

All the better to bite you with! Striking intrasexual differences in cheliceral size define two male morphs in an Amazonian arachnid

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When two mating tactics can be successfully used by different-sized males, disruptive selection may favour morphological divergence between males, resulting in intrasexual dimorphism. Here we characterize intrasexual dimorphism based on cheliceral size in males of the harvestman *Paecilaemula lavarrei*. We also describe how males of the two morphs use their chelicerae in intra- and intersexual interactions, and investigate microhabitat use to infer their mating tactics. The distribution of body and cheliceral traits was markedly bimodal, indicating the existence of a major morph (majors) with large body and cheliceral size, and a minor morph (minors) with small body and cheliceral size. Male–female interactions were similar between morphs, but only majors initiated male–male contests by biting the legs of rivals using their chelicerae. Males and females preferred tree trunks with large perimeters and containing burrows that could be used as shelters. Female spatial distribution was aggregated, whereas males of both morphs were randomly distributed. Majors seem to fight for reproductive territories that concentrate females, and minors probably rely on territory invasion to sneak copulations. Little overlap in the distribution of body and cheliceral size between morphs suggests that male dimorphism in *P. lavarrei* may not be a polyphenism, and it is associated with different mating tactics.

ADDITIONAL KEYWORDS: allometry – alternative reproductive tactics – copulatory courtship – fighting behaviour – habitat use – intrasexual male dimorphism – male–male contests – Opiliones – sexual dimorphism.

INTRODUCTION

Sexual size dimorphism is widespread in animals and, depending on the species, either males or females can be the larger sex (examples in [Fairbairn *et al.*, 2007](#)). In most cases, however, males are the sex bearing exaggerated traits, such as ornaments and weapons ([Andersson, 1994](#)). Male ornaments usually evolve in an intersexual context, and are used by females to select mating partners. Male weapons, in turn, usually evolve in an intrasexual context, and are used in contests for access to females or to resources that are critical for female reproduction (reviewed by [McCullough *et al.*, 2016](#)). As ornaments and weapons

are often costly to produce and maintain, only males in good condition are expected to develop exaggerated sexually selected traits (reviewed by [Bonduriansky, 2007b](#)). When intrasexual selection is intense, males bearing exaggerated traits may monopolize almost all copulations, so that males bearing small traits may be excluded from the mating pool. In this case, instead of fighting other males or displaying to females, males bearing small traits can adopt alternative reproductive tactics (ARTs). Whenever two or more reproductive tactics can be successfully employed by males bearing different sized traits, disruptive selection may favour morphological divergence between individuals that use different behaviours ([Gross, 1996](#)). The resulting pattern is known as ‘intrasexual male dimorphism’, formally defined as a discrete or discontinuous

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variation in sexually selected male traits (Gadgil, 1972).

Intrasexual male dimorphism has already been described in many animal groups, including vertebrates and invertebrates (examples in Oliveira *et al.*, 2008). Among insects, for instance, intrasexual male dimorphism may occur in the expression of traits that function either as ornaments, such as wing pigmentation (e.g. González-Soriano & Córdoba-Aguilar, 2003), or as weapons, such as horns and forceps (e.g. Eberhard & Gutiérrez, 1991). However, most cases of intrasexual male dimorphism are related to the size and shape of male traits used as weapons in intrasexual contests (reviewed by Brockmann, 2008 and Buzatto *et al.*, 2014a). Males bearing large weapons (i.e. 'majors') usually guard females and/or defend food or reproductive resources, using their weapons to fend off rival males. In turn, males bearing small weapons or no weapon at all (i.e. 'minors') usually exhibit ARTs that do not involve fights with other males. For instance, minors may sneak copulations, act as satellites, or even mimic females to invade the territories of majors (examples in Thornhill & Alcock, 1983).

Although arachnids are incredibly diverse, there are relatively few described cases of intrasexual male dimorphism associated with ARTs in the group. Among spiders, for instance, there are few described cases of intrasexual male dimorphism, most of them in traits not related to weaponry. Male morphs of the jumping spider *Maevia inclemens* differ in colour and mating displays (Clark & Uetz, 1993), whereas male morphs of the linyphiid *Oedothorax gibbosus* differ in the presence of a cephalothoracic gland that provides a nuptial secretion to females (Heinemann & Uhl, 2000). In other arachnid groups, intrasexual male dimorphism occurs in traits used mostly as weapons. Majors of the pseudoscorpion *Semeiochernes armiger*, for instance, have enlarged pedipalps used in contests for access to the dispersal agent, a giant timber fly (Zeh & Zeh, 2013). In some mites, majors have a thickened and pointed third pair of legs used to stab and kill other males during contests for access to females (Radwan, 1995). However, most cases of intrasexual male dimorphism in weapon traits among arachnids occur in the order Opiliones, known as harvestmen or daddy long-legs (reviewed by Buzatto & Machado, 2014). In the family Gonyleptidae, for instance, intrasexual male dimorphism related to the size of leg spines and/or length of the fourth pair of legs has evolved several times independently (Buzatto *et al.*, 2014b). Similarly to insects, harvestmen major morphs have long spines or legs used to defend territories (i.e. oviposition sites), whereas minors have short spines or legs and rely on territory invasion to sneak copulations (e.g. Buzatto *et al.*, 2011; Zatz *et al.*, 2011).

The harvestman *Paecilaemula lavarrei* (Laniatores: Cosmetidae) occurs in the Amazon forest, where individuals are found on tree trunks and fallen logs. As in many cosmetids, there is a marked intersexual dimorphism in cheliceral size, which is larger in males (Kury & Pinto-da-Rocha, 2007; Fig. 1). Males can also be recognized by the presence of swollen tarsal segments on the first pair of legs, a trait that occurs in all males regardless of body size (Fig. 1D, F). Based on analysis of a large sample of males, we found great and possibly discontinuous variation in cheliceral size, suggesting the existence of intrasexual dimorphism in this species. Recently, male polymorphism in cheliceral size and shape has been reported for the New Zealand harvestman *Pantopsalis cheliferoidea* (Eupnoi: Neopilionidae), which uses the enlarged chelicerae in contests for access to females (Painting *et al.*, 2015). Among species of the suborder Laniatores, however, there is no report of intrasexual male dimorphism based on formal statistical and allometric analyses (reviewed by Buzatto & Machado, 2014). Moreover, there is no information on how males use their enlarged chelicerae during contests or on how males with different-sized chelicerae achieve copulations. If we are to understand the elaboration and diversification of weapons at the inter- and intraspecific level, we need detailed morphological descriptions coupled with behavioural data on how males of different morphs use their weapons to acquire mates.

