

## Research



**Cite this article:** Machado G, Buzatto BA, Samia DSM. 2021 It is not always about body size: evidence of Rensch's rule in a male weapon. *Biol. Lett.* **17**: 20210234. <https://doi.org/10.1098/rsbl.2021.0234>

Received: 29 April 2021

Accepted: 28 May 2021

**Subject Areas:**  
evolution

### Keywords:

allometry, condition dependence, Opiliones, sexual dimorphism, sexual selection

### Author for correspondence:

Glauco Machado

e-mail: [glaucom@ib.usp.br](mailto:glaucom@ib.usp.br)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5459127>.

## Evolutionary biology

# It is not always about body size: evidence of Rensch's rule in a male weapon

Glauco Machado<sup>1</sup>, Bruno A. Buzatto<sup>2,3</sup> and Diogo S. M. Samia<sup>1</sup>

<sup>1</sup>LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP 05508-090, Brazil

<sup>2</sup>Department of Biological Sciences (E8C 209), Macquarie University, Eastern Road, Sydney 2109, NSW, Australia

<sup>3</sup>Centre for Evolutionary Biology, School of Biological Sciences (M092), The University of Western Australia, 35 Stirling Highway, Crawley 6009, WA, Australia

GM, 0000-0002-0321-128X; BAB, 0000-0002-2711-0336; DSMS, 0000-0002-0487-8019

In many species, sexual dimorphism increases with body size when males are the larger sex but decreases when females are the larger sex, a macro-evolutionary pattern known as Rensch's rule (RR). Although empirical studies usually focus exclusively on body size, Rensch's original proposal included sexual differences in other traits, such as ornaments and weapons. Here, we used a clade of harvestmen to investigate whether two traits follow RR: body size and length of the fourth pair of legs (legs IV), which are used as weapons in male–male fights. We found that males were slightly smaller than females and body size did not follow RR, whereas legs IV were much longer in males and followed RR. We propose that sexual selection might be stronger on legs IV length than on body size in males, and we discuss the potential role of condition dependence in the emergence of RR.

## 1. Introduction

In many animal species, sexual size dimorphism increases with body size when males are the larger sex but decreases when females are the larger sex [1]. The mechanisms leading to this macro-evolutionary pattern, known as Rensch's rule (RR), are poorly understood, but sexual selection is usually invoked as the main driving force ([2], but see [3]). The factors influencing reproductive success usually differ between sexes, and body size may hence be under different selection regimes in males and females [4]. For instance, male body size may be under positive directional sexual selection when males fight for females or resources and when females prefer large males [5]. Since males and females share most genes that control basic aspects of growth, directional sexual selection acting mostly or exclusively on male size may lead to a similar evolutionary change in female size due to cross-sex genetic correlations, the degree of which is proportional to the strength of the genetic correlations [6,7]. A partial erosion of such genetic correlations may allow the emergence of RR when males and females are under different selective regimes [2,8]. Another non-exclusive hypothesis to explain RR states that body size may have more additive genetic variation in males than females, leading to a stronger evolutionary response in males under directional selection [8,9].

The two hypotheses above should also apply to traits other than body size. When a sexually dimorphic trait occurs in both sexes, but is under directional sexual selection in males only, a pattern consistent with RR should emerge [10]. In fact, although almost all studies on RR focus on body size, Rensch's original proposal was broad in scope and included sexual differences in other traits [1,10]. Accordingly, recent studies with sexually selected male traits, such as wing pigmentation in dragonflies [11] and head shape in lizards [10], showed patterns consistent with RR. To our knowledge, however, there are no studies showing that RR applies to sexually selected traits that are present in both

sexes but enlarged only in males. This is the case in some traits used as weapons in male–male contests, such as the forceps of earwigs [12] and mandibles of some beetles [13].

Depending on the function that weapons have in male–male contests, they can be classified as (i) *pure weapons*, used to physically coerce rivals, and (ii) *threat devices*, used in the mutual evaluation of size and strength [14]. Threat devices include, for instance, mutual leg spreading in spiders and head-to-head confrontations in stalk-eyed flies [15,16]. Comparative evidence shows that directional sexual selection leads to hyper-allometry in threat devices, so that larger males have disproportionately larger traits compared to smaller males [14]. Females, in turn, do not fight, have no benefit in expressing enlarged threat devices, but may pay survival and/or fecundity costs for expressing them [6]. Thus, although females of many species also express threat devices, these structures are under different selection regimes in males and females.

