effect of male videos on male subjects: R^2=0.038, Beta=0.066, p=0.306; **(B)** effect of female videos on male subjects: R^2=0.028, Beta=−0.115, p=0.330; **(C)** effect of male videos on female subjects: R^2=0.449, Beta=0.217, p=0.014; **(D)** effect of female videos on female subjects: R^2=0.499, Beta=0.214, p=0.013. Major axis regression lines are presented only for significant associations.

whether facial femininity/masculinity (both in males and females) serves as a stimulus to trust, we addressed possible associations between partners' facial femininity (based on their facial photographs) and participants' willingness to trust those partners, and to behave trustworthily toward them. The multivariate analysis of variance performed on the facial shape Procrustes coordinates by sex revealed that facial shape differed significantly between male and female subjects. Sex explained 7% of the total variance in facial shape among the participants (N=145; p<0.001). Adding age of the participants as the first of the two independent variables (along with sex) revealed that age explained 1.3% of the variance in facial shape (p=0.03). However, after removing this component of variance, the impact of sex remained highly significant. The percent of variance explained by sex remained practically the same (var. expl. 6.8%, p<0.001). The latter suggests that variation in facial shape, which occurred due to differences in age, and variation, which occurred due to sex differences, were almost independent of each other. Figure 6 displays sexual dimorphism in the facial shape of the participants. Deformation grids (Figure 6A) and geometric morphometric morphs (Figure 6B) demonstrate facial shape change from a sexually undifferentiated face (mean shape; in the center) toward the average female shape (left) and the average male shape (right). To enhance the details, the outer configurations show these differences exaggerated by a factor of 3.

The main sex differences in facial shape occurred in the shape of the lower face and the eyes area. Women, when compared to men, had a relatively shorter and narrower lower face, while male faces were relatively longer, with wider and more robust jaws. Women also had relatively fuller lips compared to men. Female

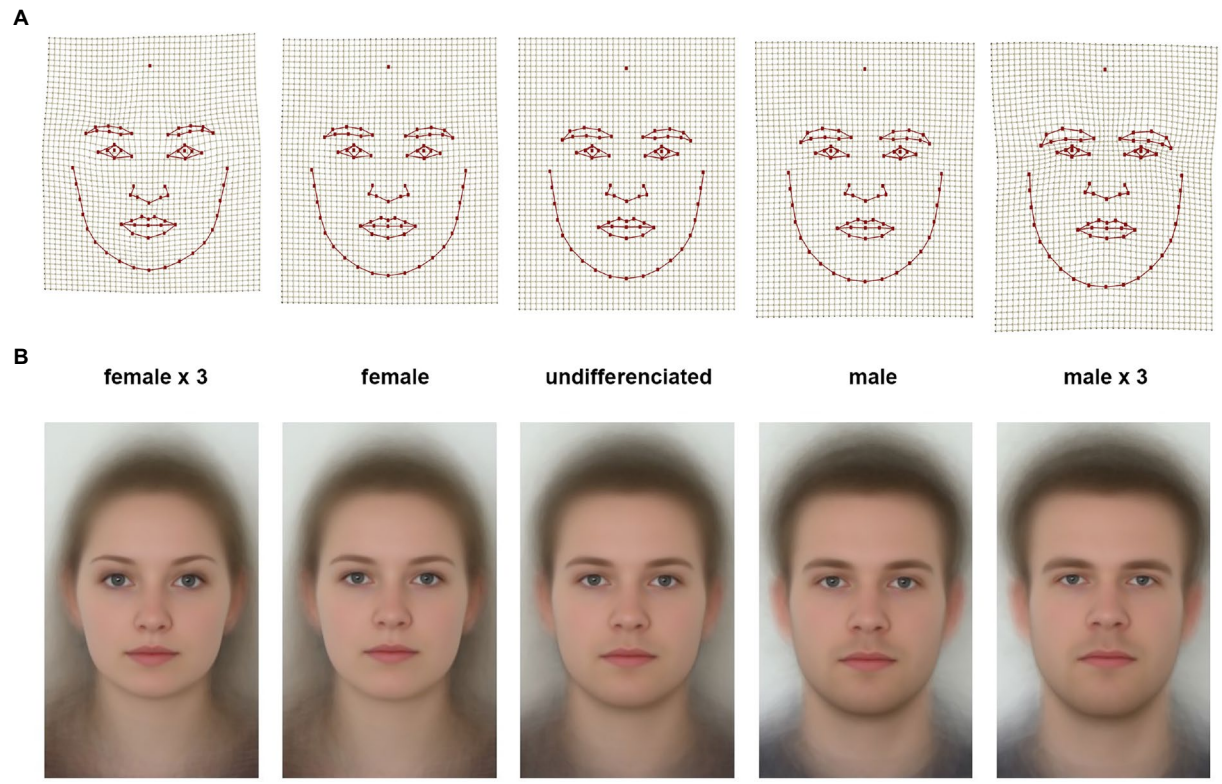

FIGURE 6
Sex differences in facial shape. **(A)** Deformation grids, and **(B)** geometric morphometric morphs display facial change from sexually undifferentiated shape (in the center) toward the average female face (left) and average male face (right). Two outer configurations display these changes exaggerated by a factor of 3. Sex differences are statistically significant (N=145, var. expl. 7%, p<0.001).

eyebrows were set more laterally and relatively higher, visible areas of the eyes were larger. Since there was only one landmark on the forehead (see Figure 1), the visualization of sex differences in the forehead area along the x-axis was not informative. One of the important components of the sex differences was degree of bilateral asymmetry. Women on average had more symmetrical faces, whereas men had a clear bilateral asymmetry with "deformation" of the left side of the face (right side of the grid).

In order to obtain a quantitative measure of facial femininity for each participant, individual shape scores were calculated using linear discriminant analysis (LDA) for two groups (males, females) performed on the Procrustes coordinates of the facial shapes of 145 individuals. The shape scores represented the degree of facial femininity for men and women based on actual sex differences in the facial shapes in our sample. Figure 7A represents distributions of the shape scores for male and female subjects.

To use these scores as a measure of femininity of male and female faces, a within-sex z-score standardization was applied, which transformed the raw scores into standard deviations from the mean value per sex (where mean per each sex was set to zero, and ±1 corresponded to ±1 SD). The distributions of z-transformed femininity scores for males and females from the general sample are presented in Figure 7B. Our aim was to test an impact of partner's facial femininity on shifts in trust and trustworthiness in the TG. Since the interaction partners shown at the videos were randomly chosen from the general sample, the z-transformed femininity scores (calculated based on facial shapes of all 145 individuals) were not distributed symmetrically between male and female partners. Although there were no statistically significant differences in femininity z-scores between male and female partners (Mann–Whitney U-test: $U = 31.000$, $p = 0.165$), there still was a small shift toward male partners having slightly higher z-scores than female partners (for details see Supplementary Figure 3A). Given a small sample size of interaction partners from the videos ($N = 20$) and repeated interactions (each partner's video was shown to 17 ± 2 subjects of the same sex) this small shift still could cause biased results. For this reason, to obtain standardized femininity scores for male and female partners, the raw femininity scores were z-transform within each sex in the subsample of partners from the videos ($N = 20$). The raw femininity scores of male and female partners were normally distributed (Supplementary Figure 3B), which allowed applying z-score transformation. The distributions of the femininity z-scores for male and female partners are displayed in Figure 7C. Since the sample size for the facial shape analysis was reduced compared to the general sample (see "Materials and methods"), the number of shifts of personalized decisions in the Trust Game (compared to anonymous ones) was also reduced.

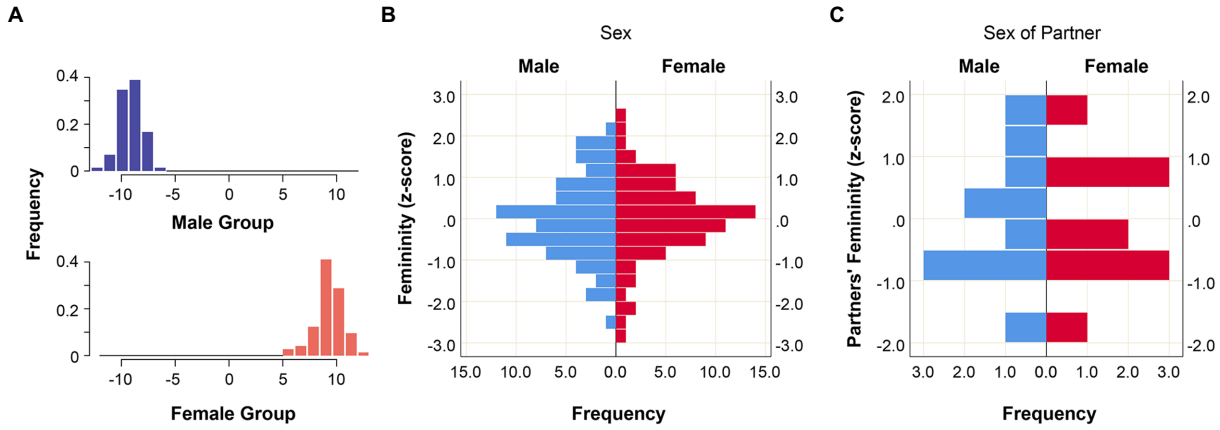

FIGURE 7
Individual facial shape scores by sex. **(A)** Facial shape scores as a result of linear discriminant analysis of Procrustes facial coordinates by sex; **(B)** distributions of femininity *z*-scores after within-sex standardization (*N*=145); **(C)** distributions of partners' femininity *z*-scores after within-sex standardization among partners (*N*=20).

There were 113 interactions with shifts in the trust part of the TG (65 shifts to trust, 48 shifts to distrust), and 110 shifts in the trustworthiness part (30 shifts in direction of increase of trustworthiness, 80 shifts to decrease of trustworthiness).

Our aim was to test whether a degree of facial femininity of a partner influenced shifts in trust elicited by that partner in male and female participants. Association of the partners' facial femininity with shifts in trust, and sexes of both partners are presented in Figure 8. Although, as discussed above, females generally elicited more trust in their interaction partners (see Figure 3; Table 1), high facial femininity of female partners elicited distrust in both male and female subjects. The effects of facial femininity/masculinity of male partners were oppositely directed for male and female subjects: male participants tended to trust men with more feminine facial shapes, and female participants trusted men with more masculine faces (Figure 8).

In order to assess statistical significance of the observed effects, we used a binary logistic model, which accounted for repeated measures (GEE) based on 113 unique interactions. Shifts toward trust or distrust were set as a binary response variable, whereas sex of decision-maker, partners' sex, and partners' facial femininity (*z*-scores) were set as predictors (Table 2). The results confirmed that the effects of partner's sex and partner's facial femininity are significant predictors of shifts in trust, and that impacts of facial femininity on shifts in trust are oppositely directed for male and female subjects.

Next, we addressed the question of whether partner's facial femininity/masculinity may also elicit change in trustworthiness of participants. Testing shifts in trustworthiness using the same approach as in the case of shifts in trust was not possible, since number of switches under some conditions was too small (for instance, there was only one unique interaction between two male partners with switch in direction of increase of trustworthiness). For this reason, in this part of the analysis, we measured shifts in behavior as the absolute differences in returned points between

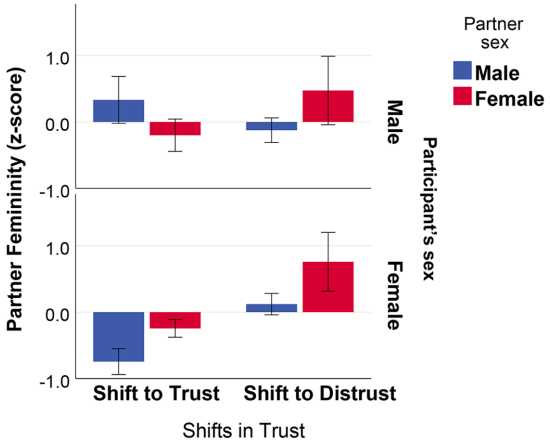

FIGURE 8
Shifts in trust, partners' facial femininity, and partners' sex. Associations between shifts in trust and facial femininity for interaction partners of both sexes. *N*[interactions]=113, *N*[partners]=20, mean values with ±1 standard error are presented.

personalized and anonymous conditions per interaction. Thus, the binary variable (shift to increase, shift to decrease) turned into continuously scaled one, which was also sensitive to the magnitudes of the elicited shifts. Analysis was performed using GEE with linear model and repeated measures based on 560 unique interactions. Continuously scaled shifts in trustworthiness were set as a response variable, and sex of decision-maker, partners' sex, and partners' facial femininity (*z*-scores) were set as predictors. The results revealed that trustworthiness was practically not related either to facial femininity or partners' sex. The only very weak association was found in directions of shifts in male and female participants, with feminine partners eliciting slight increase of trustworthiness in male subjects and slight

TABLE 2 Shifts in trust, degree of facial femininity, and partners' sex.

Dependent variable: Shift to trust in personalized setting			
Predictors	*B*	Wald X^2	*p*
Sex of decision-maker (male)	−0.559	0.652	0.420
Sex of partner (male)	**−1.473**	**8.060**	**0.005****
Femininity of partner (*z*-score)	**−2.836**	**11.679**	**<0.001*****
Sex of DM * Femininity of Partner (*z*-score)	**2.358**	**7.754**	**0.005****
Sex of partner * Femininity of partner (*z*-score)	0.926	1.293	0.255

Results of the GEE analysis with repeated measures are presented: a binary logistic model with multiple predictors, *N*[interactions] = 113. DM, decision-maker; *B*, coefficients; Wald X^2, statistics of the Wald Chi-squared test; *p*, statistical significance (**$p < 0.01$, ***$p < 0.001$). Significant results, which remained significant after Bonferroni correction for five predictors are in bold.

decrease of trustworthiness in female subjects (Figure A2). However, this effect was very weak ($p = 0.03$), and given multiple testing could occur by chance. Detailed statistics can be found in Table A2 in the Statistical Appendix A. We conclude that partner's sex and facial femininity did not affect subjects' trustworthiness.

Association of sex and sex-related facial traits with own trustworthiness

According to the obtained results, females were generally trusted more than males. At the same time, female partners with more feminine facial shape elicited more distrust in both male and female subjects, whereas male partners with more masculine facial shape were more trusted by females, and less trusted by males (Figure 8; Table 2).

Following such reactions to partners' sex and appearance, one would expect: (i) female subjects to be more trustworthy than male subjects; (ii) females with more feminine facial shapes to be less trustworthy than females with more masculine facial appearance; and (iii) male subjects with more masculine facial shape to be more trustworthy toward female subjects, and less trustworthy toward males. In order to test whether these expectations are met, we analyzed trends in trustworthiness in association with partners' sex and facial femininity.

It was already demonstrated that female subjects were not more trustworthy than males under anonymous condition (Figure 2B). Additional analysis also did not reveal sex differences in trustworthiness under anonymous conditions among 20 partners shown at the videos (Fisher's exact test: $N = 20$, $p = 0.998$). Females' trustworthiness also did not increase under personalized interactions compared to anonymous (Table 2B). These results suggest that general predisposition to trust females more than males was not justified by actual female behavior.

To address more specific patterns involving both sex and femininity, we applied additional analyses. Figure 9 represents distributions of decisions in the trustworthiness part of the TG against own facial femininity under anonymous and personalized conditions for male and female subjects. Degree of facial femininity was not a significant predictor of actual trustworthiness in any of the conditions (for statistics see legend for Figure 9).

We conclude that sex and facial femininity of an interaction partner was an important factor of eliciting trust (Figure 8; Table 2). However, own sex and degree of facial femininity of participants were not reliable predictors of their actual trustworthiness (Figure 9).

Discussion

More than two hundred studies on behavior in the anonymous Trust Game have been conducted in the last decades (games with binary-choice trust decisions: Bolle, 1998; Eckel and Wilson, 2004; Gómez-Miñambres et al., 2021; Jaeger et al., 2022; games with continuously scaled trust decisions are extensively reviewed by Ostrom and Walker, 2003; Johnson and Mislin, 2011; Van den Akker et al., 2020). Research on the effects of personalization on between-individual trust and trustworthiness became popular only recently. These personalization studies can be categorized into three lines of research. First, in quite a number of studies subjects are asked to rate neutral photographs of their interaction partners regarding various traits (e.g., trustworthiness); subsequently, these studies explore whether and how these ratings are associated with the trust and trustworthiness decisions toward these partners in the Trust Game (Bente et al., 2014; Yu et al., 2014; Li et al., 2017; Qi et al., 2018; Brustkern et al., 2021; Li et al., 2021; Shen et al., 2021). A second set of studies investigates how adding emotional facial expressions (smiles, anger displays, etc.) to a partners' image affect trust and trustworthiness (Campellone and Kring, 2013; Tortosa et al., 2013; Alguacil et al., 2015; Kret and De Dreu, 2019; Li et al., 2021). A third line of research studies whether facial self-resemblance has a positive effect on trust and trustworthiness (DeBruine, 2002; Farmer et al., 2014). Most personalization studies are based on showing pictures of the interaction partners; only a few studies investigate trust and trustworthiness under conditions of face-to-face interactions or with dynamic partner representation (videos or dynamic avatars; Krumhuber et al., 2007; Centorrino et al., 2015; Tognetti et al., 2018; Rychlowska et al., 2019). In the present work, we made use of both, a dynamic representation of the interaction partners (videos) in the Trust Game and the analysis of full-face photographs.

The design of our study allowed us to compare personalized and anonymous interactions, and to estimate whether trust directed toward particular partners is justified by the actual trustworthiness of these partners. In addition, it enabled us to investigate how the sex of interaction partners and their facial appearance (femininity/masculinity) affect trust and trustworthiness.

