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ORIGINAL PAPER

# Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones)

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**Abstract** Intense male–male competition for females may drive the evolution of male morphological dimorphism, which is frequently associated with alternative mating tactics. Using modern techniques for the detection of discontinuous allometries, we describe male dimorphism in the Neotropical harvestman *Longiperna concolor*, the males of which use their elongated, sexually dimorphic legs IV in fights for the possession of territories where females lay eggs. We also tested three predictions related to the existence of alternative mating tactics: (1) if individuals with relatively longer legs IV (majors) are more likely to monopolize access to reproductive resources, they are expected to remain close to stable groups of females more than individuals with relatively shorter legs IV (minors) do; (2) if minors achieve fertilization by moving between territories, they are expected to be less faithful to specific sites; and (3) majors should be observed in aggressive interactions more often. We individually marked all the individuals from a population of *Longiperna* during the reproductive season and recorded the location of each sighting for males and females as well as the identity of males involved in fights. Majors were more likely to have harems, and large majors were even more likely to do so. Majors were more philopatric and all males involved in fights belonged to this morph. These results strongly suggest that the mating tactic of the majors is based on resource defense whereas that of the minors probably relies on sneaking into the territories of the majors and furtively copulating with females.

**Keywords** Discontinuous allometry · Fight · Male–male competition · Mating system · Polyphenism

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## Introduction

Sexual selection in males that defend receptive females and the resources that attract females is thought to have led to the evolution of morphological traits that enable them to be more competitive in contests for females and resources (Andersson 1994; Shuster and Wade 2003). In some cases, intense male–male competition for females may also drive the evolution of male morphological dimorphism, which is generally associated with alternative mating tactics (review in Taborsky et al. 2008). Among dimorphic male species, the difference between male morphs is generally restricted to the size and shape of sexual traits that vary discontinuously with body size. *Major* males (territorial males or guards) typically have more elaborate weaponry and are frequently larger, whereas *minor* males (sneakers or satellites) have reduced weaponry (Gross 1996; Taborsky et al. 2008). Originally thought to be a rare phenomenon restricted to a few species (Gadgil 1972), male dimorphism is taxonomically widespread and, among arthropods, has

been reported for several insect orders (reviewed by Brockmann 2008), many species of crustaceans (reviewed by Shuster 2008), and a few species of arachnids (Radwan et al. 2002 and references therein; Vanacker et al. 2004 and references therein; Buzatto et al. 2010).

Most dimorphic male species in arthropods include examples of polyphenism, i.e., the ability of a single genotype to express alternative phenotypes depending on environmental conditions (West-Eberhard 2003). Therefore, every male in the population is capable of developing into either of two alternative phenotypes, and the environmental conditions faced by each individual are the main determinant of its status and consequently its morph (Gross 1996). In conditionally dimorphic male species, the status distributions of male morphs (generally measured as body size) often overlap to some extent (e.g., Emlen and Nijhout 2000; Knell 2009). According to the environmentally cued threshold model, the degree of overlap depends on the genetic variation in the distribution of the switch points that determine which morph is expressed in each value of body size (Tomkins and Hazel 2007). Consequently, although distinct male morphs may be easily distinguished by the size of the secondary sexual trait in some species, in many cases male dimorphism can only be detected by analyzing the nonlinear or discontinuous allometric relationship of the sexually selected trait (see Knell 2009).

Differences in external morphology may arise if individuals of each morph consistently exploit different reproductive alternatives; thus, correlated behavioral and morphological divergence is to be expected (Gross 1996; Shuster and Wade 2003; Taborsky et al. 2008). In most cases, major males aggressively exclude males that are competitively inferior from accessing females or reproductive territories (e.g., Shuster 1987; Emlen 1997; Kelly 2006). Although major males may have privileged access to mates, they incur several ecological and physiological costs, including the risk of injuries associated with resource defense, the production of conspicuous signals that may attract natural enemies, and the construction of energetically demanding structures to attract a mate or for protecting, providing for, and raising offspring (references in Taborsky et al. 2008). Minor males, on the other hand, may avoid agonistic interactions by sneaking copulation in the majors' territories (e.g., Shuster 1987; Emlen 1997). Although minor males do not invest as much in resource defense, they too incur costs and likely face intense sperm competition because they will generally copulate with females that have previously mated or will mate with a major male, and thus the ejaculates of both males will compete to fertilize eggs (Parker 1970).