Here we used morphological traits to characterize inter- and intrasexual dimorphism in *P. lavarrei*. We also conducted behavioural observations to understand how males of both morphs use their chelicerae in intra- and intersexual interactions. In some gonyleptid harvestmen, even when males do not have enlarged chelicerae, they are still able to use these appendages to occasionally amputate legs of rivals during contests (e.g. Buzatto *et al.*, 2011; Zatz *et al.*, 2011). Thus, we predict that majors of *P. lavarrei* would use their enlarged chelicerae as weapons in intrasexual contests. Finally, we compared microhabitat use by females and males of the two morphs. Resource defence polygyny is the most common mating system among harvestman species that exhibit marked inter- and intrasexual dimorphism (Buzatto & Machado, 2014; Machado *et al.*, 2016), and we expected that majors would be associated with high-quality reproductive sites. Unfortunately, there is no information on the breeding biology of *P. lavarrei* that could allow us to predict the characteristics of a high-quality reproductive site. However, individuals of the syntopic whip-spider *Heterophrynus longicornis* (Amblypygi) use similar microhabitats and show a preference for large trees, bearing buttresses and burrows where they hide during daytime (Dias & Machado, 2006). Thus, as a first approximation to the mating system

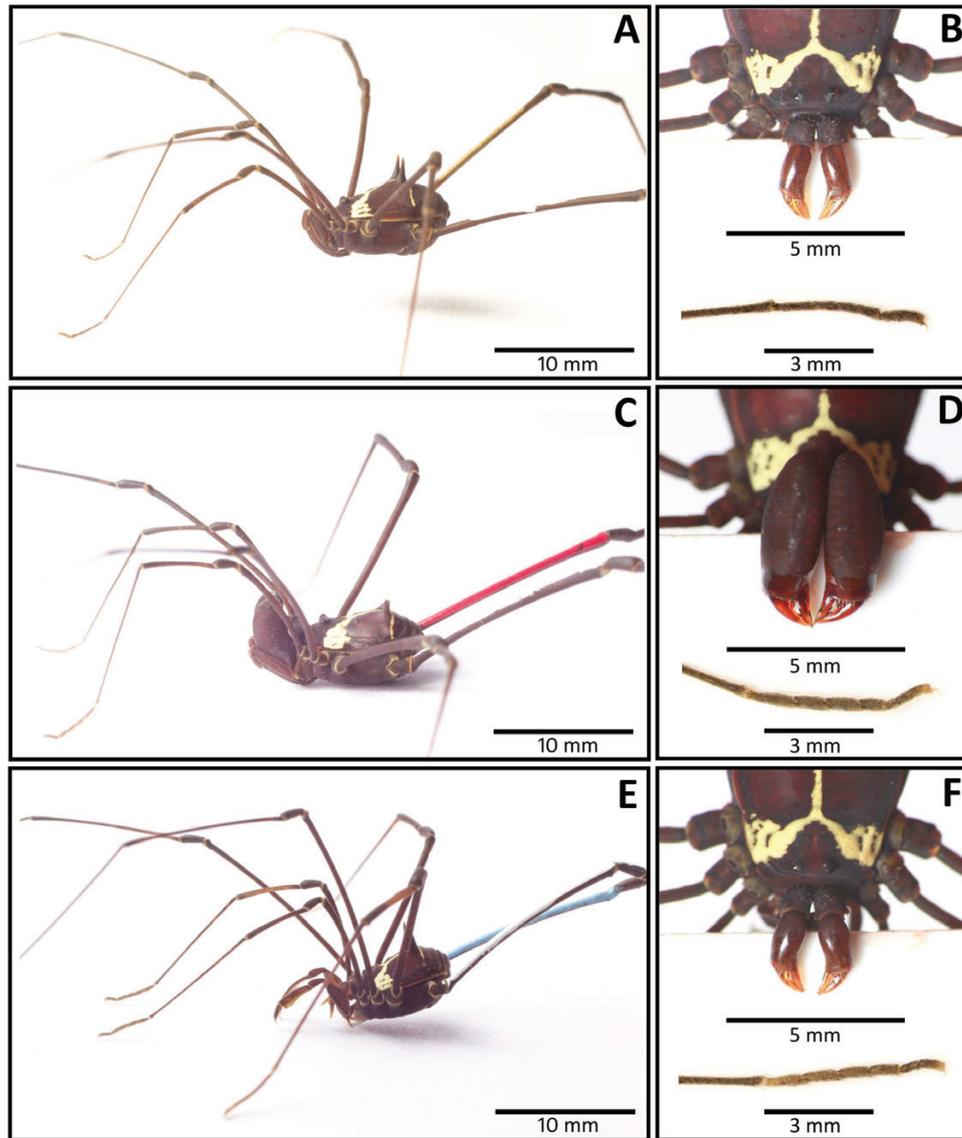


Figure 1. Inter- and intrasexual dimorphism in the harvestman *Paecilaemula lavarrei*. A, B, female in lateral view (A) and detail of her chelicerae and tarsal segments of leg I (B). C, D, major male in lateral view (C) and detail of his chelicerae and tarsal segments of leg I (D). E, F, minor male in lateral view (E) and detail of his chelicerae and tarsal segments of leg I (F). Note that tarsal segments of leg I of both male morphs (D–F) are slightly swollen when compared with the female (B). In A, C and E, the fourth pair of legs of the individuals is marked with coloured enamel painting because they were used in the behavioural observations.

of *P. lavarrei*, we used these same three features as proxies of reproductive site quality.

MATERIAL AND METHODS

STUDY SITE

We conducted the study at Adolpho Ducke Forest Reserve (02°53'S, 59°59'W), an area of 100 km² located close to the city of Manaus, state of Amazonas, Brazil.

The vegetation in the reserve is almost undisturbed and composed of *terra firme* rainforest. The local climate is warm and wet, with mean annual temperature of 26.5 °C and mean annual rainfall of 2436 mm. Rainfall is concentrated between November and June, with the highest precipitation between March and April (Marques Filho *et al.*, 1981). We visited the reserve in November 2016 and December 2017 (i.e. the beginning of the rainy period), totalling 10 days of fieldwork. In the first trip, we collected 125 individuals of *P. lavarrei*,

which were used exclusively to acquire morphological data. In the second trip, we collected 112 individuals, which were used to acquire morphological, behavioural and ecological data.

MORPHOLOGICAL DATA

All individuals collected in the first fieldtrip and most of the individuals collected in the second fieldtrip were preserved in individual vials containing 70% ethanol, and each of them received an exclusive code number. Given that harvestmen do not moult after reaching adulthood, and that adults can be easily distinguished from immature stages because they have complete tarsal segmentation, we were certain that all individuals collected in the field and used to acquire morphological data were sexually mature and belonged to the same life stage. Voucher specimens are deposited at Museu Nacional do Rio de Janeiro (MNRJ), Brazil.

In the laboratory, we took two photographs of each individual: one in dorsal view and the other in frontal view. To take the photograph in dorsal view we spread the legs of each individual laterally and positioned its dorsum as perpendicular as possible to the lens of the camera. The photograph in dorsal view allowed us to measure dorsal scute width, which is a proxy of structural body size in harvestmen, and femur length of legs I to IV (Fig. 2A). Although we have no evidence that males use their legs during intrasexual contests (see Results), we measured leg length because minors could be more vagile, leading to longer walking legs (e.g. Framenau, 2005; Kelly *et al.*, 2008) or to sensory appendages (e.g. Andersson, 1994; Herberstein *et al.*, 2017). Moreover, males intensively tap and rub their legs I on females before and during copulation (see Results), and there is evidence from other arthropods that contact courtship structures show negative allometry (e.g. Eberhard, 2002; Kilmer & Rodríguez, 2015). To take the photograph in frontal view we placed both chelicerae on a piece of white card and positioned them as perpendicular as possible to the lens of the camera (see Fig. 1B, D, F). The photograph in frontal view allowed us to measure traits that most probably show inter- and intrasexual dimorphism, namely cheliceral hand width and length, and cheliceral fixed finger length (Fig. 2B). Whenever possible, we measured the right appendages of the individuals. All individuals were photographed close to a scale bar and measurements were extracted from the images using the software ImageJ (Rasband, 2003).

