

# *Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones)*

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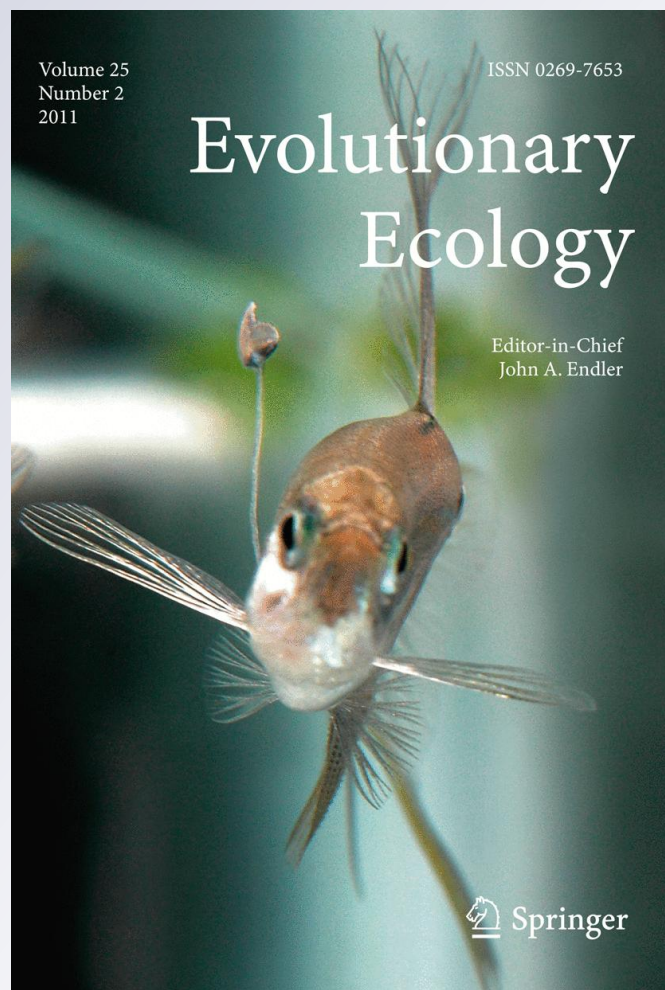
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# Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones)

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**Abstract** In arthropods, most cases of morphological dimorphism within males are the result of a conditional evolutionarily stable strategy (ESS) with status-dependent tactics. In conditionally male-dimorphic species, the status' distributions of male morphs often overlap, and the environmentally cued threshold model (ET) states that the degree of overlap depends on the genetic variation in the distribution of the switchpoints that determine which morph is expressed in each value of status. Here we describe male dimorphism and alternative mating behaviors in the harvestman *Serracutisoma proximum*. Majors express elongated second legs and use them in territorial fights; minors possess short second legs and do not fight, but rather sneak into majors' territories and copulate with egg-guarding females. The static allometry of second legs reveals that major phenotype

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expression depends on body size (status), and that the switchpoint underlying the dimorphism presents a large amount of genetic variation in the population, which probably results from weak selective pressure on this trait. With a mark-recapture study, we show that major phenotype expression does not result in survival costs, which is consistent with our hypothesis that there is weak selection on the switchpoint. Finally, we demonstrate that switchpoint is independent of status distribution. In conclusion, our data support the ET model prediction that the genetic correlation between status and switchpoint is low, allowing the status distribution to evolve or to fluctuate seasonally, without any effect on the position of the mean switchpoint.

**Keywords** Conditional strategy · Environmental cue · Male polyphenism · Phenotypic plasticity · Status dependence · Threshold

## Introduction

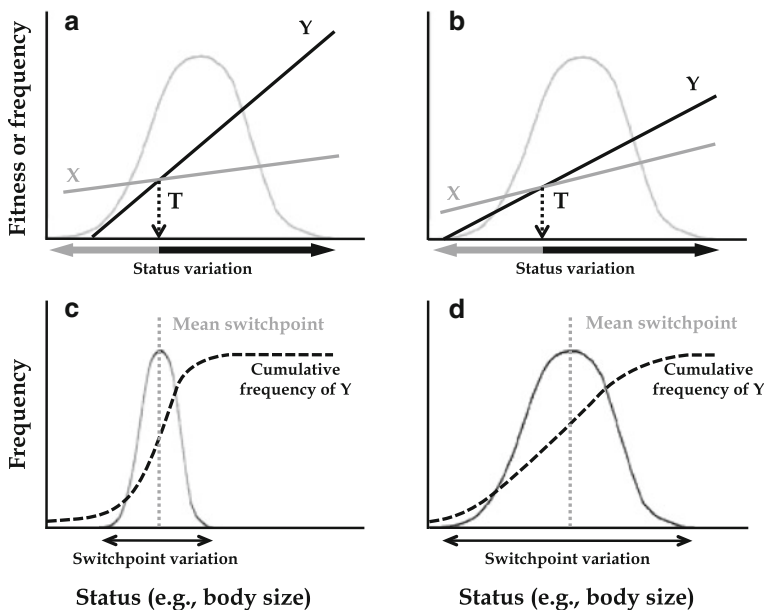
Morphological dimorphism within one sex, usually the male, is generally associated with alternative reproductive tactics: majors (the larger male morph) typically guard females or reproductive territories and have more elaborate weaponry, and minors (the smaller male morph) sneak copulations and have reduced weaponry (Gross 1996; Shuster and Wade 2003; Taborsky et al. 2008). Originally thought to be a rare phenomenon restricted to a few species of insects (Gadgil 1972), male dimorphism is now known to be taxonomically widespread (Taborsky et al. 2008), and expected to occur whenever there is intense variation in male reproductive success (Shuster and Wade 2003). In arthropods, for instance, male dimorphism has so far been documented for at least 50 species of insects (reviewed by Brockmann 2008), many species of crustaceans (reviewed by Shuster 2008), and a few species of spiders (Vanacker et al. 2003 and references therein) and mites (Radwan et al. 2002 and references therein).

The classic examples of male dimorphism consist of extreme morphological divergence between male morphs, such as the case of the coho salmon *Oncorhynchus kisutch* (Salmonidae), in which minors' body size is as small as 30% of the majors' body size (Gross 1985). However, in several male-dimorphic arthropods, the main difference between male morphs is the size and shape of sexually selected traits, such as the horns of beetles (e.g., Eberhard 1982; Eberhard and Gutierrez 1991; Emlen et al. 2007) and the forceps of earwigs (e.g., Simmons and Tomkins 1996; Tomkins 1999; Tomkins and Simmons 1996). In such cases, whereas distinct male morphs are somewhat easily distinguished by their secondary sexual traits, their body size distributions may overlap. Among arthropods, a continuous spectrum of cases exists starting with no overlap in the body size distribution of male morphs, and grading continuously into species with great overlap (examples in Knell 2009). In some of the later cases, male dimorphism can only be detected by analyzing the nonlinear or discontinuous allometric relationship of a sexually selected trait (Cook and Bean 2006; Knell 2009). Different methods of detecting such dimorphisms have been proposed (see Knell 2009), and almost all of them are based on scaling relationships (sensu Emlen and Nijhout 2000; LaBarbera 1989) of the dimorphic sexual traits on overall body size.

