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COMMENT

Sigmoid allometries generate male dimorphism in secondary sexual traits: a comment on Packard (2023)

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Abstract

The detection of male dimorphism has seen numerous statistical advances. Packard has recently criticized a widely used method, reanalyzing data from beetles and harvestmen using an alternative method. We disagree with Packard conclusions, probably due to different implicit definitions of male dimorphism. We consider that male dimorphism manifests in a distribution when it is significantly better described by a model with two values of central tendency (bimodality), rather than a model with only one (unimodality). Thus, while Packard suggests sigmoid allometries as alternatives to male dimorphism, we argue that such allometries are manifestations of mechanisms that generate bimodal distributions. Instead of focusing on this dichotomy, we propose an approach to test whether bimodality in a trait simply arises from its allometry by: (1) characterizing the trait static allometry, (2) simulating body size values based on original data parameters, and (3) generating new trait sizes using the static allometries. The percentage of simulations generating equal or greater bimodality than the data represents the likelihood that the bimodality can be explained by the allometry alone. Our method offers a null model linking sigmoid allometries and bimodal distributions, providing a test for mechanisms that accentuate trait bimodality beyond what the trait allometry generates.

Keywords Bimodality · Disruptive selection · Hartigan's dip test · Intrasexual dimorphism · Harvestmen · Mixture models

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Conditionality and morphological divergence in dimorphisms

About 130 years ago, Bateson and Brindley (1892) were intrigued by the bimodalities in the frequency distributions of secondary sexual traits (SSTs) in male earwigs, rhinoceros beetles, and stag beetles. Later, these bimodalities were linked to alternative reproductive tactics among males of the same population (Gadgil 1972), and the term *male dimorphism* has since been used for systems where males roughly fit into two categories (*morphs*) that combine a specific morphology with a reproductive behaviour. In many male-dimorphic species, *major males* (usually those exhibiting high SST values) guard females or reproductive resources, have larger bodies, and disproportionally larger weaponry, whereas *minor males* (usually those exhibiting low SST values) engage in sneak copulations, have smaller bodies, and reduced or completely absent weaponry (Taborsky et al. 2008). These alternative phenotypes can represent a simple genetic polymorphism in one locus (Shuster 2008), but more commonly result from a conditional strategy in resource allocation (Tomkins and Hazel 2007).

Conditional male dimorphism represents a case of extreme plasticity known as polyphenism, where the same genotype can develop two or more alternative phenotypes via a reaction norm with a threshold (Nijhout 1999). In this case, males initially follow the same developmental pathway and environmental conditions, such as food availability, trigger a developmental switch. As a result, individuals will either express or suppress an SST associated with one of the alternative adult phenotypes (Emlen 2008). The extent of this reprogramming event and its timing in individuals' development places species along a continuum of behavioural reversibility and morphological divergence between morphs. At one extreme, males are morphologically uniform and can dynamically switch between different reproductive behaviours (Taborsky et al. 2008), as only behavioural switches are necessary, without any developmental reprogramming. For instance, male gryllid crickets switch between a reproductive tactic based on acoustic signalling to attract females and a satellite tactic based on remaining silent near a calling male to intercept females (Hissmann 1990). At the opposite end of the continuum, males exhibit striking morphological differences, each capable of performing only one of the mating tactics, as reported for dung beetles, where large horned males aggressively defend resources in dung patches, and small hornless males engage in sneak copulations with unguarded females (Emlen 1997). In this case, both morphological and behavioural switches exist, which usually results in males fixed in a single reproductive tactic throughout their entire adult life.

