



Good body condition increases male attractiveness but not caring quality in a neotropical arachnid with male-only care

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Abstract

Female mate choice is usually based on traits that signal male quality as a sexual partner. According to the “good parent” hypothesis, female mate choice may also consider male quality as a caregiver in species with male-only care. Because parental activities may be costly, males in good condition should be more attractive to females than those in poor condition. We experimentally manipulated the body condition of non-parental and parental males of the egg-tending harvestman *Iporangaia pustulosa* and then evaluated how it affected their mating success and ability to protect eggs under field conditions. For non-parental males, individuals in good condition had twice the probability of mating than those in poor condition. For parental males, individuals in good condition had two times more chances of mating and acquired five times more eggs than those in poor condition. Surprisingly, males’ body condition had no effect on the efficiency of egg protection. Although our results indicate that the male condition is a sexually selected trait, we found no support for the “good parent hypothesis” given that an increase in body condition does not improve the survival of the offspring under male care. Instead, these findings are congruent with predictions of the “essential male care” model, which suggests that, when the costs of parental care are low (as is the case of egg attendance), most males can provide the minimum necessary care for offspring survival. However, only males in good condition can allocate surplus energy to advertise their overall quality and attract more mates.

Significance statement

Studies examining female mate choice based on condition-dependent traits that serve as reliable indicators of male caregiving quality are mostly limited to vertebrates. We present one of the first empirical examples demonstrating that male body condition influences male attractiveness in an arthropod species exhibiting male-only care. Our field-based results show that females prefer males, whether non-parental or parental, in good body condition over those in poor condition. However, we found no evidence that an increase in body condition improves the survival of the offspring under male care. We propose that males in good body condition are more attractive because the relatively low costs of egg attendance allow them to allocate their surplus energy into advertising their overall quality. Our findings are congruent with predictions of the “essential male care” model, which explores resource allocation between paternal care and sexual advertising.

Keywords Direct benefits · Female preference · Good parent hypothesis · Mate choice · Offspring survival · Paternal care

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Introduction

In species with male-only parental care, females can reduce or even eliminate their investment in post-oviposition parental activities. This enables them to forage, invest in future reproduction, and ultimately increase their lifetime fecundity (Trivers 1972; Maynard-Smith 1977; Tallamy 2000; Johnstone and Hinde 2006). However, by leaving their eggs under the protection of another individual, females should be expected to select mates based on the prospective chances of offspring survival under their partners’ care (Hoelzer 1989;

Tallamy 2000; Kelly and Alonzo 2009; Alonzo 2012). According to the “good parent” hypothesis, when males honestly advertise their quality as caregivers, females should prefer males that provide high-quality care (Hoelzer 1989). But how exactly can females assess whether a mate will be a good father?

One possible answer is that males may demonstrate their paternal abilities to potential partners during courtship. For example, in some fish species with male-only parental care, males exhibiting high rates of egg fanning also tend to have high rates of egg hatching and are preferred by females (e.g., Östlund and Ahnesjö 1998; Lindström et al. 2006). Sand goby males may even intensify their egg-fanning behavior in the presence of females, which has been interpreted as a form of sexual display (Pampoulie et al. 2004). Another possibility is that the presence of eggs under male’s protection can serve as an indicator of the male’s parental ability. This is because the survival of the eggs from their oviposition until the present moment reflects the extent of the male’s investment in offspring care (Stiver and Alonzo 2009; Kelly and Alonzo 2010). In this case, females should exhibit a preference for males with eggs under their care over males without eggs. In fact, this pattern of female preference has been observed not only in several fish species (e.g., Jamieson 1995; Östlund and Ahnesjö 1998; Pampoulie et al. 2004; Lindström et al. 2006; Hale and St Mary 2007; reviewed in Goldberg et al. 2020) but also in some arthropods (e.g., Gilbert et al. 2010; Nazareth and Machado 2010; Requena and Machado 2015; Ohba et al. 2016, 2018), and at least one frog species (Valencia-Aguilar et al. 2020). While males displaying paternal behaviors do provide cues that are readily accessible to females, an important question remains: how do males signal their prospective quality as caregivers *before* tending to their first clutch of eggs?

In this study, we tested the hypothesis that body condition could serve as a reliable indicator of males’ prospective quality as caregivers, making this trait subject to female preference. Generally, caring for offspring is a behavior that demands significant energetic expenditure (reviewed in Alonso-Alvarez and Velando 2012). Engaging in parental activities may also hinder males from foraging regularly, thereby amplifying their energetic costs (e.g., Gonçalves and Almada 1997; Requena et al. 2012). Consequently, males with limited energy reserves (i.e., in poor body condition) may find it challenging to afford the energetic demands of parental activities and may be more likely to adopt strategies such as brood desertion or filial cannibalism (reviewed in Manica 2004; see also Klug 2009 and references therein). Conversely, males in good body condition should be less likely to cannibalize eggs under their care and more likely to invest additional time and energy in activities that increase offspring survival, including defense against predators, nest maintenance, and egg aeration (e.g., Neff 2003; Takahashi

and Khoda 2004). Moreover, by selecting males in good body condition, females may confer benefits to their offspring through the transmission of good genes that could increase their fitness and/or attractiveness (Rowe and Houle 1996; Iwasa and Pomiankowski 1999; Cotton et al. 2004). Thus, in species with male-only parental care, females could potentially gain multiple fitness benefits in choosing mates based on their body condition.

In the harvestman *Iporangaia pustulosa* (Arachnida: Opiliones), females lay their eggs in clutches on the vegetation and abandon them to males for protection (Machado et al. 2004; Requena et al. 2009; Fig. 1). Males may copulate and receive additional eggs while providing care, a situation in which successful individuals take care of multiple clutches simultaneously (hereafter called “brood,” following Requena and Machado 2015, Fig. 1A). Shortly after receiving the first clutch of eggs and assuming a parental role, a male becomes almost four times more likely to copulate with another female and receive her clutch of eggs than a non-parental male (Requena and Machado 2015). However, his chance of receiving new clutches of eggs declines dramatically over time, and after 1 month, this chance becomes similar to that of a non-parental male (Requena and Machado 2015). Although each egg completes its embryonic development in approximately 30 days (Requena et al. 2012), the total period of paternal care may extend up to 4 months due to the asynchronous deposition of eggs in the brood (Requena et al. 2009). While tending their broods, parental males reduce their foraging activities, gradually depleting their body condition over the long caregiving period (Requena et al. 2012). Therefore, one possible explanation for the change in males’ mating success over the course of their caregiving period is that the decline in body condition reduces their attractiveness to females.