The majority of the cases of alternative male phenotypes in arthropods comprise examples of polyphenism, which is the ability of a single genotype to express alternative phenotypes depending upon environmental conditions (West-Eberhard 2003). In polyphenic male-dimorphic species, the expression of alternative male phenotypes is usually modeled as a single conditional evolutionarily stable strategy (Gross 1996; Repka and

Gross 1995), in which male fitness varies as a function of their competitive status. According to the ‘status-dependent selection’ model (SDS), the rate of change (i.e. the slope) in fitness with status differs between the alternative tactics (Fig. 1a, b). The functions that relate fitness to status for each phenotype intersect at a certain status value, which depicts the threshold between the alternative tactics (Fig. 1a, b; Gross 1996). As a result, males with a status higher than the threshold benefit from adopting the major phenotype (the primary tactic), whereas males with status lower than the threshold benefit from adopting the minor phenotype (the alternative tactic; Gross 1996).

In conditionally male-dimorphic species, every male in the population is capable of expressing either of two alternative phenotypes, and the environmental conditions faced by each individual are the main determinant of its status and consequently its phenotype (Gross 1996). However, individuals may differ in their response to the environmental cues



**Fig. 1** **a** Representation of the ‘status-dependent selection’ model (SDS), in which the bell-shaped curve is the normal distribution of males’ status (i.e., body size), and the lines represent how the fitness of alternative male phenotypes vary as a function of status (black line for phenotype Y; grey line for phenotype X). The fitness functions of the alternative morphs intersect at the threshold T, and individuals of status  $>T$  benefit from expressing phenotype Y, whereas individuals of status  $<T$  benefit from expressing phenotype X. Horizontal arrows indicate the proportion of males expressing each phenotype (black for Y; grey for X). These arrows gradually merge at the threshold, indicating genetic variance for switchpoint position among males. **b** In this version of the SDS model, the slopes of the fitness functions of different male morphs are not strikingly different. Therefore, the difference in the fitness of the alternative phenotypes is small for males with status close to the mean switchpoint, and the selection differential on the switchpoint is likely to be low. **c** In the ‘environmentally-cued threshold’ model (ET), genetic variance in switchpoint position between males (mean switchpoint indicated by the grey dotted line; switchpoint distribution indicated by the solid bell-shaped curve) explains why males of different morphs overlap in status, generating the cumulative normal curve of tactic expression (in this case Y; broken line). **d** In this version of the ET model, switchpoint distribution is wider, and therefore the cumulative normal curve of phenotype Y expression is more gradual than in the previous case. Scenarios (b) and (d) may account for the great overlap in the body size distributions between male morphs of the harvestman *Serracutisoma proximum*

due to genetic variation on the switchpoint that determines which of the alternative phenotypes is expressed in each value of status (see Box 2 in Tomkins and Hazel 2007). Within this context, the ‘environmentally cued threshold’ model (ET, recently reviewed by Tomkins and Hazel 2007) takes into account that conditional strategies show genetic variation for the switchpoint, which is understood as a quantitative trait with normally distributed variation that is subject to selection (Hazel et al. 1990; Tomkins and Hazel 2007; West-Eberhard 2003). The genetic variation in the distribution of switchpoints explains the degree of overlapping in body size between male morphs, so that the larger is the genetic variance in switchpoint distribution, the smoother is the cumulative frequency of the major tactic as body size increases (Fig. 1d).

Here we describe for the first time both male dimorphism and alternative reproductive tactics in a harvestman (Arachnida: Opiliones). Majors of *Serracutisoma proximum* use their elongated and sexually dimorphic second legs in ritualistic fights for the possession of territories on the vegetation where females lay eggs (Buzatto and Machado 2008). Minors possess shorter second legs and their reproductive behavior is based on sneaking into majors’ territories and furtively mating with egg-guarding females. Although the mating tactics of majors and minors are completely distinct, we show that there is a great overlap in their body size distributions. Based on this result, we estimate the magnitude of phenotypic variation for the distribution of switchpoints in the male population. Our results indicate that the switchpoint underlying male dimorphism presents a large amount of genetic variation, which probably results from weak selective pressure on this trait. Given that genetic variation for the switchpoint is great, we would not expect major morph expression to be highly costly, otherwise selection would penalize all small males that adopt the major phenotype, eroding genetic variation for the switchpoint. We provide support for this hypothesis with a 1-year mark-recapture field study in which we estimated survival rates for both male morphs. Finally, using our data on morph ratio variation along the reproductive season, we investigated whether seasonal changes in body size distribution were correlated to changes in the population mean switchpoint. According to the ET model (Tomkins and Hazel 2007), the genetic correlation between status (i.e., body size) and switchpoints in typical threshold traits should be low, enabling distinct evolutionary trajectories for these traits. We tested this prediction by investigating whether the seasonal fluctuations in *S. proximum* morph ratio were explained by seasonal variations in mean switchpoint, body size distribution, or both.

## Materials and methods

### Organism

*Serracutisoma proximum* females lay their eggs mainly on the underside of leaves hanging above small forest streams. Following oviposition, females guard their eggs and the hatched nymphs for approximately 37 days (Buzatto et al. 2007). Large males fight for territories on the vegetation next to the river, where females mate, lay, and guard their eggs. These territorial males stay the entire reproductive season (which lasts from September to April) patrolling their territories, and they promptly engage in ritualized fights with male conspecific intruders. During these fights, males hit each other with their elongated second legs, which are much longer in males than in females, and are positively related to the number of females in each males’ harem (Buzatto and Machado 2008).



## Study site

We conducted the study in the Intervalles State Park (24°14' S, 48°04' W; 800 m a.s.l.), an area covered by dense Atlantic Forest, close to the city of Ribeirão Grande, southern São Paulo state, south-eastern Brazil. There is a marked seasonality in the study site, with a wet and warm period from October to March, and a dry and cold period from April to September. During the *S. proximum* breeding season, the mean rainfall is 281.8 mm, and the mean temperature is 20.3°C. During the non-breeding season (May to August), the mean rainfall is 103.8 mm, and the mean temperature is 17°C. We carried out fieldwork in a 200 m transect with marks every 10 m on the vegetation flanking the stream that follows the Caçadinha trail. This stream is approximately 5 m wide and is flanked by abundant vegetation that partially covers the river bed in some places.