The continuum observed in conditionally male-dimorphic species generates a challenge: some males may express intermediate morphologies, raising the question of whether male dimorphism exists in the system. This debate has prompted the development of numerous statistical methods aimed at determining the presence of male dimorphism in various systems (see Knell 2009 and references therein). Initially, formal approaches focused on detecting non-linearity in the static allometries of the SST and body size (Eberhard and Gutierrez 1991; Kotiaho and Tomkins 2001). Subsequently, univariate methods were introduced to investigate the frequency distributions of SSTs and body size, assessing the presence of multiple peaks (Rowland and Qualls 2005; Rowland et al. 2005). This statistical procedure formalizes what Bateson and Brindley (1892) originally attempted visually with earwig forceps, as well as rhinoceros beetle horns and stag beetle mandibles. Implicit in the univariate approach is a definition of male dimorphism, which we now make explicit: we consider male dimorphism to manifest in a univariate distribution when it is significantly better described (statistically) by a model with two different values (parameters) of central tendency (i.e., statistical bimodality), rather than a model with only one (i.e., statistical unimodality). This operational definition is useful because bimodality can result from discontinuous or continuous sigmoid allometries and may arise either from selection against intermediate sized individuals or threshold developmental mechanisms.

Packard's (2023) criticism of univariate methods to detect male dimorphism

In the article titled "Frequency distributions, dimorphisms, and allometric variation in size of the weapon on male harvestmen (Arthropoda, Arachnida, Opiliones)", Packard (2023) raised questions regarding the existence of male dimorphism in harvestmen by reanalysing published data from five species. Although Packard used harvestmen as a model system to evaluate the method of identifying male dimorphisms through univariate tests of bimodality in trait distributions, his criticism extends beyond harvestmen studies and also applies to studies of male dimorphism in rhinoceros beetles (Packard 2021a, 2022) and stag beetles (Packard 2021b). While we hold different viewpoints from Packard on certain aspects of his contribution (addressed below), we acknowledge that his papers mark an initial step in an important re-evaluation of univariate tests.

Since the influential article by Rowland and Qualls (2005), the investigation of male dimorphisms in a single trait has been widely conducted using mixture models. This approach involves contrasting models with either one or a mixture of multiple distributions, determining the best-fitting model based on AIC values. A significant advantage of this approach is its ability to quantify uncertainty in 'morph membership' for intermediate males, calculated as probabilities from the modelled distributions. These probabilities can then be used to conservatively avoid assigning a morph to males for which the ambiguity exceeds a certain threshold. Packard challenges the findings of studies using this approach by arguing that: (1) "*the AIC protocol may be so liberal in its identification of bimodal distributions as to be generally unreliable*" (page 2), and (2) "*whereas dimorphism would very likely cause the frequency distribution to be bimodal, the presence of two modes does not in itself point to dimorphism*" (page 2). The first argument concerns test sensitivity, which Packard did not directly assess in his study. The second argument, in turn, is a semantical debate. Packard disagrees that bimodality implies dimorphism, without offering a different definition of dimorphisms. In the forthcoming sections, we will elaborate on these two points, elucidating an important underlying issue: the inherent relationship between sigmoid allometries and the frequency distributions of SSTs.

Transcending test sensitivity: why departures from unimodality are worth a second look

Packard argues that relying on AIC values for choosing between mixture models may lead to erroneous detection of bimodal distributions. Although the alternative method he used (Hartigan's dip test; HDT) aims to reduce the likelihood of type I statistical errors, it inadvertently increases the potential for type II errors. Thus, an objective protocol becomes crucial to avoid confirmation bias. Notably, Packard highlights that the HDT is recognized for its inability to detect departures from unimodality: “The test reliably identifies cases of unimodality but often fails to detect departures from unimodality when the detection level is set at $P = 0.05$” (page 4). To address this issue, the author increased the detection level to $P =$ 0.25, without any simulations or rationale to justify why this change would effectively manage the trade-off between type I and type II errors (Packard 2023; page 4, lines 3–5). While studies cited by Packard (Ameijeiras-Alonso et al. 2018; Kang and Noh 2019) incorporate simulations, none propose a standardized detection level for the analyses. Moreover, the two studies cited by Packard to back his critique of AICs in mixture models (Freeman and Dale 2013; Kang and Noh 2019) only analysed their simulated data with mixture models of symmetric distributions. The main criticism of both these papers is related to how the skewness of simulated distributions influences type I error in the detection of bimodalities by symmetric mixture models. However, the papers criticized by Packard used mixture models with skew-normal distributions, and hence all distributions modelled already accommodate asymmetries, largely resolving the issue of falsely detecting multimodality in asymmetric but unimodal distributions.