Among Neotropical harvestmen of the subfamily Mitobatinae (Opiliones: Gonyleptidae), the most evident form of sexual dimorphism is the elongation of the male's fourth pair of legs (Machado and Macías-Ordóñez 2007). In males of *Metamitobates squalidus*, for instance, these may reach 39 times the body length (Kästner 1968), while females have much shorter legs, which rarely exceed four times the body length. In this species, females are so different from males that each sex has mistakenly been described as a different species (see Kury 1992). Recent field observations have shown that males of *Longiperna concolor* (Mitobatinae) use their sexually dimorphic legs IV in fights, apparently for the possession of territories where females lay their eggs (Zatz 2010; Fig. 1). Much as in the case of the gladiator harvestman *Neosadocus maximus* (Willemart et al. 2009b), the fighting males of *Longiperna* turn so that they are back to back, but they do not intertwine their fourth pair of legs, which are very long and lack any spine or tubercle to hook onto the legs of contenders. Instead, the fighting males keep their bodies nearly 1 cm apart, and both open their fourth pair of legs widely, with the right and left femurs forming a 100–180° angle (Fig. 1a). In this split-like position, each male strikes his opponent's leg IV metatarsi with his own metatarsi IV (Zatz 2010).

Even though there is great variation in the length of femur IV in male *Longiperna* (Table 1), there is no obvious bimodality in the distribution of this trait (Fig. 2). Using modern techniques for the detection of discontinuous allometries, however, we describe male dimorphism in this harvestman species. Since allometric analyses should be considered only the first step towards convincingly demonstrating the existence of polyphenism (Knell 2009), we also compiled behavioral data and tested three predictions about the existence of alternative mating tactics in *Longiperna*. The first prediction postulates that, if major males are more likely to monopolize access to females or reproductive territories (e.g., Moczek and Emlen 2000; Kelly 2006), then they will remain close to stable groups of adult females to a greater extent than minor males do. The second prediction postulates that, if minor males achieve fertilization by moving between different territories or harems monopolized by majors, then they are expected to spend less time than major males at specific sites. Finally, our third prediction postulates that males observed in aggressive interactions are more likely to be majors because minors usually avoid or quickly break off direct confrontations with larger opponents (e.g., Eberhard et al. 2000; Karino et al. 2005).

## Materials and methods

### Study site

The study was conducted in an Atlantic forest fragment at the Intervales State Park (24°14′ S, 48°04′ W) in the state of