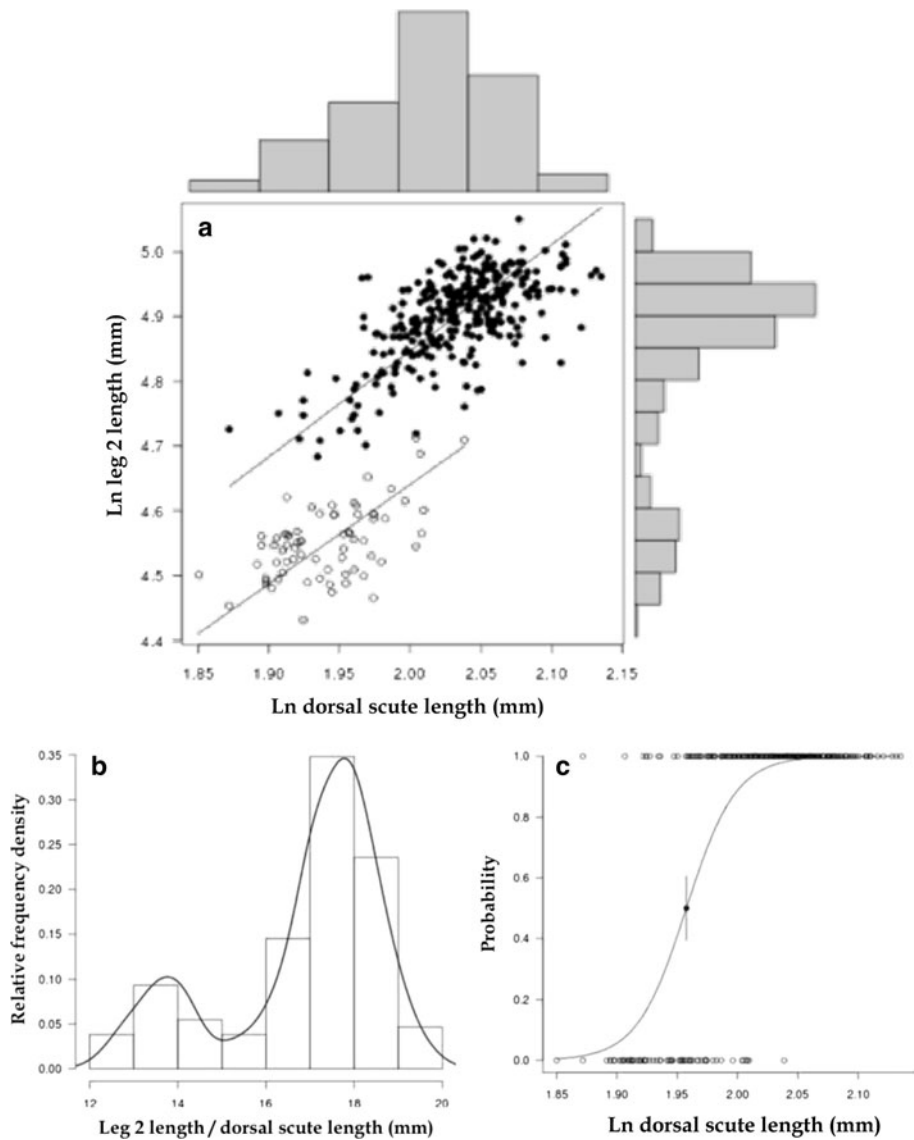
## Behavioral observations

To investigate the sexual behavior of *S. proximum*, we followed the reproductive activity of individually marked males for 2 years (comprising the reproductive seasons of 2003–04 and 2004–05). In each study period of two to seven consecutive days per month, we inspected the transect three times a day (from 08:30 to 12:00 h, from 14:00 to 17:30 h and from 20:30 to 00:00 h). We searched for adults on the vegetation flanking both margins of the stream, and measured with calipers (to the nearest 0.01 mm) all individuals we found for the dorsal scute length and right second leg length. Thereafter, we marked the individuals with unique enamel paint dots on the hind legs and/or dorsal scute (following Buzatto et al. 2007). Finally, we recorded the sex and location in the transect (to the nearest 1 m) for each marked harvestman to estimate individual movement. As a rough estimation of individual movement, we calculated the straight line distance between the two most distant points where the same harvestman was found, and compared the movements of majors and minors using a Mann–Whitney test. For this analysis, we used only individuals that were captured at least twice during the reproductive season of 2004–2005.

Between December 2006 and March 2007, we determined the exact location of several males' territories in the transect (see Buzatto and Machado 2008 for detailed information on *S. proximum* territories), and conducted intensive observations within 29 of these territories. Throughout the study, which comprised 2,300 h of field observations, we continuously recorded all copulations and agonistic interactions between individuals. We used these behavioral data to characterize the reproductive behavior of each male morph.

## Male morph discrimination

To discriminate male morphs, we fitted a kernel density function to the frequency distribution of the ratios of the dimorphic second leg length to dorsal scute length, which is a standard estimate of body size in harvestmen (see Willemart et al. 2009). Using the nonparametric kernel density estimates, we identified the minimum point between the two modes of males, and used this point as the criterion for male morph discrimination (see Knell 2009). The kernel density estimator method is preferred to Eberhard and Gutierrez (1991) and Kotiaho and Tomkins (2001) methods when there is overlap between morphs in both body size and the dimorphic sexual trait (Knell 2009), as occurs with *S. proximum* (Fig. 2a). Moreover, we estimated the allometric coefficients of the regression between dorsal scute and second leg lengths for majors and minors using the standardized major axis regression and compared the slopes between morphs with a likelihood ratio test



**Fig. 2** **a** Allometric scaling of second leg and dorsal scute length for the two male morphs of the harvestman *Serracutisoma proximum*: open circles represent minors and full circles represent majors. Notice that dorsal scute length (*top* histogram) exhibits a unimodal distribution whereas second leg length (*side* histogram) exhibits a clear bimodal distribution. **b** Histogram and kernel density estimation of the second leg length/dorsal scute length ratio used to discriminate major and minor males. **c** Generalized linear model with binomial distribution depicting the probability of becoming a major. The predicted probability value of 0.5 represents the mean switchpoint point in the population. The vertical line represents the 95% confidence interval of the mean switchpoint. Equation:  $y = e^{-95.54 + 48.81 \cdot \log \text{dorsal scute length}} / (1 + e^{-95.54 + 48.81 \cdot \log \text{dorsal scute length}})$

(Warton et al. 2006). For this analysis, we used only individuals captured in the reproductive season of 2004–2005, and transformed both morphological variables to natural logarithms (Knell 2009).



## Quantitative assessment of switchpoint variation

After assigning each male from the population into one of the morphs, we calculated the probability of males of any possible dorsal scute length having developed into a major by fitting a generalized linear model with binomial distribution and a logit link to the dataset. We coded majors as one and minors as zero, and used the logarithm of dorsal scute length as the continuous predictor variable (according to Knell 2009). The fitted line represents the cumulative frequency distribution of individuals expressing the major phenotype as body size increases. Next, we used the value of dorsal scute length in which males have a probability of 0.5 of developing into majors to estimate the mean of the underlying distribution of switchpoints (as suggested by Hazel et al. 1990). To estimate the variation of this underlying distribution of switchpoints, we used the same cumulative frequency distribution of majors and calculated the interval of dorsal scute length that comprises the probabilities between 0.1587 and 0.5 (i.e., one standard deviation from the mean switchpoint) of a male developing into a major. This value was further standardized by dividing it by the standard deviation of the overall dorsal scute length distribution in the male population. This procedure provides an objective estimation of the variance of switchpoint distribution.