For a sample of 30 males (15 majors and 15 minors) and 15 females collected in the second fieldtrip, we also measured additional traits. (1) Femur diameter (Fig. 2A) and cuticle thickness of legs I to IV: given that males can bite legs off during contests (see Results),

males should have thicker legs and thicker cuticle than females. To measure cuticle thickness, we cut the right femur transversally at the midpoint of the leg segment (Fig. 2C). Then, we photographed the cut piece from each leg (close to a scale bar) under a stereomicroscope, and measured cuticle thickness via the software ImageJ. (2) Cheliceral muscle mass and the area between movable and fixed cheliceral fingers when they are locked: given that chelicerae of males function like pliers during contests (see Results), the musculature associated with these fingers may help males to amputate legs of their rivals. The area between cheliceral fingers, in turn, is remarkably similar to that described for the chelae of the squat lobster *Munida rugosa*; in the latter species, the chela is an intrasexually selected organ adapted to inflict puncture wounds on opponents during contests (Claverie & Smith, 2007).

To estimate cheliceral muscle mass of each individual, we first removed both cheliceral hands using a scalpel. We then dried the chelicerae in an oven at 50 °C for 24 h, and weighed them in an analytical balance (precision 0.0001 g). After weighing, we placed the chelicerae in a vial containing 10% potassium hydroxide (KOH) for 24 h to dissolve the muscles. Finally, we dried the chelicerae in an oven (50 °C) for an additional 24 h before weighing them again. We used the difference in mass before and after immersion in KOH as an estimate of cheliceral muscle mass. To estimate the area between cheliceral fingers we used frontal photographs of the right chelicera as indicated in Figure 2D.

To analyse the data, we first investigated the existence of intrasexual male dimorphism in dorsal scute length (body size) and three morphological traits related to cheliceral size: length and width of cheliceral hand and length of cheliceral fixed finger (Fig. 2). We checked for bimodality in these four traits by adjusting mixture models that used one or two skew-normal distributions for each trait (cf. Buzatto *et al.*, 2014b). We then calculated the Akaike information criterion (AIC) for each model, and used the difference between AIC values of the two models (Δ AIC) to infer the existence of intrasexual male dimorphism. We considered a trait to be intrasexually dimorphic when the Δ AIC between the models with one and two skew-normal distributions was higher than 2. The mixture models were implemented using the package *mixsmsn* (Prates *et al.*, 2013) for R version 3.5.1 (R Development Core Team, 2018).

To classify each male as a minor or major for the subsequent analyses, we used estimates from the mixture model with two skew-normal distributions of cheliceral hand length, which was the trait with the highest value of Δ AIC in relation to the model with one skew-normal distribution (see Results). Based on this criterion, we assigned 98 males to their respective

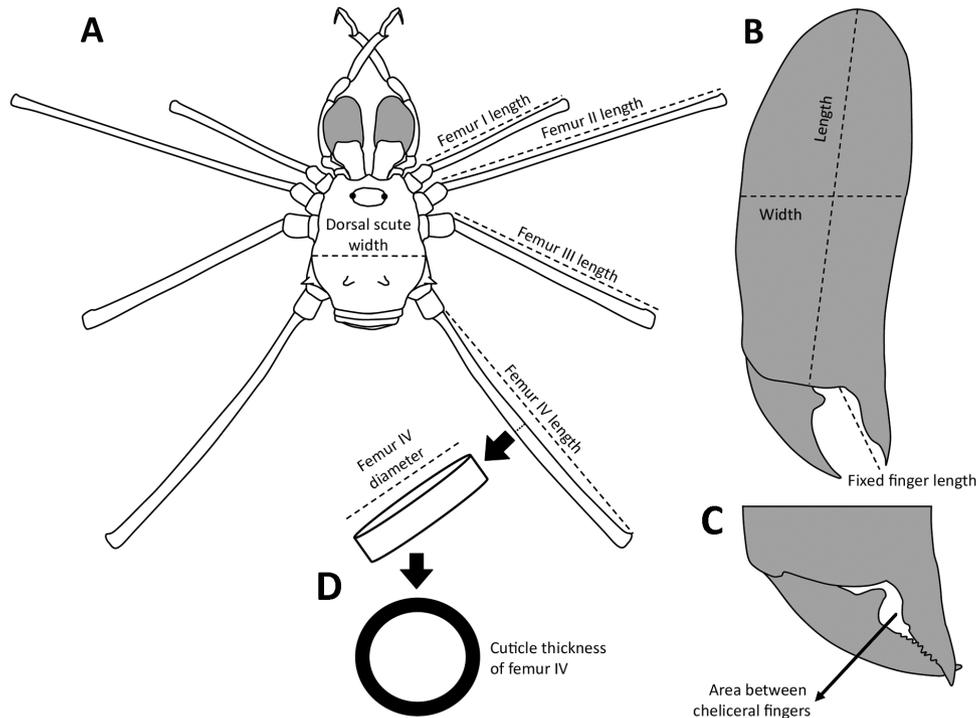


Figure 2. Scheme of all measurements taken from males and females of the harvestman *Paecilaemula lavarrei*. A, using dorsal photographs of the individuals, we measured dorsal scute width, femur length and diameter of all legs. Diameter was always taken at the midpoint of the femur. B, C, using frontal photographs of the individuals, we measured right chelicera length and width, and fixed finger length, (B) and area between cheliceral fingers (C), which was measured from the base of the fixed finger to the point where the first incisive tooth of the fixed finger touches the movable finger. D, for a sample of individuals, we removed a slice of each femur (at the midpoint of the segment) and photographed this slice under a stereomicroscope to measure cuticle thickness of all legs.

morph with 95% confidence – only two males could not be unequivocally assigned to a morph and they were removed from all analyses described below. We then used two complementary approaches to characterize intra- and intersexual dimorphism. In the first approach, we used linear models to compare the values of all morphological traits between females, minors and majors (hereafter called ‘groups’). When we found statistically significant results for a given trait, we performed a post-hoc Tukey test to identify which group(s) differed from the other(s). In the second approach, we used standardized major axis regressions between dorsal scute width and a subset of the morphological traits, namely length of legs I to IV, length and width of cheliceral hand, and length of cheliceral fixed finger. Variables were \log_{10} -transformed and for each trait we used a robust estimator in which allometric slopes are less sensitive to outliers (Taskinen & Warton, 2013). Using likelihood ratio tests, we investigated whether the slope of each group was different from 1 (isometry) and also compared the slopes between groups to investigate if they differed from each other. The linear models were performed using the package *stats*, and the standardized major axis regressions were applied using the package

smatr (Warton *et al.*, 2006, 2012) for R version 3.5.1 (R Development Core Team, 2018).

BEHAVIOURAL DATA

In both fieldtrips we made ad libitum observations of individuals, paying particular attention to male–male agonistic interactions and male–female sexual interactions. We also recorded leg amputations in the individuals we collected. In the second fieldtrip, we captured six males (three minors and three majors) and three females. These individuals were taken to the laboratory, where they were maintained inside four terraria (20 × 10 cm base, 15 cm high) containing a layer of *Sphagnum* moss as substrate and a piece of bark (c. 8 × 12 cm) that could be used as a diurnal shelter by the individuals. In each terrarium, we placed one female and one major for 7 days before behavioural observations were made. One terrarium was used only to keep the three minors. We watered each terrarium once a day and fed the individuals once a week with dead cricket nymphs. All behavioural observations were conducted from 21:00 to 00:00 h, using red lamps to avoid disturbing the individuals.