It is notable that even when the HDT employed by Packard detected significant bimodality for *Phareicranaus manauara*, he still argued that male dimorphism is unlikely: “…*nothing is untoward in the allometric analysis aside from one bin that contains an unusually small number of observations (Fig. 5c)*”. The occurrence of an unusually small number of observations in a histogram bin precisely defines a dip (the focus of the method employed) and is typically interpreted as indication of male dimorphism. While adjusting test sensitivity ideally requires simulations, we argue that the issue here transcends the trade-off between type I and type II statistical errors. The main point of this debate lies in establishing a clear expectation of how male dimorphism would be manifested in trait distributions. Agreement on the specific patterns sought is essential before discussing the optimal method to detect such patterns. We posit that whenever there is remarkably large variation in the size of a trait among conspecific males, it is worth asking whether that variation exhibits a single or multiple peaks because the latter (if objectively demonstrated) could suggest disruptive selection at the ultimate level, and threshold developmental mechanisms at the proximate level.

Selection shapes allometries and environmental conditions push individuals along reaction norms

Although not explicitly addressed by Packard, the origin of bimodalities in the distribution of SSTs is an important yet overlooked issue that permeates his contribution. It is well established that selection can ultimately shape allometries (Emlen 1996). However, it is imperative to not lose sight of the fact that males of different sizes, bearing SSTs of different sizes, are the real-world manifestation of these allometries. These males are the agents engaging in fights and mating with variable success, thereby providing the competitive contexts for the expression of SSTs. If two distinct reproductive tactics exist, each with its own phenotypic optimum, selective pressures may eliminate intermediate forms by producing sigmoid allometries. These sigmoid allometries naturally yield bimodal trait distributions on the y-axis (Fig. 1).

The presence of bimodality in the distribution of an SST becomes apparent when the allometry is simulated using a sigmoid function (in our example, the Richard's growth equation) of body size (Fig. 1b). This shows that sigmoid functions inherently produce bimodal distributions on the y-axis of a static allometry: the more sigmoid the function is, the more pronounced the resulting bimodal distribution on the y-axis. This mechanistic link supports one of Packard's assertions regarding sigmoidal curves: "*…the steep part of the curve corresponding with the low point in the histogram* [...] *that give an appearance of bimodality*" (Abstract). While we acknowledge the validity of that statement, we disagree with Packard's assertion that this does not constitute male dimorphism. This discrepancy likely stems from a difference between our operational definition of dimorphism, which entails detectable bimodality (as explained above), compared to Packard's perspective, which requires a more pronounced discontinuity in the trait, regardless of the allometry that generates such discontinuity. Unfortunately, we do not know the magnitude of discontinuity that is required to satisfy his criterion for male dimorphism. However, we argue that Packard's particular definition of dimorphism may account for his treatment of sigmoid allometries and dimorphisms as mutually exclusive phenomena.

We adopt a different perspective and propose that steep sigmoid allometries are an important mechanism that generates the pattern of bimodal distributions in SSTs. This view aligns with Emlen and Nijhout (2000), who suggest a connection of such allometries with exaggerated morphologies. The key point lies in the resulting two peaks in the distribution of the relevant male trait. This concept is not novel, as it has been recognized that male

