



## Experimental limitation of oviposition sites affects the mating system of an arachnid with resource defence polygyny



Danilo G. Muniz<sup>a, b</sup>, Glauco Machado<sup>b, \*</sup>

<sup>a</sup> Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

<sup>b</sup> LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

### ARTICLE INFO

#### Article history:

Received 16 March 2015  
 Initial acceptance 18 May 2015  
 Final acceptance 7 July 2015  
 Available online  
 MS. number: A15-00221R

#### Keywords:

alternative mating tactic  
 behavioural plasticity  
 harem size  
 Opiliones  
 sexual selection  
 sneaker  
 territoriality

The availability and spatial distribution of reproductive resources determine female distribution, thus affecting the organization of mating systems and the intensity of sexual selection. Females of the harvestman *Serracutisoma proximum* lay eggs on specific plant species, which are defended by males of the large morph (majors). After oviposition, females remain inside the major's territory, forming a harem, which may be invaded by males of the small morph (minors) to sneak copulations. We experimentally manipulated the availability of the plants used as oviposition sites, and investigated how it affected the mating system of *S. proximum*. Our results show that females and minors moved preferentially to plots with high plant availability. Plots with high plant availability had more harems, which were established on the preferred plants. In plots with low plant availability, many females laid eggs on plants where *S. proximum* clutches had never been observed previously, rather than choosing to be a part of a harem on a preferred plant. Harem invasions were accomplished by both minors and majors, and the frequency of harem invasions was not influenced by plant availability. Finally, male–male competition for harems and the potential for sexual selection were also not influenced by plant availability. Female plasticity in oviposition site use probably attenuates competition among majors, allowing males with poorly developed weaponry to establish a territory and achieve copulations. Minors apparently adjust their distribution in response to harem density, but the income of minors does not increase the frequency of harem invasions in plots with high plant availability. Plasticity in the major mating tactic probably accounts for the high frequency of harem invasions, regardless of plant availability. We argue that behavioural plasticity may thus profoundly affect our ability to make predictions about the effects of oviposition site limitation on mating systems and the intensity of sexual selection in species exhibiting resource defence polygyny.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The availability and spatial distribution of reproductive resources are key determinants of female distribution, which in turn has important consequences for the evolution of mating systems and the intensity of sexual selection (Emlen & Oring, 1977; Shuster & Wade, 2003). For instance, when reproductive resources are clumped, males may gain access to receptive females by defending territories containing these resources, characterizing a resource defence polygyny (examples in: Andersson, 1994; Thornhill & Alcock, 1983). Due to resource limitation, large males or males in good condition may be able to monopolize the reproductive resources and exclude other males from the mating pool through intrasexual competition (Emlen & Oring, 1977; Wade, 1995). When

the competition for reproductive resources is intense, small males or males in poor condition may avoid fighting for the possession of resources and adopt alternative mating tactics (Oliveira, Taborsky, & Brockmann, 2008). In some species, alternative mating tactics are associated with male dimorphism (Gadgil, 1972), so that large males have more elaborate weaponry and usually defend territories, while small males have reduced or completely absent weaponry and usually invade territories to sneak copulations (Buzatto, Tomkins, & Simmons, 2013; Gross, 1996; Oliveira et al., 2008).

In some species exhibiting resource defence polygyny, females may remain inside the male's territory, forming groups called harems (e.g. Kelly, 2006; Kunz, August, & Burnett, 1983; Leonard, 1990). The spatial aggregation of females may attract non-territorial males that sneak into the harem in order to copulate furtively with some females (e.g. Buzatto, Requeña, Lourenço, Munguía-Steyer, & Machado, 2011; Galimberti & Boitani, 1999;

\* Correspondence: G. Machado, LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP 05508-900, Brazil.