Even under anonymous conditions, trust and trustworthiness were manifested at a remarkably high level in our study

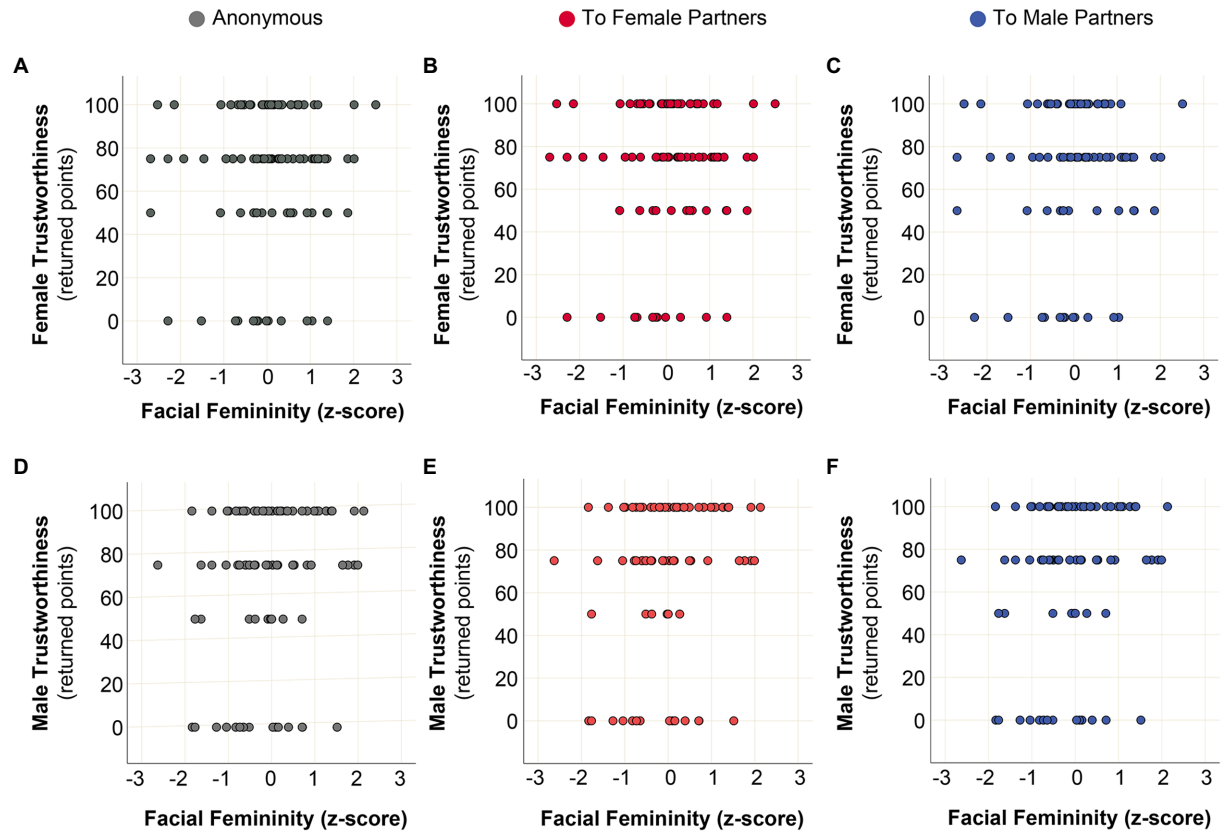

FIGURE 9
Actual trustworthiness, sex, and degree of facial femininity. **(A)** Linear regression model: response variable—female trustworthiness under anonymous condition; predictor—own facial femininity (*z*-score). N=70; B=2.999, $R2$=0.010, p=0.409. **(B)** generalized estimating equations (GEE), linear model accounting for repeated measures: response variable—female trustworthiness toward female partners (personalized condition); predictor—own facial femininity (*z*-score). N=139; B=−1.016, Wald X^2=0.050, p=0.823. **(C)** GEE, linear model accounting for repeated measures: response variable—female trustworthiness toward male partners (personalized condition); predictor—own facial femininity (*z*-score). N=138; B=6.312, Wald X^2=1.171, p=0.279. **(D)** Linear regression model: response variable—male trustworthiness under anonymous condition; predictor—own facial femininity (*z*-score). N=71; B=2.945, $R2$=0.008, p=0.463. **(E)** GEE, linear model accounting for repeated measures: response variable—male trustworthiness toward female partners (personalized condition); predictor—own facial femininity (*z*-score). N=141; B=−0.679, Wald X^2=0.023, p=0.880. **(F)** GEE, linear model accounting for repeated measures: response variable—male trustworthiness toward male partners (personalized condition); predictor—own facial femininity (*z*-score). N=142; B=−0.216, Wald X^2=0.002, p=0.968.

population: the majority of participants were generally willing to entrust goods to anonymous partners (70% of all cases), and were also trustworthy in that they frequently returned a fair share of the goods entrusted to them (46% of cases). Earlier studies by other authors revealed that in experiments trust levels tend to be higher in binary-choice variants of the trust game than in "investment games" with a continuum of choices of the trustor (Bolle, 1998; Eckel and Wilson, 2004; Gómez-Miñambres et al., 2021). At the same time, binary-scaled ("all-or-nothing") trust may also lead to a decrease in reciprocal trustworthiness (Ostrom and Walker, 2003; Gómez-Miñambres et al., 2021). However, our results confirm earlier findings (reported for both variants of the game) that in Europe and North America, a high degree of trust and trustworthiness toward anonymous strangers is quite typical in experimental Trust Games (Berg et al., 1995; Cochard et al., 2004; Eckel and Wilson, 2004; Wilson and Eckel, 2011; Wilson, 2018; Andreozzi et al., 2020; Müller and Schwieren, 2020; Gómez-Miñambres et al., 2021). Such behavior cannot be explained by economic rationality, since reciprocation cannot be enforced by the trustor, and trust can easily be exploited by returning an unfair share or even nothing. In other words, human trust and trustworthiness are far beyond purely economic self-interest. However, the literature suggests that there are considerable population differences in the level of trust. According to the World Value Survey (World Values Survey Wave 7, 2017–2021), when subjects were asked whether they trust people whom they meet for the first time the expressed levels of trust are the highest in Denmark [75.3%], followed by Sweden [73.9%] and Netherlands [71.6%], the country where our study was conducted. The lowest levels of trust toward strangers were reported for Ecuador [7.8%], Albania [8.7%], and Peru [9.0%]. Some authors suggest that the explanation for the observed population differences may be rooted in different socio-environmental factors, which moderate trusting attitudes through social learning and everyday experiences (Kwantes and Kuo, 2021; Liu and Chen, 2022). The correspondence between the level of trust in the anonymous version of our Trust

Game [70%] and the outcome of the WVS for Netherlands [71.6%] is more than a coincidence: a study across 35 countries (involving more than 23,000 subjects) revealed that the level of trust per country as measured in anonymous one-shot Trust Games aligned well with the level of trust as measured by the WVS. Interestingly, the experimentally measured trustworthiness levels were not correlated with the trust levels as measured by the WVS in those countries (Johnson and Mislin, 2012).

Under anonymous conditions, we did not find sex differences in trust or trustworthiness in our study. Earlier, van den Akker et al. (2020) conducted a meta-analysis on sex differences in trust and trustworthiness in the one-shot anonymous continuously scaled Trust Game, based on 77 articles with 174 studies in 35 countries. They concluded that men are generally more trusting than women, whereas no significant sex differences in trustworthiness are observed. As trust toward strangers is a risky behavior that may lead to higher gains, but also may lead to loss, this finding may not be unexpected, as males tend to be more risk-prone than females. In contrast to this general trend, we did not find sex differences in trust between male and female subjects under anonymous "all-or-nothing" conditions. Such inconsistency may be rooted in the differences in design (binary- vs. continuous-trust decisions) and should be studied more carefully in the future. Another explanation for this may be related to the fact that our study was conducted in Netherlands, where differences between the sexes have diminished continually in the last 50 years.

When comparing personalized with anonymous interactions, we did not observe a systematic decline or increase of trust. Generally, a high degree of consistency in individual behavior was observed across all five interactions (anonymous and personalized). There was a slight decline in trustworthiness under personalized conditions in comparison to anonymous ones. This could partly have been caused by sequence effects: the set-up of our study necessitated that anonymous interactions preceded personalized interactions, and that same-sex personalized interactions preceded opposite-sex interactions. Although this sequence may have affected our results, we tried to minimize such effects by not providing our participants with feedback on the outcomes of earlier interactions, thereby eliminating the most obvious learning effects. However, due to repetition, subjects had more time for reflection (Kahneman, 2011), which could cause a slight downward bias along the sequence of interactions.

Although there were no sex differences in trust and trustworthiness under anonymous conditions, in personalized setting, significant sex effects were revealed. In a personalized setting, females elicited an increase of trust in both male and female subjects, whereas the trustworthiness of a subject remained unaffected by the sex of the partner. This finding contrasts with conclusions drawn in the literature. One study (Scharlemann et al., 2001) found that female images elicited more trust in males, while male images elicited more trust in females. Another study (Wilson and Eckel, 2006) reports that females are more trustworthy toward males than toward females. The study investigating facial trustworthiness perception using neuroimaging (Dzhelyova et al., 2012) reports that female appearance is generally perceived as more trustworthy than male appearance. Our results support the notion that females generally elicit more trust than males, but due to the apparent plasticity of trust in different socio-cultural environments generalizations should be made with caution.

In our study, trust and trustworthiness toward the same interaction partner were strongly positively correlated in female subjects, while there was no such correlation in male subjects (Figure 5). This means that if a male participant trusted someone he did not necessarily behave trustworthily toward that partner, whereas females trusted and were trustworthy toward the same person to a similar degree. This finding suggests that male and female participants differ in behavioral strategies and/or motivations for trust.

When considering the effects of specific facial features of a partner (facial femininity/masculinity), our study revealed that, although females generally were more trusted than males, females with more feminine facial traits elicited less trust than females with less feminine faces. At the same time, males with more masculine facial traits were more trusted by female partners, but were less trusted by male partners. Although the relatively small sample of partner videos (10 males and 10 females) is a certain limitation of our study, it is reassuring that our main results are consistent with the literature. The revealed effects are a good illustration of the differential impact of male masculinization on the behavior of interaction partners of the same and the opposite sex. On the one hand, according to the literature, men with highly masculinized faces are generally perceived as less trustworthy (Stirrat and Perrett, 2010), and were reported to actually demonstrate less trustworthiness in the Trust Game (Stirrat and Perrett, 2010; Sanchez-Pages et al., 2014). On the other hand, females tend to find masculinized faces more attractive for short-term relationships (Little, 2014), which may modulate their behavior in the Trust Game (for the wrong reasons). By the same logic feminized faces should increase trust in males, while the opposite pattern was observed in our study. Indeed, a number of studies have shown that more feminine female faces are perceived as more attractive than more masculine female faces (Perrett et al., 1998; Penton-Voak et al., 2004; Rhodes, 2006). However, in one study of Hu et al. (2018), conducted in China, it was revealed that among generally attractive-looking individuals more masculine female faces were perceived as more trustworthy by both male and female subjects than less masculine faces.

Finally, we found that neither the sex nor the sex-related facial appearance of an interaction partner seems to be a reliable predictor of actual trustworthiness. This contrasts with previous studies that reported significant associations of facial features (Stirrat and Perrett, 2010; Sanchez-Pages et al., 2014) with the trustworthiness of a person in a binary-choice Trust Game. However, other studies also concluded that assigning behavioral traits to individuals with particular facial appearances (based only on visual cues) often fails to correctly predict their actual

behavioral predispositions (Bonnefon et al., 2015). A recent study (based on the same variant of the Trust Game as used in our study) also showed that people are unable to detect the trustworthiness of strangers through their facial appearance (Jaeger et al., 2022). One of the possible reasons for the lack of actual recognition may be rooted in the so-called prosocial mimicry (or "camouflage"; Dawkins, 1976; Gambetta, 2005; Mokkonen and Lindstedt, 2016) used by free-riders (or cheaters) to imitate behavior and even appearance of prosocial individuals (Rostovtseva et al., 2022a,b). Although a fraction of such "cheaters" among trustworthy-looking individuals may be small, this still can introduce noise to the data. Another possible reason is that the "trustworthiness decisions" (and their interpretation) are more complicated than "trust decisions," as the former highly depend on what one considers fair. Today it is known that the perceptual "trustworthiness stereotype" (whom to consider trustworthy? whom to trust?) is a very dynamic phenomenon, and such stereotype can be very quickly rebuilt within a single individual through social learning (Chua and Freeman, 2022).

Summarizing, our findings indicate that personalization of interactions has a clear effect on trust, but not trustworthiness. Overall, there was no positive or negative effect of personalization on trust and trustworthiness, but there was a clear effect related to sex. Our results support previous findings by other authors that females generally elicit more trust than males. However, females with more feminine facial shapes elicited less trust in both male and female partners, while males with more masculine facial shape were more trusted by females, but less trusted by males. This result indicates the differential impact of male masculinization on the behavior of interaction partners of the same and the opposite sex. Importantly, sex and sex-specific facial appearance do not seem to be reliable predictors of trustworthiness. However, one should keep in mind that our study population is 'Western, educated, industrialized, rich, and democratic' (WEIRD; Henrich et al., 2010) and therefore not representative of all humans.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: FigShare.com, the data are available at doi: 10.6084/m9.figshare.21300924.

Ethics statement

The study received approval by the Ethical Committee Psychology (ECP) of the University of Groningen (Research Code: 16250-0). Prior to the experiment, all subjects signed informed consents.

Author contributions

VR, FW, and MB contributed to conception and design of the study. VR and FW conducted the experiment, analyzed the data and drafted the manuscript. VR and AM implemented geometric morphometrics. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.925601/full#supplementary-material

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Statistical Appendix

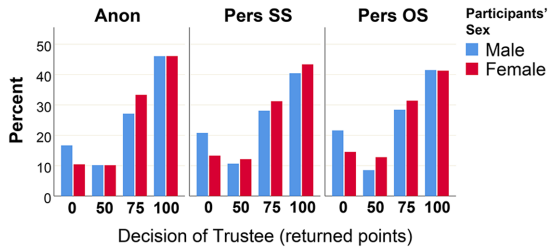

FIGURE A1
Distributions of decisions in trustworthiness part of the Trust Game. Relative frequencies (per participants' sex) of decisions in the trustworthiness part of the Trust Game under three experimental conditions: Anon, anonymous interactions; Pers SS, personalized same-sex interactions; Pers OS, personalized opposite-sex interactions. *X*-axis represents amounts of points returned to a partner.

TABLE A1 Sex-related shifts in trustworthiness.

Model	Dependent variable: Shift in points returned			
	Predictors	*B*	Wald X^2	*p*
(a)	Sex of decision-maker (male)	−0.634	0.796	0.372
	Partner's sex (male)	−0.176	0.309	0.579
	Sex of decision-maker * Partner's sex	−0.517	0.362	0.547
(b)	**Dependent variable: Shift in frequency of zero returns**			
	Predictors	*B*	Wald X^2	*p*
	Sex of decision-maker (male)	2.125	2.904	0.088
	Partner's sex (male)	−0.231	0.249	0.617

Results of the GEE with repeated measures are presented: binary logistic model with two predictors and their interactions (for the model [b] interaction of predictors was inapplicable). (a) *N*[interactions] = 136; (b) *N*[interactions] = 54. B, coefficients; Wald X^2, statistics of the Wald Chi-squared test; *p*, statistical significance.

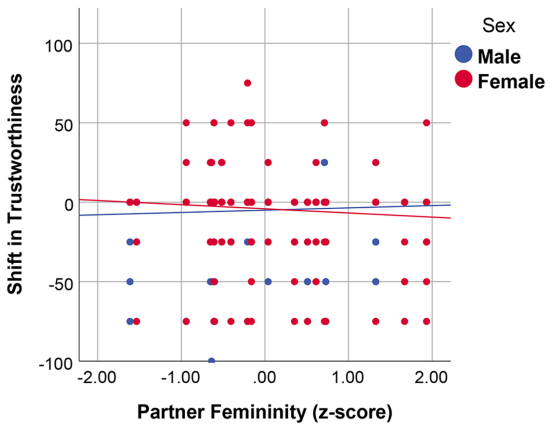

FIGURE A2
Shifts in trustworthiness, partners' facial femininity and partners' sex. Association between shifts in trustworthiness and facial femininity for interaction partners of both sexes (the figure depicts direction of the only significant association presented in Table A2), *N*[interactions]=560, *N*[partners]=20.

TABLE A2 Shifts in trustworthiness, degree of facial femininity and partners' sex.

Dependent variable: Increase of trustworthiness in personalized setting			
Predictors	*B*	Wald X^2	*p*
Sex of decision-maker (male)	−0.898	0.104	0.747
Sex of partner (male)	−2.064	3.010	0.083
Femininity of decision-maker (*z*-score)	3.558	3.099	0.078
Femininity of partner (*z*-score)	−3.076	2.740	0.098
Sex of DM * Femininity of DM (*z*-score)	−0.378	0.018	0.894
Sex of DM * Femininity of partner (*z*-score)	4.354	4.734	0.030*
Sex of partner * Femininity of DM (*z*-score)	0.972	1.292	0.256
Sex of partner * Femininity of partner (*z*-score)	0.646	0.101	0.751

Results of the GEE analysis with repeated measures are presented: a linear model with multiple predictors, *N*[interactions] = 560. DM, decision-maker; B, coefficients; Wald X^2, statistics of the Wald Chi-squared test; *p*, statistical significance (*$p < 0.05$).

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The sexual selection of creativity: A nomological approach

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Cultural innovations, such as tools and other technical articles useful for survival, imply that creativity is an outcome of evolution. However, the existence of purely ornamental items obfuscates the functional value of creativity. What is the functional or adaptive value of aesthetic and intellectual ornaments? Recent evidence shows a connection between ornamental creativity, an individual's attractiveness, and their reproductive success. However, this association is not sufficient for establishing that creativity in humans evolved by sexual selection. In this critical review, we synthesize findings from many disciplines about the mechanisms, ontogeny, phylogeny, and the function of creativity in sexual selection. Existing research indicates that creativity has the characteristics expected of a trait evolved by sexual selection: genetic basis, sexual dimorphism, wider variety in males, influence of sex hormones, dysfunctional expressions, an advantage in mating in humans and other animals, and psychological modules adapted to mating contexts. Future studies should investigate mixed findings in the existing literature, such as creativity not being found particularly attractive in a non-WEIRD society. Moreover, we identified remaining knowledge gaps and recommend that further research should be undertaken in the following areas: sexual and reproductive correlates of creativity in non-WEIRD societies, relationship between androgens, development, and creative expression, as well as the impact of ornamental, technical and everyday creativity on attractiveness. Evolutionary research should analyze whether being an evolved signal of genetic quality is the only way in which creativity becomes sexually selected and therefore passed on from generation to generation. This review has gone a long way toward integrating and enhancing our understanding of ornamental creativity as a possible sexual selected psychological trait.

KEYWORDS

creativity, intelligence, sexual selection, proximate, ultimate, mating, ornament, WEIRD

Introduction

> *"Sexual selection made our brains wasteful, if not wasted: it transformed a small, efficient ape-style brain into a huge, energy-hungry handicap spewing out luxury behaviors like conversation, music, and art."* (Miller, 2000, p. 134).

Being creative secures undeniable practical benefits for survival. Crows and chimpanzees use twigs and create tools by modifying these twigs to better perform the

desired aim (Reader et al., 2016). Chimpanzees, for instance, use such tools for termite fishing (Sanz et al., 2009). Humans have also created tools (e.g., handaxes) and various implements (e.g., clothes) that make it easier to get food and survive in diverse environments (Puccio, 2017). However, what would the evolutionary benefits be of body decoration, cave paintings, literary classics, philosophical treatises, or guitar solos?

Darwin's (1871) answer to that question was sexual selection. The ability to make tools must have evolved by viability selection, for it helped in survival in hostile environments, while the aesthetic skills required to create artistic performances and products would have evolved through sexual selection because they contributed to mate attraction. The extravagance of bird song and plumage, together with humans' conspicuous drive to produce art and other forms of ornaments (e.g., self-grooming: Valentova et al., 2022; daily behaviors: Kapoor et al., 2021; and humor: Kaufman et al., 2007) would have a common evolutionary root (Darwin, 1871). The aesthetic sensibility, artistic capacities (including musicality), creative capacities, and creative motivation necessary to produce and appreciate (two different traits) these aesthetically conspicuous manifestations (e.g., art, music, paint, dance, humor, and metaphors) constitute a mental trait named *ornamental creativity* (Figure 1).