Our study is divided into two complementary parts. In the first part, we examine how body condition influences the mating success of *I. pustulosa* males. In a field experiment, we manipulated the body condition of males in two situations: (1) in a *non-parental state*, to assess female mate choice when there is no information available regarding caregiving quality, only information about male body condition, and (2) in a *parental state*, to assess the role of body condition when females have additional information regarding caregiving quality due to the presence of eggs under males’ protection. Assuming that males in good body condition provide direct (i.e., parental care) or indirect (i.e., good genes) benefits to their mates, females should be more likely to copulate with them and lay more eggs in their broods compared to males in poor body condition. In the second part, we investigate a potential direct benefit that males in good body condition can provide to females. Given that male care in *I. pustulosa* plays a crucial role in protecting the eggs against predation by conspecifics and other arthropods

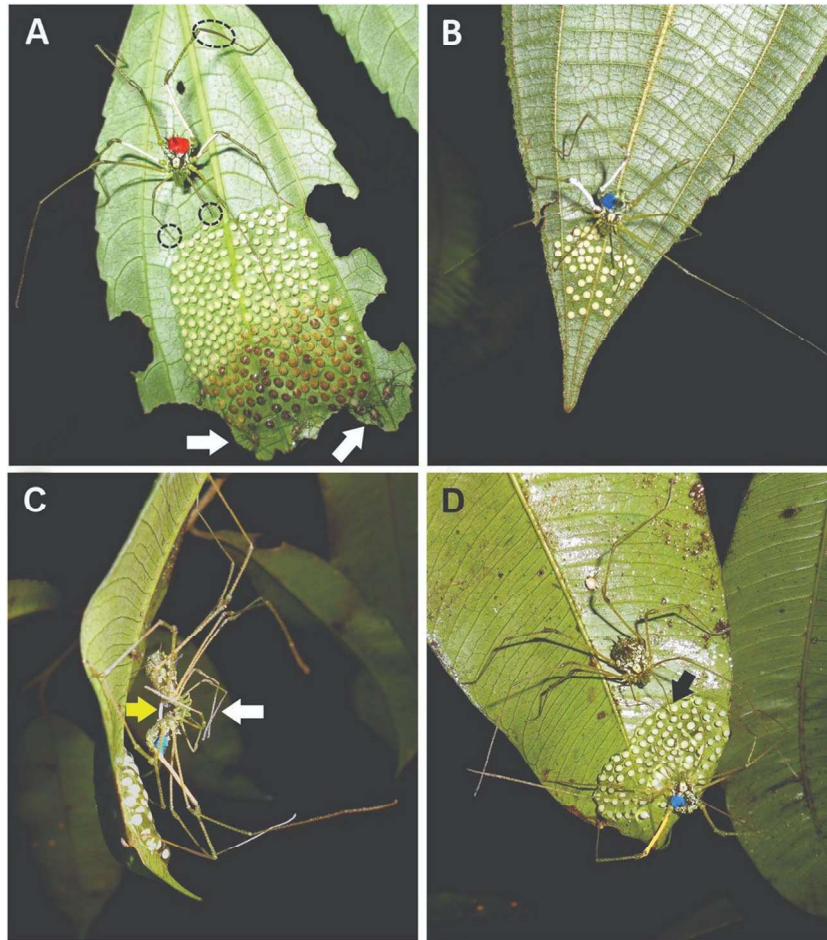


Fig. 1 Parental males of the harvestman *Iporangaia pustulosa* during egg attendance. **A** A successful male (with the body marked in red and hind legs marked in white) caring for a large brood composed of several clutches that can be recognized by differences in egg size and color. Eggs in early stages of development are smaller and white, whereas eggs in late stages are larger and dark. The brood also includes some early hatched nymphs (arrows), which disperse 3 to 5 days after eclosion. The dotted ellipses indicate the tarsus of the first pair of legs and the metatarsus of the fourth pair of legs, where males have sexually dimorphic exocrine glands that release pheromones. **B** A successful male (with the body marked in blue and right hind legs marked in white) caring for a single clutch of eggs. Note that all eggs have similar size and color, and the male keeps the tip

of his first pair of legs (where one of his sexually dimorphic exocrine glands are located) on the eggs. **C** When a receptive female arrives at the leaf, the caring male (with the body marked in blue and left hind leg marked in yellow) approaches her, and the couple starts a tactile interaction that involves mutual touches with the first and second pairs of sensorial legs. Sometimes, the female abandons the leaf without mating. When copulation occurs, the female keeps touching the male with her first pair of legs (white arrow) during penetration (the penis is indicated in the yellow arrow). **D** After copulation, the male moves to the tip of the leaf and allows the female to inspect the eggs with her first pair of legs. The female may abandon the leaf without laying eggs after this inspection or stay and add eggs to the brood. Photos: L. M. Alissa

(Requena et al. 2009), we expect that males in good body condition would be more effective in protecting the eggs from predation than males in poor body condition.

Materials and methods

Individuals of *Iporangaia pustulosa* are predominantly found on the marginal vegetation of creeks and streams. In contrast to most species within the family Gonyleptidae, in which males are typically larger than females and possess

enlarged spines used in competition for oviposition sites (Machado and Burns 2024), *I. pustulosa* males are slightly smaller than females and lack such weaponry. Throughout numerous years of field observations, we have not documented any instances of male-male fights or takeovers of broods in *I. pustulosa*, behaviors documented in other harvestman species exhibiting exclusive paternal care (Mora 1990; Nazareth and Machado 2010; Quesada-Hidalgo et al. 2019). The most prominent form of sexual dimorphism in *I. pustulosa* is the presence of two pairs of exocrine glands in males. The first pair is situated in the tarsal segments of

the first pair of legs, whereas the second pair is found along half of the extension of the metatarsus of the fourth pair of legs (Kury and Pinto-da-Rocha 1997; Fig. 1A). Males rub these glands on leaves, depositing chemicals on the substrate likely conveying information about their location (Murayama and Willemart 2015). As these glands are exclusive to males, they also likely release sexual pheromones.

Precopulatory interactions in *I. pustulosa* are consistently brief, never exceeding 30 s. These interactions either culminate in male aggression towards the female or prompt copulation without any discernible courtship (Requena and Machado 2014). On average, copulation lasts approximately 3 min, during which the couple engages in mutual tactile interaction with their first and second pairs of sensorial legs (Requena and Machado 2014; Fig. 1C). Post-copulation, females may abandon the male without laying eggs or inspect the brood using their first pair of legs, engaging in an egg-laying process that may last several hours (Requena and Machado 2014; Fig. 1D). Given that the front legs of *I. pustulosa* are covered with mechano- and chemoreceptors (Willemart and Chelini 2007), tactile and chemical signals likely play a critical role in mutual assessment during and after mating. From the female perspective, these chemical signals may convey information about male quality or attractiveness, as observed in other animal groups (reviewed in Wyatt 2003).

Study site

We carried out this study at Intervalos State Park (24° 140'S, 48° 040'W; 800 m a.s.l.), a fragment of Atlantic Forest in the State of São Paulo, Brazil. We conducted field observations and experimental manipulations using adult *I. pustulosa* individuals found on the vegetation along a 5-m-wide freshwater stream. The sampling area consisted of two transects, each running along one side of the stream for a distance of 200 m downstream and extending 1 m into the marginal vegetation. To facilitate location tracking, we affixed colored tape every 5 m along each transect. This allowed us to estimate the position of every male followed during the study. Data collection took place during the wet and warm season (between January and March 2015 and 2016), coinciding with the peak of the breeding season of *I. pustulosa* (Requena et al. 2012).

General description of the experiments

We performed two experiments in which we manipulated the body condition of both non-parental (experiment 1) and parental (experiment 2) *I. pustulosa* males, subsequently recording their mating success and number of acquired eggs under natural field conditions. In this topic, we provide an overview of our experimental manipulation, while

variations in the procedures employed in experiments 1 and 2 are explained in more detail in subsequent topics.

Upon collecting males from the field, we transported them to the laboratory, where they were individually marked with enamel ink. This procedure does not appear to influence the behavior of the individuals (e.g., Requena et al. 2009, 2012; Requena and Machado 2015). Given that harvestmen have very low basal metabolism (Santos 2007), their body condition declines slowly under resting conditions. To accelerate this process, we experimentally forced all males to decline their body condition through a series of physical exercises (i.e., forced walking) in the laboratory. Only after the forced exercise, when we were able to decline the body condition of all males, we assigned them to one of two experimental groups: (a) “good condition” group, in which males received water and food ad libitum, and (b) “poor condition” group, in which males received water ad libitum but no food. We allowed males of the “good condition” group to feed for 1 day, sufficient to induce significant food intake and, consequently, a marked increase in body condition (Fig. S1 in Supplementary Material). The criteria used to assign males to each of the two experimental groups are presented in Table S1 and Figs. S2–S4.