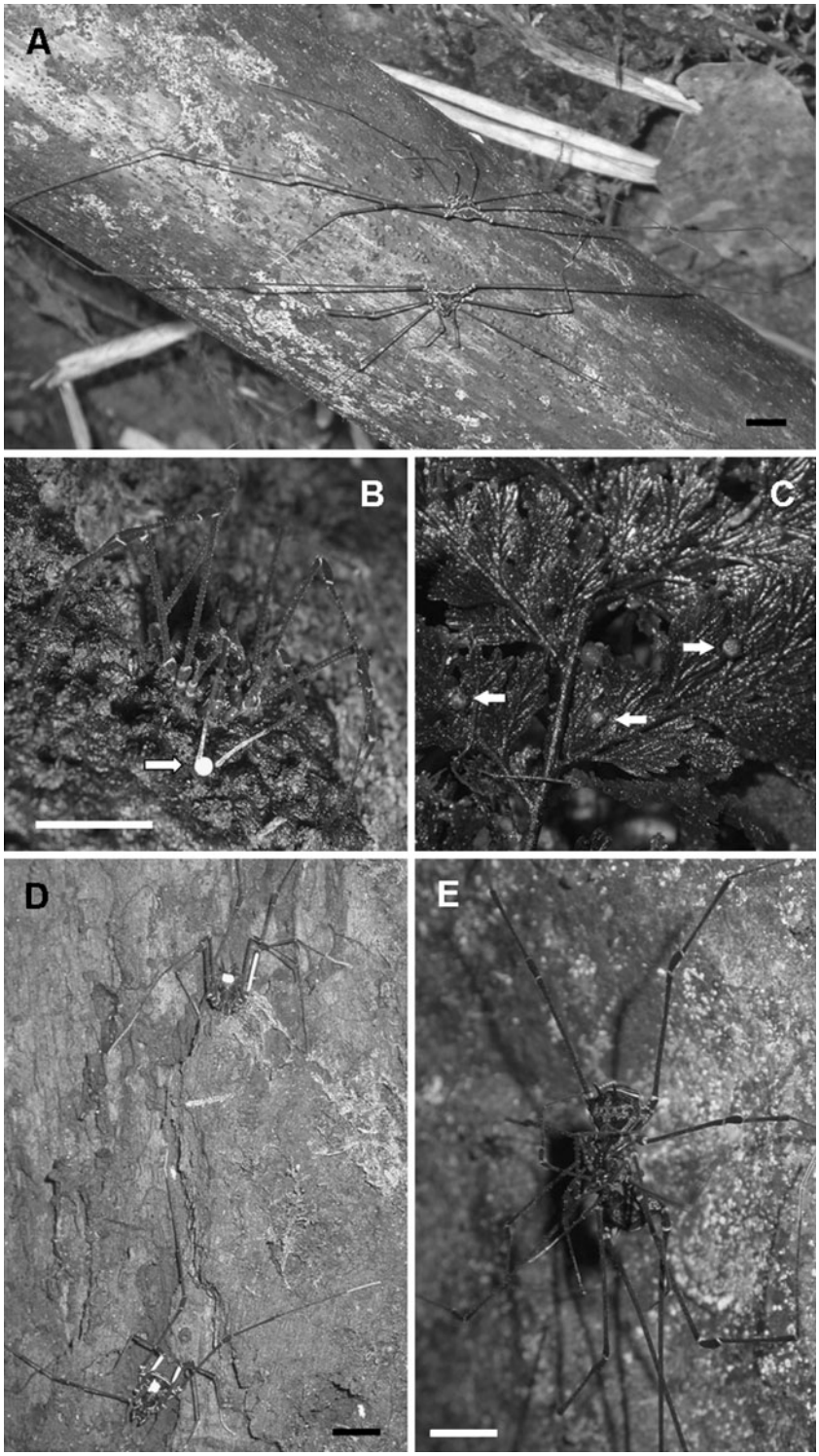


**Fig. 1** **a** Males of the harvestman *L. concolor* fighting on a fallen trunk. Both males are exhibiting the splits position in which their fourth pair of legs are widely spread, with the right and left femurs forming a 180° angle. **b** *Longiperna* female picking up debris and attaching particles to a recently laid egg (*white arrow*). Note that in females the fourth pair of legs is considerably shorter than it is in males. **c** *Longiperna* eggs (*white arrows*) on a fern leaf in a harem. Females do not guard their eggs but rather cover them with debris, which may provide protection against predators and also prevent dehydration. **d** Two marked *Longiperna* females resting on a rotten log that was used as an oviposition site. These particular individuals were captured exactly at this spot for more than ten times during the study. **e** A *Longiperna* mating pair copulating on a rock (the male is on the bottom). *Scale bar* in all photos=1 cm

São Paulo, southeastern Brazil. The region has high precipitation levels, with an average annual rainfall of 2,000 to 3,000 mm/year, and mean annual temperature ranges from 12 to 20°C. The weather is mainly subtropical, with a warm–wet season from October to March and a cold–dry season from April to September. Naturalistic observations were made along a stream, which is approximately 5 m wide and is flanked by abundant vegetation that partially covers the stream bed in some places.

## Study species

*L. concolor* exhibits marked sexual dimorphism in body size: male dorsal scute length, which is a standard estimate

**Table 1** Mean and standard deviation of the size of two body parts (in millimeters) in males and females of the harvestman *L. concolor*. The range and coefficient of variation are respectively given in parentheses. Body parts were compared between males and females using Student's *t* test

| Body part | Length | | Statistic |
|---|---|---|---|
| | Male ($n$=633) | Female ($n$=535) | |
| Dorsal scute | 5.49±0.28 (4.65–6.31; 0.05) | 6.24±0.27 (4.91–6.96; 0.04) | $t$= −45.780, df=1,166, $P$<0.001 |
| Femur IV | 39.78±10.70 (14.44–59.96; 0.26) | 12.09±0.95 (6.72–17.70; 0.07) | $t$=59.642, df=1,166, $P$<0.001 |

of body size in harvestmen (see Fig. 1 in Willemart et al. 2009b), is nearly 12% smaller than female dorsal scute length (Table 1). On the other hand, femur IV is much longer in males than in females (Table 1; Fig. 1a, b). The coefficient of variation of femur IV length is also much higher in males than in females (Table 1). While in some adult males femur IV is as long as 60 mm, in other males its length is similar to that of females, i.e., nearly 14 mm (Table 1). At the Intervales State Park, individuals of *Longiperna* are mainly found along the margins of streams where they forage, reproduce, and take shelter. The species is very abundant and individuals are active during most of the day during the wet–warm season (Zatz 2010).

Although there is little information on the reproductive biology of the Mitobatinae in the wild, laboratory observations indicate that *Promitobates ornatus* females lay their eggs individually on the substrate and cover them with debris (Willemart 2001). During our fieldwork (Zatz 2010), *Longiperna* females were also seen to lay their eggs one at a time, manipulate them with their first pair of legs, and cover them with debris ($n$=21; Fig. 1b). Oviposition sites were stones partially covered with moss ($n$=12), rotten fallen trunks ($n$=6), and fern leaves ($n$=3, Fig. 1c). Other eggs covered with debris and previously hatched nymphs were always observed close to oviposition sites (within 20–30 cm; Fig. 1c).