Recent studies seem to confirm that more creative people, particularly in the ornamental/aesthetic aspect, are considered more attractive in Western, educated, industrialized, rich, and democratic societies (see Karamihalev, 2013; Lebuda et al., 2021). Nevertheless, more than that is needed to show that creativity evolved by sexual selection.

A complete explanation must consider an ethological analysis, which holistically synthesizes evidence regarding mechanisms, ontogeny, phylogeny, and evolutionary function (Tinbergen, 1963), as well as a nomological network based on theoretical, cross-cultural, hunter-gatherer, phylogenetic, genetic, psychological, medical, and physiological evidence (Schmitt and Pilcher, 2004). The more evidence in that nomological network, the greater the chances that a mental trait is a psychological adaptation (Schmitt and Pilcher, 2004). Psychological adaptations are cognitive modules evolved to solve problems recurring in the environment of evolutionary adaptedness of a species (Schmitt and Pilcher, 2004). The consequences of these modules are flexible and adaptive behaviors, which allow them to be inherited by future generations as tendencies to develop the same modules ontogenetically (Schmitt and Pilcher, 2004). However, modules do not fossilize. How, then, to recognize them?

Human psychological adaptations can be recognized by criteria such as high efficiency, high complexity, high modularity,

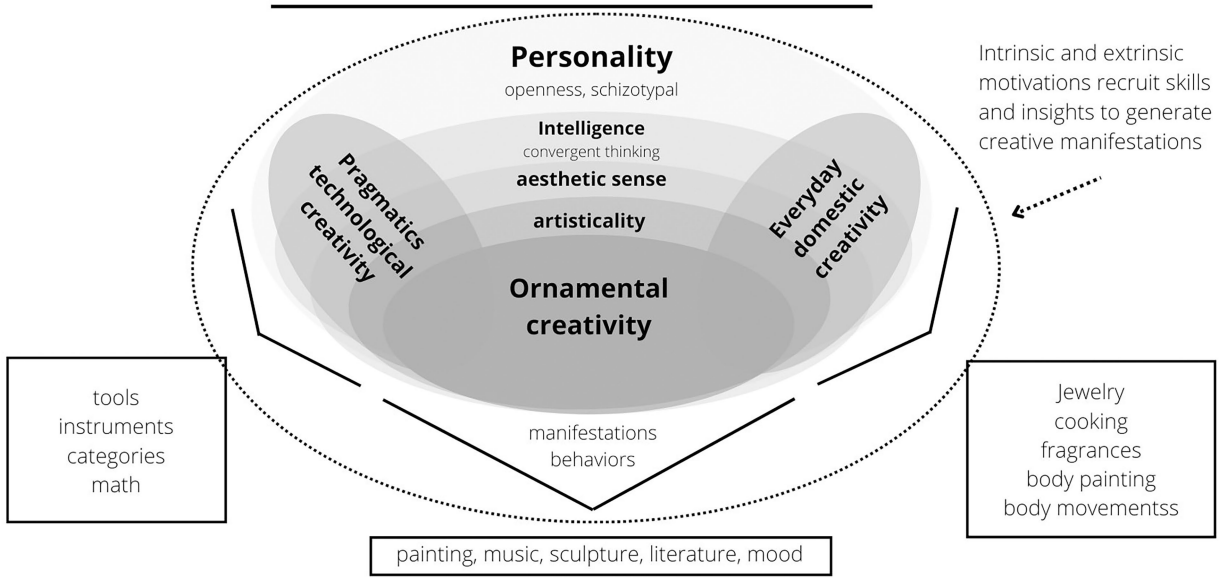

FIGURE 1
This scheme synthesizes the main variables associated with creativity and the possible relationships between them. A schematic illustration of a possible psychological structure of creativity. People who are more open to new experiences are more curious, flexible, and original, i.e., more creative and intelligent. Creativity involves divergent and convergent thinking, two characteristics associated with intelligence. Each type of creativity would operate according to its psychological mechanisms that are activated in the face of specific contexts and stimuli. These contexts and stimuli can have a reproductive nature, such as situations related to mate attraction or the visualization of a physically attractive partner. According to Feist (2001), ornamental creativity would have evolved by sexual selection because it was more conspicuous (e.g., making artistic pieces), just like the peacock's plumage (Møller and Petrie, 2002, but also Askew, 2014 and Thavarajah et al., 2016), while technical creativity would have evolved by viability selection because it was more beneficial for survival (i.e., making tools). We also propose that reproductive motivations can mobilize everyday creativity; after all, people use their creativity and aesthetic sensitivity daily to beautify themselves (e.g., using makeup and clothes that enhance the most attractive features of the face and body, respectively; Stephen and Luoto, 2021; Varella et al., 2017; Valentova et al., 2022). Importantly, sexual selection would have shaped the psychological propensities to perform these manifestations and to enjoy them.

low phenotypic variance, low genotypic variance, low heritability, universality across cultures and individuals (Miller, 2000). However, the criteria used to identify adaptations evolved by viability selection differ from those used to identify adaptations evolved by sexual selection (Miller, 2000). Some of the ornamental adaptations evolved by sexual selection are fitness indicators. Effective fitness indicators are costly and wasteful, like a peacock's plumage (Miller, 2000; Møller and Petrie, 2002; Askew, 2014; Thavarajah et al., 2016). Effective fitness indicators are also simple because they do not need to convey much information or to recruit many resources from the organism; they only need to "create a discriminable signal perceivable at a reasonable distance that reliably indicates a single quantity" (Miller, 2000). Fitness indicators must be sensitive to the covariation of different capacities to indicate their quality level, such as a peahen that notices a peacock's exuberant tail and becomes inclined to mate with it (Miller, 2000). Furthermore, fitness indicators tend to vary more in the population than adaptations shaped by viability selection (Miller, 2000). That greater variability allows individuals to be sexually selected according to the display of the most costly indicator (Miller, 2000).

This review integrates existing evidence to explore whether creativity is or is not a psychological adaptation evolved through sexual selection. There are earlier attempts to review evidence about the evolution of mental abilities (Miller and Todd, 1998; Klasios, 2013), including creativity (e.g., Karamihalev, 2013), but these earlier attempts do not use the nomological approach presented here (Miller, 2000; Schmitt and Pilcher, 2004; Lewis et al., 2017).

Before proceeding, we must make some critical caveats. We do not suppose that creativity has evolved *only* by sexual selection. The idea is that the selection of creative partners has possibly overemphasized this ability, allowing it to be co-opted for ornamental purposes (Miller, 2000, 2001; Winegard et al., 2018). We are also not assuming that a trait evolved by sexual selection originated from sexual selection. Traits can initially evolve by viability selection and then be co-opted and exapted by sexual selection (e.g., foot fetish or bodily piercings; Luoto, 2019a). We are also not saying that sexual selection is only about sex differences (see Hooper and Miller, 2008; Janicke and Fromonteil, 2021), nor only male-biased sex differences (Miller, 2013; Varella et al., 2014, 2017; Rosenthal and Ryan, 2022). Further, sexual selection is not a proximate motivation (e.g., Bach could have been religiously motivated when composing music but still could have increased mating success because of his musical success; see Miller, 2000; Varella et al., 2013). Also, sexual selection is not only mate attraction but also relationship maintenance (long-term), intrasexual competition, intersexual conflict, and parenting (Kenrick et al., 2010; Petrie, 2021; Shuker and Kvarnemo, 2021). Furthermore, we are not claiming that ornamental creative ability is the only route to differential reproduction; other such domains include, but are not limited to, sports, physical enhancements, resource acquisition, parenting skills, and nepotism (Manning and Taylor, 2001; Stephen and Luoto, 2021; Walter et al., 2021; Varella et al., 2022).

Definitions

Before approaching the multiple lines of evidence supporting creativity as a sexually selected trait, it is necessary to characterize creativity and its constituent variables (Figure 1).

Creativity, capacity, and performance

Creativity is synonymous with originality and effectiveness (Runco and Jaeger, 2012). Creativity includes original aesthetic manifestations and precise imitations (non-original) of aesthetic manifestations. Creative people are often called innovative and inventive (Said-Metwaly et al., 2017). Research on creativity has focused on individual-level cognitive aspects as divergent thinking and intelligence (Runco and Jaeger, 2012; Karwowski et al., 2016b) and personality, mainly plasticity and openness (Karwowski et al., 2016b). From a process-focused perspective, creativity is a process of blind variation and selective retention of original ideas (Jung et al., 2013). Creative products result from these individual characteristics and processes and manifest in multiple domains, such as everyday, scholarly, performance, scientific, and artistic domains (Kapoor et al., 2021).

All of these creative domains are costly because successfully navigating them depends on healthy brains, and healthy brains are costly (i.e., energy-intensive and susceptible to instabilities throughout development; Miller, 2001). However, ornamental or aesthetic manifestations may be more expensive because they require a lot of energy expenditure without the practical benefits in return (from the point of view of survival; Feist, 2001). That would be the case for creativity employed in such domains as art and body beautification.

Divergent and convergent thinking

Creativity is often operationally defined as divergent thinking, although the connection between creative capacity, creative achievement, and divergent thinking is not always clear (Hornberg and Reiter-Palmon, 2017). Divergent thinking is the ability to come up with solutions, answers, or questions in response to an open problem of a visual or verbal nature (Hornberg and Reiter-Palmon, 2017). The level of divergent thinking depends on originality and fluency, where originality is the number of responses distinct from those of other individuals, and fluency is the overall number of responses (Hornberg and Reiter-Palmon, 2017). Divergent thinking alone does not guarantee creativity, and a dose of convergent thinking is also needed, which is defined as the ability to select the most helpful ideas from among those generated by the divergent associative process (Cropley, 2006).

Personality

Openness, extroversion, and plasticity

Openness to experience and extroversion are the two personality components most consistently associated with

creativity (Karwowski and Lebuda, 2016; Hornberg and Reiter-Palmon, 2017; Vartanian et al., 2018). Individuals higher in openness to experience are flexible, curious, less conventional, and tend to seek sensations and stimulation. The search for sensations and stimulation are occasionally pointed out as characteristics of extroversion as well (Karwowski and Lebuda, 2016). Openness and extroversion make up a second-order factor called *plasticity* in a model called Big Two, which positively predicts creativity and beliefs about creative capacity (Puryear et al., 2017; Feist, 2019). Openness to experiences is divided in sub-dimensions. The *intellect* sub-dimension, linked to intellectual curiosity, predicts success in science; the *openness* sub-dimension, linked to desire of adventure, predicts success in the arts (Feist, 1998).

Schizotypal and autistic traits

Schizotypy is a personality feature that seems to be associated with creativity. Schizotypal traits are characterized by positive symptoms, such as magical thinking, unusual perceptual experiences, impulsive nonconformity, and negative symptoms, such as introversion, emotional instability, and cognitive disarray (Holt, 2019). Schizotypy is positively related to originality and divergent thinking (e.g., Wang et al., 2018; Holt, 2019). Exaggerated schizotypy leads to exaggerated and unexpected associations, which leads to exaggerated creativity, observed mainly in artists (Acar and Sen, 2013; Carter et al., 2019; Aguilera and Rodríguez-Ferreiro, 2021). Artists often display "healthy schizotypy," that is, higher creativity with no psychosis symptoms (Holt, 2019; Rantala et al., 2022). For example, poets tend to be more schizotypal, associating less obviously related ideas (Acar and Sen, 2013).

Autistic traits may also be associated with creativity (Baron-Cohen et al., 2001). Subjects with autism are inhibited in fluency and flexibility, but they have high levels of attention to details and originality; thus, subjects with autism are creative for different reasons, compared to the general population (for a meta-analysis, see Pennisi et al., 2020). Further, individuals with non-clinical autistic phenotype score lower on self-report creativity scales but exhibit greater creative performance in tasks involving drawing (Jankowska et al., 2019) and greater convergent thinking in anagram solution tasks (Abu-Akel et al., 2020).

Intelligence

Intelligence is also involved with creativity. Intelligence (i.e., *g* factor or cognitive ability) is the capacity to think, plan, solve problems, and adapt to the environment (Cattell, 1963). More specifically, intelligence is a general factor that emerges from performance in specific and interrelated domains (e.g., verbal, spatial, mathematical). It comprises the ability to reason (fluid intelligence) and the ability to acquire knowledge (crystallized intelligence; Cattell, 1963; see also Kovacs and Conway, 2019).

Solving problems requires intelligence. However, it also requires originality and thinking beyond the obvious. Thus, it is difficult to distinguish between creativity and intelligence. Creative people also tend to be intelligent (Kim, 2008; Karwowski et al., 2021). For example, a meta-analysis that included 11,418 people showed that success in mathematics (a field with performance closely linked to IQ) is associated with creativity (Bicer et al., 2021). For instance, fluid intelligence and originality are positively correlated (Silvia, 2008). Higher fluid intelligence is associated with a higher use of metaphors (Silvia and Beaty, 2012). Individuals with better memory show more divergent thinking (Silvia and Nusbaum, 2013). Those with higher divergent thinking have higher verbal, figural (Cho et al., 2010), and visuospatial reasoning (Kell et al., 2013). In other words, intelligence is a necessary condition of creativity (Guilford, 1967).

These relationships can also manifest in specific fields. Scientists need to analyze problems systematically (which demands intelligence) to reach innovative outcomes (creativity; Karwowski et al., 2021). Elaborating disruptive theories requires "thinking outside the box" and pattern recognition (Feist, 1998). On the other hand, artists can work by associating ideas more freely (Boyd, 2010; Karwowski et al., 2021). Thus, intelligence and creativity are essential to the arts and sciences, but technical fields are more cognitively loaded than the arts (Feist, 1998; Park et al., 2007).

Aesthetic sensibility

Aesthetic sensibility is the ability to assess the quality of sensory stimuli, such as abstract drawings and human faces. Eibl-Eibesfeldt (1989) describes three levels in human aesthetic psychology: (1) the basic level, which we have shared with most vertebrates and includes regularities, symmetry, harmony, and superstimuli; (2) the human-specific level, which is universal and relates to a human "sense of order" that underlies more specific attributes such as balance, rhythm, rhyme, and harmony; (3) the local culture level which is related to traditions and tastes shared within each human population.

The capacity to perform aesthetic appraisals (visual) is associated with intelligence, divergent thinking (figural but non-verbal), and personality (aesthetic openness; Myszkowski et al., 2014). Creative ornamental products are judged more on their aesthetic rather than technical merit, thus, they are expected to rely more on aesthetic sensibility (Feist, 2001). Personality also seems to be associated with aesthetic sensibility. People with greater openness to experience and schizotypy tend to appreciate artistic activities more (Feist and Brady, 2004) and have higher aesthetic motivation (Furnham, 2021).

It is necessary to emphasize that aesthetic and artistic sensibility are not synonymous. Esthetic sensitivity is a more general capability than artistic; the two are independent adaptations of each other (Varella et al., 2011). For example, many animals distinguish different types of human art; however, few animals find it as reinforcing as humans do (e.g., Varella, 2021), which points to the specificity of human artistic appreciation (Watanabe, 2013).

Levels of analysis and nomological network of evidence

Why do human beings employ their creativity in making original works of art? In line with previous proposals, we believe that part of the answer concerns sexual selection (Darwin, 1871; Low, 1979; Eibl-Eibesfeldt, 1989; Zahavi and Zahavi, 1997; Miller and Todd, 1998; Miller, 2000; Miller, 2001; De Block and Dewitte, 2007; Baer and Kaufman, 2008; Dutton, 2009; Varella et al., 2011, 2017, 2022; Verpooten and Nelissen, 2012; De Ridder and Vanneste, 2013; Karamihalev, 2013; Westphal-Fitch and Fitch, 2018; Luoto, 2019a). However, to test this hypothesis, the evidence must be collected from diverse levels of analysis (mechanisms, development, stimuli, phylogeny, and function; Tinbergen, 1963; Varella et al., 2012; Fitch, 2015). More recently, this approach has been expanded by investigating cultural, social, biological, and environmental inputs that activate psychological modules (Lewis et al., 2017; Luoto, 2019a). To answer whether creativity evolved by sexual selection, one needs to establish whether different sources of evidence converge toward indicating that ornamental creativity serves reproductive ends (Table 1).

Mechanisms

Genetic

There are polymorphisms in alleles of genes associated with dopaminergic systems, such as genes DRD2, DAT, COMT, DRD4, and TPH1, which are also associated with creative abilities and achievements (e.g., Reuter et al., 2006; Runco et al., 2011; Mayseless et al., 2013; Zabelina et al., 2016; Luoto, 2019b). Such genes also appear to play a role in sexual selection. For example, D4 dopamine receptor gene variation is linked to infidelity and sexual promiscuity (Garcia et al., 2010; Acevedo et al., 2020). Furthermore, genes associated with creativity and preference for creative partners are correlated, which shows that creativity has been subject to sexual selection at some level, perhaps by assortative mating (Verweij et al., 2014).

The selection of these genes linked to creativity has an ancient history. Modern humans have over 200 unique non-protein-encoding genes that regulate the co-expression of many other protein-encoding genes in coordinated networks underlying modern capabilities such as creativity, which are not found in chimpanzees or Neanderthals (Zwir et al., 2022).

These genes provide a part of the biological substrate necessary for creativity; however, they do not necessarily imply the development of creative capacities. Inheriting the propensity to develop the ability differs from having the ability, which depends on adequate stimulation throughout ontogenetic development as well as a host of other neurodevelopmental and biopsychosocial factors.

Neurotransmission and endocrine mechanisms

Dopamine has a role in creativity and sexuality, which suggests a link with sexual selection (Garcia et al., 2010; Acevedo et al., 2020). Dopaminergic activity is also related to psychomotor agitation behaviors such as eye blinking, that is a known clinical marker of accelerated dopaminergic activity observed in schizophrenic patients and non-clinical creative individuals (Akbari Chermahini and Hommel, 2009).

Testosterone is also related to creativity. For instance, men and women usually present a peak of musical talent from puberty (Hassler, 1992). Testosterone seems to enhance musical performance up to a certain level, but performance drops above this level (Hassler, 1992). Hassler (1992) conjectures that the positive effect of the hormone on musical creativity is mediated by its influence on spatial reasoning. In fact, children trained in a musical instrument have better indicators of intelligence and creativity (Benz et al., 2016; but see Mosing et al., 2014 for a discussion of genetic and practice effects). Artists of both sexes have a lower 2D:4D ratio, which suggests these individuals sustained more influence of testosterone during intrauterine development (Sluming and Manning, 2000; Crocchiola, 2014). Furthermore, there is a positive correlation between lower 2D:4D, amount of Nobel prizes, and scientific publications (van der Linden et al., 2020). On the other hand, concentrations of salivary testosterone and preference for sophistication levels of music are negatively correlated (Doi et al., 2018).