Harvestmen (Arachnida: Opiliones) show a great diversity of male weapons [17]. In the subfamily Mitobatinae (Gonyleptidae), the fourth pair of legs (legs IV) is used as walking appendages in both sexes, but also as threat devices in male contests for the possession of territories on rocks and fallen logs where females lay eggs [18]. During the contests, males position themselves back-to-back, hold their elongated legs IV laterally extended and repeatedly hit each other with the tips of legs IV. Although leg hitting does not impose injuries or physically coerces rivals, leg length is probably used as a signal of size and/or strength of the opponent in intrasexual assessment, since individuals with longer legs IV are more likely to win contests and hold a territory [18]. This finding suggests that legs IV are a secondary sexually selected trait in males.

Here, we investigated whether two traits of Mitobatinae harvestmen follow RR: body size and the elongated legs IV. If directional sexual selection on males' legs IV length partially drags along females' legs IV length due to weak cross-sex genetic correlations, we expect that this trait would follow RR. If this prediction is corroborated, we have further evidence that RR is not restricted to body size, but rather also applies to traits used as weapons.

## 2. Material and methods

### (a) Source of the data

We obtained most of our data from specimens in four arachnological collections from Brazil: Instituto Butantan, Museu de Zoologia da Universidade de São Paulo, Museu Nacional do Rio de Janeiro and Universidade Federal de Minas Gerais. We complemented these data with individuals previously collected in the Brazilian Atlantic Forest (see electronic supplementary material, table S1). We photographed all individuals next to a ruler (for scale) and took measurements on *ImageJ* [19]. For each individual, we recorded sex, body size (dorsal scute length) and right femur IV length, which is a proxy for total leg length [18,20].

### (b) Phylogeny

Our dataset includes 25 species of Mitobatinae, comprising all genera and 56% of the known diversity of the subfamily. To account for the non-independence of data due to the phylogenetic relationships between species, we employed comparative methods using a working phylogeny of the Mitobatinae based

on the topology by Bragagnolo & Pinto-da-Rocha [21], with small modifications. Eight species present in the phylogeny but not included in our dataset were pruned from the tree with the function `drop.tip` from the R package `phytools` [22]. Moreover, two species included in our dataset were not present in the original phylogeny: we placed *Mitobatula sponsa* as the sister species to the congeneric *M. castanea*, and *Mitobates elegantulus* as the sister species to all congeners, assuming both genera as monophyletic. Finally, we standardized branch lengths in the final topology using Grafen's [23] method with the function `compute.brlen` from the R package `APE` [24].

### (c) Statistical analyses

To test RR, we performed a phylogenetic reduced major axis (pRMA) regression with the female trait in the  $x$ -axis, the male trait in the  $y$ -axis (following [25]) and the null hypothesis set to an allometric coefficient of 1. A non-significant relationship means the allometric coefficient does not differ from 1, i.e. the trait scales isometrically in males and females, a result that refutes RR. To support RR, the allometric coefficient should be significantly higher than 1, indicating that the trait scales hyper-allometrically in males. We conducted the pRMA regressions with the function `phil.RMA` from the package `phytools` [22] in R v. 3.2.2 [26].