Marked *Longiperna* females rarely moved during the time that we were sampling, and 53.7% of the females captured at least two times were found on exactly the same stone or trunk that they used as their oviposition site

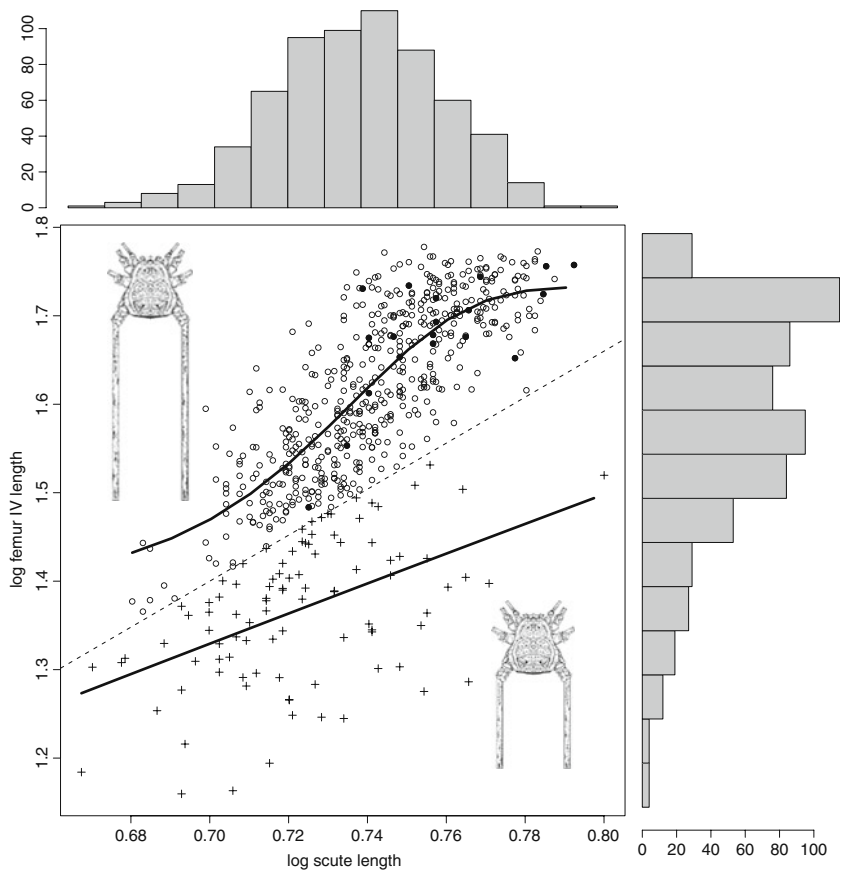


**Fig. 2** Allometric relationship between dorsal scute length and femur IV length in males of the harvestman *L. concolor*. The *dashed line* is the switch line that separates the population into majors (*circles*) and minors (*crosses*) using Knell's (2009) procedure. The *solid lines* represent the best models explaining each male morph data set analyzed independently (Table 2), i.e., a Weibull growth curve sigmoidal model for major males and a Michaelis–Menten sigmoidal model for minor males (barely distinguishable from a straight line). The *solid circles* represent males involved in fights. Notice that both body size (*top histogram*) and leg size (*side histogram*) exhibit continuous variation

(Fig. 1d). Adult *Longiperna* males were frequently found at these oviposition sites, sometimes copulating with females ($n$=4; Fig. 1e). Based on these field observations, *Longiperna* is hypothesized to be a harem-defending polygynous species (sensu Shuster and Wade 2003), similar to related species of harvestmen (Buzatto and Machado 2008).

## Morphometric measures and analyses

The study population of *Longiperna* was censused monthly by inspecting a 170-m-long transect along the stream from October 2008 to April 2009. The vegetation on both sides of the stream was inspected twice a day (from 14:00 to 18:00 h and from 20:30 to 01:30 h) on four consecutive days per month. All captured males were measured to the nearest 0.01 mm using calipers for the length of the dorsal scute (as an indicator of body size) and the right femur IV, which is the longest and strongest leg segment used as a weapon in male–male contests (Zatz 2010). Morphometric data from these monthly inspections and data collected during two field trips specifically for the observation of aggressive interactions (see below) were pooled for the morphometric analyses.

To identify any allometric relationship between dorsal scute length and femur IV length in males and potential male dimorphism, several models were tested on a log–log scale and their AIC values compared (according to Knell 2009): (1) a linear model, (2) a quadratic model using Eq. 1 described in Eberhard and Gutierrez (1991), (3) the best of five different sigmoidal models (logistic, four-parameter logistic, asymptotic regression, Michaelis–Menten, and Weibull growth curve; see Chapter 20 in Crawley 2007) also selected based on AIC values, (4) a nonlinear model that includes a breakpoint (Muggeo 2003, 2008) using the segmented package developed for *R*, version 7.1 (R Development Core Team 2009), and (5) a model that included a two-level morph factor and dorsal scute length as the covariable. To assign each individual to one of the two morphs in the fifth model, a switch line function was estimated using Knell's (2009) method (the *R* code was provided by this author), testing the model with all the combinations of a given range of intercept and slope values suggested by visually inspecting the plot (in our case, intercepts between 0 and 2 on 0.02 steps and slopes between 2 and 5 on 0.1 steps) and picking the combination of values with the highest $R^2$ value. This and all ANCOVA models described in the following section were subjected to simplification (deletion test) to eliminate unnecessary parameters (see Chapter 12 in Crawley 2007). As the two-morph model had the lowest AIC value and was thus selected (see "Results"), data for each morph were subsequently analyzed as independent data sets, and the linear, sigmoidal (all five), and segmented models were tested and compared again to pick the one that best described the allometric relationship for each morph.