After the manipulation of body condition, we returned each male to the exact location of capture within our transects. During subsequent visits to the field, a team of four researchers actively surveyed the transects for 3 consecutive days. They searched for marked males during the afternoon (between 14:00 h and 18:00 h) and the night (between 20:00 h and 00:00 h). During each inspection visit, we recorded whether the recaptured males were successful or unsuccessful in acquiring eggs. To ensure that males were not tending to any clutches, upon encountering a marked male, we carefully searched the vegetation within a 2-m radius around him. Given that males significantly reduce their movement while caring for eggs (Requena et al. 2012), this searching procedure allowed us to confirm whether a male was successful or unsuccessful in acquiring eggs. For successful individuals, we took photographs of their broods to quantify the number of eggs acquired during the sampling interval, which spanned from one inspection visit to the next.

Experiment 1: manipulation of non-parental males

We captured a total of 136 non-parental males in January 2015. These males were transported to our laboratory at the Universidade de São Paulo, Brazil, where they were maintained under controlled conditions: temperature = 25–27 °C, relative humidity = 80%, and light:dark photoperiod = 12:12 h. We accommodated groups of six males in each container (base, 20 × 45 cm; height, 30 cm). The body condition manipulation lasted 15 days, during which all males were forced to walk 30 min a day (a total of

7 h of exercise) by a consistent touching stimulus (Fig. S5). Following the 15-day period of forced exercise, we assigned 68 males to the “good condition” group and 68 males to the “poor condition” (6 males from the latter group died in captivity, leaving us with 62 males for release back into the field). Males in the “good condition” group were provided with abundant sardine and moist cat food for 1 day, while males belonging to the “poor condition” group received no food. After the manipulation of body condition, we returned each male to the exact location where they had been initially captured in the transects. Finally, we visited the transects between February and April 2015 to search for the manipulated males at three time points: 7, 27, and 46 days after their return to the field. These three inspection visits will be referred to as *visits 1, 2, and 3*, respectively. Given that the focus of experiment 1 is on *non-parental* males, when a manipulated male was found with eggs (that is, changed its status to parental), we scored him as successful, and he was not accounted in subsequent visits.

When studying non-parental males, it is possible to keep the individuals in the laboratory for a long period and slowly reduce their body condition, simulating a long period of starvation. The 15-day period used here represents nearly half of the time a clutch of *I. pustulosa* takes to hatch (Requena et al. 2012). Thus, considering that parental males do not feed (or feed with a very low frequency) during the caring period (Requena et al. 2012), the duration of our experimental manipulation falls within a normal range of starvation experienced by the males in the field. Regarding the amount of food offered to the males, it is equivalent to a substantial meal, such as the corpse of a large katydid, moth, or caterpillar, all food items that we have already recorded in the field (Fig. S1A).

To assess whether the experimental manipulation successfully altered body condition in the desired direction, we used a paired *t*-test to compare the body condition (as described in the topic “[Estimation of body condition](#)” below) of males of each experimental group at the beginning and at the end of the 15-day period. The results clearly indicate that males in the “good condition” group experienced a marked increase in their body condition, whereas males in the “poor condition” group exhibited a decline in their body condition (Fig. S6 and Table S2).

Experiment 2: manipulation of parental males

Due to the relatively low proportion of *I. pustulosa* males that copulate, receive eggs, and assume parental roles (Requena and Machado 2015), we found a smaller number of parental males compared to non-parental males within the transects. Therefore, we had to carry out experiment 2 on three separate sampling occasions to achieve a substantial sample size. On each sampling occasion, we removed

the parental males from their broods and relocated them to a laboratory at the Intervales State Park, where they were maintained under natural conditions, i.e., a temperature of approximately 25 °C, humidity ranging from 80 to 90%, and a light:dark photoperiod of 14:10 h. Immediately after the removal of a parental male, we took photographs of his brood to count the initial number of eggs and enclosed the leaf on which the eggs were deposited with a plastic bag to protect them from predation. It was not possible to perform the same long-term manipulation conducted in experiment 1 because prolonged periods with parental males in the laboratory and absent from their clutches can result in high egg mortality and the hatching of juveniles inside the plastic bags.

In 2015, during the manipulation of body condition for both the first and second sampling occasions, all males were subjected to 1 h of daily forced exercise for 2 consecutive days, totaling 2 h (Fig. S5). Males in both experimental groups had access to water ad libitum but were not provided food during this 2-day period of forced exercise. After the forced exercise, only males assigned to the “good condition” group received abundant sardine for one whole night. Similar to experiment 1, we employed a paired *t*-test to compare the body condition of males of each experimental group at the beginning and at the end of the manipulation period. The analysis combined data from the two sampling occasions. As expected, males assigned to the “good condition” group exhibited an increase in their body condition, whereas males assigned to the “poor condition” group experienced a decline in their body condition (Fig. S7 and Table S2). The magnitude of the difference between the experimental groups was slightly smaller in the first two sampling occasions of experiment 2 in comparison to experiment 1 (Table S3), which can likely be attributed to the higher total intensity of forced exercise in experiment 1 (7 h).

To increase the sample size for experiment 2, we conducted a third sampling occasion in 2016, during which we subjected males to a total of 6 h of forced walking over one night (Fig. S8). Similar to the two previous sampling occasions, after the forced exercise, only males assigned to the “good condition” group were provided with abundant sardine for 1 day. As expected, males assigned to the “good condition” group exhibited an increase in their body condition, whereas males in the “poor condition” group experienced a decline in their body condition (Fig. S9 and Table S2). Moreover, the magnitude of the body condition change for both experimental groups in the third sampling occasion was higher than in the two previous sampling occasions (Table S3). The difference we found between sampling occasions 1–2 and 3 is likely due to the higher total intensity of forced exercise in the latter (6 h). When analyzing the data from experiment 2, we examined whether including the different sampling occasions as a variable in our models

would explain variance in the chances of males being successful in acquiring eggs. However, since incorporating the variable “sampling occasions” did not result in a reduction in the residual variance of your models and did not yield significant effects (Table S4), we opted not to include the variable “sampling occasions” in our final analyses.

After conducting the manipulation of body condition in the three sampling occasions, we subsequently returned each male to their respective brood within the transects. During the first sampling occasion in February 2015, we captured a total of 33 parental males, with 16 assigned to the “good condition” group and 17 to the “poor condition” group. Our visits to the transects occurred between February and April 2015 to search for the manipulated individuals at 7, 19, and 37 days after their return to the field. For the second sampling occasion in April 2015, we captured a total of 37 parental males, with 19 assigned to the “good condition” group and 18 to the “poor condition” group. Subsequent visits to the transects occurred between April and May 2015 to search for the manipulated individuals at 7, 21, and 40 days after their return to the field. Finally, during the third sampling occasion in February 2016, we captured a total of 36 parental males, with 18 assigned to the “good condition” group and 18 to the “poor condition” group. Our visits to the transects occurred between February and March 2016, with searches for the manipulated individuals conducted at 3, 15, and 28 days after their return to the field. The initial visit of each sampling occasion will be referred to as *visit 1*, the second as *visit 2*, and the third as *visit 3*.

Estimation of body condition

There are different ways to estimate body condition in arthropods (reviewed in Moya-Laraño et al. 2008). One of them involves calculating body density, determined by dividing an individual’s body mass by its corresponding body volume. Given that lipidic acid molecules occupy a greater volume per unit of mass compared to proteins or water, individuals with higher fat content exhibit lower body density, indicative of better body condition. Body density has already been used in a previous study on the energetic costs of egg attendance by *I. pustulosa* males (Requena et al. 2012). Thus, we adopted the same approach to ensure the comparability of our results with the previously published data.