In the first phase of behavioural observations, which lasted 6 days, we randomly selected one major and transferred it (hereafter ‘intruder’) to another terrarium containing a female and another major (hereafter ‘resident’). We then followed the individuals for 1.5 h and recorded all behavioural interactions using a video camera (Sony Handycam HDR-CX405). We repeated this procedure every other night until each major had acted once as resident and once as intruder. In the second phase, which lasted 18 days, we transferred the three females to a single terrarium containing a randomly selected major (resident). The other two majors were maintained isolated in two different terraria with no female. After 3 days, we transferred one major (intruder) to the terrarium containing the three females and the resident major. We then followed the individuals for 1.5 h and recorded all behavioural interactions using a video camera. We repeated this procedure every other night, with each major acting once as resident and once as intruder. The same procedure was repeated with the minors to record possible agonistic interactions between them, and also sexual interactions between minors and females. Finally, in the third phase, which lasted 7 days, we first placed the three females and a major (resident) in the same terrarium. After 3 days, we placed one minor (intruder) in the same terrarium and followed the individuals for 1.5 h. All behavioural interactions were recorded using a video camera. Every other night we repeated this procedure with the other two minors.

At the end of the three phases, each major male was used three times as resident and twice as intruder, and

each minor male was used once as resident and twice as intruder. We used the behavioural data gathered in the three phases to describe how males of both morphs use their chelicerae and legs in agonistic male–male interactions and also in pre-copulatory and copulatory interactions with females. Due to the qualitative nature of our observations and the low number of individuals, no statistical test was performed.

ECOLOGICAL DATA

In the second fieldtrip, we compared the spatial distribution of females and males of the two morphs. We used the trail network that crosses the reserve to establish four plots. These plots were all 8 m wide (4 m either side of a trail), but varied in length from 160 to 350 m, so that the total sampled area was 7760 m². We actively searched for individuals of *P. lavarrei* using UV lamps because the yellow Y-shaped patch on the dorsum of the individuals glows under UV light (Fig. 3A). Inside each plot, we scanned all trees with perimeter at breast height (PBH) ≥ 30 cm (c. 10 cm in diameter), from a height of nearly 2 m down to the ground. We also scanned all fallen logs with perimeter ≥ 30 cm (regardless of their length). Each plot was searched only once and the sampling was conducted on four consecutive nights (from 18:00 to 00:00 h). The trees and fallen logs where the individuals were found received a numbered tag, which was also used to identify the vial of each individual we collected. In the afternoon after each sampling, we measured the PBH of all trees and the perimeter of all fallen logs inside the plots, recording those on which individuals

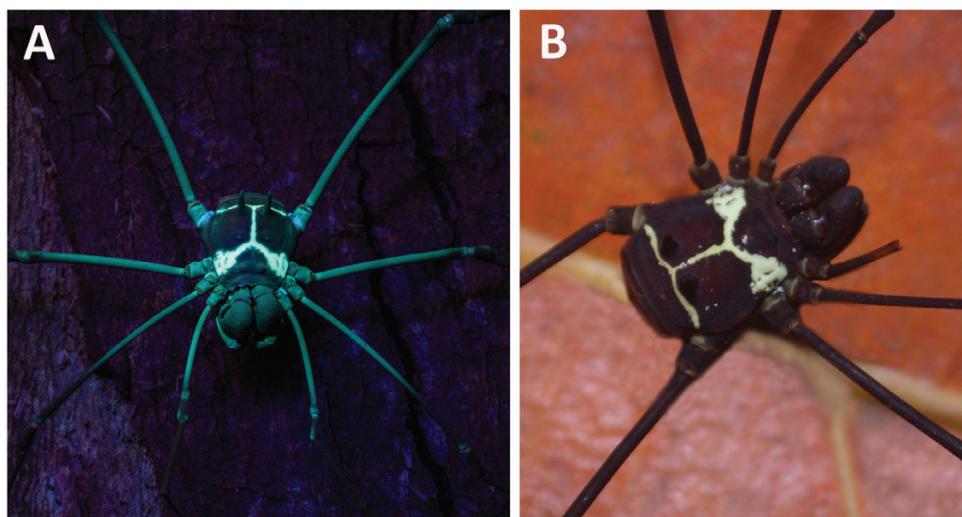


Figure 3. Major males of the harvestman *Paecilaemula lavarrei*. A, individual photographed under UV light. The yellow Y-shaped patch on the dorsal scute glows under this type of light. B, male found in the field with leg I amputated at the middle of the femur.

were present vs. those on which they were absent. For both tree trunks and fallen logs, we also recorded the presence or absence of natural cavities ('burrows'). These burrows could be either on the ground at the base of the trunk/fallen log or on the trunk/fallen log per se, and had to have opening diameter ≥ 5 cm and depth ≥ 10 cm. Finally, for all trees, we recorded whether buttressing was present or absent. In the laboratory, we identified the sex and male morph of the individuals captured in the plots.

We analysed the ecological data using generalized linear models (GLMs). In the first analysis, we tested whether individuals of *P. lavarrei* showed any preference for tree trunks or fallen logs. The predictor variable was the type of microhabitat (tree trunks or fallen logs) and the response variable (with binomial error distribution) was the presence or absence of individuals. This analysis was performed for females, minors and majors separately. In the second analysis, we investigated which features of tree trunks and fallen logs could influence the occurrence of individuals. The predictor variables were PBH (\log_{10} -transformed), presence or absence of buttressing, and presence or absence of burrows. The response variable (with binomial error distribution) was the presence or absence of individuals. Again, the analysis was performed for females, minors and majors separately. In both analyses we used a logit link function (Zuur *et al.*, 2005). The GLMs were performed using the package *stats* for R version 3.5.1 (R Development Core Team, 2018).

Finally, we calculated dispersion coefficients (DCs) to compare the spatial distribution of females, minors and majors. The DC is calculated as the ratio between the standard deviation and the mean number of individuals collected per sampling unit (i.e. tree trunks and fallen logs). A DC > 1 indicates that the spatial distribution of individuals is aggregated, a DC < 1 indicates regular spatial distribution and a DC ~ 1 indicates random spatial distribution. Because the number of sampling units containing no individual was very high (nearly 95%

of all trunks/fallen logs), DC values for females and males of both morphs would invariably result in aggregated distributions. Considering that the probability of finding individuals increases with PBH (see Results), we used only the data of the upper two quartiles of the PBH distribution, which contains 589 trunks/fallen logs. Thus, based on a subsample of all trunks/fallen logs that includes 95% of the individuals, we used a chi-square test to determine whether the DC of females and males of each morph was statistically different from 1 (following Brower *et al.*, 1997).

RESULTS

INTRA- AND INTERSEXUAL DIMORPHISM

We found intrasexual male dimorphism for dorsal scute width, cheliceral hand length and width, and cheliceral fixed finger length (Table 1). The distribution of these four morphological traits was clearly bimodal, sometimes with little overlap between each morph (Fig. 4). After we classified males as minors and majors based on cheliceral hand length, the trait with lowest overlap between morphs (Fig. 4A), we also found that minors were smaller than majors in femur length, diameter of legs I, III and IV, cheliceral muscle mass, and area between cheliceral fingers (Table 2).