## 3. Results

### (a) Data description

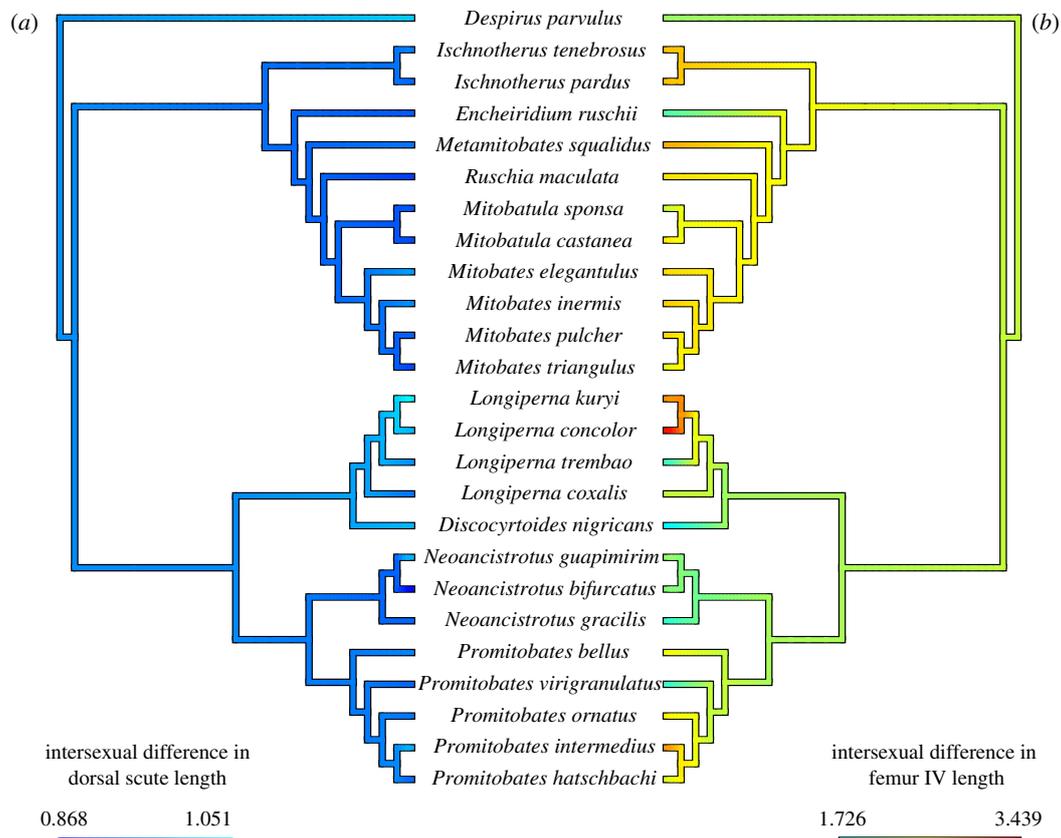
Females had slightly longer dorsal scutes than males (figures 1a and 2a). The mean intersexual difference (males divided by females) in dorsal scute length was 0.959 (bootstrapped 95%CI: 0.944–0.975; electronic supplementary material, table S2). In all species, males' femur IV was much longer than that of females (figure 1b). The mean intersexual difference (males divided by females) in femur IV length was 2.487 (bootstrapped 95%CI: 2.335–2.628; electronic supplementary material, table S2).

### (b) Test of Rensch's rule

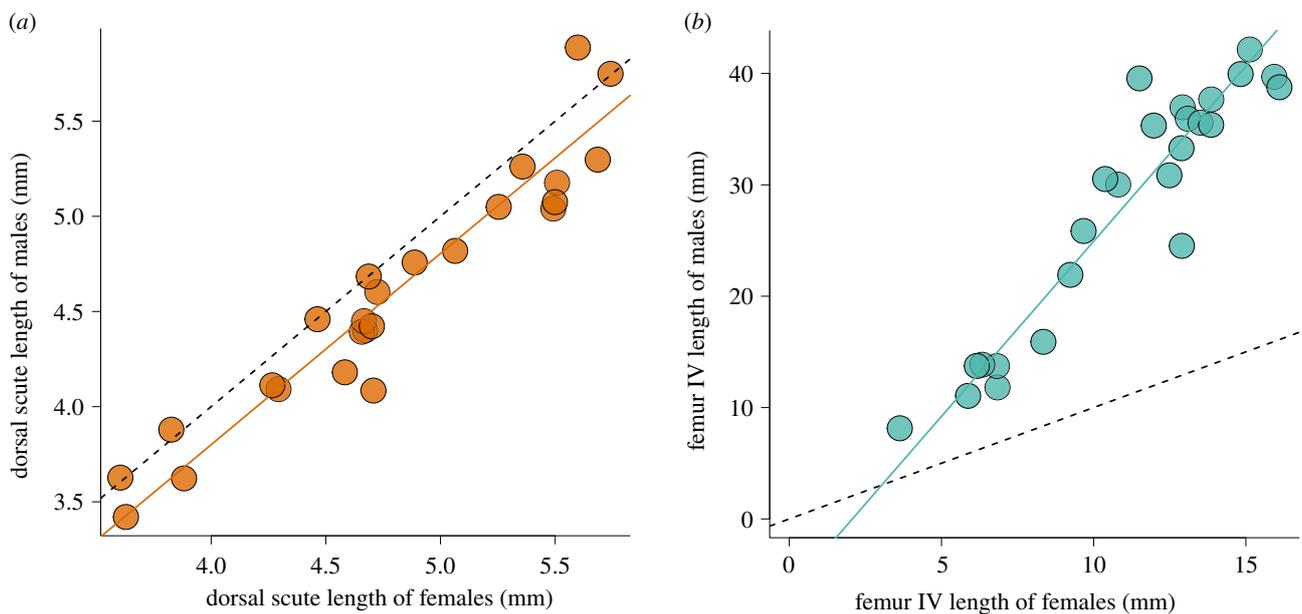
We found an isometric relationship for dorsal scute length ( $b = 1.004$ ,  $t = 0.07$ ,  $p = 0.94$ ), indicating that an increase in this trait in females is followed by a similar increase in the same trait of males (figure 2a). Conversely, we found a hyper-allometric relationship for femur IV length ( $b = 3.367$ ,  $t = 13.29$ ,  $p < 0.001$ ), indicating that an increase in the females' femur IV length is associated with a higher increase in the same trait of males (figure 2b). An analysis on femur IV relative length (controlling for body size within species) returned similar results (electronic supplementary material, figure S1).