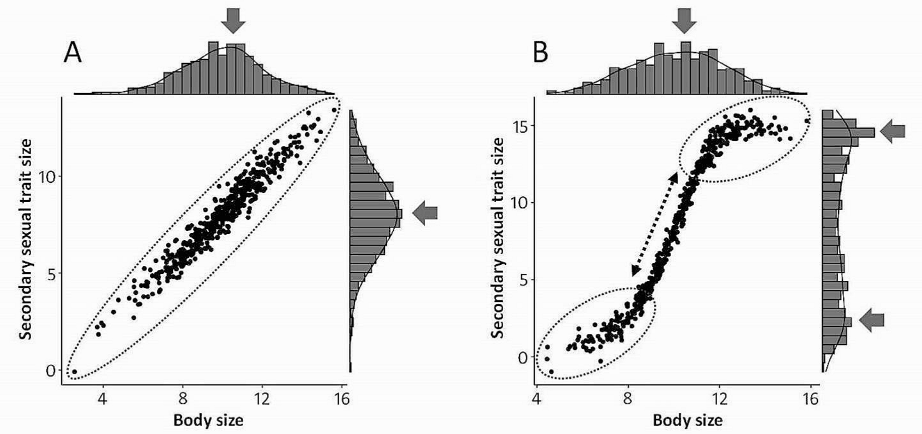

Fig. 1 (**A**) Simulated linear static allometry of a secondary sexual trait, depicting histograms illustrating the univariate distribution of this trait (displayed on the right) and that of body size (on top); both distributions are unimodal. (**B**) Simulated sigmoid static allometry using the same simulation parameters for body size as in (A) but employing a Richard's growth equation to simulate the values of the secondary sexual trait. Solid arrows indicate the peaks of distributions. In (B), the sigmoid allometry naturally causes individuals to cluster towards the extremes (rather than the centre) of the allometry (depicted by dotted circles), resulting in the secondary sexual trait distribution appearing bimodal, even when the underlying body size is clearly unimodal. We propose that the sigmoid static allometry suggests either selection against intermediate values of the sexually selected trait or for extreme values (disruptive selection). Dotted arrows show the directions individuals have been pushed towards by selection

dimorphism in insects can arise from highly positive allometries that reach an asymptote (Tomkins and Moczek 2009). While Packard seems to consider an "*unexpected pattern of allometric variation*" a constraint, we suggest that in some cases it could represent an adaptive response to selection against intermediate sized males.

We hence agree with Packard that, in certain cases, the shape of the sigmoid allometry can adequately explain the departure from unimodality observed in the distribution of a trait. However, we hypothesize that there are potential further mechanisms at play, as environmental conditions and selection might 'push' males along the reaction norms of the trait allometry, resulting in a concentration of males around different sections of that allometry. In this scenario, selection against intermediate SST values could accentuate the bimodal distribution in the trait beyond what the sigmoid allometry alone can generate. If a particular range of intermediate SST values is underrepresented in the population, this suggests disruptive selection on male phenotypes, presumably linked to alternative reproductive tactics in the study system. We conceptualize this notion through a simulated sigmoid allometry (Fig. 1b), followed by the sequential random removal of individuals with intermediate SST values (Fig. 2). In our simulation, the percentage of removed males correlates with the degree of bimodality observed in the distribution of the SST (Fig. 2), which is to be expected. Whereas the degree of removal of intermediate males intuitively correlates with the intensity of bimodality in the SST, this eventually starts becoming apparent in the distribution of body sizes as well (Fig. 2). This conceptualization opens the opportunity to investigate disruptive selection in sigmoid allometries by explicitly modelling whether the bimodality in the distributions of SSTs naturally arises from the sigmoid shape of such allometries, which can be done by contrasting the simulated bimodality with the observed bimodality in natural populations.