To estimate body density, we first weighted the males using an electronic scale (with precision to the nearest 0.001 g) to obtain their body mass (BM). In the case of harvestman, the last five opisthosomal segments are interconnected by a highly elastic membrane (Fig. S1), which allows great expansion of this body part after a large meal. Thus, the body volume of individuals can vary considerably depending on whether they are poorly or well-fed (see examples in Fig. S1). To calculate body volume (BV), we

took photographs of each male in dorsal and lateral views and measured the following traits using the software *ImageJ* (Schneider et al. 2012): total body length (TBL), body width (BW) at the widest point of the dorsal scute (i.e., carapace), and body height (BH) at the highest point of the opisthosoma (see measured traits in Fig. S1). Using these three measurements, BV was approximated as an ellipsoid using the formula: $BV = 4/3 \times \pi \times TBL/2 \times BW/2 \times BH/2$. Finally, we divided the value of BM by the value of BV to estimate body density (g/mm^3). As we previously mentioned, males in good body condition should have higher fat content and, therefore, lower body density when compared to males in poor body condition.

Estimation of offspring mortality

In the third sampling occasion of the experiment 2, conducted in 2016, we monitored the broods of both experimental groups over a 3-day period, totaling 15 to 19 inspections per brood. During each inspection, we recorded the presence or absence of males with their broods. Out of the 36 males (18 in the “poor condition” and 18 males in the “good condition” group), no instances of permanent male desertion were detected. Additionally, the proportion of inspections in which the caring male was present was similar between the two experimental groups: 67% in the “poor condition” and 68% in the “good condition” (Fig. S10). These data indicate that males resumed their parental activities after being kept in the laboratory without their broods and that the potential stress caused by the manipulation did not induce brood desertion. Thus, we used the number of egg loss in broods protected by parental males in the two experimental groups of experiment 2 to test whether body condition influences the quality of male care.

By comparing pictures of the same brood taken at two different moments, it is possible to determine if some eggs were removed during consecutive visits, which we assumed to be due to egg predators’ attacks. This procedure can be confidently applied only to eggs in the early stages of embryonic development because eggs in later stages may hatch and the nymphs may disperse in a few days. Thus, egg hatching followed by nymph dispersal may be confounded with egg predation. To avoid this problem, we recorded egg loss only for eggs that were in stages 1 to 3 according to the classification proposed by Requena et al. (2012). These eggs in the initial stages of embryonic development were expected to be present in their clutches during the following visits, and any egg loss is certainly the result of egg predation (for an example of the procedure, see Fig. S11). It is important to highlight that, in a collective effort of four students and two researchers who have been studying the *I. pustulosa* reproductive system for more than 20 years, no instance of filial cannibalism by males has been observed. Moreover, eggs

in the final stages of embryonic development are usually located at the tip of the leaf (Figs. 1 and S11) and are likely less accessible to ambulatory predators that approach the brood from the leaf petiole. Thus, predation events probably are concentrated on eggs in the initial stages of embryonic development.

Data analyses

Females are expected to prefer mating with males in the “good condition” group, both in the non-parental (experiment 1) and parental state (experiment 2). This way, we predicted that a greater proportion of males in the “good condition” group would successfully mate and receive eggs from females than males in the “poor condition” group. Moreover, the successful males in the “good condition” group would receive more eggs than successful males in the “poor condition” group. To analyze male mating success, we categorized males as successful or unsuccessful (binary data) depending on whether they received at least one clutch of eggs between inspection visits. After this, using the data only from the successful males in each experimental group, we analyzed another component of their success, the number of eggs they received (count data).

Our first set of analyses, conducted for both experiments 1 and 2, evaluated whether the male mating success was significantly affected by the experimental group (i.e., “poor” and “good condition”) and the period after body condition manipulation (i.e., visits 1–3). For experiment 1, we used a dataset with all visits merged and created two generalized linear models (GLMs) with a binomial distribution of errors. In one of these models, the proportion of successful and unsuccessful males was the response variable, with an additive effect (i.e., not including the interaction between the variables) between experimental groups and visits as the explanatory variable. The second model had the proportion of successful and unsuccessful males as the response variable, with an interactive effect between experimental groups and visits as the explanatory variable. We then compared the models to determine which of them better explained the variation in male mating success. The same statistical procedure was applied to analyze the data in experiment 2. The only difference is that, since we sampled some parental males in multiple visits, we created generalized linear mixed models (GLMMs) and included male identity as a random effect in our models.

After finding that male mating success in both experiments is significantly affected by an interaction between experimental groups and visits (see topics “[Experiment 1: attractiveness of non-parental males](#)” and “[Experiment 2: attractiveness of non-parental males](#)” in the “[Results](#)” section), we analyzed the data separated for each visit (1–3). This allowed us to detect differences between the

experimental groups in the probability of male mating success and egg acquisition within each visit. For the data with non-parental males (experiment 1), we created two GLMs with binomial distribution of errors for the data observed in each visit, in which the proportion of successful and unsuccessful males was the response variable. One of the models included the experimental groups as the predictor variable, while the other was a null model without any predictor variable. To analyze differences in egg acquisition between the experimental groups in experiment 1, we created two GLMs with a negative binomial distribution of errors, with the number of eggs received by successful males between visits as the response variable. Again, one of the models included the experimental groups as the predictor variable, while the other was a null model.

To test the predictions for parental males (experiment 2), we employed the same analytical structure, but this time using GLMMs because we included male identity as a random effect. Additionally, we analyzed one last component of males’ success in experiment 2, focusing on the cumulative egg acquisition across all visits. Again, we used data only from successful males in each experimental group. We created two GLMMs with a negative binomial distribution of errors, taking the total number of eggs received by successful males across all visits as the response variable and considering male identity as a random effect. One of the models included the experimental groups as the predictor variable, while the other was a null model.

In experiment 2, we also expected that parental males in the “good condition” group would provide better paternal care than males in the “poor condition” group. Thus, we predicted that broods under the protection of males in the “good condition” group would have lower chances of being attacked by predators than broods of males in the “poor condition” group. To test this first prediction, we categorized each male’s brood as either having at least one missing egg (coded as 1) or having no missing egg (coded as 0) between visits. Moreover, we predicted that the broods of males in the “good condition” group would experience less egg predation compared to the broods of males in the “poor condition” group. Similar to what was done for the analyses of male mating success, we first tested whether there was a significant interaction between the experimental group (i.e., “poor” and “good condition”) and the categorical variable visit (1–3) affecting the chances of a male’s brood being attacked by egg predators. Using the dataset with all visits merged, we created two GLMMs with a binomial distribution of errors. In one of these models, the proportion of broods with and without eggs consumed was the response variable, with an additive effect (i.e., not including the interaction between the variables) between experimental groups and visits as the explanatory variable and we included male identity as a random effect. The second model had the proportion of broods with and without eggs consumed as the

response variable, with an interactive effect between experimental groups and visits as the explanatory variable and male identity as a categorical random variable. We then compared the models to determine which of them better explained the variation in male mating success.

Following the analyses checking the interaction between the experimental group and visit on egg predation, we proceeded to test, in each visit, whether male experimental group affected the chances of a brood being attacked by egg predators and the amount of eggs consumed. For the first prediction, we used the categorization of having at least one missing egg (coded as 1) or having no missing egg (coded as 0) between visits (binary data) as the response variable and created a pair of GLMs with a binomial distribution of errors: one model included the experimental groups as the predictor variable, and the other was a null model. To test this second prediction, we used the proportion of eggs that went missing from each brood between visits as the response variable (providing an estimate of the chances of each individual egg being eaten by predators). Then, we created a pair of GLMs with a negative binomial distribution of errors: one model included the experimental groups as the predictor variable, and the other was a null model. We repeated this model comparison structure between the model including the experimental groups and the null model for each visit (1, 2, and 3).