## 4. Discussion

Here we show that body size is only slightly sexually dimorphic and does not follow RR, whereas legs IV are extremely dimorphic (on average 148.7% longer in males) and follow RR in Mitobatinae harvestmen. Sexual selection is probably the main process generating RR, but there are two hypotheses that provide specific mechanisms [8]. First, directional sexual selection acting mostly or exclusively on a male trait may lead to correlated evolutionary change in the homologous trait in females due to cross-sex genetic correlations, the strength of which should determine the magnitude of the



**Figure 1.** Evolution of sexual dimorphism in (a) dorsal scute length and (b) femur IV length in Mitobatinae harvestmen (male divided by female). (a) In several species, females have a larger body size than males, but in at least six species males are slightly larger than females. (b) In all 25 species included in the analysis, males have longer legs IV than females and extreme elongation of legs IV occurred at least three times in the clade.



**Figure 2.** Allometric relationship of (a) dorsal scute length and (b) femur IV length between males and females of 25 species of Mitobatinae harvestmen. The dashed line illustrates a perfect isometric relationship between male and female traits. The solid line shows the relationship fitted by a pRMA regression. Whereas the coefficient of dorsal scute length does not differ from 1 (isometry), the coefficient of femur IV length is significantly higher than 1 (hyper-allometry).

correlated changes. Second, more additive genetic variation in a sexually selected male trait should lead to a stronger evolutionary response to selection when compared to the homologous trait in females. These two mechanisms are integral parts of the concept of *condition-dependent sexual dimorphism*, according to which variation at numerous loci affecting resource acquisition and allocation efficiency in a secondary sexual male trait can result in phenotypic differences

between females and high-condition males [7,27]. The fact that Mitobatinae harvestmen present condition-dependent sexual dimorphism is supported by the consistently steeper allometric slopes of male femur IV across species (electronic supplementary material, table S2), although direct evidence for condition dependence is still lacking. According to the theory, stronger condition dependence in male traits may be linked to sex differences in the variation in resource allocation,

potentially due to sex-linked allocation genes [28]. Hereafter, we discuss how condition dependence may explain the emergence of RR, offering a path for future work.

Strong directional sexual selection on a trait expressed in both sexes with different optima promotes intralocus sexual conflict [29]. Whereas males gain fitness benefits expressing an exaggerated sexually selected trait, females maximize their fitness expressing low values of this same trait due to viability selection [30]. A widespread mechanism that attenuates cross-sex genetic correlations and facilitates the evolution of sexual dimorphism in secondary sexual traits is condition dependence [31]. When a male trait is condition dependent, its expression is affected by variation at numerous loci related to resource acquisition and/or allocation. In turn, the expression of the trait in females is condition-independent and influenced by fewer loci. The sex-limited epistasis promoted by condition dependence requires a sex-linked genetic switch to activate the genes related to the expression of the male trait. Because these genes are expressed only in males, they facilitate the evolution of condition-dependent sexual dimorphism [7]. Experimental studies with arthropods show that the more condition-dependent a trait, the more sexually dimorphic it is [28,32,33]. However, condition dependence does not mean that the evolution of shared traits is uncorrelated in males and females. A review showed that the mean genetic correlation between males and females in morphological traits is 0.80 [34]. Although the authors do not analyse the data separately for condition-dependent and condition-independent traits, the cross-sex genetic correlations are probably lower in the former. In *Mitobatinae* harvestmen, the main form of sexual dimorphism is the elongation of legs IV, suggesting that this trait is highly sensitive to condition, and that its exaggeration in males is not severely constrained by cross-sex genetic correlations [17,18]. Lower values of cross-sex genetic correlations may allow exaggeration of legs IV length in males, generating a macro-evolutionary pattern consistent with RR.