## Mark-recapture methods

To investigate the survival costs of expressing the major morph, we carried out a mark-recapture analysis in the studied population to estimate recapture and survival probabilities of adult males and investigate if these parameters differ between morphs. The study comprehended nine visits to the site of two to up to seven days from September 2004 to May 2005 (i.e., the entire reproductive season). Within each visit there were six to up to 14 mark-recapture sessions (total of 83 mark-recapture sessions). As previously mentioned, all males were marked with a unique enamel paint combination, so we were able to identify each individual and follow its encounter history. Moreover, the individual marks allowed us to assign a posteriori each male to the major or minor morph using the procedure described in the topic ‘Male morph discrimination’.

Mark-recapture analyses have the great advantage of dissociating survival from recapture using the encounter histories of individuals along time through maximum likelihood techniques (Lebreton et al. 1992; Williams et al. 2002). The discrimination of recapture rates of the two morphs is important because majors are territorial (Buzatto and Machado 2008) and therefore likely to have higher detection probability when compared to minors. Not taking this important biological feature into account would lead to a bias in survival estimates (Munguía-Steyer et al. 2010; Williams et al. 2002).

We evaluated the goodness of fit of the global model using the median  $\hat{c}$  approach implemented in MARK 5.1 software (White and Burnham 1999). The median  $\hat{c}$  approach applies a logistic regression to simulated and replicated data with an increasing degree of overdispersion and assumes that the best estimate of  $\hat{c}$  is obtained when deviance  $\hat{c}$  (deviance of the model divided by the degrees of freedom of the model) corresponds to the median of all possible generated  $c$  values. We performed simulations with  $c$  adopting values between 1 and 3 in 20 equally spaced points and 20 replicates for each point. The global model  $\varphi_{(\text{group} \times \text{time})} p_{(\text{group} \times \text{time})}$  presented a slight overdispersion  $\hat{c} = 1.126$  (SE = 0.0175), far from serious structural problems or violation of the assumptions, i.e.,  $\hat{c} > 3.0$  (Lebreton et al. 1992; Williams et al. 2002). As our best supported model contained

variation in time and morph identity in recapture rates parameters (see “[Results](#)”), we estimated the mean recapture rates for each morph using the variance components approach. Moreover, since there were irregular time intervals between the eight visits done along the year, we standardized survival and recapture probabilities to a 1 month time interval.

Model selection and ranking of competing models were performed using the Akaike Information Criterion for overdispersed data (QAIC) (Burnham and Anderson 2002). Competing models originated from the different combinations of the predictors that could potentially explain survival and recapture rates: group identity (majors or minors), time, sampling effort, group:time and group:sampling effort interactions. Sampling effort was only considered as a possible predictor for recapture rates. We used MARK 4.3 software (White and Burnham 1999) to estimate survival and recapture parameters contained in the competing models and rank them according to their QAIC values.

### Seasonality of morph frequency, status and switchpoint distribution

To test the ET model prediction that status and switchpoint are not significantly correlated (page 527 in Tomkins and Hazel 2007), we initially investigated whether there were seasonal changes in the recruitment of adult males of both morphs, which are likely to result from changes in the status distribution or mean switchpoint along the reproductive season. To do that, we plotted the number of new minors and majors recorded monthly in the population from August 2004 to May 2005. Next, the dataset of male dorsal scute and second leg lengths was divided in two different periods along the reproductive season: the first one being from August to December 2004 ( $N = 134$  males) and the second one from January to February 2005 ( $N = 133$  males). These two periods were chosen because they differ drastically in the monthly numbers of subadults that developed into majors—15–25 subadults per month between August and December and 40–69 subadults per month between January and February (see “[Results](#)”). They also show a marked difference in the number of ovipositing females, with a peak of reproductive activity between January and February (see “[Results](#)”).

Finally, we repeated the analysis on mean switchpoint position and switchpoint standard deviation described in the topic ‘Quantitative assessment of switchpoint variation’ for the two periods of the reproductive season. To test whether the position of the mean switchpoint changes seasonally, we performed a generalized linear model with binomial distribution, with the two periods, dorsal scute length, and their interaction as predictor variables, and male morph as the dependent binary variable. To test if the interaction between dorsal scute length and period was significant, we performed a likelihood ratio test between the generalized model that contained this predictor and a reduced model that did not. A significant interaction between dorsal scute length and period would indicate that a shift in the mean switchpoint took place over the course of the reproductive season. Alternatively, if mean switchpoint position is really independent of status distribution (i.e., if there is a low genetic correlation between status and switchpoint), seasonal fluctuations in dorsal scute length (status) distributions alone could explain the different proportions of male morphs recruited in each month, even if the mean switchpoint position had not shifted along the reproductive season (see Box 2 in Tomkins and Hazel 2007). We further tested this alternative using a Spearman correlation to investigate a possible association between average dorsal scute length and relative frequency of new majors in each month.

## Results

### Male morph discrimination

The kernel density function showed a clearly bimodal distribution of the second leg length to dorsal scute length ratios (Fig. 2b). The minimum value between the two modes was 15.058, so that individuals with a second leg to dorsal scute length ratio lower than this value were categorized as minors and the rest as majors. Therefore, out of the 365 *S. proximum* males captured, 295 (80.8%) were assigned to the major morph and 70 (19.2%) to the minor morph. The allometric slopes for majors ( $b = 1.632$ ;  $CI_{95\%} = 1.497\text{--}1.781$ ) and minors ( $b = 1.532$ ;  $CI_{95\%} = 1.255\text{--}1.871$ ) did not differ ( $\chi^2 = 0.329$ ,  $df = 1$ ,  $P = 0.566$ ; Fig. 2a).