We conducted deviance analyses to compare the model that included the experimental groups as the predictor variable with its corresponding null model. Deviance analyses are based on a likelihood ratio test that calculates the goodness-of-fit between the two models and generates a p -value by approximating the deviance value to a chi-square distribution (Lekdee and Ingsrisawang 2010). If male condition is indeed important for male success (i.e., the mating probability and the number of eggs received) and for the quality of care provided by the males (i.e., the probability of egg loss and the number of eggs lost), the model including the experimental groups should have a better fit than the null model, and the deviance analysis should return a p -value lower than 0.05. We used the package `glmmTMB` (Brooks et al. 2017) for building the models and conducting model fitting protocols. All analyses were performed in the software R version 4.0.2 (R Core Team 2022). The data files and the R Notebook with the analyses are available in the Dryad repository (<https://doi.org/https://doi.org/10.5061/dryad.3n5tb2rpz>).

Results

Experiment 1: attractiveness of non-parental males

In visit 1, conducted 7 days after returning manipulated males to the field, no male received eggs (Fig. 2A), and

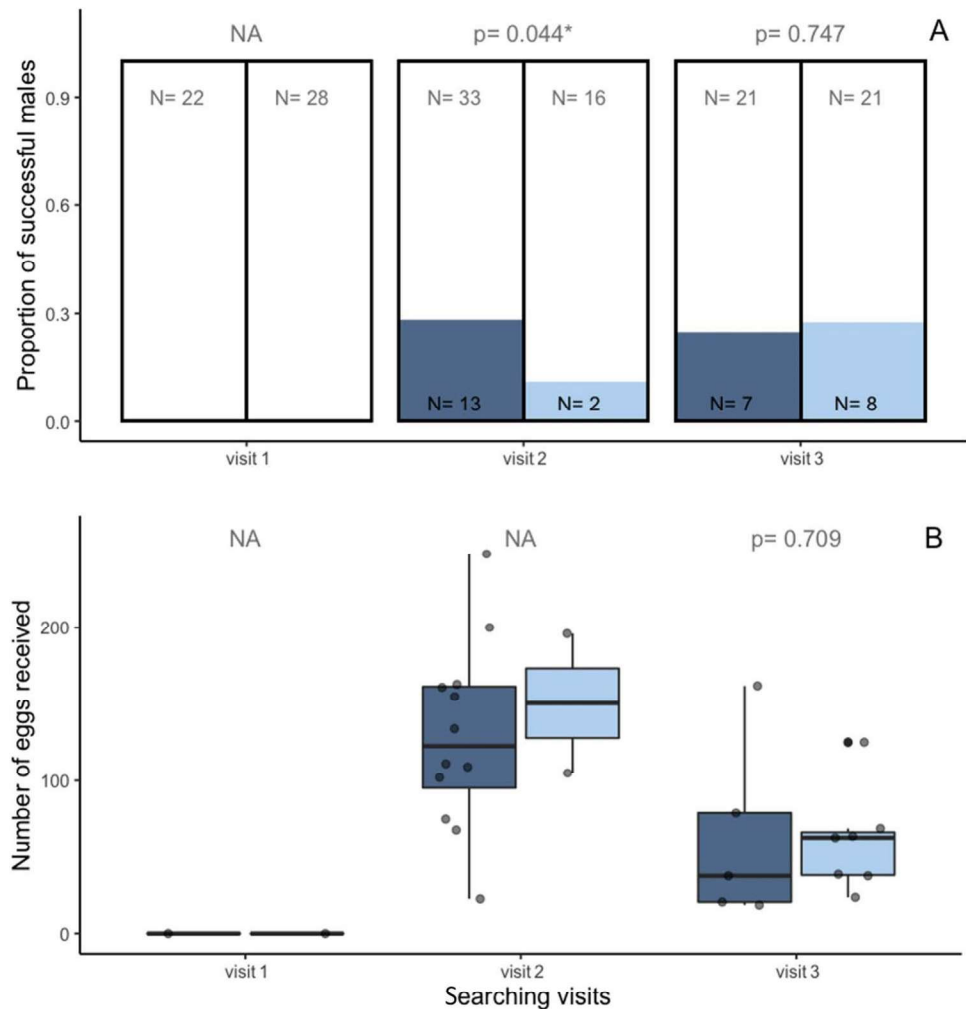
thus this visit was removed from the analyses. The analysis of the dataset with visits 2 and 3 merged indicated that the mating success of non-parental males was affected by the interaction between the experimental group and visit (deviance = 4.370; $df = 1$; $p = 0.037$). In visit 2, conducted 27 days after returning manipulated males to the field, the proportion of successful males in the “good condition” group (28.3%) was more than two times higher than in the “poor condition” group (11.1%) (deviance = 4.056; $df = 1$; $p = 0.044$; Fig. 2A). In visit 3, conducted 46 days after returning manipulated males to the field, the proportion of successful males was similar between the two experimental groups (25% in the “good condition” group and 27.5% in the “poor condition” group) and comparable to that in the “good condition” group in visit 2 (deviance = 0.103; $df = 1$; $p = 0.747$; Fig. 2A).

Due to the lack of successful males in both experimental groups in visit 1 and the low number of males in the “poor condition” group that received eggs in visit 2 ($N = 2$), we were unable to statistically compare the experimental groups in these two visits (Fig. 2B). In visit 3, however, the mean number of eggs received per male was 63 (median = 38; range, 19–162 eggs; $N = 7$ broods) for males in the “good condition” group and 60 (median = 63; range, 24–125 eggs; $N = 8$ broods) for males in the “poor condition” group (Fig. 2B). The number of eggs received by the males in visit 3 was not affected by the experimental group (deviance = 0.138; $df = 1$; $p = 0.709$).

Experiment 2: attractiveness of parental males

The analysis of the dataset with all visits merged indicated that the mating success of parental males was significantly affected by the interaction between the experimental groups and visits (deviance = 15.605; $df = 2$; $p < 0.001$). In contrast to what happened with non-parental males, parental males from both experimental groups promptly received eggs in the interval between their return to the field and visit 1 (Fig. 3A). In visit 1 (3–7 days after manipulation), the proportion of parental males that received additional eggs was not affected by the experimental group: 13.2% in the “good condition” group and 19.2% in the “poor condition” group (deviance = 0.704; $df = 1$; $p = 0.401$; Fig. 3A). The pattern was similar in visit 2 (15–21 days after the manipulation), with 30.43% of successful males in the “good condition” group and 15.6% in the “poor condition” group (deviance = 1.701; $df = 1$; $p = 0.192$; Fig. 3A). In visit 3 (28–40 days after the manipulation), however, the proportion of males in the “poor condition” group that received additional eggs remained roughly constant (i.e., 18.2% of males), while the proportion of successful males in the “good condition” increased to 70% (deviance = 6.033; $df = 1$; $p = 0.014$; Fig. 3A).