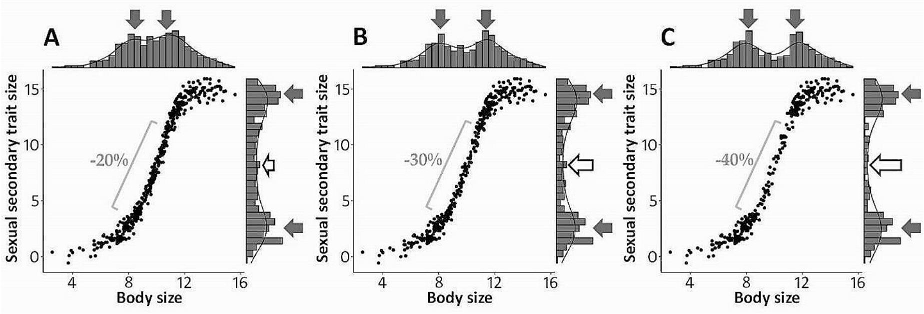

Fig. 2 The same sigmoid static allometry of a secondary sexual trait presented in Fig. 1, but with the subsequent random removal of (**A**) 20%, (**B**) 30%, and (**C**) 40% of the individuals exhibiting intermediate trait values, simulating selection against them. The random removal targeted individuals with secondary sexual trait sizes between 25% and 75% of the possible trait sizes. Solid arrows indicate the peaks of distributions, and now all univariate distributions become increasingly bimodal, with the bimodality being directly proportional to the percentage of individuals with intermediate trait values removed from the dataset. Open arrows show the valleys/dips between the peaks in the distributions of trait sizes, which progressively turn into more pronounced gaps between individual morphs. For a "control" of this simulation (with no intermediates removed), refer to Fig. 1B

A null model linking static allometry and bimodality of secondary sexual traits

We consider that the most important implications of Packard's contribution are: (1) the importance of clearly defining dimorphism and expected levels of discontinuity in distributions/allometries, and (2) the necessity of an approach to test whether the observed bimodal distribution of a trait is solely due to the shape of its allometry or also due to other mechanisms generating discontinuity. Therefore, we employed the approach we proposed above through a four-step process. For step 1, we gathered the same data used by Packard (2023) and modelled the static allometry of the trait for each species using different non-linear models. We chose non-linear models due to their capability to fit the data with different types of sigmoid functions or asymptotes.

We used the '*minpack.lm*' package for fitting the non-linear models. This package estimates upper and lower parameter bounds, ensuring accurate estimation of the static allometries (Elzhov et al. 2023). We used the '*grofit'* package (v1.1.1-1) to fit a Richard's growth equation to the data (Kahm et al. 2010), along with a self-starting non-linear logistic model from the '*stats'* package. Subsequently, we compared both the Richard's growth equation and the logistic model through their AIC_c values. We adhered to the common method of selecting the model with the lowest AIC_c (as long as $\Delta AIC_c > 2$). In cases where the models displayed $\Delta AIC_c < 2$, we opted for the simpler model, i.e., the one with the fewest number of parameters. The models fitted and the distribution of each trait for each species can be seen in Fig. 3.

For step two, we employed the mean and standard deviation of the actual distributions of male body sizes to generate 10,000 new sets of body sizes for each species, maintaining the same sample size as the original datasets. Using the best-fit allometric models specific to each case from step 1, we predicted SST values for all simulated male body sizes. Next, in step 3, we modelled the distribution of new trait sizes for each simulation as a single skew-normal distribution or as mixtures of two skew-normal distributions using the *mixsmsn* package (Prates et al. 2013). The ΔAIC_c between one distribution and a mixture of two distributions was recorded for each iteration. Moving to step 4, we compared the ΔAIC_c values obtained from the randomly generated SST sizes with the observed ΔAIC_c value from the original dataset. For each species investigated, our final metric of interest was the percentage of ΔAIC_c values obtained in the simulations that exceeded the observed value in the real dataset.

In summary, step 1 involves incorporating the original allometry in the data, while step 2 is employed to simulate null distributions of the SST based on the allometric equation. Step 3 is identical to the univariate statistical approach conventionally used in detecting male dimorphism in the literature (e.g., Rowland and Qualls 2005; Buzatto et al. 2014; Palaoro et al. 2022), and step 4 quantifies the influence of static allometries on male dimorphisms. Step 3 can be replaced by any bimodality test, including the HDT. The percentage of simulations that generated a distribution that is as bimodal or more bimodal than the value obtained by the real data is interpreted to represent the likelihood that the data bimodality can be explained by the allometry alone.