Hormonal influence in creative expressions can be detected in the patterns of drawings made by boys and girls. For instance, between 5 and 6 years old, boys draw more objects, use fewer colors and prefer cool colors, while girls draw more people and flowers, using more colors (Abraham, 2016). Girls with congenital adrenal hyperplasia (who consequently produce more androgens than the female average) present drawing patterns more akin to those made by boys (Iijima et al., 2001).

Though women with high testosterone display intense creative activity, the pattern seems more consistent in men. The masculine peak of artistic output happens in married men from 30 to 40 years old, extending beyond 40 for singles (Kanazawa, 2000). Men write 10 times more books and other literary outputs, accounting for more entries in the *Guinness World Records* (Lange, 2011; Lange and Euler, 2014).

So what, after all, is the role of testosterone in creativity? Androgen levels may be positively linked to increased performance and personality. For example, increasing performance in skills such as spatial reasoning and increasing willingness to take risks, compete, and seek novelty (Feist, 2019; Luoto and Varella, 2021). That would partially explain the male prominence in scientific and artistic fields, even without differences in creativity averages between the sexes (see Goldin and Rouse, 2000; Mosing et al., 2015).

TABLE 1 Predictions based on sexual selection and supporting evidence.

Question	Yes	No
Is there genetic influences in creativity?	Reuter et al. (2006) – polymorphisms of the dopamine D2 receptor gene DRD2; mathematical talent and convergent thinking; Runco et al. (2011) – genes DRD2, DAT, COMT, DRD4, TPH1 for verbal and figural fluency; Zabelina et al. (2016) – COMT and DAT for good cognitive flexibility and medium top-down control; Mayseless et al. (2013) – 7R polymorphism in the dopamine receptor D4 gene DRD4 in participants with higher divergent thinking scores and particularly flexibility scores; Mosing et al. (2014) – associations between music practice and music ability were predominantly genetic; Tan et al. (2014) – gene AVPR1A and SLC6A4; Zwir et al. (2022) – modern humans have genetic basis for creativity that chimpanzee and Neanderthal do not	
Is individual differences in creativity partially heritable?	Coon and Carey (1989) – Yes, but the effects of common environment were almost always larger; Grigorenko et al. (1992) – 0.44 in creative thinking in adolescents; Velázquez et al. (2015) – creative personality 50%–54%; Velázquez et al. (2015) – 38%–47% in creative drawing; Vinkhuyzen et al. (2009) – 60% in arts; Vinkhuyzen et al. (2009) – 83% in creative writing; Piffer and Hur (2014) – 61% in creative achievement; Kandler et al. (2016) – 62% in perceived and 26% figural creativity; Piffer and Hur (2014) – 43%–67% in creative achievement; Roeling et al. (2017) – 67% in the choice of artistic professions and of 43% in scientific professions; Mosing et al. (2015) – 51% among women regarding musical aptitude; 57% for men, and 9% for women in musical achievement; Mosing et al. (2014) – music practice was substantially heritable, 40%–70%	
Are androgens (T) associated with creativity?	Fukui (2001) – music listening decreased T in men and increased in women; Hassler (1992) – the better the musical performance, the wider the T range; Crocchiola (2014) – both male and female artists had significantly lower 2D:4D ratios, i.e., more T; Sluming and Manning (2000) – musical ability within the orchestra were associated with lower male 2D:4D, i.e., more T; van der Linden et al. (2020) – positive association between T indicators, intelligence and scientific achievement; Iijima et al. (2001) – girls with congenital adrenal hyperplasia make drawings typical of normal boys; Kanazawa (2000) – The productivity of single scientists takes longer to drop compared to married ones, and being married is associated with a drop in T	
Is there sexual dimorphism in creativity?	Baer and Kaufman (2008) – sex differences in specific domains of creativity; Beaussart et al. (2012) – men have a higher drive for creative display; Cheung and Lau (2010) – girls in the junior high grades excelled boys in verbal flexibility, figural fluency, figural flexibility, figural uniqueness, and figural unusualness; Ellis et al. (2008) – meta-analysis showing more precursors of appreciation art related traits in women/girls and precursors of production art-related traits in men/boys; Greengross et al. (2020) – meta-analysis showing that men have higher humor production ability and women have higher humor appreciation; He (2018) – female superiority in creative thinking-drawing during childhood and early adolescence; He and Wong (2011) – girls outperformed boys in thoroughness of thinking, boys outperformed girls in boundary-breaking thinking; Hemdan and Kazem (2019) – females' creative performance was significantly better than males' in the Creativity Index score; Hora et al. (2021) – meta-analysis showing male advantage in creative performance; Lange (2011) – men are more prone to verbal display production than women; Lange and Euler (2014) – most literature is produced by men of reproductive age, in a sample with 18th-, 19th-, and 20th-century writers; Low (1979) – ornamentation occur in both sexes, according with social status, wealth and power; Nakano et al. (2021) – Most studies reported gender differences, with 45.20% in favor of women, 23.28% in favor of men, and 31.50%, oscillating according to the content evaluated; Savage et al. (2015) – predominance of male music performances; Varella et al. (2017) – review showing higher women's inclination toward artistic domains; Varella et al. (2022) – women showed higher score in Visual arts and Musical arts, while men scored higher in Literary arts, Sport, and Circus arts; Varella et al. (2010) – women like to sing and men like to play musical instruments	Baer and Kaufman (2008) – review showing no sex differences in creative ability or creative achievement in general; Varella et al. (2010) – no sex difference in the amount to music listened per day

(Continued)

TABLE 1 (Continued)

Question	Yes	No
Is there only greater male variability in creativity?	He (2018) – greater male variability in China; He et al. (2013) – greater male variability in adolescents in China; He and Wong (2011) – greater male variability in China	Karwowski et al. (2016b) – greater male variability in originality and unconventionality and greater female variability in adaptiveness; Karwowski et al. (2016a) – higher variability of creative ability between males and females in Meru, Kenya; He et al. (2015) – greater female variability in young children and greater male variability in young adults; Ju et al. (2015) – The greater male variability hypothesis in creativity is generally supported., but is inconsistent across samples; Lau and Cheung (2015) – both male variability and female variability increased with time, according to the responses to both verbal and figural stimuli; Taylor and Barbot (2021) – no differences in drawing, writing and divergent thinking in american men and women adults and adolescents
Is creativity attractive in other cultures?	Buss and Barnes (1986) – WEIRD and non-WEIRD cultures; Kamble et al. (2014) – India; Li et al. (2011) – United States and Singapore; Souza et al. (2016) – Brazil; Chang et al. (2011) – China; Varella et al. (2022) – Brazil and Czech	Lebuda et al. (2021) – Meru
Does creativity increase attractiveness?	Madison et al. (2018) – mate value ratings were generally increased by MPQ for raters of both sexes; May and Hamilton (1980) – men were found to be more attractive when paired with specific music styles; Marin and Rathgeber (2022) – male faces paired with music were considered more attractive; Marin et al. (2017) – women, but not men, gave significantly higher ratings of facial attractiveness and dating desirability after having listened to music than in the silent control condition; Watkins (2017) – male creativity impacted attractiveness more than facial beauty; Gao et al. (2017) – Male faces paired with novel metaphorical compliments were rated as more attractive by women than those paired with literal ones; Greengross et al. (2020) – women prefer men high in production ability and men prefer women high in appreciation ability; Lange et al. (2014) – the main effect of verbal proficiency on attractiveness was supported	Bongard et al. (2019) – results show that musicians' profiles were not generally rated as more attractive than non-musicians; Lebuda et al. (2021) – creative potential negatively predicted the number of offspring
Is there an association between short-term sexual strategy (e.g., number of sex partners) and creativity?	Beaussart et al. (2012) – the link between creative activity and number of sexual partners was only significant for males; Clegg et al. (2011) – more successful male artists had more sexual partners than less successful artists but this did not hold for female artists; Nettle and Clegg (2006) – unusual experiences and impulsive nonconformity positively predicted the number of partners, when mediated by creative activity; Clegg et al. (2011) – more successful male artists had more sexual partners; Harrison and Hughes (2017) – greater musical ability had higher sex/drugs milieu scores, especially in women; Lange and Euler (2014) – literature production was correlated with number of mates; Mosing et al. (2015) – men with higher scores on the music achievement scale had more children; Varella et al. (2022) – positive association between literary arts, short-term mate value and sociosexual desire; women showed positive association between musical arts, short-term mate value; in men, circus arts were positively predicted by short-term mate value; White et al. (2018) – pursuing a short-term mating strategy was associated with selecting more atypical flirting behaviors	Harrison and Hughes (2017) – musicians and non-musicians do not differ in the number of sex partners; Varella et al. (2022) – in women, literary arts were not predicted by sociosexual behavior and not by the number of short-term relationships; in women, visual arts were not predicted by sociosexual behavior, attitude or desire and not by the number of short-term relationships; in women, musical arts were not predicted by sociosexual behavior and desire and not by the number of short-term relationships; in women, circus arts were not predicted by sociosexual behavior and desire and not by the number of short-term relationships; in men, literary arts, musical arts, circus arts and visual arts were not predicted by sociossexuality and also not by the number of short-term relationships

(Continued)

TABLE 1 (Continued)

Question	Yes	No
Is there an association between long-term sexual strategy and creativity?	Gao et al. (2017) – compliments on appearance using novel metaphors were preferred by women in a long-term relationship during the fertile phase; Kennair et al. (2022) – humor is more effective as flirtation when used by men in long-term context; Madison et al. (2018) – women's preference for long-term relationships increased in the face of exposure to better musical performance quality; Mosing et al. (2015) – males and females who scored higher on the musical aptitude or music achievement measures scored lower on sociosexuality; Prokosch et al. (2009) – men perceived as more intelligent are more desirable for long-term relationships; Varella et al. (2022) – in women, engagement in literary art was negatively correlated with SOI-Attitudes; in women, engagement in visual arts was predicted positively by parenting effort; women showed that musical activities were predicted negatively by SOI-Attitudes; in men, esthetically enhance bodily movements are positively related to the number of long-term partners; in men, literary arts were predicted positively by long-term mate value	Varella et al. (2022) – in women, literary arts were not predicted by sociosexual behavior and not by the number of long-term relationships; in women, visual arts were not predicted by sociosexual behavior, attitude or desire and by the number of long-term relationships; in women, musical arts were not predicted by sociosexual behavior and desire and not by the number of long-term relationships; in women, circus arts were not predicted by sociosexual behavior, desire but were by the number of long-term relationships; in men, literary arts, musical arts, circus arts and visual arts were not predicted by sociossexuality and also not by the number of long-term relationships
Is there an association between ovulatory phase, production and appreciation of creative manifestations?	Charlton (2014) – woman only preferred composers of more complex music as short-term sexual partners when conception risk was highest; Haselton and Miller (2006) – fertile women prefer creative over wealthy men for short-term relationship; Galasinska and Szymkow (2022) – women ideas were the most original during the phase of ovulation; Galasinska and Szymkow (2021) – positive correlation between the probability of conception and both creative originality and flexibility; Gao et al. (2017) – compliments on appearance using novel metaphors were preferred by women in a relationship during the fertile phase; Miller et al. (2007) – female dancers earned more tips in the ovulatory period, which suggests an increase in aesthetic sense and/or creativity to perform more seductive movements	
Does mating motives enhance creativity?	Griskevicius et al. (2006) – short-term or a long-term mating goal increased creative displays in men, but in women, only long-term mating goal increase creative displays	
Is creative tendencies spontaneous, precocious and intrinsically motivated?	Amabile and Gitomer (1984) – extrinsic motivation decreases children's creative performance; Bispham (2009) – intrinsic motivation makes people engage in music very early; Frois and Eysenck (1995) –creative and aesthetic capacities does not need artistic training; Morris (1962) – anedotic evidence that extrinsic motivation decreases creative performance of a chimpanzee; Trevarthen (1999) – early motivated to draw and dance; Varella (2021) – greater intrinsic motivation in students of artistic areas	
Does creativity and other g-loaded traits indicate genetic quality?	Arden et al. (2009a) – intelligence was a significant positive predictor of six of the eight abnormality counts, controlling for life style; Arden et al. (2015) – genetic relationship between intelligence and lifespan; Gajos and Beaver (2017) – Paternal age at birth appears to have a marginally significant nonlinear relationship with male children's verbal IQ scores; Banks et al. (2010) – meta-analysis showing that smarter people are a bit more symmetrical; Spencer et al. (2005) – adult male canaries, Serinus canaria, infected with malaria, Plasmodium relictum, as juveniles, develop simpler songs as adults compared to uninfected individuals, and exhibit reduced development of the high vocal center, HVC, song nucleus in the brain; Mosing et al. (2015) – in women, there was a positive correlation between musical aptitude and music achievement with genetic quality measures; in male, only between musical aptitude and general intelligence	Arslan et al. (2014) –higher paternal age at offspring conception did not predict offspring intelligence; DeLecce et al. (2020) – no evidence for a relationship between intelligence and ejaculate quality; Garamszegi et al. (2018) – the study did not find statistical evidence for MHC allelic diversity being related to either the estimates of song output and complexity or syllable composition

(Continued)

TABLE 1 (Continued)

Question	Yes	No
Does other species manifest creative behaviors and dispositions?	Bandini and Harrison (2020) – review of innovation in chimpanzee; Catchpole (1987) – review showing song birds as a trait evolved by sexual selection; Endler (2012) – according to some definitions of art, Great Bowerbirds are artists, judge art, and therefore have an aesthetic sense; Garamszegi et al. (2018) – males performing song bird in sexual selection; Kawase et al. (2013) – male puffer fishes construct large geometric circular structures on the seabed that played an important role in female mate choice; Lefebvre (2013) – review of innovation and intelligence in birds and primates; Lefebvre et al. (2004) – review of innovation and intelligence in birds and primates; Macdougall-Shackleton (1997) – review showing song birds as a trait evolved by sexual selection; Taylor (2014) – review showing that corvids have complex cognition, use tools and think in complex ways; Reader and Laland (2001) – evidence that individual variation in the propensity to innovate in terms of sex, age, and social rank in primates; van Schaik et al. (2016) – orangutans seem innovative only or mostly in captivity	
Does creativity (and other g-loaded traits) generate reproductive success in other species?	Coleman et al. (2007) – mimetic vocalizations accuracy predicted male mating success; Boogert et al. (2011) – review indicating sexual selection of cognitive traits in non-human vertebrates; Catchpole (1987) – males with more elaborate songs attract females before males with lesser elaborate songs; Chen et al. (2019) – female budgerigars shifted their preference to previously non-preferred males after these males demonstrated the ability to solve a problem that stumped the originally preferred males; Keagy et al. (2009) – problem-solving ability predicts mating success; Macdougall-Shackleton (1997) – review showing that song bird contributes to sexual selection as well peacock's tail; Minter et al. (2017) – females preferred mating with males who had better initial inhibitory control, a proxy for intelligence; Östlund-Nilsson and Holmlund (2003) – females were more attracted to males with nests containing sticks and spangles than to males with undecorated nests; Shaw et al. (2019) – superior male memory performance was associated with efficient offspring provisioning; Spritzer et al. (2005) – males with better spatial ability had larger home ranges and made more visits to different nestboxes than did males with poorer spatial ability	
Do human ancestors show sexual dimorphism in relation to creative manifestations?	Snow (2013) – persons who made hand stencils in the caves were predominantly females	Mackie (2015) – hand sprays were created by children and adults of both sexes suggesting non-exclusivity in activities associated with rock art creation; Rabazo-Rodríguez et al. (2017) – 11 hands belong to women and 10 to men

Neurobiological

Could brain architecture influence creativity and thus affect mate selection? More creative people exhibit brain laterality leaning to the right; however, the findings are mixed. For example, more schizotypal people use the right hand less (Somers et al., 2009) and show greater left asymmetry in the use of the senses (Lindell, 2014), which suggests greater right lateralization of the brain hemispheres. Whereas the left hemisphere is associated with access to more specific semantic networks, the right hemisphere is connected to more diffuse networks, connecting more general ideas in the semantic network, which may explain the activation of this hemisphere during divergent thinking (Lindell, 2014).

Lateralization of the brain hemispheres appears to be associated with testosterone. For example, boys with higher testosterone levels at puberty show greater right brain lateralization (Beking et al., 2018). Boys with higher levels of intrauterine testosterone showed the opposite lateral (i.e., left) activation at puberty (Beking et al., 2018), which seems more associated with an autistic profile (Castelli et al., 2002).

Social mechanisms

Universal preference for creative partners

If creativity evolved through sexual selection, it would logically follow that creative partners will be in higher demand. Studies have shown that creativity is a trait desired in romantic partners by Americans (Buss, 1989; Buss et al., 1990; Li et al., 2011), Brazilians (Souza et al., 2016; Novaes, 2022), Chinese (Chang et al., 2011), Singaporeans (Li et al., 2011), Indians (Kamble et al., 2014), and others (Buss et al., 1990; Watkins, 2017; but see Lebuda et al., 2021). The importance given to creativity varies. Creativity, especially of the ornamental/aesthetic type (Kaufman et al., 2016; see Figure 1), starts

to matter in mating as soon as primary preferences (such as physical beauty) are satisfied (Li et al., 2002). Creativity is so essential in attractiveness that it can make someone more attractive than social status (Buss and Barnes, 1986; Novaes, 2022), physical appearance (Watkins, 2017), or intelligence (Prokosch et al., 2009).

Creativity keeps partners together

The power of creativity can explain the universal preference for creative partners in partner retention. Couples that engage in novel and stimulating activities become closer (Aron et al., 2005). Thinking about romantic relationships stimulates creativity more than thinking about casual sex (Campbell and Fletcher, 2015). However, the consequences change depending on the type of creativity considered. For example, while everyday creativity increases romantic love, artistic creativity decreases it – but they did not elaborate explanations for these results in evolutionary terms (Campbell and Kaufman, 2017).

Psychopathological mechanisms

Fitness indicators are subject to instability in their development, affecting their carriers' reproductive success (Klasios, 2013). For example, peacocks may have trouble developing their extravagant plumage because of deleterious mutations, environmental stress, or parasites (Møller and Petrie, 2002; Askew, 2014; Thavarajah et al., 2016). Likewise, developmental problems can impair brain development and the display of mental and, by extension, creative ornaments (Miller and Todd, 1998; Shaner et al., 2004; Del Giudice et al., 2010). Some psychological disorders may result from ontogenetically or evolutionarily disturbed mental adaptations (Figure 2; Rantala et al., 2019, 2021, 2022).

Schizotypal traits are linked to mental ornaments that involve creativity and can be displayed in various ways, such as verbally and visually (Shaner et al., 2004). Dysfunctional levels of schizotypy characterize schizophrenic people, and they suffer from verbal difficulties, such as a disorganized expression of thoughts through language (Shaner et al., 2004). Despite high levels of schizotypy, schizophrenic and bipolar people have difficulty expressing creativity (Acar and Runco, 2012; Acar et al., 2018). The association between schizotypy and creativity follows an "inverted U" shape, growing to a point beyond which one decreases while the other increases (Abraham, 2014). That explains the ambiguous findings on disorders and creativity (Acar and Runco, 2012; Acar and Sen, 2013; Acar et al., 2018).