Fig. 2 **A** Proportion of non-parental males of the harvestman *Iporangaia pustulosa* that were successful in receiving eggs over the study period (blue fill with sample size in black = successful males; white fill with sample size in gray = unsuccessful males). Males were assigned to two experimental groups: “good condition” (dark blue) and “poor condition” (light blue). We conducted three visits at 7, 27, and 46 days after returning the experimentally manipulated males to the field. **B** Boxplot showing the number of eggs received by successful males in the “good condition” (dark blue) and “poor condition” (light blue) groups. In both **A** and **B**, the p -value comparing the two experimental groups is presented above the data for each visit (significant values are indicated with an asterisk). Due to an insufficient number of successful males in some visits, we were unable to statistically compare the experimental groups (indicated by NA)



In visit 1, the mean number of eggs received per successful parental male was 28 (median = 24; range, 7–75 eggs; $N=7$ broods) in the “good condition” group and 20 (median = 17; range, 7–45 eggs; $N=10$ broods) in the “poor condition” group (Fig. 3B). The number of eggs received by parental males in visit 1 was not affected by the experimental group (deviance = 0.328; $df=1$; $p=0.566$; Fig. 3B). Although males in both experimental groups had similar chances of receiving eggs in visit 2 (Fig. 3A), the number of eggs received by parental males was affected by the experimental group (deviance = 4.827; $df=1$; $p=0.028$; Fig. 3B). The mean number of eggs received per successful parental male in the “good condition” group (mean = 61 eggs; median, 64 eggs; range, 26–98 eggs; $N=7$ broods) was twice as high as that in the “poor condition” group (mean = 30 eggs; median = 25 eggs; range, 12–54 eggs; $N=5$ broods; Fig. 3B). In visit 3, due to the low number of successful parental males in the “poor condition” group, we were unable to statistically compare the experimental groups. The median cumulative number of eggs received per parental male (considering all visits together) in the “good condition”

group (median = 103.5 eggs; range, 11–191 eggs; $N=12$ broods) was almost five times higher than that in the “poor condition” group (median = 22 eggs; range, 11–306 eggs; $N=12$ broods) (deviance = 4.638; $df=1$; $p=0.031$, Fig. 4).

Caring quality

We did not observe any instances of filial cannibalism during the visits to the field. In contrast to the patterns observed for egg gain, egg loss was pervasive, occurring throughout the entire experimental period and at higher incidence (Fig. 5A). In the analysis with all visits merged into the same dataset, we found that neither the experimental group nor the visit nor their interaction affected the chances of a parental male losing at least one egg from his brood between visits (deviance = 1.250; $df=2$; $p=0.535$).

In visit 1, the proportion of parental males in the “good condition” group that had eggs consumed by predators was 61.5%, while in the “poor condition” group, it was 51.9% (Fig. 5A). During visit 2, 73.9% of males in the “good condition” group and 81.2% in the “poor condition” group had

Fig. 3 **A** Proportion of parental males of the harvestman *Iporangaia pustulosa* that were successful in receiving additional eggs over the study period (green fill with sample size in black = successful males; white fill with sample size in gray = unsuccessful males). Parental males were assigned to two experimental groups: “good condition” (dark green) and “poor condition” (light green). We conducted three visits at 3–7, 15–21, and 28–40 days after returning the experimentally manipulated males to their broods in the field. **B** Boxplot showing the number of eggs received by parental males of the “good condition” (dark green) and “poor condition” (light green) groups. In both **A** and **B**, the *p*-value comparing the two experimental groups is presented above the data for each visit (significant values are indicated with an asterisk). Due to insufficient number of successful males in the “poor condition” group in visit 3, we were unable to statistically compare the experimental groups (indicated by NA)

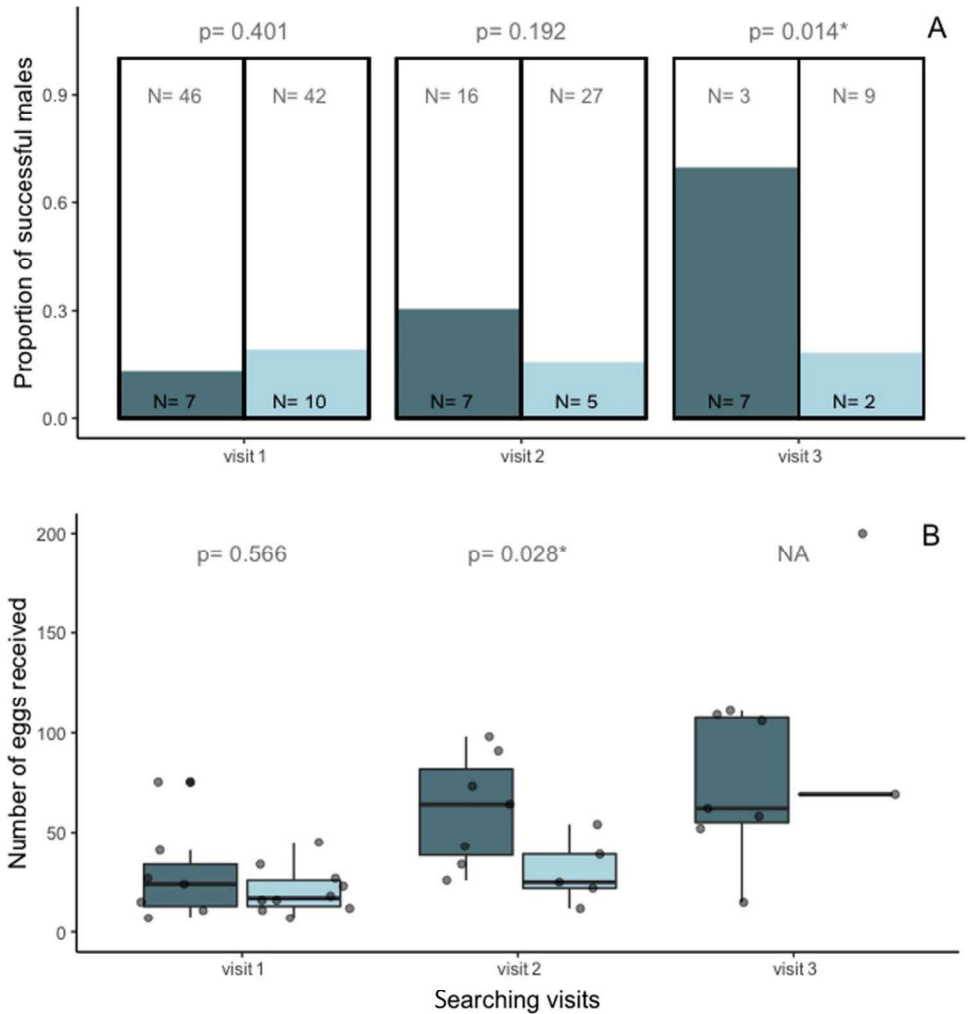
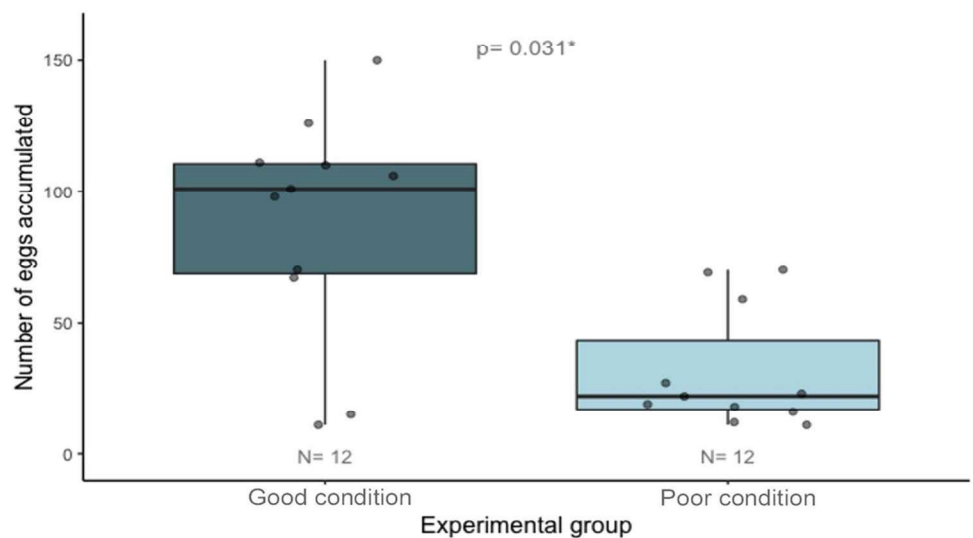