The aforementioned approach was implemented using R version 4.3.1 (R Core Team 2022). All data and scripts are available as supplementary files and on GitHub (see Data Accessibility). A comparative figure illustrating the difference between the real datasets and

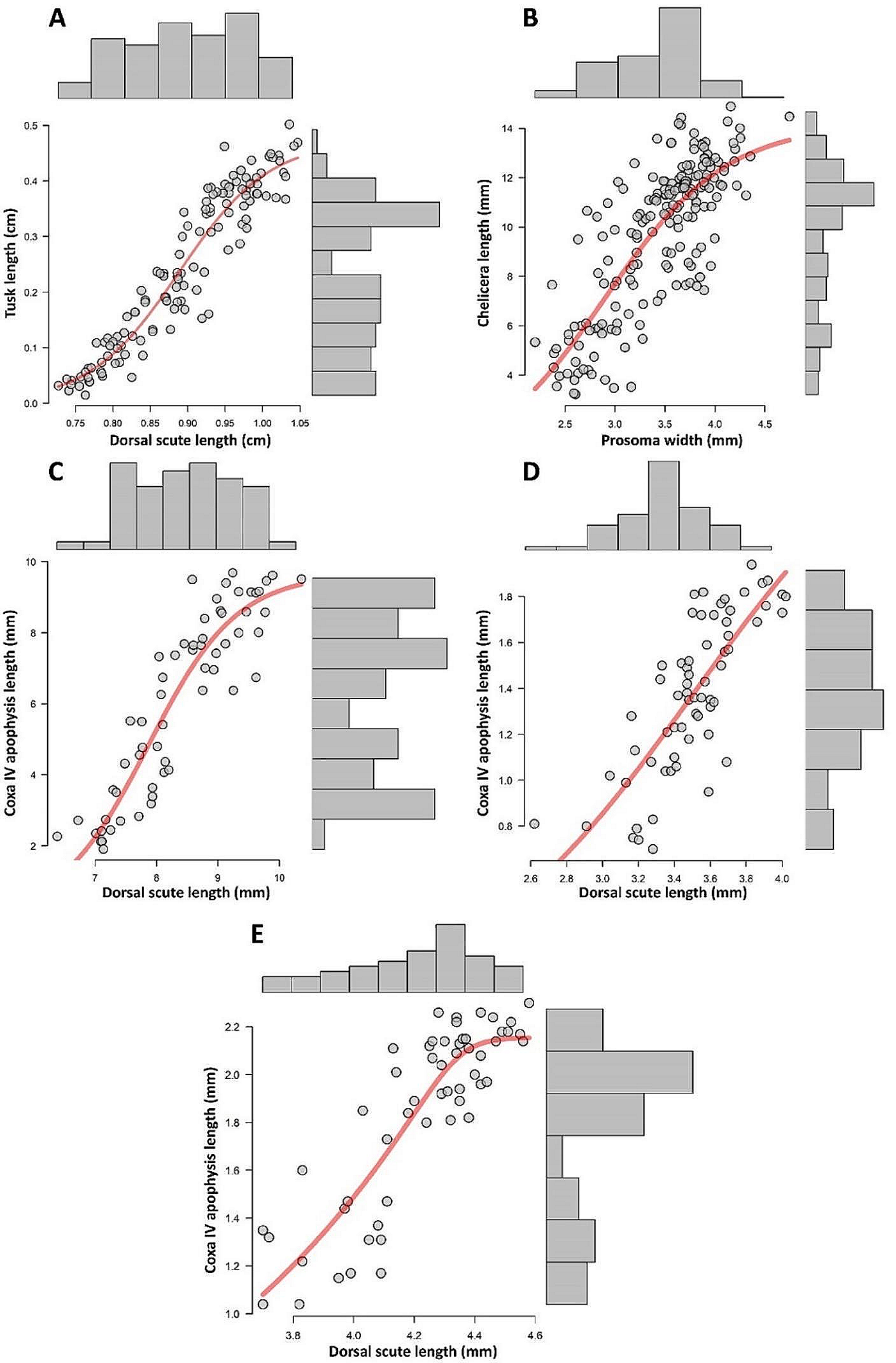

Fig. 3 Non-linear allometries (red lines) fitted for each species reanalysed by Packard (2023), with histograms illustrating the distributions of the body sizes (x-axis) and the secondary sexual trait sizes (y-axis). Each dot represents an individual of a specific harvestman species: (**A**) *Phareicranaus manauara*, (**B**) *Fosteropsalis pureora*, (**C**) *Cobania picea*, (**D**) *Neoancistrotus gracilis*, and (**E**) *Promitobates bellus*

a random sample of one tenth of each simulated dataset is provided in the Supplementary Materials (Figures S1-S5).

Simulations of the examples presented in packard (2023)

Employing the method described in the previous section, our results indicate that the connection between the allometries and the extent of bimodality in the distribution of SSTs differs across species (Fig. 3). Specifically, for *Phareicranaus manauara, Fosteropsalis pureora*, and *Cobania picea*, the likelihoods that the sigmoid allometries alone generated the observed deviation from unimodality are only 0.14%, 0.11% and 0.31% (Table 1). This suggests that additional mechanisms (e.g., disruptive selection) accentuate bimodal distributions that are not fully explained by the traits' sigmoid allometries. Conversely, in *Promitobates bellus*, there is a 44% likelihood that allometry explains the bimodality observed in the analysed trait. Despite these variations, we maintain our interpretation that these four species exhibit male dimorphism in the analysed SSTs, as in all of them disruptive selection (whether in survival or differential reproduction) might have shaped these