Mood disorders are also associated with creativity only to a certain extent. A meta-analysis showed that (verbal) creativity and bipolarity are positively associated (Taylor, 2017). Epidemiological analyses reveal a higher prevalence of bipolar disorder among academics and artists (Kyaga et al., 2011). Likewise, people with a high expression of autistic traits are more prevalent in fields such as engineering and mathematics (Morsanyi et al., 2012). However, the association between creativity and success declines as the severity of psychopathological symptoms increases (Pennisi et al., 2020) – see Figure 2.

The shared genetic basis between mental disorders, personality, and creativity can explain these associations. In other words, the genetic risk of developing schizophrenia and bipolar disorder predicts artistic achievements positively (Power et al., 2015). More precisely, higher polygenic risk for bipolar disorder is associated with a higher tendency for divergent thinking (Takeuchi et al., 2021). Also, the polygenic risk of developing schizophrenia is positively associated with risk behavior (Li et al., 2020), which is linked to creativity (Feist, 2019). The same genetic component involved in verbal ability is involved in schizophrenia, which may explain verbal proficiency drawbacks in schizophrenic patients (Jonsdottir et al., 2021). Similarly, autism shares some of the genetic basis of intelligence, which can explain the relation of the autistic phenotype with the improvement in cognitive performance and convergent thinking, which are essential to creativity (Crespi, 2016). In addition, there may be some relationship between autism, creativity, and artisticality (Kellman, 1998; Spikins et al., 2018).

Mechanisms associated with personality

The connection between creativity and personality occurs on many levels. For example, creativity, intelligence, openness to experience, and extraversion share a genetic basis (Kandler et al., 2016), which may be a consequence of assortative mating (Conroy-Beam et al., 2019). This genetic basis is involved in dopaminergic systems (Gocłowska et al., 2019). Such systems are activated during process that constitute creative thinking, such as divergent thinking, exploratory activities, and the search for novelty (Vartanian et al., 2018; Gocłowska et al., 2019), commonly associated with individuals high in extroversion and openness (Feist, 2019).

In relation to sex differences, studies have shown that women are more open to experiences than men, whereas others found no gender distinction (Weisberg et al., 2011; Natividade and Hutz, 2015; Schmitt et al., 2017). Differences may be found in the openness to experience subfactors, with women more open than men and men more intellectual than women (Weisberg et al., 2011). Regarding extroversion, women, on average, are more extroverted than men (Weisberg et al., 2011; Natividade and Hutz, 2015; Schmitt et al., 2017).

Psychological mechanisms: Capacity, perception, and motivation

Creative behaviors may result from psychological structures evolved to solve adaptive problems. Such psychological structures consist of capacities, perceptions, and motivations shaped to generate adaptive outputs (Lewis et al., 2017). This framework has recently been applied to "artisticality" (Varella et al., 2011, 2017; Luoto, 2019a; Varella, 2021) and "musicality" (Bispham, 2009). Here,

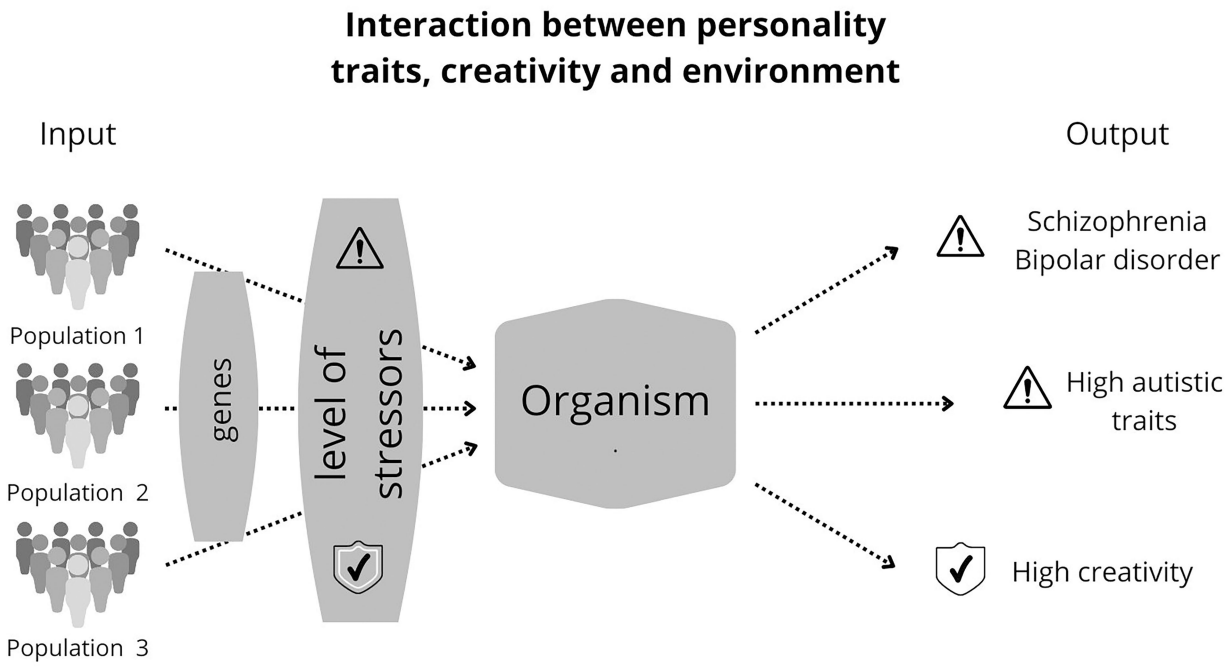

FIGURE 2
Consequences of stress on people with schizotypal and autistic traits. Creative people are moderately schizotypal. In other words, schizotypal people are often imaginative, associating ideas in unusual ways. People with schizophrenia and bipolar disorder also have these characteristics, sometimes manifesting them in a "dysfunctional way," e.g., in a paranoid way, but not in an artistic way. That "dysfunctional manifestation" of creativity can occur because of stressors that disrupt normal nervous system development. Thus, individuals with the same genetic propensities for high creativity may manifest it in the form of a disorder or the neurotypical form, depending on how much the stressors have affected ontogeny. This figure shows three examples of populations, each subjected to different levels of environmental stress. The symbol with "!" means high levels of stressors, while the symbol "ok" means tolerable levels of stressors, that is, those that do not significantly impair neural development.

we propose a similar psychological framework for creativity. That is, creative behaviors of any kind (everyday, academic, performative, scientific, and artistic; Kapoor et al., 2021) will result from evolved psychological structures (creative capacity, aesthetic sense, and motivation) capable of generating cultural creative outputs.

Psychological adaptations are related to intrinsic motivation to perform certain activities. In fact, children and adults from different cultures exercise their creative capacity in games and other activities in search of fun, pleasure, and affective social interactions (Boyd, 2010; Moraes et al., 2022). This creative play may or may not involve aesthetic sensibility (e.g., drawing and painting; Myszkowski et al., 2014, 2018). Further, this exercise of creative and aesthetic capacities is so spontaneous that it does not even need artistic training (Frois and Eysenck, 1995; Boyd, 2010).

In other words, there is motivation early on in development to put creative and aesthetic capabilities into action. Motivation can be defined as organizing and coordinating aspects of behaviors that arise from a wide variety of internal, environmental, and social sources and is manifested at many levels of behavioral and neural organization (Shizgal, 2001). There is intrinsic and extrinsic motivation. Intrinsic motivation is the will or impulse to engage and sustain engagement in a given activity; extrinsic motivation involves engaging in an activity to have rewards external to the activity itself (Ryan and Deci, 2017). People often engage in creative activities because they are intrinsically motivated by the activity, as in the case of involvement with music (Bispham, 2009) and art (Varella, 2021). It is not by chance that individuals who choose art-related courses are more motivated by intrinsic reasons (e.g., using their talents) than extrinsic ones (e.g., parental and media influence, earnings, status; Varella, 2021).

Furthermore, intrinsic motivation did not vary significantly between arts careers (e.g., music, dance, theater, visual arts, and literary studies), suggesting a specific motivational system for general artistic abilities that underlies the expression of all artistic modalities (Varella, 2021). Offering rewards (extrinsic motivation) for creative performance can even decrease the quality of products generated by children (Amabile and Gitomer, 1984) and possibly in other animals, as anecdotally observed in a chimpanzee (Morris, 1962). Motivation in this area appears very early in development (Bispham, 2009; Varella, 2021). Children already draw, and babies are entertained by the mother's vocalizations and movements, which may indicate the perception of rhythm, fundamental for appreciation and aesthetic productions in music and dance (Trevarthen, 1999; Bispham, 2009).

Ontogenesis

Some people are more creative than others, which is spontaneously evidenced since childhood (Feist, 2004). As children

age, more cognitive maturity ensues, and it may be accompanied by a greater investment of creativity in specific domains, such as visual art, music, literature, or science (Barbot and Tinio, 2015). If creativity has evolved by sexual selection, it is expected that its increase follows changes beginning at puberty, when there is a boost in the release of androgens (Miller, 2000; Miller, 2001). However, that boost is not linear. During puberty, there is a drop in gray matter and the number of dopamine receptors; this likely explains the decrease in the cognitive aspect of creativity and the increase of the aspects related to personality, such as openness, thrill-seeking and novelty (Barbot and Tinio, 2015).

The relationship between androgens and creative expression could indicate the existence of sexual dimorphism in creativity, but, considering physical and psychological characteristics in general, humans have milder sexual dimorphism than other species (Janicke and Fromonteil, 2021). More specifically, humans tend to be more monomorphic because both sexes are heavily invested in offspring and, therefore, more selective in choosing mates (Stewart-Williams and Thomas, 2013). That likely led both females and males to evolve and develop fitness indicators for mate attraction (Stewart-Williams and Thomas, 2013). That would explain the similarity in creativity between men and women and the greater variability in different creative domains in both sexes (details in Table 1; Varella et al., 2017; Nakano et al., 2021).

Evidence on the variability of creativity in childhood is mixed (Lau and Cheung, 2015; He, 2018). There is evidence of greater male variability in adulthood (He and Wong, 2011; He, 2018), which has been replicated in several countries in African (Karwowski et al., 2016a) and European (Karwowski et al., 2016b) continents, as well as the United States (Taylor and Barbot, 2021), with a few exceptions (He et al., 2013; Ju et al., 2015; Lau and Cheung, 2015). For instance, a study conducted in Poland reported greater male variability in all ages in the performance at a task that involved completing a drawing as creatively as possible (Karwowski et al., 2016b). In a second study, various domains of creativity were examined in a sample of people of diverse ages and schooling. There were no sex differences in the means in performance or potential, but there was sex differences on specific domains of creativity (e.g., Karwowski et al., 2016b), as well as a greater male variability (e.g., Karwowski et al., 2016b).

However, the variability in creativity in each sex may also depend on the creative domain evaluated. He (2018) measured divergent thinking and creative problem-solving in Hong Kong university students. Greater male variability was found in divergent thinking tasks involving images but not verbal tasks (He, 2018). See Table 1.

Average creativity between men and women is highly variable among studies, even among creative domains (Abraham, 2016). In childhood, girls perform better than boys (Cheung and Lau, 2010; Hemdan and Kazem, 2019). In adults, most studies show female superiority (45.2%), while others find no sex differences (31.5%; Nakano et al., 2021). In a study on 3–7-year-olds, girls were better represented at the top of creativity distribution, while in the age range of 19–23-year-olds, the boys had the best representation at the top (He et al., 2015). In a longitudinal study that lasted four years in Hong Kong, boys and girls from 8 to 11 years old displayed improvement in creativity, with female superiority (He, 2018), but boys' creativity increased from age 15 and surpassed that of girls at 16 (He, 2018).

The disparity between men and women may also be perceived in personality traits associated with creativity. For example, teenage girls are more extroverted and open to experiences (personality traits associated with creativity) than boys of the same age, which corroborates the evidence of higher creativity in girls in this age range (De Bolle et al., 2015). These disparities in personality may stem from male and female timing in sexual maturation. Girls enter puberty earlier, which seems to explain their improvement in socialization and cognitive performance ahead of boys (De Bolle et al., 2015).

Phylogenesis

If creativity is a result of evolution, it is to be expected that there would be similar characteristics in other species (e.g., Cauchard et al., 2013). Likewise, if this process is partly due to sexual selection, it makes sense to assume that creativity plays a role in the reproduction of humans and other species.

Creativity and innovation in other species

Species that develop in hostile and unstable environments tend to have an intense social life, large brains, extended youth, and an ability to learn; that is to say, these species are marked by higher phenotypic plasticity, which carries advantages in solving adaptive and new problems (Lefebvre, 2013). This is the case with some primates, including *Homo sapiens*, and birds, like crows (Lefebvre et al., 2004; Sanz et al., 2009; Lefebvre, 2013; Bandini and Harrison, 2020). For instance, crows choose hook-shaped twigs, ideal for "fishing" food from hard-to-reach places (Taylor, 2014). Chimpanzees fashion sprigs to feed on termites from inside trunks (Bandini and Harrison, 2020). An anecdotal sample showed that a male chimpanzee used plant leaves and branches to emit specific sounds that caught females' attention (Bandini and Harrison, 2020).

Animals more inclined to be innovative tend to be neophilic, i.e., they run more risks and seek novelty and sensations (Kaufman et al., 2011). Orangutans illustrate the case of a neophobic primate known for innovating less in natural environments; on the other hand, chimpanzees are more neophilic (van Schaik et al., 2016; Bandini and Harrison, 2020). Just like humans, these plastic behaviors are associated with dopamine in various brain systems (Kaufman et al., 2011).

There has been shown sex differences in innovation. Creativity can be used by the less dominant sex as an alternative sexual and foraging strategy, as it happens among chimpanzees, where females are the most habitual tool users (Reader and Laland,

2001). However, Lefebvre (2013) states that males innovate more than females not only in primates, but also in birds and in ancestral humans. Using tools to enable more accessible food gathering brings evident benefits for survival and less obvious ones for reproduction. Males with privileged access to food gain advantages in the social hierarchy, ensuring access to allies and females (Reader and Laland, 2001).

Ornamental creativity: The case of bowerbirds

Some displays of creativity are more ornamental or aesthetic than pragmatic, impacting mating (Miller, 2001). The bowerbird is a classic example of an ornamental manifestation of cognition in non-human animals. The male satin bowerbird increases its reproductive success by decorating the bower with blue objects (Borgia, 1986). To do this, males need an aesthetic sense to decorate the bower, just as females need an aesthetic sense to evaluate the best-decorated bower. Depending on the definition of art and aesthetics used, the bowers produced and appreciated by bowerbirds can be considered non-human examples of art (Endler, 2012). This aesthetic sense needs a certain cognitive complexity typically present in altricial species (Boogert et al., 2011).

In fact, females in several non-human animal species seem to prefer males who tend to exhibit better cognitive performance. For instance, males that build the fanciest bowers have greater reproductive success, and these males are better at problem-solving (e.g., getting food from a box; Keagy et al., 2009). Also, female budgerigars remain closer to males that manifest more complex problem-solving (Chen et al., 2019). The same behavior is observed in eastern meadow voles (*Microtus pennsylvanicus*) and North Island robins (*Petroica longipes*; Spritzer et al., 2005; Shaw et al., 2019). These behaviors suggest that males who exhibit greater cognitive complexity tend to attract females. However, research is unclear as to whether exhibiting cognitive behaviors attracts females or whether some other trait, indirectly correlated with cognition, generates that attraction.

Ornamental creativity in *Homo sapiens*

As an altricial species (or a secondary altricial species, see Portmann, 1969), humans also have a large brain and prolonged development that favor cognitive flexibility. The genus *Homo* seems to have been expressing itself creatively for thousands of years. *Homo erectus* already used pigments 800,000 years ago likely for decorative purposes in Southern Africa; 450,000 years ago, they already scratched arbitrary lines on mollusk shells, just as chimpanzees seem to do; 40,000 years ago, *Homo sapiens* made cave paintings and decorated tools from the American continent to Asia (Høgh-Olesen, 2018).

The advent of decorated tools suggests that technical and ornamental displays of creativity have co-evolved. Tools probably started to be produced to solve practical problems, but ornamenting these tools could have social functions (e.g., identification in the group hierarchy), which characterize weapons and uniforms in more recent human history (Menninghaus, 2019). However, these creative and artistic manifestations may be collective activities of the whole group, not restricted to specialized individuals, i.e., professional artists (e.g., Mackie, 2015; Rabazo-Rodríguez et al., 2017).

A specific (and controversial) hypothesis about Paleolithic tools' pragmatic and ornamental function is that of the sexy handaxe (Kohn and Mithen, 1999). According to this hypothesis, handaxes would have the same ornamental function as the bowerbird's decorated bower (Kohn and Mithen, 1999). An effective handaxe just for hunting would not need to be overly symmetrical, big, or heavy, making them difficult to use as a weapon (Menninghaus, 2019). Thus, such artifacts could also have social functions, such as signaling identity and potential as a reproductive partner, which could indicate the level of status, dominance, and/or aesthetic skills. It is also possible that the symmetry of artifacts takes advantage of sensory system biases that make specific patterns more attractive than others (such as more symmetrical faces; Gangestad and Thornhill, 2003). In the aggregate, such findings as reviewed above suggest that displaying aesthetic and ornamental capabilities linked to creativity is not restricted to the present but also to the evolutionary past.

Function

The available evidence indicates that creative manifestations—mainly ornamental ones, but also pragmatic ones—may play a unique role in attractiveness. But why? In the following sections, we will examine evidence related to various theories (see also Davis and Arnocky, 2022).

Good genes and mental fitness

According to the good genes model, traits selected by sexual selection confer indirect advantages to the offspring, such as genetic quality (see Davis and Arnocky, 2022). "Providing" good genes is essential in species with low male parental investment (Trivers, 1972; Zahavi, 1975). For example, peacocks display their striking plumage, and bowerbirds display their decorated bowers that serve as honest signals of genetic and/or phenotypic quality (Zahavi, 1975; Borgia, 1986). The mental fitness hypothesis uses the same logic applied to the mind. According to that hypothesis, higher-than-average creativity and intelligence would lead to improved reproductive success by indirectly indicating genetic quality (Miller and Todd, 1998; Miller, 2000, 2001; Karamihalev, 2013). Genetic quality means fewer harmful mutations (Klasios, 2013). These mutations can disrupt the organism's development, including the brain (Klasios, 2013). Therefore, displaying creative products ultimately indicates that the producer is healthy and has an efficient brain (Miller and Todd, 1998; Klasios, 2013).