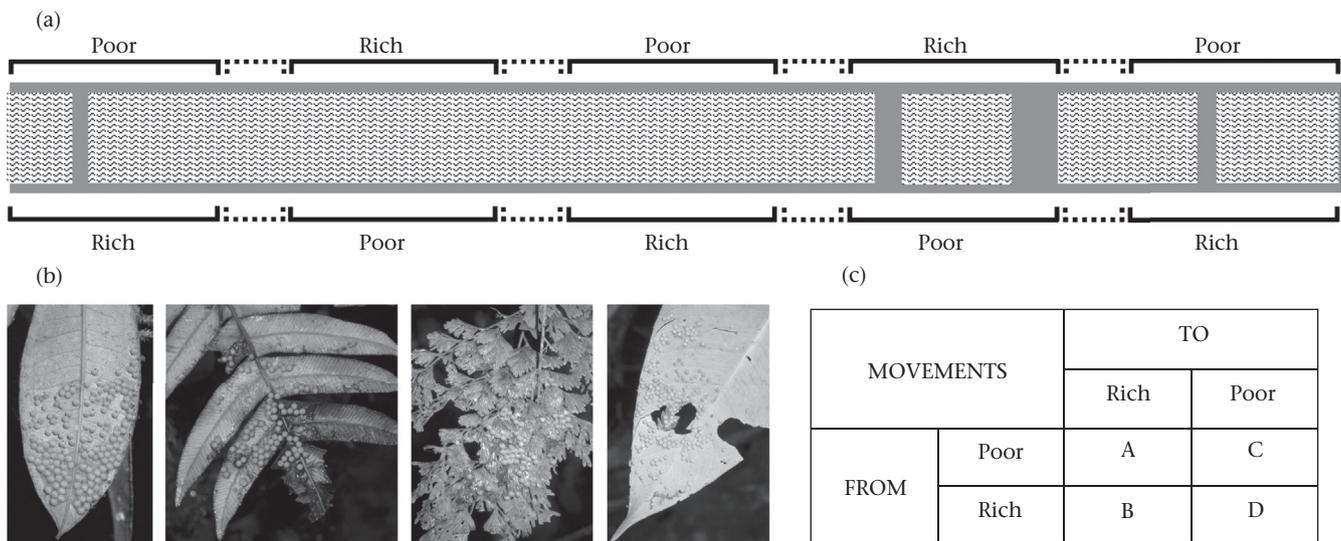
E-mail address: [glaucm@ib.usp.br](mailto:glaucm@ib.usp.br) (G. Machado).

Shuster, 1987). When reproductive resources are scarce and highly clumped, the spatial distribution of females becomes so aggregated that only a few large harems are found in the population, and the mean harem size is expected to be high (e.g. Almada, Gonçalves, Oliveira, & Santos, 1995; Campbell, Akbar, Adnan, & Kunz, 2006). As harem size increases, it becomes easier for a sneaker male to invade a territory and copulate with a female, since territorial males are generally unable to effectively guard all females inside large harems (e.g. Byers & Kitchen, 1988; Munguía-Steyer, Buzatto, & Machado, 2012). Moreover, when intrasexual competition for reproductive resources is strong, less competitive territorial males may adopt alternative mating tactics, increasing the probability of harem invasion (e.g. Borg, Fosgren, & Magnhagen, 2002; Muniz, Guimarães, Buzatto, & Machado, 2015). Therefore, the availability and spatial arrangement of reproductive resources also affects the success of alternative mating tactics (e.g. Bessert, Brozek, & Ortí, 2007; Formica, Gonsler, Ramsay, & Tuttle, 2004).

Previous studies have investigated how the availability of oviposition sites limits reproduction and influences both the organization of mating systems and the intensity of sexual selection in vertebrates, including fishes (e.g. Almada et al., 1995; Bessert et al., 2007; Borg et al., 2002; Forsgren et al., 1996; Lehtonen & Lindström, 2008; Mousseau & Collins, 1987; Reavis & Barlow, 1998; Reichard, Ondracková, Bryjová, Smith, & Bryja, 2009; Singer, Kvarnemo, Lindström, & Svensson, 2006), anurans (e.g. Heying, 2004) and birds (e.g. Gustafsson & Sutherland, 1988; Jacot, Valcu, van Oers, & Kempenaers, 2009; Newton, 1994; Robertson & Stutchbury, 1988; Village, 1983). Many of these studies used a nonmanipulative approach, comparing isolated populations living in habitats with contrasting resource availability, and/or an experimental approach conducted under controlled laboratory conditions. Here we experimentally manipulated the availability of oviposition sites directly in the field and evaluated the demographic and behavioural responses of the harvestman *Serracutisoma proximum* (Arachnida: Opiliones), a species with male dimorphism that exhibits resource defence polygyny. Large males