## Behavioral observations

At the time of the first capture, males and females were individually marked with enamel paint applied to the dorsal scute (males and females), legs III (males and females), and/or legs IV (only females). This marking procedure has been widely used in studies with harvestmen because it does not affect behavior and lasts for more than 2 years (e.g., Buzatto et al. 2007). During each inspection, we recorded the sex and location along the transect (to the nearest 1 m) for each individual. These data were used to estimate the descriptive residency index (RI) calculated as $\frac{N_m}{n} \times 100$, where $N_m$ is the number of times an individual was found at its modal recapture site (i.e., the point in the transect where this individual was recaptured most frequently) and $n$ is the number of times each individual was recaptured during the study period. RI is zero when an individual is never found in the same place twice (i.e., there is no modal recapture site) and is 100% when an individual is always found in the same place along the transect. RI was only calculated for individuals that were recaptured for two or more times.

To test the first prediction, which states that major males will monopolize reproductive territories and reside close to groups of adult females, the distribution of all females captured for at least three times in the same place was mapped in the transect. RI was high for these females (median=100%; $n$=225 females), i.e., relatively stable groups with one to 12 females (which were interpreted as possible harems) were clearly identified in the transect. After detecting these groups of females, harem ownership was assigned to the males according to two criteria: (1) the modal recapture site of the male matched the harem site and (2) the male was captured at the harem site for at least four times. The latter criterion was applied to avoid assigning ownership to males that were only sporadically recaptured at the harem site as that is not congruent with territorial defense. Following these criteria, nearly 50% of the harems had two and up to five owners. Multiple ownership can be explained by both temporal changes in the owner of a given territory over the study period and by perceptual constraints in males. Among harvestman species, two or more males may share the same territory without noticing each other (Macías-Ordóñez 1997) because individuals rely almost exclusively on tactile and close-range chemical cues to detect conspecifics (Willemart et al. 2009a). The frequency of individuals holding a harem was compared between morphs using chi-square test. This and other contingency table tests described below were one-tailed as the predictions behind them had one direction (Rice and Gaines 1994). Additionally, a logistic regression was performed to test the effect of morph and dorsal scute length (covariable) on the probability of a male holding a harem or not (dependent variable). In this and all following similar analyses, morph was consistently introduced as the first

factor before model simplification since some collinearity was detected between both variables (scute length accounted for about 12% of the deviance in morph under a logistic regression), and factor order affects the deviance attributed by the model to each factor when data are not orthogonal (Crawley 2007, p. 328).

Residency was also used as a proxy to test the second prediction, which states that minor males will be less faithful to specific sites. The RI value, however, was avoided in the analysis because, in addition to other problems (Jasieński and Bazzaz 1999), ratios promote a substantial widening of the sampling variation compared to that of the original variables. Instead, a generalized linear model using a proportional response variable with binomial error was generated (see Chapter 16 in Crawley 2007). The proportional response variable was a two-vector object based on the number of times a male was found in its modal recapture site ($N_m$) and the number of times a male was not found at that site ($n-N_m$). For harem ownership, the continuous predictor variable was dorsal scute length (covariable) and the categorical factor was the morph. Additionally, the proportion of individuals captured once or more was compared between morphs using a chi-square test.

Throughout the study, male fights were recorded and a detailed description of these fights is given in Zatz (2010). To increase the sample size of male–male fights, two field trips were made with the expressed purpose of making behavioral observations in January (10 days) and February 2009 (15 days) when the reproductive season peaks for *Longiperna* (Zatz 2010). On these field trips, the study transect was searched from 09:00 to 02:00 h and 13 fights involving 19 different males were recorded. Males were considered to be involved in a fight only when observed in the split position (Fig. 1a).

To test our third prediction, which states that males observed in aggressive interactions will belong mostly to the major morph, the frequency of individuals involved in aggressive interactions was compared between morphs using Fisher's exact test. Additionally, a logistic regression was also done to test the effects of morph and dorsal scute length (covariable) on the probability of a male being involved in a fight (dependent variable). This and all other behavioral analyses were performed using the R statistical package, version 2.10.1 (R Development Core Team 2009).

## Results

### Allometric dimorphism in males

Table 2 shows the AIC values, ΔAIC, and Akaike weights for all five models tested on the log–log relationship between dorsal scute length and femur IV length for all *Longiperna* males. A two-morph model had the lowest AIC values for data from the males. The switch line that defined the best two-morph model classified 536 males as majors and 97 as minors (Fig. 2). Table 2 also shows the AIC values for each morph analyzed independently and the linear, quadratic, sigmoidal, and segmented breakpoint models along with their respective parameters. The allometric relationship between dorsal scute length and femur IV length for major males was best explained by a sigmoidal model (Weibull growth curve; Fig. 2), although the Akaike weight was closely followed by the segmented breakpoint model. The data for minor males were also best explained by a sigmoidal model (Michaelis–Menten; Fig. 2), although the Akaike weight of the linear model was very similar.