Genetic quality of creative individuals

If the mental fitness hypothesis is correct, there will be associations between creativity (and related cognitive variables) and indicators of genetic quality, and these indicators may be associated with health (Zahavi, 1975; Miller, 2000). One of the cognitive performance indicators most associated with health is intelligence (possibly the cognitive part of creativity). Higher intelligence is related to longevity and a lower risk of suffering from certain diseases, such as hypertension, heart problems, and Alzheimer's disease (Arden et al., 2009a, 2015; Deary et al., 2019). That can be explained by the fact that intelligent people have healthier behaviors and would be subject to less risk (Gale et al., 2010).

Biological factors can also explain the relationship between intelligence and health. Deleterious mutations cause instabilities in the organism's development, impairing brain development and cognitive performance (Gajos and Beaver, 2017). Paternal age is a known indicator of detrimental mutations (Gajos and Beaver, 2017). Children of older fathers are more at risk of having autism, attention-deficit/hyperactivity disorder, bipolar disorder, schizophrenia, and depression (D'Onofrio et al., 2014; Gajos and Beaver, 2017; Woodley of Menie and Kanazawa, 2017). More specifically, older fathers tend to have a little less intelligent children (even controlling for other variables), with a reduction of.84 to 1.23 points in *g* factor for each additional decade in paternal age since conception (Arslan et al., 2014; D'Onofrio et al., 2014; Woodley of Menie, 2015; Gajos and Beaver, 2017).

It is expected that characteristics affected by instabilities in development are interrelated. For instance, developmental disturbances lead to higher bilateral asymmetry in the body; the higher the asymmetry, the lower the IQ (Banks et al., 2010). Genetic mutations that hinder normal development also impact the quality of sperm (Jeffery et al., 2016). One study found a positive correlation between sperm quality and intelligence (Arden et al., 2009b); however, another, more recent one, did not (DeLecce et al., 2020).

Geary (2019) suggested that detrimental mutations that affect cognitive performance involve small inefficiencies in cellular processes. More precisely, genetic problems would affect the workings of cellular organelles, such as mitochondria, in charge of cell energy production and operation of the immune system and the brain; difficulties in cellular energy production would affect neurons, which in turn would impact brain functioning (Geary, 2019). Up to now, this notion seems largely speculative, though promising (see Savi et al., 2020; Ujma and Kovacs, 2020). However, other studies provide little supporting evidence for this hypothesis, while some studies have even reported contradictory evidence. For example, Mosing et al. (2015) showed significant correlations between musical aptitude and genetic quality measures only in females, when one would expect to find this result also in men.

Health and cognitive performance may also be associated in other species. For instance, better cognitive performance in bees often indicates an absence of parasites (Gegear et al., 2006). That happens because fighting infectious agents is as costly as investing in complex cognition; thus, there is a trade-off between immune function and cognitive performance (Boogert et al., 2011). Thus, being healthy, and having good learning and problem-solving skills simultaneously, can reflect high levels of genetic quality, or low parasite load. That is compatible with evidence showing that males who are better at problem-solving and learning and have better inhibitory ability have healthier offspring and are, on average, preferred in mating contexts (Spencer et al., 2005; Minter et al., 2017).

Though cognitive qualities imply health, these qualities may be valuable in the mating market for providing more advantages in obtaining resources that may later increase reproductive success (Stephen and Luoto, 2021). Cauchard et al. (2017) suggest this by showing that males of a bird species with better cognitive performance care more about their offspring. However, this hypothesis does not explain why females of promiscuous species (i.e., in which the females do not need the male's resources) also mate with males having good cognitive qualities (Borgia, 1986; Keagy et al., 2011, 2012).

Variability and sexual dimorphism

Fitness indicators vary more than traits evolved for other functions not related to fitness. This variation is due to the number of genes associated with these traits (pleiotropy), the susceptibility to mutations that affect development, and the sexual selection pressure that selects the trait according to the "more is better" logic (Miller, 2000). The heritability of attributes, manifestations, and achievements in a creative domain in men and women suggests that creativity can be a fitness indicator (details in Table 1).

If creativity is a mental adaptation evolved by sexual selection to indicate fitness potential, then it is expected to show high variability in the population due to the large number of genes involved in the expression of this adaptation (pleiotropy; Miller, 2000). Creativity shows high heritability and high variability in men and women, depending on the creative domain considered (see Miller, 2013; Varella et al., 2017; Table 1).

Yet what role does creativity have in attractiveness? Are there sex differences in the role of creativity in attractiveness? Men seem more interested than women in creative activities, and more engaged than women in creative behaviors in the past, according to a scale used to measure interest in creative activities and creative behaviors (Beaussart et al., 2012). Men are also more creative with unexpected flirting behaviors (White et al., 2018). A recent meta-analysis showed a male advantage in creative performance that the authors attributed to cultural factors (Hora et al., 2021). However, previous reviews found no sex/gender differences in creative ability or creative achievement in general but in specific domains of creativity (Baer and Kaufman, 2008).

Why are men more engaged and prominent in art than women, despite their similar creative performance? Men and women can use their creative potential in different ways. For instance, in comedy women use their creativity more in assessing

humor, while men use theirs more in producing humor (Greengross et al., 2020). Similarly, one study mentioned the presence of more women (69%) than men in the front rows of music concerts (Sluming and Manning, 2000).

Sociocultural factors can also play a role in these sex differences. Indeed, men are better represented in artistic fields, but it is also a fact that for most of history, women have had fewer chances and fewer incentives to engage and achieve prominence in art (Varella et al., 2017; Rosenthal and Ryan, 2022). A meta-analysis of cross-cultural studies shows that women are "more artistic," which suggests that sex differences in engagement in these fields may vary culturally (Ellis et al., 2008). Varella et al. (2010) found that women actually appreciate more than men an unknown instrumental piece of music, that women report to appreciate more music in general than men, and that women also report singing more than men. Another study showed a greater number of women in samples of gifted students in art-related courses (Holahan et al., 1995). Given the divergent findings, further studies are needed to verify whether sex differences concerning artistic manifestations exist and whether are more explainable by psychological or cultural factors (Hora et al., 2021).

The influence of creativity on attractiveness

Anecdotal evidence suggests that creativity is attractive. Creative geniuses in art and science (e.g., Lord Byron, Albert Einstein, Pablo Picasso, Van Gogh, and Charles Chaplin) are known for having had many casual sex partners, marriages, and children (Karamihalev, 2013). We have already shown evidence that creativity is universally attractive, but in this section, we will discuss specific evidence in more detail.

It is difficult to say whether this is a causal relationship or merely an association, but studies have shown that, for example, men with a larger artistic output (e.g., poets and painters) have a larger number of sexual partners (Clegg et al., 2011; Beaussart et al., 2012; Lange and Euler, 2014). Mosing et al. (2015) showed that boys had higher music achievement than girls. Furthermore, there was a negative association between sociosexuality, music aptitude and achievement in both sexes (Mosing et al., 2015). The authors indicated that these results are in accordance with the mutual mate choice model, in which both sexes utilize music to attract partners in a long-term reproductive strategy. But other studies show the opposite in terms of reproductive strategy. For instance, female and male poets and painters had more sexual partners (i.e., short-term reproductive strategy) than controls from other non-artistic professions (Nettle and Clegg, 2006). After reading vignettes describing a man with different levels of creativity and resources, women consider creative men with fewer resources as more attractive than less creative men with abundant resources; an limitation of this study was the low number of participants (41 women; Haselton and Miller, 2006). Male faces become more attractive if presented alongside creative text or music (Marin et al., 2017; Watkins, 2017; Marin and Rathgeber, 2022). The attributed attractiveness is even greater when men produce more complex (compared with less complex) musical patterns (e.g., Charlton, 2014; see Bongard et al., 2019). Furthermore, men, more than women, prefer songs with more complex, technical musical patterns and those less present in popular styles of music (Colley, 2008; Ord, 2020). The male preference for complex and technical music may be explained as a consequence of the evolved aesthetic propensities to impress women (which contradict the mutual mate choice model). An alternative explanation is that observed male preference is a byproduct with no signaling component *per se*. Artists and other creative people tend to be more open to experiences than other professionals, and more open people are likely to be more erotically inclined and less sexually restricted (Nativídade and Hutz, 2016).

But the artistic propensities of both sexes can be used to attract mates (intersexual selection) and to compete for mates (intrasexual competition; Varella et al., 2022). For example, women propensities to visual and circus arts were related to intersexual selection, while literary and musical arts were related to both elevated inter-and intrasexual selection (Varella et al., 2022). In men, circus arts were related intersexual selection and visual arts with intrasexual competition (Varella et al., 2022).

Everyday displays of creativity also seem to impact attractiveness. For instance, women are attracted by men who can employ metaphors, make them laugh at jokes, and have significant verbal prowess (Lange et al., 2014; Gao et al., 2017; Greengross et al., 2020). Summing up, ornamental signs of creativity seem to be mainly linked to male attractiveness, though some suggest they also increase the attractiveness of creative women (Kaufman et al., 2016). However, some studies contradict the association between creativity, openness, and unrestricted sexuality. For instance, though better musical performance increases attractiveness (Madison et al., 2018), individuals with a more prominent musical output take longer to have their first intercourse, and women have fewer sexual partners as their musical output grows (Mosing et al., 2015).

Creativity, attractiveness, and reproductive strategy

In general, costly signaling develops in promiscuous species, in which the only expected male investment is genetic quality. Humans are diversified in their reproductive strategies and may enter short-term relationships in some situations, a kind of partnership akin to the promiscuity of other species (Gangestad and Simpson, 2000; Schmitt, 2005; Buss and Schmitt, 2019). Hence, if creativity signals good genes, it is expected that creative and original people are more attractive for casual relationships, as it seems to occur among bowerbirds (Borgia, 1986; Miller, 2001; Keagy et al., 2009). Findings regarding a preference for creative partners for short-term relationships are inconclusive at best. Some studies propose that women prefer creative men for long-term partnerships (Madison et al., 2018), for short-term ones (Haselton and Miller, 2006; Charlton, 2014; Mosing et al., 2015), or both (Griskevicius et al., 2006; Prokosch et al., 2009).

For instance, Madison et al. (2018) and Charlton (2014) have shown that presenting men with music increased their

attractiveness for short-term relationships. Prokosch et al. (2009) recorded men as they performed four activities demanding verbal intelligence and creativity and then showed the videos for women to evaluate them. Intelligence predicted male attractiveness for long-term relationships, while creativity predicted attractiveness for short-and long-term relationships (Prokosch et al., 2009). Similarly, in two studies, male artists had a greater interest in long-term relationships, but one of the studies showed an association between being more successful in the career and the larger quantity of children, a sign of a larger reproductive effort characteristic of short-term relationships (Clegg et al., 2011; Mosing et al., 2015). The attractiveness of creativity in short-and long-term relationships may contradict the relationship between creativity and good genes; but it may also indicate that, precisely because it signals good genes, creativity becomes attractive in long-term relationships, in which people are more demanding (for other evolutionary theories, see Dissanayake, 2008; Luoto, 2019a; Mehr et al., 2021; Savage et al., 2021).

Fertile window

If creativity is a kind of costly signaling, creative men will be more desirable to women in the fertile window of the menstrual cycle. The higher chance of getting pregnant at this time would heighten sexual appeal (Stern et al., 2021) and the preference for men with a better genetic constitution (see Thomas et al., 2021). Some evidence confirms that women in their fertile window would rather have casual relationships with creative men (e.g., Charlton, 2014; Marin et al., 2017). Haselton and Miller (2006) showed that women in the fertile window preferred short-term relationships with creative men (regardless of the men's amount of resources). Furthermore, women were more creative during their fertile phase (Galasinska and Szymkow, 2021; Galasinska and Szymkow, 2022).

Lack of reproductive success in psychopathological scenarios

Some psychopathologies may be dysfunctional expressions of ornamental creativity as if the fitness indicator had failed or overshot its optimum. Indeed, people with schizotypal traits attract partners using metaphors and verbal proficiency (Lange et al., 2016; Gao et al., 2017). On the other hand, people with schizophrenia have cognitive and linguistic problems that make it difficult to express such "verbal ornaments" and, therefore, also impair their attractiveness (Shaner et al., 2004). Schizophrenic symptoms peak at puberty, when levels of circulating androgens increase, influencing secondary sexual traits. The increase in symptom severity is related to dopaminergic antagonists, which in humans and other animals are associated with sexuality and reproduction (Shaner et al., 2004; Del Giudice et al., 2010). In addition to being associated with creativity, schizotypal and autistic traits would theoretically be linked to short-and long-term reproductive strategies, respectively (Del Giudice et al., 2010). That may explain the relationship between creativity, personality, and sexual selection. Individuals with an autistic phenotype invest more in offspring and favor long-term relationships (Del Giudice et al., 2014; Ponzi et al., 2016). Autistic creativity is mainly characterized by convergent thinking, exhibiting greater pragmatic creativity. According to Del Giudice et al. (2010), the prevalence of autism is currently linked to the selection of genes that are associated with greater systematization, greater attention to detail, and the ability to innovate in technical fields, which may have become more helpful from the Holocene, a period characterized by agriculture (Harpending and Cochran, 2002). However, attention to detail is also crucial in archeological cave paintings (Kellman, 1998; Spikins et al., 2018). These psychological skills would be worth greater prestige and access to resources in these cultural contexts, also leading to a higher number of mating opportunities for individuals with these skills, particularly men (Henrich and Gil-White, 2001; Del Giudice et al., 2010). That would suggest that the reproductive benefit of this kind of creativity lies in facilitating the acquisition of resources, not necessarily in signaling good genes.

On the other hand, schizotypal individuals may have occupied the role of shamans in traditional societies (Dein and Littlewood, 2011). That would explain ancestral artistic displays as part of religious rituals rather than pure art, the latter being more common in contemporary art (Høgh-Olesen, 2018). Theoretically, artistic skills and a more original personality would improve access to short-term relationships, which is difficult to infer from ancestral societies, yet studying a hunter-gatherer population, Smith et al. (2017) found that the value of good storytellers is reflected in the fact that they also have increased reproductive success and receive more resources than less-skilled storytellers. It is also conceivable that this ornamental creativity associated with schizotypy does not guarantee many privileges in these societies. A study of the Meru, a semi-nomadic tribe in Kenya, showed that more creative people had more resources, although they had fewer children, fewer grandchildren, and fewer wives/husbands (Lebuda et al., 2021). That is the opposite of what is expected from an adaptive perspective, namely that creativity leads to reproductive success. One possible explanation is that the attraction to creative partners is recent in human history, in societies that value disruption, innovation, and rapid change. Traditional societies value stability, traditions, and rules. Or, yet, creativity was adaptive from a sexual selection point of view in our environment of evolutionary adaptedness (EEA), but is not adaptive anymore because societies and environments (including the Meru) have changed so drastically.

Context

Socioecological stimuli and contexts exert an important influence on creativity. The stimuli and contexts that inspire men and women to perform more creatively may reveal the influence of sexual selection. For instance, men behave more creatively (produce better creative descriptions of abstract paintings) after seeing photos of attractive women. That

suggests that a romantic stimulus activates cognitive/neural mechanisms linked to reproduction, leading men to perform better on tasks that might impress women. The increase in male creativity was maintained even when participants performed creative tasks after imagining themselves having a short-term or long-term relationship (Griskevicius et al., 2006). Nevertheless, female creativity increased in the face of greater assurance that the potential partner would invest in a long-term relationship, which may indicate that creativity was selected in the female sex to deal with a reproductive strategy more focused on attracting investment from partners in a committed relationship (Griskevicius et al., 2006).

This study reinforces the idea that creativity evolved by sexual selection in men and women (Baer and Kaufman, 2008; Varella et al., 2011, 2014, 2017; Miller, 2013). The increase in female creativity, given the possibility of short-and long-term relationships, indicates that ornamental creativity may have evolved for signaling both good genes and an ability to acquire resources.

Resources

It is common for females to select males based on their ability to contribute resources to offspring (Andersson, 1994; Davis and Arnocky, 2022). Parental care is very important to the human species, and resources are one of the forms of parental investment (Andersson, 1994), which is why men with more access to resources are universally considered more attractive, all other things being equal (Buss and Schmitt, 2019; Walter et al., 2020), regardless of the level of gender equality (Zhang et al., 2019). Indeed, intelligence and creativity are critical to activities that implicate access to resources, e.g., academic and professional activities, increasing attractiveness in modern societies (see Lebuda et al., 2021). Intelligence and creativity may not be attractive in themselves but as markers of resource-related potential. Thus, it is possible that intelligence and creativity are not considered attractive in societies (as may be the case with the Meru) where access to resources does not depend on intelligence or creativity.

A possible counter-argument is that even if creativity is attractive because it increases access to resources, this would not necessarily exclude its possible role as an indicator of good genes (Luoto et al., 2019a). After all, individuals able to obtain resources in a given context must be healthy enough to participate in activities that require physical and cognitive effort. As a consequence, it may be that the more attractive women think they are, the more they prefer men who rank high on signs of health and social status, because women's attractiveness is a fungible currency on the mating market that can be "exchanged" for traits that women seek (Buss and Shackelford, 2008). Creativity can be a reliable sign of both health and status. This would explain why women prefer creative men for short-term and long-term relationships (e.g., Griskevicius et al., 2006; Prokosch et al., 2009).

Cognition as a weapon in the struggle for status

According to Winegard et al. (2018), cognitive resources increase attractiveness only when they provide culturally valuable assets. More precisely, inventing new technologies or artistic products confer prestige, which can be "exchanged" for resources and mate partners (Henrich and Gil-White, 2001). This model emphasizes intrasexual competition more than intersexual selection (Winegard et al., 2018). Intrasexual and intersexual competition are two main mechanisms of sexual selection (Darwin, 1871; Puts, 2016). In intrasexual competition, individuals (usually males) compete with others of the same sex for access to the opposite sex, which leads to the evolution of ornaments (e.g., plumage, singing, dancing) and/or weapons (e.g., horns, talons, fangs); whereas in intersexual selection, males mostly display their ornaments and weapons directly to the opposite sex (Berglund et al., 1996). In humans, males and females are involved with intersexual selection and intrasexual competition (see, e.g., Stewart-Williams and Thomas, 2013). It is possible that ornamental creativity evolved to be useful in intrasexual competition as a way of impressing other men, in addition to being useful in intersexual selection (Winegard et al., 2018). Accordingly, Winegard et al. (2018) mention historical, philosophical, and literary treatises written when most women were not able to read. The contents of such treatises do not seem to appeal to female interests (as pointed out by feminist authors; e.g., Irigaray, 1985) since they deal with war, politics, military strategy, and metaphysics. Men who were more prolific in these fields garnered more prestige among other men, securing access to valuable social assets, such as resources and protection for themselves and their families (Henrich and Gil-White, 2001; Winegard et al., 2018). Thus, men with superior cognitive abilities will also tend to rise in social status hierarchies.