There was marked intersexual dimorphism in most of the morphological traits analysed, even when females were compared with minors (Table 2; Fig. 4). Dorsal scute width of females was greater than that of minors, but lower than that of majors. Cuticle thickness of legs I and II did not differ between males and females, and cheliceral muscle mass did not differ between minors and females. For all other traits females were smaller than males, regardless of the morph.

All cheliceral traits in males (regardless of the morph) were hyperallometric, i.e. they had allometric slopes significantly above 1 in males (Table 3; Fig. 4).

Table 1. Results of the mixture models used to test whether males of the harvestman *Paecilaemula lavarrei* show a bimodal distribution in four morphological traits

Trait	AIC		Δ AIC	Conclusion
	One size distribution	Two size distributions		
Dorsal scute width	69.73	2.43	67.3	Dimorphic
Cheliceral hand width	105.22	-54.18	159.4	Dimorphic
Cheliceral hand length	305.35	81.13	224.22	Dimorphic
Cheliceral fixed finger length	-114.94	-164.95	50.01	Dimorphic

For each trait we present the AIC value for one and two skew-normal distributions. When the best model (highlighted in bold) describes a mixture of two skew-normal distributions, we concluded that trait is intrasexually dimorphism.

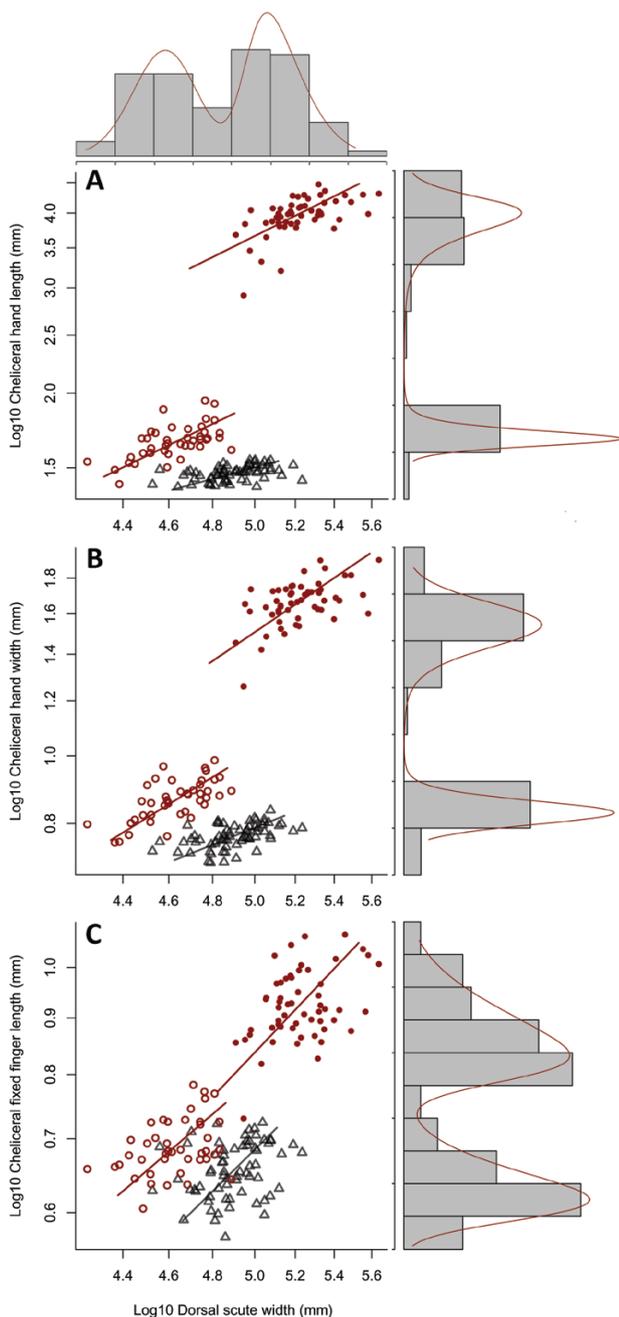


Figure 4. Allometric relationships of three morphological traits that show inter- and intrasexual male dimorphism in the harvestman *Paecilaeumula lavarrei*: A, cheliceral hand length; B, cheliceral hand width; and C, cheliceral fixed finger length. Triangles represent females and circles represent males (empty = minors, filled = majors). The histograms on the right show the fit of a mixture model with two skew-normal distributions, indicating that the three cheliceral traits have a bimodal distribution (see Table 1). The histogram at the top shows the fit of a mixture model with two skew-normal distributions, indicating that dorsal scute width (i.e. body size) also has a bimodal distribution (see Table 1). Slope values are presented in Table 3.

Only the allometric slope of cheliceral hand width was higher in majors than in minors. The allometric slope of cheliceral hand length in females did not differ from 1, and was lower than the slopes of both male morphs. In turn, cheliceral hand width and cheliceral fixed finger length in females showed slopes higher than 1. The slope of cheliceral hand width in females was lower than the slopes of both male morphs, but the slope of cheliceral fixed finger length in females did not differ from the slope of males. Finally, the slope of femur length for all legs did not differ from 1, and showed no significant difference between sexes or morphs.

MALE–MALE AND MALE–FEMALE INTERACTIONS

During the two fieldtrips, no male–male contest was observed, but several individuals had amputated legs (Fig. 3B). Considering all collected individuals ($N = 237$), we found six females, four minors and one major with amputated legs. Females had one amputation in leg I, one in leg II, two in leg III and two in leg IV. Minors had one amputation in each of the four leg pairs, and the major had amputation in leg I (Fig. 3B).

In laboratory observations, we recorded nine male–male contests. Eight of these contests were initiated by the resident major approaching the intruder male (minor or major) and one contest was initiated by an intruder major. During the contests, resident majors bit the femur ($N = 8$), tibia ($N = 2$) or tarsus ($N = 1$) of intruders with their chelicerae (see Supporting Information, Video S1). Most of the attacks were directed to legs IV ($N = 6$), but legs III ($N = 2$) and II ($N = 1$) were also bitten during the contests. When the femur of leg II was bitten, we saw haemolymph release, implying that the cuticle was fractured. In 33% of contests, the intruder male (minor or major) counterattacked by biting the legs IV of the resident major. In all other cases, the intruders ran away from the attacks of the resident majors. Male–male contests occurred regardless of the number of females in the terrarium (one female: 66% of trials; three females: 87% of trials). When there was only one female, the resident major usually stayed less than 1 cm from her, preventing the intruders from approaching. During ($N = 2$) or after a contest ($N = 5$), we observed males (always majors) strongly biting the legs of nearby females. In one case, the bite promoted haemolymph release in the femur of leg III of a female. We never observed minors initiating a contest, even when they were residents. Thus, when the intruder and the resident were both minors, no contest was recorded.