### Alternative mating tactics

Throughout the reproductive season, 535 *Longiperna* females were marked at the study site, and 225 (captured at least three times at the same place) were assigned to 102 harems containing one to 12 females. For 92 harems, it was possible to unequivocally identify at least one male owner, i.e., an individual captured at least four times at the same harem site. Of the 180 males holding harems, 161 (89.4%) belonged to the major morph, a frequency higher than expected by chance given their relative abundance ($\chi^2$=3.909, df=1, $p$<0.024). Also, the minimum model (model deviance=29.24, null residual deviance=759.49, df=632) indicates that the probability of holding a harem was positively influenced by dorsal scute length (Δdeviance=5.00, df=1, $p(\chi^2)$=0.025), male morph (Δdeviance=18.26, df=1, $p(\chi^2)$<0.001), and their interaction (Δdeviance=5.96, df=1, $p(\chi^2)$=0.015). For major males, scute length correlated positively with the probability of holding a harem (Δdeviance=23.89, df=1, $p(\chi^2)$<0.001), but this was not found for minors (Δdeviance=0.35, df=1, $p(\chi^2)$=0.55).

*Longiperna* males were captured from one to 32 times over the study period. The proportion of minors captured only once (36 out of 97, 37.1%) is more than two times higher than the frequency of majors captured only once (87 out of 536, 16.2%) ($\chi^2$=21.560, df=1, $p$<0.0001). The median residency index was 62% for majors (range=0–100%) and 50% for minors (range=0–100%). The minimum model for residency using a proportional response variable (model deviance=19.27, null residual deviance=1,149.27, df=510) indicates that both morph (Δdeviance=8.25, df=1, $p(\chi^2)$=0.004) and body size (Δdeviance=12.61, df=1, p($\chi^2$)<0.001), but not their statistical interaction, affected residency. Thus, major males and larger males tended to spend more time at specific sites than smaller and minor males did.

**Table 2** Models fitted to the allometric relationship between dorsal scute length and femur IV length in males of the harvestman *L. concolor*. The upper panel compares models applied to all males. The middle and bottom panels show within-morph model comparisons. The best models in each comparison are in bold and the remaining models are sorted below by increasing AIC value

| | Model | AIC | ΔAIC | Akaike weight | Parameters |
|---|---|---|---|---|---|
| All males | **Two morphs** | **−1,824.17** | **0** | **>0.9999** | **$Slope_{majors}$=3.56** |
| | | | | | **$Intercept_{majors}$=-1.02** |
| | | | | | **$Slope_{minors}$=1.71** |
| | | | | | **$Intercept_{minors}$=0.13** |
| | Sigmoidal Weibull growth function | −1,292.20 | 531.98 | <0.0001 | Asymptote=1.73 |
| | | | | | Drop=0.54 |
| | | | | | Lrc=5.97 |
| | | | | | Power=18.74 |
| | Segmented breakpoint | −1,291.60 | 532.57 | <0.0001 | $Slope_{left}$=4.68 |
| | | | | | Breakpoint=0.76 |
| | | | | | $Slope_{right}$=1.15 |
| | Quadratic | −1,286.97 | 537.20 | <0.0001 | $\alpha_0$= −10.82 |
| | | | | | $\alpha_1$=29.45 |
| | | | | | $\alpha_2$= −17.13 |
| | Linear | −1,278.39 | 545.78 | <0.0001 | Slope=4.19 |
| | | | | | Intercept= −1.52 |
| Major males | **Sigmoidal Weibull growth function** | **−1,619.27** | **0** | **0.5598** | **Asymptote=1.73** |
| | | | | | **Drop=0.34** |
| | | | | | **Lrc=8.01** |
| | | | | | **Power=26.35** |
| | Segmented breakpoint | −1,618.79 | 0.49 | 0.4387 | $Slope_{left}$=3.97 |
| | | | | | Breakpoint=0.76 |
| | | | | | $Slope_{right}$=1.35 |
| | Quadratic | −1,607.26 | 12.01 | 0.0014 | $\alpha_0$= −6.99 |
| | | | | | $\alpha_1$=19.69 |
| | | | | | $\alpha_2$= −10.89 |
| | Linear | −1,602.48 | 16.80 | 0.0001 | Slope=3.56 |
| | | | | | Intercept= −1.02 |
| Minor males | **Sigmoidal Michaelis–Menten** | **−233.10** | **0** | **0.2722** | **Asymptote=3.33** |
| | | | | | ***K*=1.86** |
| | Linear | −233.04 | 0.07 | 0.2630 | Slope=1.72 |
| | | | | | Intercept=0.13 |
| | Segmented breakpoint | −232.85 | 0.25 | 0.2398 | $Slope_{left}$=2.55 |
| | | | | | Breakpoint=0.73 |
| | | | | | $Slope_{right}$=0.56 |
| | Quadratic | −232.72 | 0.38 | 0.2250 | $\alpha_0$= −5.77 |
| | | | | | $\alpha_1$=17.99 |
| | | | | | $\alpha_2$= −11.21 |