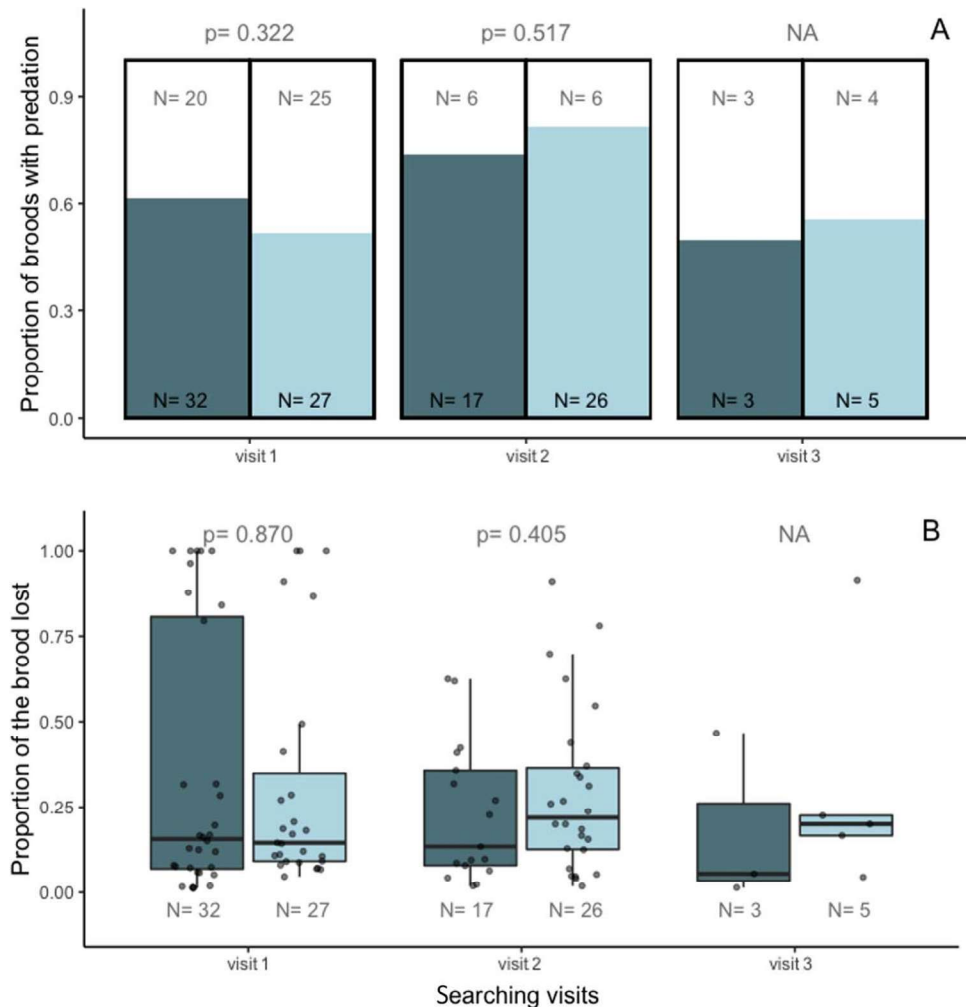
Fig. 4 Boxplot showing the cumulative number of eggs (including all visits) received by parental males of the harvestman *Iporangaia pustulosa* belonging to two experimental groups: “good condition” and “poor condition.” The *p*-value comparing the two experimental groups is presented above the data. To improve visualization, two outliers (one brood with 191 eggs in the “good condition” group and one brood with 306 eggs in the “poor condition” group) were omitted from the graphic, but not from the analysis



at least one egg consumed by predators. In visit 3, predation events occurred in the broods of 50% of the males in the “good condition” group and 55.5% of the males in the “poor

condition” group (Fig. 5A). The chances of a brood being attacked by predators were similar in the two experimental groups and throughout the entire experimental period.

Fig. 5 **A** Proportion of broods of the harvestman *Iporangaia pustulosa* that lost at least one egg to predation over the study period (green fill with sample size in black = broods attacked by predators; white fill with sample size in gray = broods not attacked by predators). Parental males were assigned to two experimental groups: “good condition” (dark green) and “poor condition” (light green). We conducted three visits at 3–7, 15–21, and 28–40 days after returning the experimentally manipulated males to their broods in the field. **B** Boxplot showing the proportion of eggs consumed by predators in broods of the “good condition” (dark green) and “poor condition” (light green) groups. In both **A** and **B**, the p -value comparing the two experimental groups is presented above the data for each visit. Due to insufficient number of broods in both experimental groups in visit 3, we were unable to statistically compare them (indicated by NA)



In visit 1, the median percentage of the brood lost to predation per parental male was 15.6% (range, 1.2–100%; $N = 32$ broods) for males in the “good condition” group and 14.6% (range, 4.7–100%; $N = 27$ broods) for males in the “poor condition” group (Fig. 5B). In visit 2, the median percentage of the brood lost to predation per male was 13.4% (range, 1.8–62.5%; $N = 17$ broods) for males in the “good condition” group and 21% (range, 1.8–91.1%; $N = 26$ broods) for males in the “poor condition” group (Fig. 5B). The number of eggs lost to predation was not affected by the experimental group either in visit 1 (deviance = 0.026; $df = 1$; $p = 0.870$) or in visit 2 (deviance = 0.690; $df = 1$; $p = 0.405$; Fig. 5B). In visit 3, only five parental males in the “poor condition” group and three in the “good condition” group were still caring for their broods (Fig. 5B). Therefore, we were unable to statistically analyze the effect of the experimental group on the number of eggs lost to predation in this last visit.

Discussion

After manipulating the body condition of non-parental and parental males of a harvestman species in which males are solely responsible for egg attendance, we assessed whether males in good body condition had higher mating success than males in poor body condition under natural field conditions. Our results indicate that, irrespective of their parental status, males whose body condition was experimentally improved had greater chances of copulating and receiving a clutch of eggs from females than males whose condition was experimentally reduced. Taken together, these findings support our hypothesis that body condition is a sexually selected trait and that females prefer males in good condition both before and after they acquire a first clutch.

Several male traits, such as body size, ornament size, and calling effort, are condition-dependent and can be

subject to directional sexual selection via female choice (Hunt et al. 2004). Since females cannot directly assess male condition, they rely on condition-dependent traits to evaluate potential mates (Iwasa and Pomiankowski 1999). In addition to visual and acoustic signals, the profile of cuticular hydrocarbons (CHC), a contact pheromone in terrestrial arthropods, may also exhibit condition dependence (e.g., Berson and Simmons 2018). Despite harvestmen not producing sounds that attract mates and lacking the ability to form images, they are highly sensitive to tactile and chemical signals used in intraspecific communication (Willemart et al. 2009). In *I. pustulosa*, copulation is preceded by intense leg tapping between male and female (Requena and Machado 2014; Fig. 1C), during which females may assess the body condition of potential mates using information from their CHC profile. Moreover, males have conspicuous sexually dimorphic exocrine glands on the first and fourth pair of legs, used to deposit chemicals on the substrate (Murayama and Willemart 2015; Fig. 1A). The role of these chemicals is not yet fully understood, but females may use them to evaluate the body condition of potential mates. Mating decisions based on glandular products released by parental males have already been reported for the fifteen-spined stickleback, *Spinachia spinachia*. Females of this fish prefer to lay their eggs in nests with higher levels of tangspiggin, a condition-dependent glycoprotein produced by males and released to shape the nest structure (Östlund-Nilsson 2001). Regardless of the specific cues used by *I. pustulosa* females to assess male condition, our results demonstrate their capability to do so and use this information in mate choice.