During the fieldtrips, we found two mating pairs of *P. lavarrei*: one was copulating on a large tree trunk and the other was copulating on a large fallen log. In both cases, the male was a major. We also recorded

Table 2. Inter- and intrasexual dimorphism in the size of several morphological traits of the harvestman *Paecilaemula lavarrei*

Trait	Females	Minor males	Major males	Statistics
Dorsal scute width (mm)	4.90 ± 0.14 ^a (N = 124)	4.63 ± 0.15 ^b (N = 42)	5.23 ± 0.17 ^c (N = 56)	$F_{2,219} = 199.9, P < 0.001$
Cheliceral hand width (mm)	0.77 ± 0.03 ^a (N = 66)	0.87 ± 0.06 ^b (N = 42)	1.66 ± 0.12 ^c (N = 53)	$F_{2,158} = 2207, P < 0.001$
Cheliceral hand length (mm)	1.47 ± 0.04 ^a (N = 66)	1.66 ± 0.11 ^b (N = 42)	3.96 ± 0.29 ^c (N = 53)	$F_{2,158} = 3416, P < 0.001$
Cheliceral fixed finger length (mm)	0.66 ± 0.04 ^a (N = 66)	0.69 ± 0.04 ^b (N = 42)	0.93 ± 0.07 ^c (N = 56)	$F_{2,161} = 481.4, P < 0.001$
Cheliceral muscle mass (µg)	0.35 ± 0.26 ^a (N = 15)	0.41 ± 0.16 ^a (N = 15)	3.27 ± 1.57 ^b (N = 14)	$F_{2,23.19} = 112.38, P < 0.001$
Area between cheliceral fingers (µm ²)	3.93 ± 2.4 ^a (N = 15)	7.84 ± 3.1 ^b (N = 15)	44.13 ± 8.84 ^c (N = 15)	$F_{2,25.14} = 141.41, P < 0.001$
Leg I femur length (mm)	6.12 ± 0.19 ^a (N = 124)	6.31 ± 0.22 ^b (N = 42)	6.44 ± 0.20 ^c (N = 56)	$F_{2,119} = 52.52, P < 0.001$
Leg II femur length (mm)	12.34 ± 0.38 ^a (N = 124)	12.73 ± 0.48 ^b (N = 42)	12.80 ± 0.43 ^b (N = 56)	$F_{2,219} = 29.3, P < 0.001$
Leg III femur length (mm)	9.06 ± 0.27 ^a (N = 124)	9.33 ± 0.33 ^b (N = 42)	9.53 ± 0.29 ^c (N = 56)	$F_{2,219} = 55.15, P < 0.001$
Leg IV femur length (mm)	12.24 ± 0.37 ^a (N = 124)	12.83 ± 0.48 ^b (N = 42)	13.15 ± 0.39 ^c (N = 56)	$F_{2,219} = 109.8, P < 0.001$
Leg I femur diameter (mm)	0.31 ± 0.02 ^a (N = 15)	0.34 ± 0.02 ^b (N = 15)	0.36 ± 0.02 ^c (N = 15)	$F_{2,42} = 28.99, P < 0.001$
Leg II femur diameter (mm)	0.32 ± 0.02 ^a (N = 15)	0.35 ± 0.01 ^b (N = 15)	0.36 ± 0.02 ^b (N = 15)	$F_{2,42} = 26.35, P < 0.001$
Leg III femur diameter (mm)	0.42 ± 0.03 ^a (N = 15)	0.50 ± 0.02 ^b (N = 15)	0.53 ± 0.02 ^c (N = 15)	$F_{2,42} = 85.85, P < 0.001$
Leg IV femur diameter (mm)	0.43 ± 0.02 ^a (N = 15)	0.52 ± 0.02 ^b (N = 15)	0.55 ± 0.02 ^c (N = 15)	$F_{2,42} = 119.27, P < 0.001$
Leg I femur cuticle thickness (mm)	0.047 ± 0.008 (N = 15)	0.046 ± 0.004 (N = 15)	0.051 ± 0.007 (N = 15)	$F_{2,42} = 2.14, P = 0.13$
Leg II femur cuticle thickness (mm)	0.057 ± 0.007 (N = 15)	0.064 ± 0.011 (N = 15)	0.058 ± 0.007 (N = 15)	$F_{2,42} = 2.83, P = 0.07$
Leg III femur cuticle thickness (mm)	0.065 ± 0.010 ^a (N = 15)	0.099 ± 0.013 ^b (N = 15)	0.100 ± 0.013 ^b (N = 15)	$F_{2,42} = 51.35, P < 0.001$
Leg IV femur cuticle thickness (mm)	0.067 ± 0.014 ^a (N = 15)	0.120 ± 0.019 ^b (N = 15)	0.130 ± 0.022 ^b (N = 15)	$F_{2,42} = 47.85, P < 0.001$

For all traits we present mean ± standard deviation and sample size in parentheses. Different letters indicate significant differences in a post-hoc Tukey test.

20 male–female interactions in the laboratory. Males usually approached the females frontally or laterally, tapping the dorsum and legs of the females with their legs I and/or II ($N = 18$). Once physical contact had been established, the male gently bit the spines on the dorsal scute of the female ($N = 2$) or the basal segments of her legs ($N = 18$), a behaviour we called ‘cheliceral massage’. Sometimes, during cheliceral massage, the mouth parts of the male were in direct contact with the legs of the female (see Video S1). The male also used the tarsus of his legs I to tap the lateral margins of the female’s dorsum ($N = 20$) and the basal segments of her legs ($N = 20$), a behaviour we called ‘leg tapping’. After cheliceral massage and leg tapping, the male held the female by her coxa or trochanter of legs I or II using his pedipalps ($N = 20$), a behaviour we called ‘female grasping’. In this position, the male intensively rubbed the swollen tarsal segments of both legs I, which contain an intersexually dimorphic gland, on the coxa, trochanter, and proximal portion of the female’s femora ($N = 20$), a behaviour we called ‘leg rubbing’. During female grasping, the mating pair raised the frontal region of their bodies, the male everted his penis and penetration occurred (see Video S1). Females remained quiescent during penetration, but in a few cases the female’s mouth parts were in direct contact with the penis of her partner ($N = 2$). Penetration lasted from 48 s to 4 min 18 s and all male–female behaviours were recorded for both minors and majors, with no clear difference between them.

HABITAT USE

We scanned 1034 tree trunks and 143 fallen logs with PBH ≥ 30 cm inside the four plots. In total, we found 103 individuals: 60 females, 18 minors and 24 majors (the morph of one male could not be assigned with 95% confidence). Females were found on 30 tree trunks (2.9% of the total) and nine fallen logs (6.7% of the total). The relative frequency of females was higher in fallen logs than in tree trunks (Table 4). Minors and majors were found on 29 tree trunks and six fallen logs, without any significant preference (Table 4). Individuals (regardless of the sex and morph) were more likely to be found on larger tree trunks and fallen logs, especially if they had burrows (Table 4; Fig. 5). The presence of buttressing, however, had no influence on the probability of finding individuals (Table 4).

The DC of minors and majors did not differ from 1, indicating that their spatial distribution on tree trunks and fallen logs was random (minors: DC = 1.10; $\chi^2 = 781.18$, d.f. = 588, $P = 0.993$; majors: DC = 1.33; $\chi^2 = 646.63$, d.f. = 588, $P = 0.999$). For females, the DC was significantly above 1, indicating that their spatial distribution was aggregated (DC = 2.35; $\chi^2 = 1381.43$, d.f. = 588, $P < 0.001$).