The recorded male–male fights ($n$=13) lasted from 1 to 90 min, and 11 of them occurred without any conspecific female around (i.e., within 50 cm of both fighting males). All males involved in fights during the study ($n$=19, some males involved in more than one fight) were classified as majors. Even though major males were more abundant than minor males, the frequency of fighting majors was significantly higher than expected by chance (Fisher's exact test, $p<0.040$). The logistic regression produced a minimum model (model deviance=17.96, null residual deviance=170.65, df=632) in which both morph (Δdeviance=6.43, df=1, $p(\chi^2)=0.011$) and dorsal scute length (Δdeviance=11.54, df=1, $p(\chi^2)<0.001$), but not their interaction, were significantly associated with the probability of fighting. Thus, major and

larger males were more likely to be involved in fights (Fig. 2).

## Discussion

### Male dimorphism

In this study, we have shown that the males of *L. concolor* are dimorphic and that this dimorphism is expressed in the length of the fourth pair of legs, a sexually selected trait used as weapon in male–male fights. In contrast to other well-studied model species, such as horn beetles and earwigs (e.g., Eberhard and Gutierrez 1991; Tomkins et al. 2005), intrasexual dimorphism in *Longiperna* is challenging to detect, whether based on frequency distributions or by the simple visual inspection of allometric scatter plots (Fig. 2). Majors and minors do not express strikingly different morphologies and, at a first glance, the variation in leg IV or body length between morphs could be regarded simply as continuous (Fig. 2). Yet using a recently proposed method for the detection of discontinuous allometries (Knell 2009), we found that the best-supported model is the one that considers two male morphs (Table 2). This method does not separate the morphs using a switch point (for either the dorsal scute or femur IV) but rather divides the bivariate plane with a transverse switch line (Fig. 2). As with the discontinuous allometry in the mandible of the male fig wasp described by Cook and Bean (2006), femur IV allometry in *Longiperna* overlaps notably on both the $x$ and $y$ axes. For these cases, methods that are based on switch points dividing the bivariate plane into two using either a vertical (Eberhard and Gutierrez 1991) or a horizontal straight line (Kotiaho and Tomkins 2001) are clearly ineffective (Knell 2009).

Given that individuals of the order Opiliones do not molt after adulthood, male dimorphism in *Longiperna* leg IV length represents a case of irreversible developmental plasticity (sensu Shuster and Wade 2003). The concept of a phenotypically plastic threshold trait (Via and Lande 1985) provides a putative explanation for the genetic architecture underlying the alternative male morphologies in *Longiperna*. As a result, the expression of the long legs IV in major males would depend on some underlying normally distributed and heritable phenotypic trait that varies according to the individuals' status (Tomkins and Hazel 2007). At least among insects, body size is the main determinant of status and often has a large environmental component (Emlen 1994; Tomkins 1999). Thus, if body size exceeds some threshold value the major phenotype is expressed, and if it fails to exceed the threshold value the minor phenotype is expressed. According to the environmental threshold model, there may be a genetic variation among individuals in the response of a sexually selected trait (such as the long legs IV of *Longiperna* majors) to some environmental cue, which could be the individual's own condition (Tomkins and Hazel 2007). Therefore, the great overlap between *Longiperna* male morphs in both body size and leg IV length (Fig. 2) probably indicates that there is a great genetic variation in the threshold (Tomkins et al. 2004). Moreover, the existence of many different genetic switch points in the population suggests that the selection for this trait is weak (Buzatto et al. 2010).

The best model for describing the allometric relationship between dorsal scute length and femur IV length for major males was sigmoidal, and there is a clear asymptote suggesting that the limit for log femur length in the largest majors is around 1.73 (Table 2; Fig. 2). In fact, the slope of many allometric relationships between the size of sexually selected traits and body size actually decreases for the largest body sizes, resulting in curved rather than straight allometries (Knell et al. 2004). These curved allometries are interpreted as a consequence of two processes that are not mutually exclusive: (1) the increasing cost of having large sexually selected traits (Huxley 1932) and (2) the limited availability of resources for the rapidly growing imaginal disks that produce these traits—an explanation that applies only to insects (Nijhout and Wheeler 1996). Therefore, according to the hypothesis that the decrease in slope is caused by the greater cost of large sexually selected traits, as the length of femur IV becomes more exaggerated (and probably more costly), the deviation of the curve from linearity becomes greater. This pattern can be observed in Fig. 2 when we analyze only the individuals of the major morph—for which allometry is steeper among small males but smoother among the largest males—or when we compare the curvature of the allometric curve for the two morphs.