In the case of body size, condition dependence is probably not so strong, and it seems that this trait is not under strong fecundity selection because females are only slightly larger than males. Estimating selection gradients is beyond the scope of the present study, thus our discussion about the strength of selection is inferential, rather than directly drawn from data. If our assumptions about the strength of selection on legs IV and body size in males and females are correct, then the cross-sex genetic correlations in body size are expected to be higher than that of legs IV. This means that directional selection on the body size of one sex (e.g. fecundity selection on females) drags along the body size of the other sex with similar intensity, generating an isometric macro-evolutionary pattern inconsistent with RR. Studies on odonates showed similar results: wing pigmentation, which is highly sensitive to condition and is under directional sexual selection only in males [35], follows RR [11]; body size, which is less sensitive to condition and probably under stabilizing viability selection [35], does not [36]. These findings provide additional support for the suggestion that condition dependence has an important role in the emergence of RR.

Condition dependence allows individuals to optimize the trade-off between viability selection and sexual selection on a trait [7]. Given that exaggerated secondary sexual traits are costly to produce and maintain, only individuals in good condition can pay the costs of expressing high trait values

[37]. We do not know how costly the production and maintenance of legs IV in *Mitobatinae* is, but the great elongation in males might hinder locomotion, especially in the structurally complex riparian vegetation where most species live. Moreover, the maintenance of exaggerated weapons with heavy muscle mass probably imposes physiological costs on males. In a recent comparative study with arthropods, the physiological costs of weapons were positively related to muscle mass associated with them [38]. Thus, great leg elongation promoted by directional sexual selection may have both ecological and physiological costs for *Mitobatinae* males, displacing them from the phenotypic optimum favoured by viability selection. Because sexual selection on males' legs IV length leads to a correlated change in females' legs IV length, females are also displaced from their viability-selected optimum and probably pay costs, such as reduced fecundity (e.g. [39]). The fact that *Mitobatinae* females often present hyper-allometric femur IV (12 out of 25 species in electronic supplementary material, table S2), even though they only use those legs to walk, suggests that this trait has been at least slightly displaced from its viability-selected optimum in many species.

In conclusion, among known mechanisms that resolve intralocus sexual conflict [31], we argue that condition dependence is the best explanation for the emergence of RR. Thus, we predict that the level of condition dependence in a secondary sexual trait present in both sexes, but under directional sexual selection in only one of them (most frequently males, but also females, see [8]), will be positively related to the degree of hyper-allometry in the evolutionary scaling of sexual dimorphism in this trait. Given that several traits, such as ornaments and weapons, are condition-dependent and are under directional sexual selection in only one sex, patterns congruent with the RR should be found for many other traits.

**Ethics.** According to the Brazilian law and the rules of Universidade de São Paulo, this research does not require ethical approval. Collection permits were granted by Instituto Chico Mendes de Conservação da Biodiversidade – Sistema de Autorização e Informação em Biodiversidade (no. 26.501-1).

**Data accessibility.** The data are provided in the electronic supplementary material [40].

**Authors' contributions.** G.M. and D.S.M.S. conceived the study. D.S.M.S. and B.A.B. conducted the analyses. G.M. and D.S.M.S. collected the data and wrote the first draft of the manuscript. B.A.B. revised the manuscript and incorporated suggestions of reviewers. All authors are accountable for the content and approved the final version of the manuscript.

**Competing interests.** We declare we have no competing interests.

**Funding.** G.M. and D.S.M.S. were supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (grant nos. 2015/10448-4 and 2015/06734-1). G.M. is also supported by a research grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant no. 306550/2014-8).

**Acknowledgements.** We thank John Uribe and Andrés García for helping with taking photos of museum specimens, Solimary García-Hernández for helping with collecting specimens in the field, Adriano B. Kury for identifying some harvestman species, Antonio D. Brescovit (Instituto Butantan), Ricardo Pinto-da-Rocha (Museu de Zoologia da Universidade de São Paulo), Adriano B. Kury (Museu Nacional do Rio de Janeiro), and Adalberto J. Santos (Universidade Federal de Minas Gerais) for granting us access to the arachnological collections under their responsibility, and Russell Bonduriansky and four anonymous reviewers for comments on the manuscript.

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