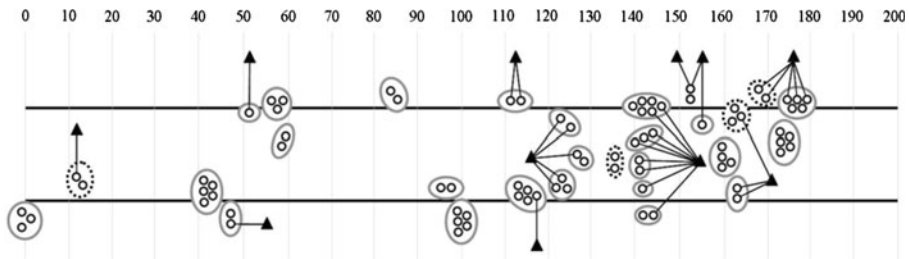
### Behavioral differences between male morphs

Besides the morphological differences between the two male morphs described in the previous section, there are also numerous differences in their reproductive behavior. All male fights observed in the field ( $N = 42$ ) occurred between majors. Furthermore, 72 (61%) of the copulations observed were accomplished by majors and the remaining 46 (39%) by minors. These proportions were different than what would be expected by the relative frequency of minors and majors in the studied population, indicating that minors copulate proportionately more frequently than majors ( $\chi^2 = 42.258$ ,  $df = 1$ ,  $P < 0.001$ ). The pre-copulatory and copulatory courtship behaviors of minors were similar to what has been previously observed for majors (Buzatto and Machado 2008). Additionally, the duration of copulation was not different for minors (median = 292 s; range: 20–967 s;  $N = 24$  copulations) compared with majors (median = 380.5 s; range: 180–1200 s;  $N = 8$  copulations) ( $U = 72.0$ ;  $P = 0.296$ ). However, after copulating, mate guarding was more frequently performed by majors (45 out of the 72 males, i.e., 62.5%) than by minors (only 1 out of 46 males, i.e., 2.2%) (Fisher exact test,  $P < 0.001$ ).

Finally, majors were seen copulating only with females inside their own territories, whereas some minors were seen copulating with egg-guarding females from more than one territory (Fig. 3). Instead of defending a small area on the vegetation as majors do (Buzatto and Machado 2008), minors invaded one or more territories to mate (Figs. 3, 4a). Of all the 65 observed invasions of territories by minors, 46 (70.8%) were successful and resulted in copulations. Only on 19 (29.2%) occasions the owner of the territory detected and repelled the minor (Supplemental material), with aggressive strikes of pedipalps and chelicerae, before the intruder could achieve copulation. Minors were more vagile (median movement distance = 7 m; range 0–138 m;  $N = 32$  males) than majors (median movement distance = 4 m; range 0–171 m;  $N = 177$  males) ( $U = 2202.5$ ;  $P = 0.046$ ), probably as a consequence of the different mating behaviors reported here.

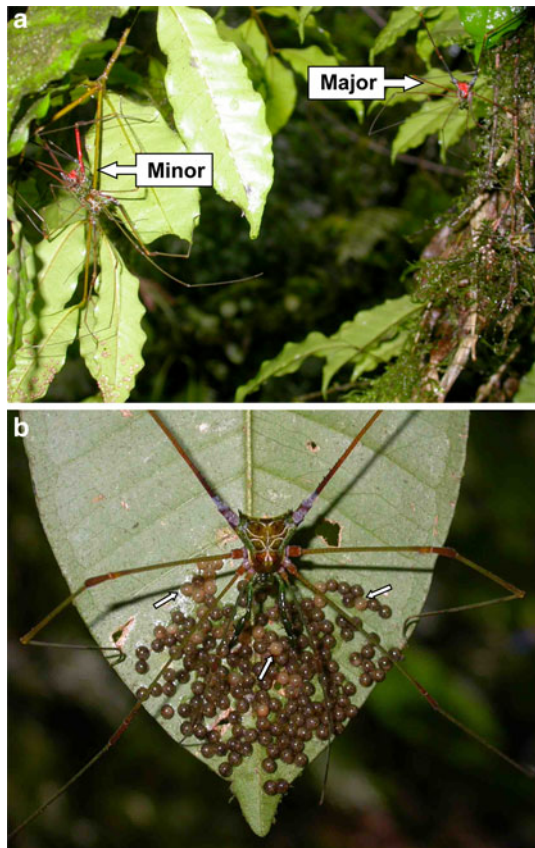
### Switchpoint variation

The generalized linear model that assessed the probability of becoming a major indicated that the mean switchpoint (predicted major probability of 0.5,  $CI_{95\%} = 0.39\text{--}0.61$ ) occurred at the dorsal scute length of 7.08 mm (Fig. 2c). Dividing the standard deviation of the distribution of switchpoints (0.24 mm) by the standard deviation of the distribution of



**Fig. 3** A schematic view-from-above representation of 29 harems of the harvestman *Serracutisoma proximum* at the study site during the reproductive season of 2006–2007. The numbers indicate the distance (in meters) from the beginning of the study transect. The two dark horizontal lines represent the river margins, and harems drawn between them were located on the vegetation that hung above the river. The larger circles represent the harems of territorial males (majors), and the smaller open circles contained inside them represent egg-guarding females. Harems represented by a dashed circle are those whose ownership shifted between two different majors over the course of the reproductive season. Sneakers (minors) are represented by small dark triangles, and the lines connecting them to females represent copulations by these males. Two females between 150 and 160 m were never seen guarded by a major

**Fig. 4** **a** Minor male of the harvestman *Serracutisoma proximum* copulating with an egg-guarding female inside a harem while the owner of the territory (major) cleans his second pair of legs on a trunk nearby. **b** Female of *S. proximum* guarding a clutch on a leaf hanging above the stream. The white arrows indicate lighter eggs that are in earlier stages of embryonic development. These eggs result from the long-lasting oviposition by females and are probably sired by sneakers



dorsal scute length of all males (0.40 mm), we found that switchpoint variation corresponds to 60.2% of dorsal scute length variation.

### Recapture and survival rates

During the mark-recapture study, we marked and measured 284 males, 59 (20.8%) were minors and 225 (79.2%) were majors. Furthermore, 32 minors (54.2%) and 154 majors (68.4%) were recaptured at least once. Survival rates showed no variation along time and did not vary between morphs (Table 1), with the male monthly survival probability estimated by the best model as 0.812 (SE = 0.028, CI95% = 0.751–0.860). Recapture rates differed between morphs and varied along time in the most supported model (Table 1). Mean recapture rate was 0.509 (SE = 0.094) for majors and 0.333 (SE = 0.082) for minors.

### Seasonality of morph frequency, status and switchpoint distribution

The relative frequency of new males from each morph varied along the reproductive season, with a peak of majors recruited between January and February (Fig. 5a), which also corresponds to the peak of the reproductive activity of females (Fig. 5a). Even though the number of new major males during the peak of the reproductive season is markedly different from that in the previous months, the mean switchpoint position was not different for males that became adults between August and December 2004 (Fig. 5b) and for males that became adults between January and February 2005 (Fig. 5c). There was also no significant interaction between dorsal scute length and period ( $\chi^2 = 0.368$ ,  $df = 1$ ,  $P = 0.544$ ). However, there was a positive correlation between average dorsal scute length and the frequency of new majors in each month (Spearman,  $r_s = 0.833$ ,  $P = 0.018$ ,  $N = 9$  months).