The curved allometry of femur IV length in *Longiperna* also suggests that sexual selection continues to favor positive allometry in individuals that invest relatively more in weaponry despite the limits imposed by exaggerated leg length in the largest males (see discussion in Knell et al. 2004). It is worth noting that, although both morphs greatly overlap at smaller body sizes and they can be distinguished by the relative size of femur IV, the size range roughly above a log scute length of 0.76 is mostly composed of major males (Fig. 2). This value corresponds to the breakpoint of the segmented model (almost as good as the sigmoidal model according to AIC values; Table 2), above which there is a decrease in the allometric slope of femur IV for these males. The sigmoidal model describing the same allometric relationship for minor males is virtually indistinguishable from a straight line (Fig. 2). Furthermore, unlike the curve for major males, that of the minor males curves upwards very slightly on the right end, consistent with the predicted asymptotic value of 3.3 (Table 2), and far above the leg size range for the species. In other words,

minor males are virtually absent in the body size range that would approach a leveling of the allometric relationship. In fact, they are virtually absent within the body size range where the curve of major males levels off. Therefore, there may be a switch point around a log scute length of 0.76, above which individuals rarely turn into minor males.

## Alternative mating tactics

Besides the morphological differences between the two male morphs, we also found behavioral evidence for alternative mating tactics in *Longiperna*. The majors' mating tactic is probably based on resource defense because: (1) the great majority of the males holding harems were majors, (2) major males were more strongly associated with specific sites than minors were, and (3) all of the males involved in fights were majors. In resource defense polygynies, successful males are expected to be associated with the limiting resources used by females (such as oviposition sites), both in the presence and absence of breeding females (Ostfeld 1987). Consequently, if major *Longiperna* males fight for reproductive territories, these fights should occur regardless of female presence. In fact, numerous majors were regularly recaptured at sites without females (data not shown), and most fights occurred without any female around the fighting males. Additionally, *Longiperna* females were highly philopatric, as they were regularly found in the same places they used as oviposition sites, i.e., on rocks and fallen trunks, which were monopolized by large majors. Thus, the length of femur IV in majors may be related to their resource holding power (RHP), as occurs in the harvestman *Serracutisoma proximum*, the males of which use their long second pair of legs to strike opponents in territorial fights (Buzatto and Machado 2008).

Because the breeding females in the harems of large males are temporally and spatially aggregated, there is an opportunity for the evolution of sneaking behavior as an alternative mating tactic (Shuster and Wade 2003). Indeed *Longiperna* minors probably rely on this tactic because the individuals of this morph—nearly 15% of the males in the population—hold harems less frequently and seem to be more mobile along the stream margins, resulting in low philopatry when compared to majors. In at least two other species, a damselfly (Romo-Beltrán et al. 2009) and a swordtail fish (Zimmerer and Kallman 1989), sneakers have been shown to be behaviorally plastic and exhibit the alternative tactic (referred to as territorial in damselflies and courter in swordtails), apparently when more females are available or larger males are absent.

Moreover, minors were never found fighting other males, and there are at least two explanations—not mutually exclusive—for this pattern. Fights are expected to be shorter when individuals are highly asymmetrical or when at least one contender has a low RHP (Taylor and Elwood 2003). Thus, fights involving at least one minor may be much shorter than fights involving two majors, and the probability of observing those fights would therefore be much lower. In this case, our results would be the consequence of a sampling bias against short fights involving minors. Alternatively, if majors are, in fact, better able to monopolize the resources needed by females, they would comprise the majority of territory owners, and minors would account for the majority of intruders (e.g., Kelly 2006). In this situation, poorly armed intruders (minors) would give up the fight even sooner, or avoid it altogether, if they follow a role-respecting fighting strategy (Maynard-Smith and Price 1973). Only large and better armed intruders (majors) would engage in fights against similar residents.

This study is the second description of alternative mating tactics in arachnids of the order Opiliones—the first was the study of the Neotropical harvestman *S. proximum* (Buzatto et al. 2010). Majors of *S. proximum* use their elongated and sexually dimorphic second legs in fights for the possession of territories on the vegetation where females lay eggs (Buzatto and Machado 2008). Minors, on the other hand, possess shorter second legs and their reproductive behavior is based on sneaking into the territories of majors and furtively mating with egg-guarding females. The sneaking tactic in *S. proximum* seems possible only because the egg-guarding females may take up to 15 days to complete the oviposition and since a major may have up to six females in his territory so that it might be difficult for him to guard all of his mates effectively. If the reproductive activity of females was asynchronous and females completed the oviposition over a short time interval, majors would probably be able to fertilize all of the females' eggs (Buzatto et al. 2010). *Longiperna* females do not exhibit maternal care but rather lay isolated eggs throughout the reproductive season (Fig. 1c), which makes it nearly impossible for majors to monopolize all of the fertilizable eggs inside a harem. Moreover, like other harvestmen (Macías-Ordóñez et al. 2010), *Longiperna* females are most likely able to store sperm from previous copulations, allowing minor males that succeed in copulating with harem females to sire at least some offspring. Therefore, *Longiperna* and similar harvestman species may be good model organisms for studying sperm competition games (sensu Parker 1990) between minor and major males.

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