DISCUSSION

Our morphological analyses confirmed that males of the harvestman *P. lavarrei* show intrasexual dimorphism

Table 3. Inter- and intrasexual dimorphism in the slope of allometric relationships of several morphological traits of the harvestman *Paecilaemula lavarrei*

Trait	Females	Minor males	Major males	Statistics
Cheliceral hand width (mm)	1.37 (1.10–1.72)^a (N = 66)	2.10 (1.62–2.73)^b (N = 42)	2.33 (1.78–3.04)^c (N = 53)	LR test = 10.47, d.f. = 2, P = 0.005
Cheliceral hand length (mm)	1.07 (0.87–1.33) ^a (N = 66)	1.92 (1.48–2.50)^b (N = 42)	1.99 (1.52–2.59)^b (N = 53)	LR test = 17.06, d.f. = 2, P < 0.002
Cheliceral fixed finger length (mm)	2.13 (1.65–2.74)^a (N = 66)	1.85 (1.38–2.46)^a (N = 42)	2.27 (1.70–3.02)^a (N = 56)	LR test = 1.06, d.f. = 2, P = 0.058
Leg I femur length (mm)	0.97 (0.81–1.15) ^a (N = 124)	1.10 (0.88–1.46) ^a (N = 42)	0.98 (0.75–1.28) ^a (N = 56)	LR test = 0.580, d.f. = 2, P = 0.748
Leg II femur length (mm)	1.05 (0.88–1.26) ^a (N = 124)	1.17 (0.88–1.56) ^a (N = 56)	1.03 (0.78–1.38) ^a (N = 42)	LR test = 0.498, d.f. = 2, P = 0.779
Leg III femur length (mm)	0.97 (0.81–1.17) ^a (N = 124)	1.11 (0.86–1.46) ^a (N = 42)	1.00 (0.76–1.33) ^a (N = 56)	LR test = 0.767, d.f. = 2, P = 0.682
Leg IV femur length (mm)	1.04 (0.87–1.25) ^a (N = 124)	1.19 (0.89–1.58) ^a (N = 42)	0.99 (0.75–1.31) ^a (N = 56)	LR test = 0.922, d.f. = 2, P = 0.630

For all traits we present the slope b , the 95% confidence interval of the slope, and the sample size in parentheses. Different letters indicate significant differences in the slopes based on likelihood ratio (LR) tests. Values in bold indicate significant positive allometry (i.e. $b > 1.0$).

in cheliceral size. Behavioural data showed that males of the major and minor morphs use their chelicerae to gently bite the legs of females before copulation and to powerfully bite the legs of rival males during contests. Although our sample size is small, only majors were observed initiating a contest, biting the opponent. However, both minors and majors responded to the attacks with bites on the opponent's legs. Some bites may lead to leg amputation and, in fact, we collected individuals missing parts of their legs in the field. Ecological data showed that individuals occurred preferentially on large tree trunks and on fallen logs with burrows. Moreover, the spatial distribution of females was aggregated, but the spatial distribution of males of both morphs was random. Hereafter, we integrate morphological, behavioural and ecological data to discuss the implications of our findings.

Although intersexual dimorphism is the rule in arachnids, intrasexual male dimorphism has been rarely described. Most such cases occur in the order Opiliones, especially in the suborder Laniatores, in which the morphs usually differ in the size of spines on legs IV and/or the length of legs II or IV (reviewed by Buzatto & Machado, 2014). These intrasexually dimorphic traits are used to harm or to threaten opponents during contests (e.g. Willemart *et al.*, 2009; Buzatto *et al.*, 2011; Zatz *et al.*, 2011). Here we provide the first formal statistical evidence of intrasexual male dimorphism in cheliceral size for a species belonging to the suborder Laniatores. Majors of *P. lavarrei* use their enlarged chelicerae as cutting pliers in male–male contests and may inflict serious damage to the opponent's legs. Traits used as weapons in contests usually show hyper-allometric slopes (Bonduriansky, 2007a). In fact, all cheliceral traits we measured had allometric slopes greater than 1 in majors. However, the allometric slopes of these same cheliceral traits were also greater than 1 in minors, and two traits showed slopes greater than 1 even in females. Given that all cheliceral traits are present in females and males of both morphs, the independent evolution of inter- and intrasexual dimorphism is probably constrained by shared genetic architecture manifested as cross-sex and cross-morph genetic correlations (Poissant *et al.*, 2009). Thus, directional sexual selection acting more strongly on majors may lead to a correlated but weaker evolutionary change in the allometric slope or in the reaction norm of cheliceral traits of both females and minors.

A single reported case of intrasexual male polymorphism in harvestmen related to cheliceral size has previously been reported. In *Pantopsalis cheliferoideis* (suborder Eupnoi), Painting *et al.* (2015) described males with long-slender chelicerae, with short-broad chelicerae and with short-slender chelicerae. Males of these three morphs have a much longer basal segment of the chelicerae in

Table 4. Results of the generalized linear models used to investigate habitat use by females, and major and minor males of the harvestman *Paecilaemula lavarrei*

Variable	Females	Minor males	Major males
Habitat type (tree trunk)	-0.776 ± 0.389 <i>Z</i> = -1.992, <i>P</i> = 0.046	-0.732 ± 0.567 <i>Z</i> = -1.293, <i>P</i> = 0.196	-0.248 ± 0.633 <i>Z</i> = -0.393, <i>P</i> = 0.695
Perimeter	2.316 ± 0.752 <i>Z</i> = 3.077, <i>P</i> = 0.002	2.415 ± 1.071 <i>Z</i> = 2.256, <i>P</i> = 0.024	4.885 ± 4.885 <i>Z</i> = 4.101, <i>P</i> < 0.001
Burrows (present)	2.041 ± 0.405 <i>Z</i> = 5.039, <i>P</i> < 0.001	1.977 ± 0.612 <i>Z</i> = 3.232, <i>P</i> = 0.001	2.318 ± 0.695 <i>Z</i> = 3.338, <i>P</i> < 0.001
Buttressing (present)	0.354 ± 0.451 <i>Z</i> = 0.785, <i>P</i> = 0.433	0.375 ± 0.634 <i>Z</i> = 0.592, <i>P</i> = 0.554	0.066 ± 0.612 <i>Z</i> = 0.109, <i>P</i> = 0.914

In a first analysis, we evaluated preference for tree trunks or fallen logs. Then, we evaluated the effects of perimeter, presence of burrows and buttressing on the probability of finding individuals. For each predictor variable we present the estimated coefficient and its standard error, the result of the test (*Z*), and the significance value (*P*)

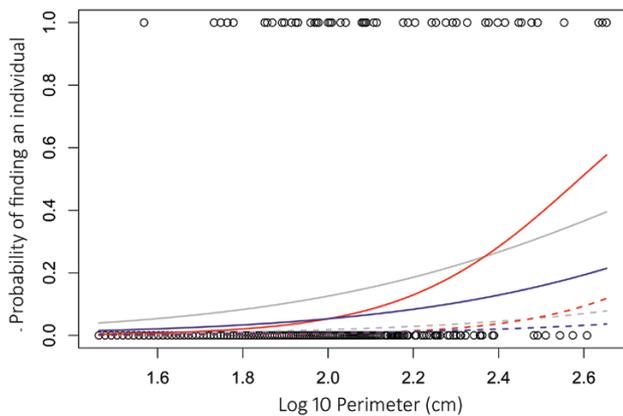


Figure 5. Logistic regressions showing the probability of finding females (grey), minors (blue) and (C) majors (red) of the harvestman *Paecilaemula lavarrei* on tree trunks and fallen logs according to trunk perimeter and the presence (solid lines) or absence (dashed lines) of burrows. The coefficients of the model are presented in Table 4.

comparison with *P. lavarrei*. Moreover, the fighting style in *Pantopsalis cheliferoideis* is very different from that found in *P. lavarrei*. Males of the long-slender morph wave their chelicerae and occasionally jab the opponent, whereas males of the short-broad morph use their chelicerae to stab the opponent – no fight between small-slender males was observed (Painting *et al.*, 2015). Thus, although male polymorphism in *P. lavarrei* and *Pantopsalis cheliferoideis* is related mainly to differences in cheliceral size, the general shape of the chelicerae is markedly different between these two harvestman species, which reinforces the notion that weapon morphology is related to the fighting style adopted by the individuals (McCullough *et al.*, 2014).