## Discussion

### Conditional male dimorphism and alternative reproductive tactics

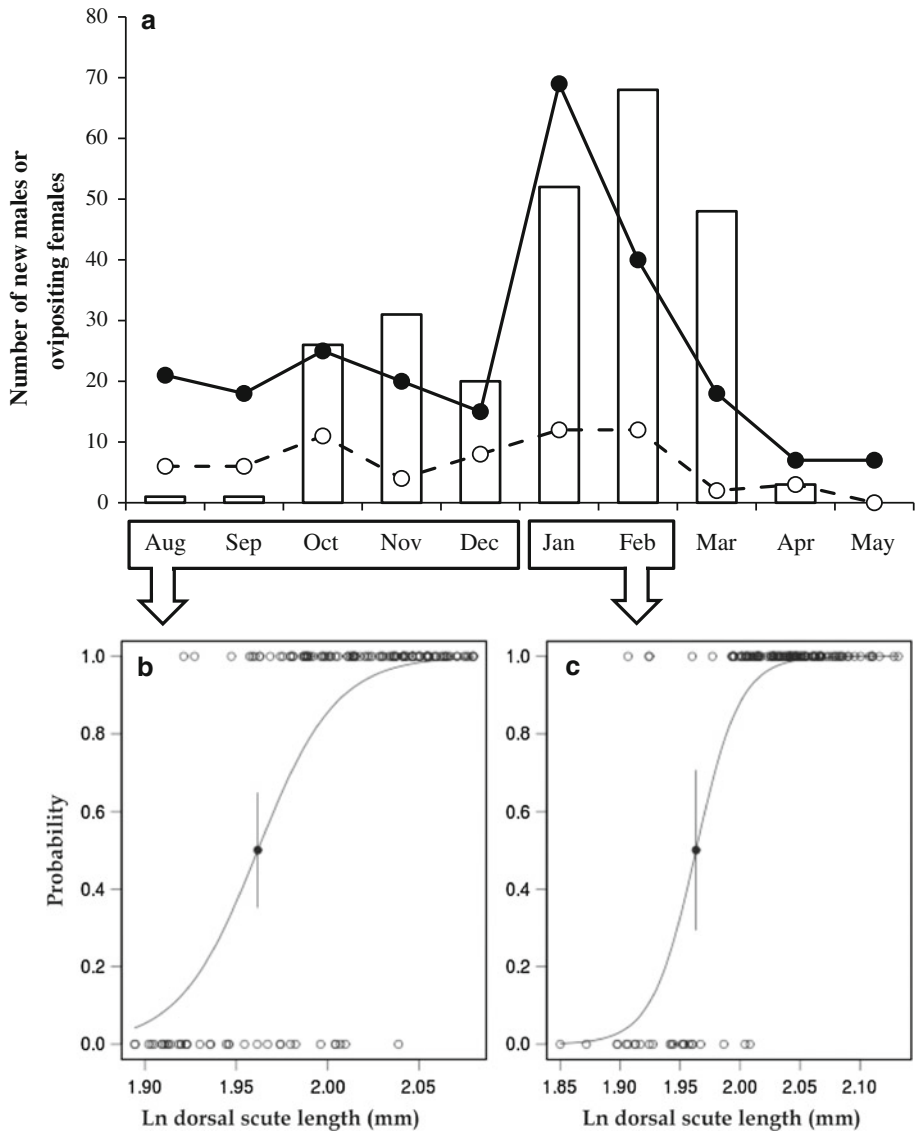
The static allometry of second legs of the Neotropical harvestman *S. proximum* indicates that major phenotype expression depends on body size, which shows a clear unimodal distribution (Fig. 2a). This scenario suggests a conditional evolutionarily stable strategy (Gross 1996; Repka and Gross 1995) in which males' body size is determined by multiple environmental factors, resulting in a normal size distribution, whereas males' morph is probably determined by body size. However, the extent to which male morph determination in *S. proximum* is conditional on the environmental factors that influence body size, such as diet for example, deserves further attention. In fact, studies that manipulate the nutrition of juveniles and experimentally test the status dependence of conditional male dimorphism are still scarce (but see Emlen 1994; Moczek and Emlen 1999; Tomkins 1999). In species of the genus *Serracutisoma*, in particular, this experimental manipulation would require a long term study, since the last nymphal stage may last up to 3 months (Gnaspini 1995).

Although male dimorphism is already known to taxonomists of the Opiliones for a long time (e.g., Forster 1954), we demonstrate here for the first time that this dimorphism is

**Table 1** Model selection for effects of male morph identity, time, and sampling effort on the survival and recapture probabilities of the harvestman *Serracutisoma proximum*

Model description		QAIC	QAIC weight	No. of parameters	Deviance
Survival probability	Recapture probability				
$\varphi$ (.)	p (morph + time)	1066.63	0.607	10	216.72
$\varphi$ (morph)	p (morph + time)	1068.65	0.220	11	216.71
$\varphi$ (morph)	p (time)	1071.61	0.050	10	221.75
$\varphi$ (time)	p (morph + time)	1071.80	0.045	15	211.51
$\varphi$ (.)	p (time)	1073.13	0.024	9	225.33
$\varphi$ ()	p (morph * time)	1074.25	0.013	17	209.75
$\varphi$ (morph + time)	p (morph + time)	1075.77	0.006	17	211.27
$\varphi$ (morph)	p (morph * time)	1076.24	0.005	18	209.61
$\varphi$ (time)	p (morph + sampling)	1076.26	0.005	11	224.32
$\varphi$ (morph + time)	p (morph + sampling)	1077.26	0.003	12	223.24
$\varphi$ (time)	p (morph * sampling)	1077.26	0.003	12	223.24
$\varphi$ (group + time)	p (time)	1077.57	0.003	16	215.17
$\varphi$ (group + time)	p (sampling)	1077.68	0.002	11	225.74
$\varphi$ (group + time)	p (group * sampling)	1077.73	0.002	13	221.62
$\varphi$ (group * time)	p (group + time)	1077.96	0.002	20	207.08
$\varphi$ (time)	p (time)	1078.94	0.001	15	218.65
$\varphi$ (time)	p (morph * time)	1079.50	<0.001	22	204.33
$\varphi$ (time)	p (sampling)	1080.02	<0.001	10	230.15
$\varphi$ (morph + time)	p (morph * time)	1081.63	<0.001	23	204.31
$\varphi$ (morph * time)	p (morph * time)	1083.00	<0.001	25	201.35
$\varphi$ (morph * time)	p (time)	1083.57	<0.001	21	210.54
$\varphi$ (morph * time)	p (morph + sampling)	1083.62	<0.001	17	219.12
$\varphi$ (time)	p (morph)	1084.71	<0.001	10	234.85
$\varphi$ (morph * time)	p (morph * sampling)	1085.23	<0.001	19	216.48
$\varphi$ (morph + time)	p (morph)	1085.53	<0.001	11	233.59
$\varphi$ (morph * time)	p (sampling)	1086.41	<0.001	17	221.90
$\varphi$ (time)	p (.)	1088.48	<0.001	9	240.68
$\varphi$ (morph * time)	p (.)	1094.91	<0.001	16	232.51
$\varphi$ (.)	p (morph + sampling)	1100.44	<0.001	4	262.86
$\varphi$ (.)	p (morph * sampling)	1100.81	<0.001	5	261.20
$\varphi$ (morph)	p (morph * sampling)	1101.93	<0.001	6	260.28
$\varphi$ (morph)	p (morph + sampling)	1102.06	<0.001	5	262.45
$\varphi$ (morph)	p (sampling)	1102.84	<0.001	4	265.26
$\varphi$ (.)	p (sampling)	1104.46	<0.001	3	268.91
$\varphi$ ()	p (morph)	1145.22	<0.001	3	309.66
$\varphi$ (morph)	p (morph)	1146.57	<0.001	4	308.99
$\varphi$ (morph)	p (.)	1147.46	<0.001	3	311.89
$\varphi$ (.)	p (.)	1148.29	<0.001	2	314.75