When assessing the positive effect of body condition on the mating probability of non-parental males, female preference emerged about 4 weeks post-manipulation. Within this timeframe, males in good body condition had twice the mating probability of those in poor body condition (Fig. 2A, visit 2). Nearly 7 weeks post-manipulation, males in good body condition still maintained their attractiveness. Only then males in poor body condition achieved a similar mating probability, finally eliminating the effect of the body condition manipulation (Fig. 2A, visit 3). Males initially in poor condition likely had time to forage and improve their body condition over this extended period. Consequently, several weeks post-manipulation, the mating probability and the number of eggs acquired by males in both experimental groups were similar. These results emphasize that when females lack information about the prospective male caregiving quality, primarily due to the absence of eggs under their care, male body condition becomes a relevant factor. We expect females of other taxa with male-only parental care to exhibit similar mate choice patterns. In some fish and frog species, for instance, males cease feeding while

caring for the eggs, and their body condition also declines over time (reviewed in Goldberg et al. 2020 and Machado and Macedo-Rego 2023). Thus, by selecting non-parental males in good body condition, females could increase the chances of egg care until hatching, reduce the risk of filial cannibalism or egg desertion, enhance egg aeration and/or hydration, and provide more efficient protection to the eggs (e.g., Neff 2003; Takahashi and Khoda 2004).

When quantifying the positive effect of body condition on the mating probability of parental males, female preference in the first 3 weeks post-manipulation was independent of males' body condition. However, contrary to experiment 1, in which non-parental males received the first eggs only 3 weeks after we returned them to the field, in experiment 2, parental males promptly received new eggs. This finding reinforces the findings of a previous observational study with *I. pustulosa* that showed that parental males are more attractive than non-parental males (Requena and Machado 2015). Studies on other species exhibiting male-only parental care have also reported female preference for parental males (arthropods: e.g., Gilbert et al. 2010; Nazareth and Machado 2010; Ohba et al. 2016, 2018; fish: e.g., Jamieson 1995; Lindström et al. 2006; Hale and St Mary 2007; frogs: Valencia-Aguilar et al. 2020). Taking a step further, our study reveals that the presence of previous eggs interacts with body condition to influence mating probability and the number of eggs received by parental males. Approximately 4–6 weeks post-manipulation, parental males with improved body condition acquired more mates and eggs than those in poor condition (Fig. 3A, visit 3). Thus, as expected, parental males in good condition appear to extend their reproductive window during which they are preferred by females. Males in poor condition, on the other hand, experience a decline in body condition over the course of the caring period, limiting their attractiveness to the baseline level determined solely by their parental status (Requena and Machado 2015).

Males taking care of previous eggs and in good body condition received almost two times more eggs than parental males in poor body condition. Cases of female choice based on multiple cues are widespread in animals, including those with male-only parental care (Candolin 2003; see also Pizzolon et al. 2012 and references therein). For instance, in the sand goby, *Pomatoschistus minutus*, neither body size nor the size of the nest alone affects male attractiveness, but the combination of a large body size and a large nest greatly increases the chances of parental male being selected by a female (Lehtonen et al. 2007). In the case of *I. pustulosa*, we argue that females are also better able to evaluate potential partners when using multiple sources of information, such as the presence of eggs under the males' protection and some phenotypic trait that signals males' body condition. Moreover, the greater number of eggs received by parental males in good body condition suggests that they either attract more

mates or gain more eggs from each female. If females indeed increase the number of eggs laid with males in good condition (i.e., high-quality mates), this finding would represent a case of positive differential allocation (Sheldon 2000). However, we emphasize that detailed information on the number of eggs laid by individual females is necessary to understand how they allocate their eggs in response to male condition.

Based on the direct benefits that females could gain from leaving their offspring under male care, we expected a positive relationship between the high attractiveness of males in good body condition and the quality of their paternal care (Hoelzer 1989; Kokko 1998). However, we found that an increase in male body condition (in the magnitude of our manipulation) did not result in improved male caregiving quality in *I. pustulosa*. If males in good body condition are not better at protecting eggs from predators, then why are they preferred by females? We propose two hypotheses, which are non-mutually exclusive. Firstly, assuming that a male's body condition correlates with his overall health and lifespan, as already reported for some arthropod species (e.g., Jacot et al. 2005; Kelly et al. 2014; McKay et al. 2016), females may prefer males in good body condition due to indirect benefits linked to good genes for their offspring (Hunt et al. 2004).

A second possibility is that males in good condition allocate their extra energy into advertising their quality as mates. Condition is determinant for the expression of several advertisement traits, such as sexual ornaments (e.g., Cotton et al. 2004), weapons (e.g., Johns et al. 2014), and pheromones (e.g., South et al. 2011). A theoretical model known as “essential male care” suggests that, when males are the sole responsible for parental care and the costs of such care are low, most males can provide the minimum necessary care for offspring survival. However, only males in good condition can allocate surplus energy to advertise their overall quality and attract more mates (Kelly and Alonzo 2009). Thus, while male advertisement can signal an important aspect of quality (e.g., body condition), it should not trade-off with his caregiving quality, as has already been reported for the peacock blenny, *Salaria pavo*, in which males are the sole responsible for egg attendance (Pizzolon et al. 2012). Egg attendance is considered one of the less demanding forms of parental care (Tallamy and Schaeffer 1997; Gilbert and Manica 2010; Smiseth et al. 2012). If this holds true for *I. pustulosa*, the low costs associated with paternal behavior could explain why males from both experimental groups were equally efficient in protecting the eggs. Thus, assuming that care does not impose significant costs and most males have enough energy to achieve the minimum parental care necessary for high offspring survival, we should expect males in good body condition to invest more in advertisement and be more attractive to females. This expectation

is congruent with our findings and suggests that the theoretical predictions of the “essential male care” model have empirical support.

Studies examining female mate choice based on condition-dependent traits, which serve as reliable indicators of male caregiving ability and/or quality, are predominantly limited to vertebrates, especially birds and frogs with biparental care (e.g., Badyaev and Qvarnström 2002; DeMory et al. 2010; Pettitt et al. 2020) and fish with male-only parental care (e.g., Pizzolon et al. 2012). Here, we present one of the first empirical examples demonstrating that male body condition influences male attractiveness in an arthropod species exhibiting male-only parental care. Our field-based results show that females prefer males, whether parental or non-parental, in good body condition over those in poor condition. However, the benefits to females as a result of their preference for males in good condition remain to be understood, as we found no evidence that an increase in body condition improves the survival of the offspring under male care. Based on the “essential male care” model, which explores male allocation of resources between sexual advertising and parental activities in species with male-only care (Kelly and Alonzo 2009), we propose that *I. pustulosa* males in good body condition are more attractive because the relatively low costs of egg attendance allow them to allocate their surplus energy into advertising their overall quality. Future studies are necessary to formally test the applicability of the theoretical predictions of the “essential male care” model to our study system. An interesting research direction would be to investigate if the higher attractiveness of males in good body condition is related to changes in the CHC profiles or to a higher production of exocrine glandular secretions that work as sexual pheromones.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03439-6>.

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Data availability The datasets generated and/or analyzed during the current study are available in the Dryad repository, <https://doi.org/10.5061/dryad.3n5tb2rpz>.

Declarations

Ethical approval The procedures used in this study comply with Brazilian legislation regarding the collection and handling of invertebrates.

Competing interests The authors declare no competing interests.

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