For many insects and arachnids studied so far, intrasexual male dimorphism seems to represent

a polyphenism (e.g. Buzatto *et al.*, 2014a; Buzatto & Machado, 2014), i.e. the differential expression of alternative phenotypes from a single genotype depending on environmental conditions (West-Eberhard, 2003). According to the polyphenic model, male body size is likely to be determined by environmental factors experienced during development, such as food availability, resulting in a normal distribution. The expression of exaggerated traits, in turn, emerges from an interaction between male body size and a genetic switch point that determines which of the alternative phenotypes will be expressed in each value of body size (Tomkins & Hazel, 2007). In many polyphenic species there is extensive overlap in both body and weapon size, indicating great individual variation in the genetic switch point determining the expression of the morphs (Tomkins & Hazel, 2007). Our findings, however, indicated that the distribution of most weapon traits and also of male body size was bimodal, showing little overlap between morphs, which contrasts with other harvestman species studied so far (e.g. Buzatto *et al.*, 2011; Zatz *et al.*, 2011). There are three hypotheses to explain this pattern. First, selection on the individual genetic switch point is strong, and thus males that express a morph incompatible with their body size pay high survival or reproductive costs. Second, the bimodal distribution of body sizes could be a consequence of males maturing at two different instars, each one with a different distribution of body size, as in the harvestman *Equitius doriae* (Hunt, 1979) and the Wellington tree weta *Hemideina crassidens* (Kelly & Adams, 2010). Finally, male dimorphism may not be a case of polyphenism, but rather a genetic polymorphism determined by one or a few loci of major effect with Mendelian inheritance, which would lead to more discrete differences between male morphs, as described for some marine isopods (reviewed by Shuster, 2008).

Besides inter- and intrasexual differences in body and cheliceral traits, we also found differences in leg traits. Females had shorter legs than males, and minors had shorter walking legs (I, III, IV) than majors. Regardless of the sex and male morph, the allometric slopes of all legs were isometric, which indicates that individuals invest in leg length proportionally to their body size. High male investment in leg length is frequent in arthropods showing a scramble competition polygyny mating system, in which males actively search for females (reviewed by [Herberstein et al., 2017](#)). Although the mating tactic of minors probably requires that they move more than majors (see below), minors do not have proportionally longer walking legs. Considering that the evolution of allometries seems not to be limited by developmental constraints (e.g. [Frankino et al., 2005](#)), our finding suggests that the selective pressure favouring increased vagility and longer legs is not strong enough to produce hyperallometric slopes for minors.

Females had smaller leg diameter than males for all legs, and minors had smaller leg diameter than majors for legs I, III and IV. Cuticle thickness of legs III and IV showed only intersexual differences, with females having cuticle nearly 50% thinner than males. Our behavioural observations shed some light on these morphological patterns. Males use their chelicerae to bite rivals and mating pairs, but the function of these bites is very different. Gentle bites on the legs of females (i.e. cheliceral massage) are probably a form of pre-copulatory courtship accomplished by both male morphs to stimulate potential mating partners. This behaviour has never been reported in harvestmen (reviewed by [Machado et al., 2015](#)), but scorpion males perform a similar cheliceral massage on females before sperm transfer, and this behaviour is interpreted as pre-copulatory courtship (e.g. [Carrera et al., 2009](#)). Strong bites on the legs of males during fights, in turn, are clearly a way of imposing injuries to rivals. Occasionally, fighting males may misdirect strong bites to nearby females, which may explain why some females found in the field also had amputated legs. However, assuming that strong bites are more frequently directed against rivals of both male morphs, males but not females should protect their legs from amputation, especially those that receive more attacks, such as legs III and IV. Similar protective countermeasures to avoid injuries during male–male contests have also been described for fiddler crabs (e.g. [Swanson et al., 2013](#)) and mantis shrimps (e.g. [Taylor & Patek, 2010](#)).

In many arthropod species each male morph is associated with a different mating tactic (reviewed by [Brockmann, 2008](#); [Shuster, 2008](#); [Buzatto et al., 2014a](#)). Our behavioural and ecological results suggest that *P. lavarrei* majors may fight for the possession

of territories, which are probably used by females as shelters or oviposition sites. Territories are probably established in large tree trunks and fallen logs with burrows, where males and females can hide during the day and find protection against predation and stressful abiotic conditions. A preference for trunks/fallen logs with larger perimeters may occur because they provide higher numbers of small arthropod prey climbing from the ground at night, as suggested for the whip-spider *Heterophrynus longicornis* ([Dias & Machado, 2006](#)). Given that massive trees and fallen logs with burrows are rare, they can be aggressively monopolized by large majors. Small majors, and perhaps some large minors, may establish territories in trunks/fallen logs with smaller perimeters. However, most trunks/fallen logs have no males and aggressive interactions between males make cohabitation unlikely; these two factors may explain the random spatial distribution of males. As occurs with other harvestmen with resource defence polygyny (e.g. [Buzatto et al., 2011](#); [Zatz et al., 2011](#)), receptive *P. lavarrei* females probably stay inside male territories during the breeding season. Thus, cohabitation is more frequent among females, which could explain their aggregated spatial distribution.

In conclusion, we have formally demonstrated that cheliceral size is intrasexually dimorphic in an Amazonian harvestman. Contrary to other intrasexually dimorphic male traits of insects and arachnids, overlap in the distribution of several traits related to cheliceral size is small between male morphs. Moreover, in contrast to many insects and arachnids, male body size is also intrasexually dimorphic. Together, these results suggest that intrasexual male dimorphism in *P. lavarrei* may not be a case of polyphenism. In fact, discrete body size distribution between morphs could be better explained either by males maturing at two different instars or by a genetic polymorphism with simple Mendelian inheritance. Regardless of the proximate causes, the morphological differences between morphs seem to be associated with different mating tactics. Future studies should follow marked individuals in the field to better understand the mating system of this species and answer the following questions: (1) Are the mating tactics of majors and minors really based on territory defence and territory invasions, respectively? (2) Are minors more vagile than majors? (3) Is the size of majors related to territory quality and/or harem size? (4) What factors influence the outcome of male–male fights? (5) Do females move between different territories during the breeding season? (6) How does mating success compare between morphs? There is a huge gap in our knowledge of the behaviour of intrasexually dimorphic arthropods under natural field conditions, and *P. lavarrei* offers a good opportunity to explore some questions that have been rarely addressed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Video S1. Intra- and inter-sexual interaction in the Amazonian harvestman *Paecilaemula lavarrei*.