**Fig. 5** **a** Variation in the number of ovipositing females (bars), as well as new adult majors (full circles and solid line) and minors (open circles and broken line) of the harvestman *Serracutisoma proximum* along the reproductive season of 2004–2005. There is a period when the relative proportion of both male morphs is nearly constant (August–December;  $N = 134$  males), and another period when the relative proportion of majors markedly increases (January–February;  $N = 133$  males). **b–c** Generalized linear models with binomial distribution depicting the probability of becoming a major for males that molted to adults in two periods of the reproductive season that differ in the relative proportion of both male morphs. Predicted values at  $P = 0.5$  represent the estimated mean switchpoints in the periods of August–December (dorsal scute length = 7.11 mm) and January–February (dorsal scute length = 7.12 mm). Lines represent the 95% confidence interval of the respective mean switchpoints. Equations: **b**  $y = e^{-91.35 + 46.57 \cdot \log \text{dorsal scute length}} / (1 + e^{-91.35 + 46.57 \cdot \log \text{dorsal scute length}})$ ; **c**  $y = e^{-106.83 + 54.42 \cdot \log \text{dorsal scute length}} / (1 + e^{-106.83 + 54.42 \cdot \log \text{dorsal scute length}})$

coupled with alternative reproductive tactics in a harvestman. We had previously shown that *S. proximum* majors' mating tactic is based on territorial and female defense, and that the length of their second legs is positively correlated with the number of females in their harems (Buzatto and Machado 2008). Here we showed that minors do not patrol nor defend females and territories, but instead adopt an alternative reproductive tactic based on furtively invading large males' harems and sneaking copulations with egg-guarding females inside the territories. Because breeding females inside large males' harems are temporally and spatially aggregated, there is opportunity for the evolution of the sneaking behavior as an alternative reproductive tactic (Shuster and Wade 2003).

But why are minors seeking copulations with females that are already guarding eggs? The answer probably relies on the fact that oviposition by *S. proximum* females takes a long time. Although nearly 80–90% of the eggs are laid in the first 24 h after copulation with territorial males (Buzatto et al. 2007), females may take up to 14 days to complete oviposition (Buzatto, unpublished data). During this first 24 h period, territorial males (majors) invest intensively in mate guarding (Buzatto and Machado 2008), reducing the access of sneakers to the guarded females. After the first day of oviposition, however, territorial males generally reduce the frequency of mate guarding and minors have the opportunity to invade territories and probably sire at least some of the last eggs that females lay (Fig. 4b). Successful copulations by minors are facilitated because majors have up to six females within their territories, and it is impossible for them to guard all their mates inside the harem. Thus, when territorial males are copulating or temporarily leave the harem to forage, at least some females are not well-guarded, representing potential mates to the sneakers.

By copulating with several males, females may benefit through increased fertility assurance and/or through increased genetic diversity and fitness of their offspring. In fact, we hypothesize that females' reproductive behavior has played an important role in the evolution of alternative reproductive tactics among males of *S. proximum*. The sneaking tactic is only possible because females present a long-lasting oviposition behavior. If females reproductive activity during the breeding season were asynchronous and females completed the oviposition in a short period of time, as occurs with other harvestman species exhibiting maternal care (Machado 2002), majors would probably be able to secure the fertilization of all females' eggs. Given that theory predicts benefits for females that mate more than once (Arnqvist and Nilsson 2000), it is possible that the long-lasting oviposition of *S. proximum* has evolved as a females' strategy to overcome majors' monopoly, and gain an opportunity to mate with other males.

#### Ecological factors affecting recapture and survival rates of male morphs

Our mark-recapture analyses revealed that the recapture rate of majors is higher than that of minors. This result is in accordance with our behavioral observations in the field, which showed that majors are territorial and highly phylopatric when compared to minors, whose mating tactic includes moving between different harems. Similar results have recently been reported for the damselfly *Paraphlebia zoe* (Megapodagrionidae), in which the territorial black-winged morph has higher recapture rates than the sneaker hyaline-winged morph (Munguía-Steyer et al. 2010). Higher recapture rates of majors in both *S. proximum* and *P. zoe* are likely to be a consequence of fidelity to the reproductive territories, and are not necessarily related to differences in survival rates between majors and minors. In fact, our mark-recapture analyses showed that there is no difference regarding survival rates between the two male morphs. Once more, this result is similar to that obtained by *P. zoe*,

in which there is a clear morphological and behavioral distinction between territorial and non-territorial morphs, but no difference in their survival rates (Munguía-Steyer et al. 2010).

Although territorial defense could probably make *S. proximum* majors more conspicuous than minors on the vegetation, it seems that territoriality does not result in higher predation by active hunting predators. Moreover, the fact that minors are more vagile than majors does not mean that they are more prone to be caught by ambush predators. We speculate that both male morphs are subject to similar mortality factors because they use the same microhabitat, are active at the same period of the day, and both are attacked by an unidentified phorid parasitoid, which may infest up to 10% of the individuals in the population, irrespectively of sex or male morph (B.A. Buzatto, unpublished data). This phorid fly is likely to be an important mortality factor for adult *S. proximum* in the study site, which may explain why the monthly survival rate we estimated for females ( $\varphi = 0.857$ ;  $CI_{95\%} = 0.808\text{--}0.895$ ) in a previous study conducted in the same population studied here is very similar to the values estimated for both male morphs (Buzatto et al. 2007). Thus, regardless of the differences in investment on reproductive traits between individuals of each sex or male morph, there is no survival bias among females, majors and minors. This finding has important implications for understanding the great overlap in the body size distributions of male morphs and the magnitude of phenotypic variation for the distribution of switchpoints in the male population (see below).