allometries in the first place. In *P. bellus*, this appears to be enough to explain the dimorphism in the species (Table 1). Meanwhile, in the first three species, we suggest that additional mechanisms pushed individuals further apart in the reaction norms and accentuated trait bimodality. We opted against reanalysing the data for *Neoancistrotus gracilis*, as both Buzatto et al. (2014) and Packard (2023) previously reported absence of male dimorphism in that species.

Species selection influenced packard's (2023) conclusions

Packard's criticism may carry significant implications for harvestmen biology. Is male dimorphism really prevalent within this major arachnid order (Buzatto and Machado 2014), or could it be an erroneous inference resulting from type I error in using mixture models (based on AIC values) for detecting bimodalities? Packard's contribution implies the latter,

Table 1 Comparison of male dimorphism across all harvestman species analysed by Packard (2023). Observed values of AIC_c were obtained using the dataset provided by the authors in the original papers. Simulated values of AIC_c consist of 10,000 iterations calculated using our four-step process described in the main text

Dataset	Species	Observed AIC_c(1 peak; 2 peaks; ΔAIC_c)	Dimorphism originally detected	Mean simulated AIC_c (1 peak; 2 peaks; ΔAIC_c)	% of simulated ΔAIC_c > observed ΔAIC_c
Palaoro et al. (2022)	*Phareicranaus manauara*	(-132.61; -183.26; -50.65)	**Yes**	(-163.80; -177.60; -12.10)	0.14
Powel et al. (2020)	*Fosteropsalis pureora*	(921.03; 907.83; -13.21)	**Yes**	(821.80; 828.70; 7.48)	0.11
Buzatto et al. (2014)	*Cobania picea*	(278.07; 261.13; -16.94)	**Yes**	(261.50; 265.30; 3.76)	0.31
Buzatto et al. (2014)	*Neoancistrotus gracilis*	(44.41; 45.84; 1.43)	No	(18.44; 23.63; 5.20)	11.8
Buzatto et al. (2014)	*Promitobates bellus*	(29.10; 23.44; -5.66)	**Yes**	(1.77; -4.59; -6.36)	43.9