of *S. proximum* (hereafter called 'majors') establish territories at river margins in areas containing the plants that are preferentially used by females as oviposition sites (hereafter called 'host plants'). Majors fight each other for the possession of territories using their elongated second pair of legs to whip the opponent (Buzatto & Machado, 2008). The territories may be visited by females, which copulate with majors, lay their eggs on the under surface of leaves within the territory, and remain caring for the clutch until the nymphs disperse (Buzatto, Requena, Martins, & Machado, 2007). Successful majors may have harems containing as many as 10 egg-guarding females (Munguía-Steyer et al., 2012). Small males (hereafter called 'minors'), do not have an elongated second pair of legs, do not fight for the possession of territories, and their mating tactic is based on the invasion of territories to mate furtively with egg-guarding females that still retain some mature eggs in their reproductive tract (Buzatto et al., 2011).

In our experimental approach we created contiguous plots of high and low abundance of host plants (Fig. 1a), so that individuals could adjust their distribution to the availability of oviposition sites. Our first prediction is related to demography and postulates that (1) individuals, particularly females, would move from plots with low host plant availability to plots with high host plant availability, seeking the preferred oviposition sites. The high availability of oviposition sites, as well as the directional movement of females, may bring consequences to the organization of the mating system. Specifically, we predicted that in plots with high host plant availability females would become dispersed among the abundant host plants, thus resulting in (2) more harems, (3) lower mean harem size and (4) more clutches established on the preferred host plants when compared with plots with low host plant availability. In plots with low host plant availability, we predicted that (5) sexual selection would be more intense and (6) only majors with a long second pair of legs would be able to secure harems as the outcome of more intense disputes for the possession of scarce reproductive resources. Finally, given that an increase in mean harem size may facilitate the invasion by minors (Munguía-Steyer et al., 2012), our



**Figure 1.** (a) Schematic view, from above, of the 190 m long transect where we conducted the experiment of manipulation of host plant availability. The grey background represents the marginal vegetation where we conducted our observations. The white background filled with small black waves represents the river. Note that there were some vegetation bridges connecting the two margins of the river. Rich and poor plots (1 m wide and 30 m long) had a high and low availability of host plants, respectively. Between two adjacent plots there was a 10 m long buffer area (dotted lines) where we removed all host plants. (b) Some host plants used by females of the harvestman *Serracutisoma proximum* as oviposition sites. From left to right: *Myrcia brasiliensis* (index of standardized plant quality, SPQ = 15.30; see Table 1), a tree belonging to the family Myrtaceae; *Blechnum binervatum* (SPQ = 10.77) and *Vandemboschia radicans* (SPQ = 5.68), two epiphytic ferns belonging to the families Blechnaceae and Hymenophyllaceae, respectively; and *Philodendrom ochroritemon* (SPQ = 1.53), a hemi-epiphytic herb belonging to the family Araceae. (c) Notation used in the formula of the preference index  $\beta$ , representing all possible transitions of individuals moving between plots of high resource availability (rich) and low resource availability (poor).

last prediction was that (7) the frequency of harem invasions would be higher in plots with low host plant availability, where successful majors are predicted to have larger harems.

## METHODS

### Study Site

We conducted the study at Intervalas State Park, an area of Atlantic Forest in the state of São Paulo, southeastern Brazil. The region has high precipitation (2000–3000 mm/year) and average annual temperature between 17 °C and 19 °C. The climate is subtropical, with a warm-wet season from October to March and a cold-dry season from April to September. We studied a population of *S. proximum* living on the vegetation flanking the stream that follows the Caçadinha Track (24°14'S, 48°04'W; Fig. 1a). For more details on this area, please refer to Requena, Buzatto, Martins, and Machado (2012) and Muniz et al. (2015).