#### Switchpoint variation and the costs of expressing the major phenotype

Even though the reproductive behavior of *S. proximum* male morphs is fundamentally distinct, their body size distributions overlap significantly. Our analyses revealed that one standard deviation of the switchpoint distribution in the studied population corresponds to nearly 60% of one standard deviation of body size distribution. This overlap in the body sizes of male morphs could result from at least three different, but non excluding mechanisms. Firstly, overlap in body size between morphs may arise if the timing of morph determination occurs early in male ontogeny, as demonstrated for the dung beetle *Onthophagus taurus* (Moczek 2002). If adult morph in *S. proximum* is determined before the nymph stops feeding to molt, variation in food intake after morph determination could result in large minors or small majors. Secondly, in addition to the sensitivity to body size, the switchpoint between male phenotypes may also be sensitive to other environmental cues that have not been measured in the present study, such as population density. Although the ET model acknowledges the possibility of multiple cues in condition-dependent traits (Tomkins and Hazel 2007), few empirical cases have been described so far, probably because the exact moment of morph determination is unknown for most studied species and also because it is difficult to experimentally manipulate the putative environmental cues (but see the case of the mite *Sancassania berlesei* below). Finally, overlap in body size between morphs may be understood as the result of great variation among individual genotypes in the position of the switchpoint determining the body size that needs to be achieved for the major phenotype to be expressed (Tomkins and Hazel 2007). Given that the variation in the distribution of switchpoints in *S. proximum* is large, selection on this trait has probably been weak in the population's recent history. Although we have no evidence to support the first two mechanisms, we provide evidence for the third mechanism with results that showed that major phenotype expression does not result in survival costs, so that a small major does not pay survival costs for expressing this phenotype in a small value of body size.

According to the ET model, the selection differential on the mean switchpoint is a function of the following components: (a) the variance on the distribution of switchpoints along the population; (b) differences in the slopes of fitness plotted on status (i.e., body size) for each morph; and (c) the frequency distribution of status (Tomkins and Hazel 2007). If the fitness functions of male morphs have strikingly different slopes (Fig. 1a), the selection differential on the mean switchpoint is high, and selection strongly penalizes small majors and large minors, eroding the genetic variation for the switchpoint. Conversely, the selection differential on the mean switchpoint is low when the fitness functions of male morphs do not have strikingly different slopes (as in Fig. 1b). In this case, the difference between the fitness that can be achieved by each alternative phenotype is small for males with body size close to the mean switchpoint. This scenario is consistent with the results of our mark-recapture study, which indicates that survival rates do not differ between major and minors in *S. proximum*. Therefore, a small male that expresses the major phenotype should not be severely penalized by this decision. Although assessing the slopes of the fitness functions of the distinct male morphs (as has been done with the dung beetle *O. taurus*, Hunt and Simmons 2001) was beyond the scope of the present study, the similar survival rates of male morphs and the great variation in the distribution of switchpoints suggest similar slopes for these functions (as depicted in Fig. 1b). Alternatively, if the slopes are not fixed over evolutionary time, but rather depend on demographic factors such as the relative frequencies of male morphs or population density, the strength of selection on the mean switchpoint would fluctuate, being weak at times.

Similar to what we found for *S. proximum*, the two male morphs of the mite *S. berlesei* (Acaridae) overlap greatly in body size, indicating that there is also a great amount of genetic variation for the switchpoint in this species (Tomkins et al. 2004). Contrary to what would be predicted by this great switchpoint variation, the weight and length of fighters (majors) is lower than scramblers (minors) that had the same weight during the last nymphal instar, indicating a clear physiological cost majors pay for developing thickened and sharp third legs (Radwan et al. 2002). The significant costs of major morph expression in a species with a large amount of genetic variation for the switchpoint contrast with the idea that weak selection on the switchpoint should be linked to low costs of major morph expression. Yet, the fitness functions of majors and minors of *S. berlesei* are affected by colony density, so that in large and high-density populations, fighters are more often killed in male-male contests than scramblers, resulting in an important mortality cost of the fighter phenotype (Radwan 1993). Thus, temporal shifts in colony density constantly alter the status where the fitness functions of both male morphs intersect. As colony density is likely to be dynamic, the large genetic variation for the switchpoint in *S. berlesei* could be maintained because of the fluctuating selective pressure on this trait. This influence of demography on how the fitness functions from alternative phenotypes intersect was first recognized by Gross (1996, see below).

### The independence between status and switchpoint distributions

Environmental and demographic parameters may ultimately influence the relative fitness of alternative male tactics (Kokko and Rankin 2006). In species with conditional male dimorphism, population density, for instance, affects the switchpoint between the alternative phenotypes through changes in the functions that relate fitness to body size for each tactic (Tomkins and Brown 2004). If only one of the male mating tactics involves fighting, for instance, the relative costs of this tactic increase in higher population

densities, when encountering rival males is more likely. Population density hence alters the selective pressure on each morph, making the alternative tactic (sneaking, for example) profitable over a wider range of body sizes (Moczek and Nijhout 2003). This kind of density effect drives the evolution of the switchpoints in mites (Radwan 1993), dung beetles (Moczek 2003; Moczek and Nijhout 2003), and earwigs (Tomkins and Brown 2004).

Here we tested the influence of demographic parameters on the evolution of the switchpoints in the harvestman *S. proximum*. Although the frequency of new majors was very dynamic, fluctuating between 65 and 100% in the same reproductive season, monthly oscillations in the proportion of new majors were not the result of fluctuating selective pressure on the switchpoint. In fact, the mean switchpoint position was not significantly different for males emerging in different periods of the reproductive season. On the other hand, monthly average body size was positively correlated with the monthly frequency of new majors. Because monthly shifts in status (measured as body size) around a stagnant mean switchpoint can explain the differential recruitment of majors along the reproductive season, without any shifts in mean switchpoint position, status and switchpoint seem to be independent traits in *S. proximum*. These results support the ET model's prediction that truly environmentally cued threshold traits have a low genetic correlation between status and switchpoint, enabling each trait to independently fluctuate and be altered by selection (Tomkins and Hazel 2007). Therefore, we have additional support for our hypothesis that the elongated second legs of *S. proximum* majors are a typical environmentally cued threshold trait.

Our results contrast greatly with what was previously found for the dung beetle *Onthophagus acuminatus* (Scarabaeidae), in which seasonal fluctuations in the mean switchpoint value for major expression tracked similar fluctuations in the body size distribution of the population (Emlen 1997). On the contrary, switchpoint distribution also seems to be independent to body size distribution in the mite *S. berlesei*, in which artificial selection on male morph caused a response in switchpoint distribution, but not in body size (Unrug et al. 2004). Thus, the current evidence from mites and harvestmen support the ET model prediction that the genetic correlation between status and switchpoint is low, allowing the status distribution to evolve or to fluctuate seasonally, without any effect on the position of the mean switchpoint, or vice versa (Tomkins and Hazel 2007). We think it is a future challenge to investigate why in other conditionally male-dimorphic taxa, such as dung beetles, the population mean switchpoint seems to track temporal changes in the distribution of male status, suggesting a high genetic correlation between status and switchpoint in these animals. This genetic correlation challenges the ET model, and a putative explanation is that male dimorphism in dung beetles, contrary to earwigs and harvestmen, is probably not a typical threshold trait, but rather the consequence of an extreme positive allometry in the continuous reaction norm of the sexual trait (Tomkins and Moczek 2009).

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