but his rationale for selecting the reanalysed species was not provided, and his failure to detect dimorphism in certain species appears to be due to a sampling artifact. The original study by Buzatto et al. (2014) investigated dimorphisms in two SSTs that can be used either individually or in concert in male-male fights depending on the species: the length of the apophysis on the fourth coxa (C4A) and the length of the fourth femur (F4). These traits were measured across 48 species belonging to 10 subfamilies of Gonyleptidae. Packard selected one trait (C4A) from three species across two subfamilies. Notably, two of these species (*P. bellus* and *N. gracilis*) belong to the subfamily Mitobatinae, where the highly dimorphic male trait is F4, and not C4A (Machado et al. 2021). Thus, the choice of C4A for *P. bellus* and *N. gracilis* appears unusual and lacks support from behavioural data on the reproductive biology of the species, in which males use their elongate F4 to fight each other, and the C4A are never employed in the fights (Zatz et al. 2011). Moreover, the original analysis of *N. gracilis* did not detect male dimorphism in the C4A. Non-surprisingly, Packard's promoted method (HDT) also failed to detect male dimorphism is this species, but he refrains from acknowledging the alignment of his conclusion with the original analysis.

It is unfortunate that the species and traits chosen for reanalysis by Packard were not randomly or systematically selected from Buzatto et al. (2014) to encompass the range of male dimorphism intensities observed in that study. Instead, the selection of some of the least dimorphic traits in that original study might have biased Packard's results. Moreover, given that Packard's statistical inference still (even when biased) remained consistent for two out of the five traits reanalysed — both the mixture model and the HDT approaches detected significant dimorphism for *P. manauara* and no dimorphism for *N. gracilis* —, it appears unlikely that reanalysing all species from Buzatto et al. (2014) with the HDT would yield significantly different conclusions. Therefore, we argue that Packard's contribution does not shed light on the prevalence of male dimorphism in harvestmen.

Conclusion

Packard's criticism regarding the detection of male dimorphism in harvestmen presents a valuable opportunity for a comprehensive re-examination of the methods employed in this field. While we hold different viewpoints on certain aspects of Packard's arguments, we agree that sigmoid allometries contribute to male dimorphism to some degree. The central issue, however, lies in how we perceive the links between bimodality/dimorphism, static allometry, and selection processes. Current statistical approaches are only capable of testing and quantifying patterns evident in the data, such as the extent of bimodality. Here, we propose a new alternative approach that generates specific null hypotheses that explicitly link diverse allometric patterns with univariate distributions of the trait of interest. With this approach, we showed that the likelihood that the sigmoid allometries of the five species of harvestmen analysed are sufficient to explain the bimodalities in their SSTs varies significantly between species. Sigmoid allometries can suggest disruptive selection, as they are linked to a deficit of intermediate males, but other mechanisms might be at play. In at least three of these species (*P. manauara, F. pureora*, and *C. picea*), there is evidence for additional mechanisms increasing the bimodality in SSTs. It is possible that individuals in these species are able to assess environmental conditions and plastically accommodate their body sizes along the reaction norms of the allometries, leading to even stronger deficit of intermediate males and more striking bimodality. This suggests that some mechanisms (e.g., disruptive selection, environmental conditions) are moving individuals along the allometric reaction norms, generating more bimodality than the shape of the sigmoid allometry itself can explain. We hope our new approach broadens the existing statistical methods and stimulate further discussion on the relationship between sigmoid static allometries of traits and their polymodal univariate distributions.

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Author contributions B.A.B, A.V.P and G.M. conceived the project, B.A.B and A.V.P performed the analyses, B.A.B, A.V.P and G.M. interpreted the results and wrote the manuscript.

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Data availability All data, codes, and simulated data generated are available at the GitHub page of one of the authors (A.V.P.; https://github.com/alexandrepalaoro/simulations-bimodality).

Declarations

Ethical approval Not applicable.

Conflict of interest We have authored four of the five studies that originated the data reanalysed by Packard (2023), and we therefore support the conclusions of those original studies. We declare no further conflicts of interest.

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