This model based on competition for status shows advantages over the "cultural courtship" model championed by Miller (2000). Miller (2013) states that men and women have been shaped by evolution to display mental abilities indicative of genetic quality (see also Stewart-Williams and Thomas, 2013). A possible flaw in this hypothesis is the belief that humans have always chosen their partners freely and individually. Actually, for most of human history, and still in most traditional cultures, marriages are arranged, i.e., the bride's family, usually fathers and brothers-in-law, interfere in the groom's choice (Apostolou, 2017). In other words, throughout history, mate selection has been about advertising one's attractiveness to other men.

Many male physical traits seem to bear on dominance, but not necessarily on attractiveness, such as a male face, beard, and muscles (Puts, 2010). Creativity seems to have its use in intrasexual competition, and lyrics about the male world seem to illustrate that (e.g., Black Sabbath, ACDC, and Metallica); but it is also true that some such cultural expressions are directed toward the opposite sex (e.g., 'N Sync and Back Street Boys; see Winegard et al., 2018). For example, among professional male guitarists, the

time spent playing the instrument positively predicted desire for casual sex with women, and the speed in playing positively predicted a desire to impress other men (DeLecce et al., 2022). Varella et al. (2022) showed that men and women use their artistic propensities in intersexual selection (female-biased) and intrasexual competition (male-biased). Creativity and aesthetic sense also probably participated in the female intrasexual competition since body beautification is universally crucial in female attractiveness (Varella et al., 2017).

Sensory exploration, "sexy son" and "runaway selection"

The theories of costly signaling and mental fitness (Zahavi, 1975; Miller, 2000, 2001) have become very popular in explaining the existence of abnormal phenotypes in many species, including creative manifestations in humans (Luoto et al., 2019a). However, Darwin (1871) believed something else: for him, sexual selection picked flashy traits for arbitrary aesthetic reasons (Prum, 2012; Davis and Arnocky, 2022). There is evidence that Darwin's insight was correct. In many species, individuals are selected to mate through a process called sensory exploration (Verpooten and Nelissen, 2012). For instance, female guppies tend to copulate with males with more markedly orange spots around their bodies. That is not so because these males are genetically better, but because their orange spots co-opt the female's sensory system, shaped by natural selection to find food of the same color (see Verpooten and Nelissen, 2012). This sensory co-optation process may lead to a "runaway selection," in which each new generation of males develops phenotypes ever more extravagant and unrelated to any underlying aptitude (Prum, 2012).

Showy phenotypes may also arise if they make the offspring attractive (this is known as the "sexy son hypothesis"). In this process, the alleles of the most selective females spread and are inherited by their offspring, as daughters become more selective and sons showier (Prokop et al., 2012). Such dynamics feedback on themselves on the grounds of attractiveness advantage (which is, in this case, more arbitrary than in the selection based on "good genes"). Hence, while sexual selection based on the "sexy son" phenomenon promises more reproductively successful offspring for being more attractive according to arbitrary patterns, selection based on "good genes" provides offspring that are successful because of better health (Prokop et al., 2012).

However, to Miller (2001), the process of sensory exploration (and, one assumes, the benefits based on "sexy son") would not continue to be arbitrary under all possible scenarios. Miller (2000) has suggested that ornaments would become so intricate that they will come to depend on the expression of ever more genes; at this stage in complexity, pleiotropy would grow, as well as the threshold of genetic quality required to go on sporting an ever costlier phenotype. Furthermore, sexual selection based on sensory exploration should be more common in not very social species, where the first step to mating is finding a partner. However, primates are social species; thus, locating a potential partner is no problem. On the contrary, the hard part is selecting the best option (Miller, 2000; Verpooten and Nelissen, 2012). Thus, if Miller (2000) is correct, genetic quality becomes a part of sexual selection at some point.

What are the implications of this plurality of mechanisms of sexual selection for the evolution of creativity? Creativity may have evolved by viability selection and also by sexual selection (Luoto et al., 2019a), but the details of this transition are uncertain. Creativity may have begun to grow initially due to general cognitive growth, which is useful for problem-solving. Its effects would have then started to affect other traits that are more useful in partner selection, such as the ability to get food (which in Neolithic humans may happen as social status increases: Winegard et al., 2018). The pressure on expanding cognitive performance would have enhanced this ability to the point that it could only be sustained by individuals having at least enough genetic quality to afford its energy costs (Miller, 2000). From a certain point on, practical benefits of cognitive ability do not increase together with the growth in cognitive ability, which is when conspicuous (i.e., ornamental, fruitless) forms of cognitive ability and creativity to exhibit fitness may arise.

Ornamental traits may be an exaptation, i.e., pragmatic creative capacities evolved initially by viability selection and were later co-opted by sexual selection as phylogenetic exaptations related to aesthetic and artistic production and appreciation (Varella et al., 2011; Luoto et al., 2019a). For instance, probably the first handaxes built by human ancestors would have been used to assist in taking down prey and cutting up carcasses; however, they would gradually be co-opted for aesthetic uses, acquiring ornaments and a more symmetrical look (Mithen, 2003). As an extension of this point of view, creative individuals can reap advantages through functional and/or ornamental extended phenotypes that they have created or acquired. For instance, clothes, cars, and houses were invented for practical reasons (e.g., protection, locomotion) and later acquired ornamental functions that signal (and extend) personal attributes, such as interest in certain forms of romantic involvement, intelligence, and creativity (Luoto, 2019a).

The role of culture in creativity may go beyond exaptations or extended phenotypes. Recently, many traits have been studied that would result from gene–culture coevolution (Bender, 2019). Briefly, this evolutionary process is characterized by selecting genes based on cultural pressures. The evolution of the ability to write is an enlightening example. Human beings did not evolve to read and write. Writing is a result of learning specific cultural techniques that co-opt brain areas shaped initially to deal with other adaptive issues (Parkinson and Wheatley, 2015); however, as soon as writing spreads and starts generating social benefits, genes associated with a greater ability to learn to read and write were selected (Overmann, 2016). This process in which learned responses acquire a genetic base is called the Baldwin effect, which has been used to explain complex aspects of human cognition (Baldwin, 2018).

That process may have supported the fast growth in complexity in hominine cognitive abilities (see recent proposals of this idea in the context of music: Podlipniak, 2017, 2021; Mehr et al., 2021; Savage et al., 2021). Neuroplasticity may have allowed learning ornamental techniques that initially aimed at reinforcing intergroup cohesion and establishing some form of individual or group identity (Garofoli, 2015). These distinctive ornaments may have begun to bring reproductive advantages for cultural reasons, which is when Baldwin effect's ability to produce ever more complex ornaments may have been genetically incorporated. The use of the Baldwin Effect here is admittedly speculative. Further studies are needed to explore the relations between culture, plasticity, genetics, and evolution.

Discussion

Did creativity evolve by sexual selection? This article aimed to answer this question considering a pluralistic Tinbergian perspective (Tinbergen, 1963; Fitch, 2015) and a nomological network of evidence (Schmitt and Pilcher, 2004; Konner, 2021). That is the most up-to-date and comprehensive review to integrate and organize an interdisciplinary body of evidence to answer this question about creativity. In summary, our findings suggest that sexual selection likely influenced the evolution of creativity (Table 1); however, the sub-process behind this influence is unclear. Creativity has multiple adaptive functions regarding sexual selection (for an example on musicology, see Fitch, 2015). More specifically, creativity may have evolved by sexual selection not only because it indicates good genes, potential to acquire resources, dominance, or because it is a useful ability in the production of artifacts (e.g., bowers, paintings, music) that co-opt sensory biases to attract attention. It is probable that creativity is connected to all of these aspects. Evolutionary psychologists must test hypotheses derived from processes of sexual selection other than good genes and costly signaling (Luoto, 2019a; Davis and Arnocky, 2022).

Evidence related to sex differences supports that both sexes have developed fitness indicators (Miller, 2013; see Table 1). Overall, no evidence was found of average differences in creative ability or achievement between adult men and women (Baer and Kaufman, 2008), but sexual dimorphism shows up when specific creative domains are evaluated (Ellis et al., 2008; Varella et al., 2010; Savage et al., 2015; Greengross et al., 2020; Hora et al., 2021; Nakano et al., 2021). Other evidence suggests greater creativity among women (Varella et al., 2017; Nakano et al., 2021). Women showed higher mean and greater variability, compared with men, in creative tasks involving language; men showed higher mean and greater variability in creative tasks involving figures and drawing (He et al., 2015; Lau and Cheung, 2015; Karwowski et al., 2016a,b; Taylor and Barbot, 2021). Such sexual differences are compatible with those found in academic and professional preferences, in which women predominate in areas that involve language and men, in areas that involve spatial reasoning (e.g., Wright et al., 2015).

Furthermore, greater variability appears positively associated with greater phenotypic plasticity, which has been linked to the action of androgenic and dopaminergic systems (Del Giudice et al., 2018; Janicke et al., 2021; see Table 1). Creativity is related with greater phenotypic plasticity (Feist, 2019), dopaminergic system (Reuter et al., 2006; Runco et al., 2011; Mayseless et al., 2013), and testosterone levels in both sexes (Hassler, 1992; Sluming and Manning, 2000; Crocchiola, 2014). However, paradoxically, testosterone promotes left brain lateralization, but creativity is linked to right lateralization (Beking et al., 2018). Future studies should investigate the possible role of androgens in male and female creativity and the mechanisms that promote this association.

Evidence on the relationship between psychopathology and creativity supports the predictions of the mental fitness theory (Miller and Todd, 1998; Miller, 2001). Disorders such as schizophrenia, bipolarity, and autism seem to be dysfunctional manifestations of schizotypal and autistic phenotypes linked to creativity, possibly due to genetic predisposition, developmental instabilities, and evolutionarily novel lifestyle factors such as low-grade systemic inflammation and chronic stress (Rantala et al., 2021, 2022).

Evidence shows that creativity is sexy: it is considered attractive in potential mating partners, at least in WEIRD societies (Buss, 1989; Li et al., 2011; Kaufman et al., 2016; Souza et al., 2016). Future studies should verify the role that creativity plays in attractiveness in traditional societies (e.g., Lebuda et al., 2021). Furthermore, future studies should verify the theoretical framework (e.g., good genes) that explains the attractiveness and evolutionary function of different types of creativity (e.g., aesthetic and pragmatic).

According to the mental fitness theory, ornamental manifestations of creativity would be more attractive in short-term relationships (e.g., Haselton and Miller, 2006; Charlton, 2014; Mosing et al., 2015) because they indicate good genes. But other studies suggest that ornamental creativity may also evolved to retain partners in a long-term relationship (Varella et al., 2017; Winegard et al., 2018). Alternatively, artistic capacities could have evolved because they are able to produce something that the human mind finds beautiful (Darwin, 1871; Prum, 2012).

Limitations

Despite making an important contribution to the literature on mating preferences by bringing together multiple studies and interpreting how much they support the hypothesis of the evolution of creativity by sexual selection, there are limitations to this review, which future studies may overcome. The first is that, despite the extent of the review performed here, this article is not a systematic review or a meta-analysis.

A second limitation is the focus on mental fitness theory. This focus resulted from our deliberate choice to consider theories and evidence supporting (or not) the evolution of creativity by sexual selection. It was for this reason that we added a discussion about

creativity being attractive because it signals good genes or because it almost always (at least in WEIRD societies) equates to resource acquisition. Future evolutionary research on creativity should compare evidence related to sexual selection and other theories, such as exaptations, co-opted by-product and cultural evolution (Luoto, 2019a). This review has gone a long way toward integrating and enhancing our understanding of ornamental creativity as a possible sexual selected psychological trait.

Author contributions

FN: main argument, writing, and formatation. JN: main argument and revision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Evolution of parental roles in phase portraits of bimatrix asymmetric games

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In this paper, we address the evolutionary dynamic of parental roles using game theory. The main purpose of the article was to expand a classical list of evolutionary dynamic parental conflicts by adding some important cases which hitherto have not been intensively studied. Our models are apt to deliver some novel insights into the evolution of parental care. We also introduced several hypothetical events that served as illustrations of an arising alteration in cost-benefits for both parents and simulated a subsequent evolutionary endpoint. Our models revealed that evolutionary outcomes for reproductive decisions of both parents could be completely predicted by certain payoff matrices, which serve as proxies for a Darwinian fitness gain. In this sense, the result of a frequency-dependent selection on reproductive traits would inevitably depend on fitness costs and benefits arising for both parents in various circumstances. We demonstrated that population division could be a plausible evolutionary consequence for any human mating game where 'reproductive defection' represents the best response to any action by the reproductive opponent. We conclude that future evolutionary studies of human reproductive behavior should be more oriented on estimating a sex-biased asymmetry in potential fitness gains obtained by cooperative and deceptive parents in diverse environments and cultures.

KEYWORDS

sexual conflict, parental care, evolutionary outcome, asymmetric games, parental cooperation

1. Introduction

Parental care requires a sufficient amount of bioenergetical resources and time (Kaplan et al., 2000). The innate goal of any living creature is to gain the individual and inclusive fitness through successful reproduction resulting in viable and fertile offspring, while the absence of reproduction would soon lead to the extinction of life forms. Nevertheless, from biological perspectives there is a potential for intense reproductive conflict that can lead to maladaptive outcome. Because each parent could gain certain fitness benefits by saving energy, meanwhile their partner devotes to successful common reproduction relatively more efforts (Lessells, 2006; Royle et al., 2016). Apparently, this conflict has various intensity levels in different taxa. Although females are more frequently the caregivers, diversification of parental roles can take a variety of forms (Kokko et al., 2012). In its extremum, an intense parental conflict could be resolved in favor of one sex or another by establishing male-only or female-only care practices. Observed

inequality in parental efforts between males and females in different taxa reflects the essence and nature of sexual disputes over parental care and results in a profound dimorphism of sexual, parental and behavioral roles. Revealing mechanisms underlying the resolution of evolutionary conflict over parental care is still an important research task in biology (Royle et al., 2016).

A generally accepted explanation for sexually dimorphic roles implying the prevalence of female care is based on the theoretical concept of the initial difference in the female and male gametes' size–anisogamy (Lehtonen and Kokko, 2011). Dimorphism at the gamete size and their level results in competition among gametes, and in the scarcity (or abundance) of gametes of the opposite mating type (Lehtonen et al., 2016). Hence, sexual selection among members of the sex with the more numerous gametes (typically males) is stronger than in sex with larger but limited in number gametes (typically females). In connection with the above, it was supposed that the probability of paternal care was significantly lower (Trivers and Campbell, 1972). It is evidenced by the fact that male care practices are relatively seldom observed in mammals (Eisenberg and Gould, 1970). However, the initial anisogamy, as a mechanism, that sets classical sexual roles, is not universally realized in various taxa and biological classes of animals if we consider the entire subtype of vertebrates. For instance, in fish, amphibians and birds, parental care, defined as investment in offspring after fertilization, is not an exception at all but an ordinary phenomenon (Salthe and Mecham, 1974); likewise, the majority of species diversity of birds demonstrate variation of social monogamy and biparental effort for a clutch (Lack, 1968).

In this paper, we are using gamy theory to illustrate a dynamic shaping parental role and thus to reveal a potential mechanism specifying a share of care each parent should provide to common offspring. Nowadays, evolutionary game theory is widely used to explain the distribution of parental investments and diversification in sexual roles (Maynard Smith, 1982, 1984; McNamara and Weissing, 2010) *via* modeling optimal reproductive solutions for each sex in terms of fitness (McNamara et al., 2000, 2003; Johnstone and Hinde, 2006). An important feature of this approach is that evolutionary game theory allows to simulate a parental conflict which has been acting during the evolutionary time in a given population, describe an iterative (evolutionary) change in strategies for two groups of players, and predict a final outcome of a continuous selection pressure acting on each sex separately (Dawkins and Carlisle, 1976; Schuster and Sigmund, 1981; Maynard Smith, 1982; Maynard Smith and Hofbauer, 1987; McNamara and Weissing, 2010).

Sexual, and parental dimorphism is ubiquitous (Lehtonen et al., 2016), and therefore interactions between females and males are almost always asymmetric. Asymmetry can be caused by physiological (genetic) differences among two groups of players (sexes) or due to preexisting environmental heterogeneity, including inequality in the social environment, or it could be a combination of both factors. Such asymmetric interactions are recognized as an important application in evolutionary game theory. Asymmetric evolutionary games correspond to the realm of bimatrix games in classical game theory. In game theory, a bimatrix game is a simultaneous two-player game in which each player has a finite number of possible decisions. It is generally thought, that in the case of reproduction, each agent (parent) can make two decisions: either caring for the offspring or refusing to care (deserting; McNamara and Weissing, 2010).

The first and most complete classification of evolutionarily stable strategies for asymmetric games was carried out by Maynard Smith (1982). He also examined cases with paradoxical solutions of mutual rejection of cooperation and cyclical dynamics in players strategies.

Our paper expands a classical list of evolutionary dynamic parental conflicts by adding some important cases which hitherto have not been intensively studied. To understand parental behavior, we also propose several hypothetical events that may serve as illustrations for certain changes in matrix payoffs for two-player games. Proposed mathematical calculations and phase portraits can also be useful in analyzes of various interactions in a wide range of two interacting classes of players, such as: parent-offspring, host–parasite, owner-intruder, etc.

2. Methods

2.1. Mathematical calculation and graphical representations

Mathematical calculations and graphical representation of phase portraits were realized using *Wolfram Mathematica* 13.0 (and 13.2.0) computational software program.

2.2. Methodology

An evolution of strategies in a conflict of the sexes over parental investment could be elucidated by means of a simple dynamic system using the game-theoretic approach (Schuster and Sigmund, 1981).

Considering that, for each subsequent generation the rate increase in the quantity of cooperative males adopted first strategy, $\frac{d\,x_1(t)}{dt}$, given by $a_{11}y_1 + a_{12}y_2$, will be the difference between the payoff obtained by caring males and average males' payoff in a previous generation, given by $a_{11}x_1y_1 + a_{12}x_1y_2 + a_{21}x_2y_1 + a_{22}x_2y_2$. A similar argument applies to changing in the proportion of females applying two different strategies, $\frac{d\,y_1(t)}{dt}$.

By solving the equations $f(x,y) = 0$, and $g(x,y) = 0$, for $\frac{d}{dt}x(t) = f(x,y)$, $\frac{d}{dt}y(t) = g(x,y)$, the fixed points could be obtained. To analyze the stability, the Jacobian matrix at this fixed point was performed.

2.3. Strategies specification

Taking into account substantial variation across different species (Royle et al., 2016), in most parental desertion games, the first strategy constitutes a cooperative tactic implies successful reproduction followed by care. By contrast, the second strategy is a deceptive tactic implying exploitation of the other's investment. Usually, a defecting parent avoids any sort of care (desert). Considering internal

fertilization, in mammals a defecting female can also exploit her social partner's investment and benefit from extra-pair maternity.

Absence of care could also be manifested through reproductive reluctance avoiding pregnancy, refusing to have sexual intercourse, also getting rid of the fetus or infanticide a newborn; for a review, see (Hrdy and Hausfater, 1984), which could be more applicable for females.

2.4. Payoff matrices

In classical game theory models' matrices payoffs are proxies for a Darwinian fitness (Maynard Smith and Price, 1973).

$$A := \begin{pmatrix} aii & aij \\ aji & ajj \end{pmatrix}; \quad B := \begin{pmatrix} bii & bij \\ bji & bjj \end{pmatrix};$$

Where a_{ij} is the payoff for a male using strategy X_i against a female playing strategy Y_j, with b_{ji} corresponding to payoff for a female using second strategy Y_j against a male playing strategy X_i.

Let fitness payoffs for males be in matrix A, and females' payoffs in matrix B. The upper row of each matrix corresponds to fitness costs for a cooperative and caring parent; the lower one reflects benefits for a deceptive strategy. The left column corresponds to changes in the individual fitness gains in cases of interacting with a cooperative partner; the right column corresponds to instances when an individual interacts with a defecting partner.

2.5. Phase portrait characteristics

Modeled phase portraits represent a one-unit square posed on a coordinate system, where zero denotes a deserting strategy, and one corresponds to a cooperation and care strategy. Any point inside the portrait could be seen as a stage in an ongoing evolutionary dynamic. For instance, within any evolutionary moment the share of males adopting the first strategy (childcare) could be traced on the *x*-axis; it could be obtained by drawing the vertical line through a point on the *x*-axis. Similarly, the proportion of caring females can be seen on the *y*-axis. The arrows indicate selections direction over an evolutionary time scale and the expected shift in the proportions of males and females that adopted these two strategies.

3. Models and phase portraits

Evolution of a novel function starts from random genetic changes as a precondition for a Darwinian natural selection which further operates on a given spontaneous variation (Darwin, 1871; Nei, 2013). These evolutionary innovations can equip individuals with "tools" that would have been favored by Darwinian selection. Hence, a spread of a novel persistent trait/allele enables bearers with a sufficient reproductive fitness advantage. The most striking example is the occurrence of lactation in mammals. Phase-portraits presented in Figure 1A demonstrated such a selection force which guided the evolution of female-only care as a pervasive reproduction model in a given population. The point (0;1) here constitutes an *evolutionary attractor* (see McNamara and Weissing, 2010).

The phase portrait in Figure 1A illustrates the Dawkins and Carlisle theoretical prediction on parental dispute resolution: a deserting partner probably would be the one who could do it first (Dawkins and Carlisle, 1976). Later, Maynard Smith (1982) supposed that the sharing of parental burden would depend on whether the players had information about the intentions and stable roles of each sex (see also McNamara and Weissing, 2010). In this regard, internal fertilization and lactation could be the key factors that determine female form of care in mammals.

The next model (Figure 1B) represents a dynamic of decreasing the propensity for paternal care; males may lose if they do cooperate, so male cooperation should be punished (− 1 point). The parenting evolution will lead away from the male-only care point. This point is called an *evolutionary repellor* (McNamara and Weissing, 2010). Interestingly, there is always an increase in female cooperation, independent of the starting point, but it will only reach 100% female-care if in the starting point proportions of cooperating males and females in sum were higher than 1.

A selection dynamic is very similar to the previous example is shown in Figure 2A. However, the interactions here are more complicated. After the initial tendency toward female-only care and male defection, the model achieves the only possible outcome of a continuously stable strategy–biparental care (Figure 2A).

The next famous example of nonlinear relationships between the two players was described in the classical example of an asymmetric conflict, the battle of the sexes by Dawkins (1978). This model has become classical for biological and ecological studies of sexual conflicts (see Schuster and Sigmund, 1981; Figure 2B).

Figure 3A shows mutual refusal of cooperation. Here reproductive defection could become an adaptive strategy for both sexes. These paradoxical dynamics, as it was defined by Maynard Smith (1982), dominate when a partner's cheating reduces an individual's fitness more than in the case of mutual rejection of reproduction and care (see Figure 3A, asymmetric *Prisoners Dilemma* game).

The next case is called *evolutionary branching* (McNamara and Weissing, 2010), where a disruptive selection becomes a possible outcome (Figure 3B).

Of the many possible scenarios of bimatrix asymmetric games, here we have discussed six. Depending on the payoff matrix, different evolutionary trajectories and outcomes are possible, leading to stable female care only (Figure 1A), stable defecting strategy (Figure 3A), stable biparental care (Figure 2A), to all possible outcomes except paternal care only (Figure 1B), to vortices of mixed strategies (Figure 2B) and to mixed strategy (Figure 3B). It is interesting to note, that the outcomes of the four figures (Figures 1A, 2A, 3A,B) are all individual cases among plenty of possible outcomes contained in Figure 1B. Hence, the currently observed outcomes (prevalent strategies) of any population do not allow any conclusion about the evolutionary trajectory, while latter could be completely predicted by a certain payoff matrix.

4. Discussion

Parental care is costly for parents, because care expends resources that parents would otherwise allocate to their own somatic effort and future reproduction (Alexander, 1987; Morita et al., 2016; Royle et al., 2016). Inequality in parenting costs for males and females leads to

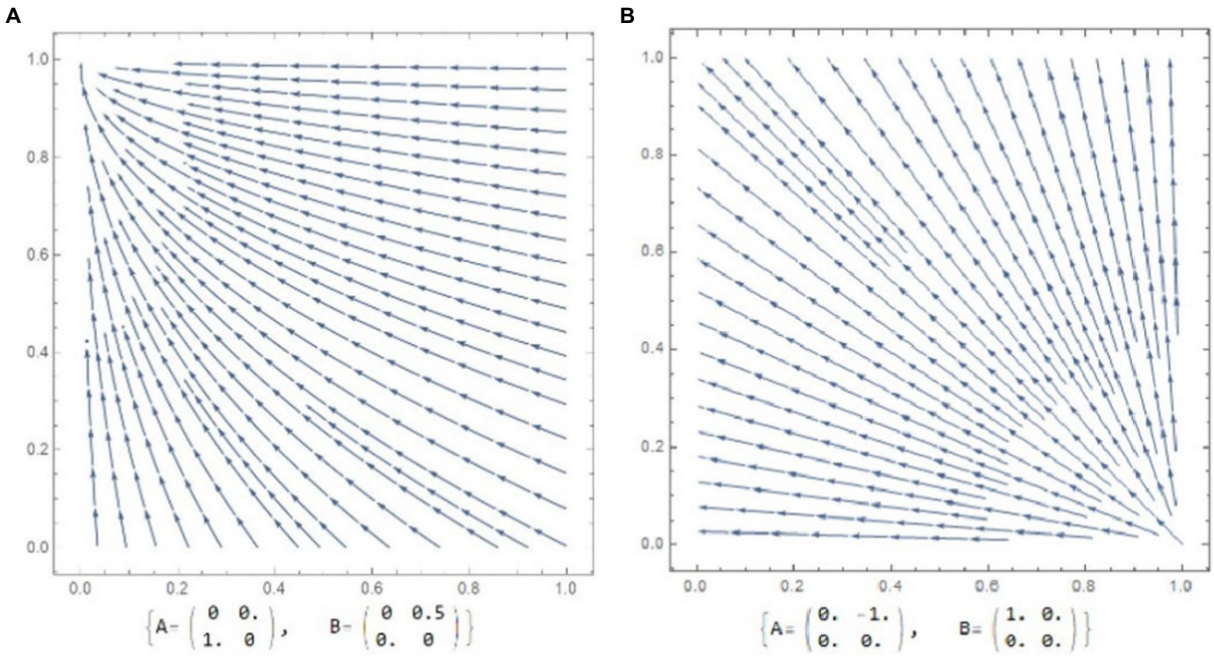

FIGURE 1
Phase portrait and corresponding payoff matrices for males and females. The arrowheads depict evolutionary trajectories. **(A)** An evolutionary dynamic directed toward female-only care. **(B)** An evolutionary dynamic where male population would be specifically selected against male-only care.

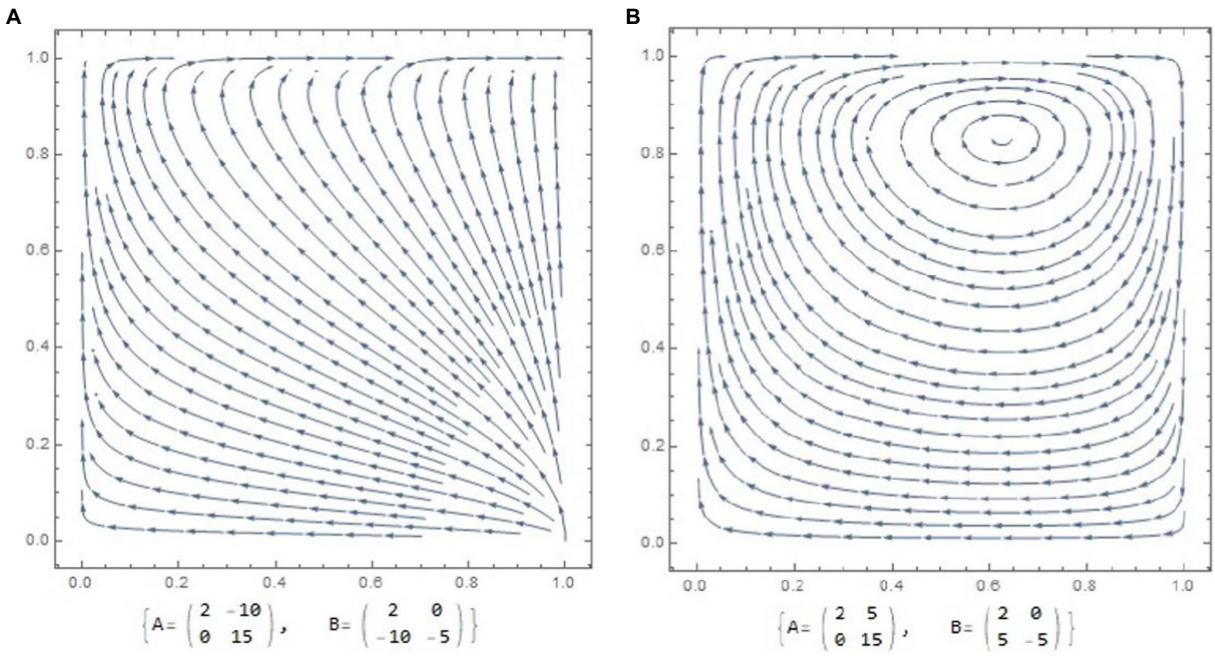

FIGURE 2
Phase portrait and corresponding payoff matrices for males and females. The arrowheads depict evolutionary trajectories. **(A)** selection favors cooperative parental strategies; hence population evolves toward the equilibrium state–biparental care. While male populations would be specifically selected against male-only care practice. **(B)** Phase portrait of dynamical forces, describing battle of the sexes according to payoff matrix proposed by R. Dawkins. The model leads to endless oscillations.

profound variation in parental care patterns and creates prerequisites for a sexual conflict through diversification of selection pressures on each sex.

Previous attempts to determine the share of care each parent provides utilizing the concept of an initial anisogamy, had not contributed exhaustive answers to the origins of the variety of

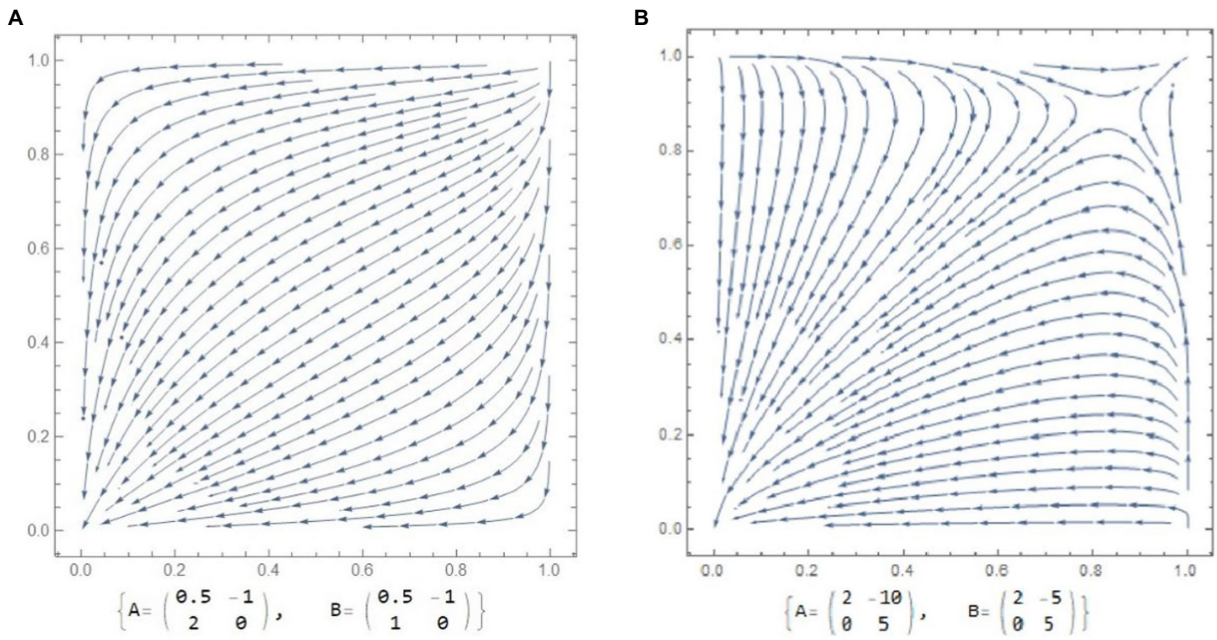

FIGURE 3
Phase portrait and corresponding payoff matrices for males and females. The arrowheads depict evolutionary trajectories. **(A)** Evolution of care avoidance and mutual reproductive rejection as equilibrium state. Even if the system had started at biparental care, small mutations would have sent it into a state of mutual defection. **(B)** population is disruptively selected for opposite parenting strategies. This would lead to populations with either exclusively biparental care or populations with a mutual defection strategy (care avoidance).

observed parental roles in different taxa (Royle et al., 2016). To disclose a complex dynamic within a parenting dispute over care, we turned to an evolutionary game theory (Maynard Smith, 1982, 1984; McNamara and Weissing, 2010).

Of particular interest to this paper is the notion that alteration in fitness gains could lead to remarkable evolutionary consequences. For instance, in different models' iterative evolutionary changes and corresponding social dynamics could be highly similar. However, the final evolutionary outcomes would be entirely different (Figures 1B, 2B). In this sense, mating system evolution under a frequency-dependent selection would inevitably depend on certain asymmetry preexisting in males' and females' reproductive positions substantially varying in different circumstances. The resulting outcome is not always obvious, and sometimes even contradicts the logical conclusions (McNamara and Weissing, 2010) drawn using the classical analysis of the linear interaction of cause (predictor) and effect (response value). Rational fitness-maximizing individual decisions can sometimes lead to apparently maladaptive reproductive behavior – mutual rejection of care and parenting (Kokko and Jennions, 2014).

Paradoxical solutions of mutual deception as equilibrium states are presented in Figure 3A.

Gaming conditions for a case of mutual rejection of parenting imply that in terms of fitness there always would be a high risk of deception for caring parents of both sexes (Morita et al., 2016). In this example (Figure 3A) the costs for being the only care giver are high, whereas defecting is rewarded. In the next figure (Figure 3B), the payoff of not providing any parental care is positive for both parents and higher then when both cooperate. Both scenarios could be applied to sexual conflict in humans, where child rearing is long and costly, and this dynamic is created by extremely destructive risks of partner defection. For women partner defection bring a serious burden of single parenting. Firstly, production of ovum, gestation, and lactation is still a biologically taxing process for women. And if women do not receive male support, they will practice "gene shopping" (Marlowe, 2000). Prevalence of deceptive tactic in females (e.g., extra-pair conception) intensifies males' selection against care, making it more and more difficult for females to count on partners help. On the other hand, increasing costs of raising a child, forcing woman to become more persistent in searching male investment, which will prolong birth intervals. In the model presented on Figure 3A, the selection force will counteract the cooperation of the players and potentially oppress reproduction (Semenova and Butovskaya, 2021). And if care is essential for offspring's survival, there would be the only option for successful reproduction–relay on help of various kin or non-relative alloparents (Hrdy and Hausfater, 1984).

Theory predicts that intense sexual conflict over care (e.g. mismatching males and females interests in reproductive payoffs) leads to a fitness minimum, which could reinforce the rate of evolutionary novelty and potentially promote speciation (for a review; Parker and Partridge, 1998; Gavrilets, 2000). An invasion of a novel mutant with a sustain cooperative strategy could facilitate an establishment of two opposite evolutionarily stable outcomes (McNamara et al., 2000): biparental care or mutual deception (Figure 3B). The last model suggest that cooperators could survive by forming clusters within which they interact more often with their own type and hence lowering the probability of meeting an opponent's defection (Axelrod, 1984). In this sense, population division with the emergence of strict norms of reproductive practices (e.g. moral and marriage norms) should be seen as a plausible evolutionary consequence for any mating game where 'reproductive defection' represents the best response to any action by the opponent.

Clusterization in groups of individuals which had adopted cooperative reproductive strategies could occur in geographically (Hauert, 2006) or even in religiously structured populations (Alexander, 1987), for instance, *via* imposing monogamy.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material: www.wolframcloud.com/obj/9930a448-532f-4551-8d08-9ce712cbea4e.

Author contributions

MB conceived of the presented original idea. OS and MB outlined the theoretical framework. AB developed the theory. AB performed the mathematical calculations. AB made numerical simulations and resulting phase portraits. All authors discussed the results. OS wrote the manuscript with confirmation from AB and MB. AB verified the analytical methods. All authors and approved the final version of this paper.

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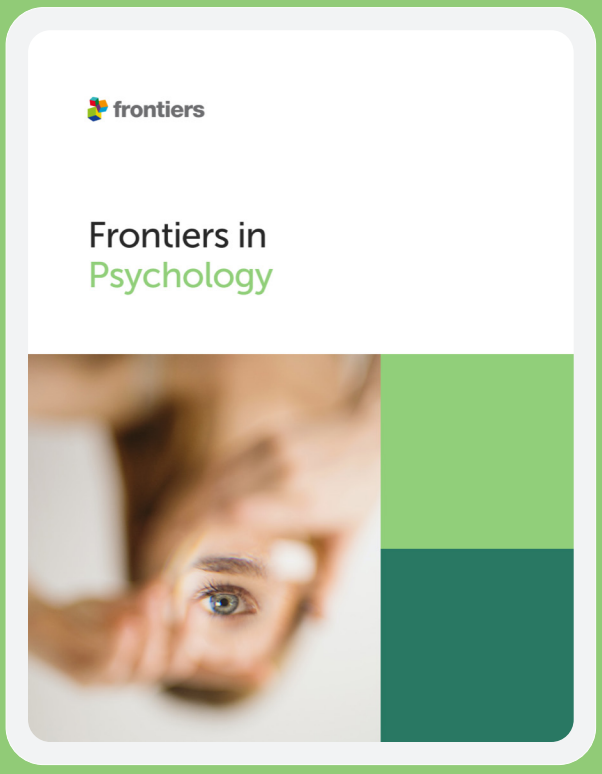

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