### Oviposition Site Manipulation

In a previous paper conducted in the same study area, 25 host plants species used by *S. proximum* females over the course of two reproductive seasons have been catalogued (Buzatto & Machado, 2008). This list includes different plant life-forms, showing a wide variety of leaf sizes and morphologies (Table 1, Fig. 1b). We used the same data set on host plant use and availability presented in Buzatto and Machado (2008), but we quantified plant quality in a different way. Our proxy of plant quality was an index given by  $w_i = u_i/a_i$ , where  $w_i$  is the preference for the host plant species  $i$ ,  $u_i$  is the proportion of clutches in the host plant species  $i$ , and  $a_i$  is the proportion of plants in the study area belonging to the host species  $i$ . This preference value is then standardized as

$$\left( \frac{w_i}{\sum_{x=1}^n w_x} \right) \times 100,$$

where  $n$  is the total number of host plant species in the study area. The standardized plant quality (SPQ) provides quantitative data of preference, so that higher values indicate that a host plant is used proportionally more than its relative frequency (Requena & Machado, 2015). The underlying assumption of this proxy is that preferred host plants represent better oviposition sites. However, we stress that the benefits that *S. proximum* females acquire by laying eggs on particular host plants are still unknown. Some possible reasons may include leaf longevity, which may decrease the risk of losing a clutch due to leaf abscission, and chemical defences, which may decrease the risk of herbivory in leaves bearing a clutch.

To evaluate the effect of oviposition site availability on the mating system of *S. proximum*, we performed a field experiment manipulating the abundance of the host plants, taking into account their SPQ. First, we established a 190 m long transect along the stream, and inspected the vegetation flanking both margins at a maximum distance of 1 m from the water to map and quantify the number of individuals of the 25 host plants species listed in Table 1. Then, we divided each margin of the transect in five 30 m long experimental plots separated from each other by 10 m long buffer areas (Fig. 1a). Finally, we calculated resource availability in each plot as

$$\left( \sum_{i=1}^n l_i \times q_i \right),$$

where  $n$  is the number of host plant species observed in the plot,  $l_i$  is the number of individuals from host plant species  $i$ , and  $q_i$  is the SPQ of host plant species  $i$ .

We assigned half the experimental plots as high-resource-availability plots (hereafter called 'rich plots') and the other half as low-resource-availability plots (hereafter called 'poor plots'). These plots were intercalated along each margin of the stream as depicted in Fig. 1a. We did not manipulate oviposition site availability in rich plots, maintaining within them a large number of individuals of the preferred host plants (i.e. those with high SPQ

**Table 1**  
Plant species used as oviposition sites by females of the harvestman *Serracutisoma proximum*

Plant species	Plant life-form	SPQ
<i>Calyptanthes grandifolia</i> (Myrtaceae)	Tree	39.77
<i>Myrcia brasiliensis</i> (= <i>Gomidesia schaueriana</i> ) (Myrtaceae)	Tree	15.30
<i>Blechnum binervatum</i> (Blechnaceae)	Epiphytic fern	10.77
<i>Vandenboschia</i> (= <i>Trichomanes</i> ) <i>radicans</i> (Hymenophyllaceae)	Epiphytic fern	5.68
<i>Ardisia guianensis</i> (Primulaceae)	Treelet	3.98
<i>Olfersia cervina</i> (Dryopteridaceae)	Ground fern	3.44
<i>Myrceugenia myrcioides</i> (Myrtaceae)	Tree	3.06
<i>Zollernia ilicifolia</i> (Fabaceae)	Tree	2.65
<i>Rudgea jasminoides</i> (Rubiaceae)	Treelet	2.21
<i>Psychotria</i> sp. (Rubiaceae)	Treelet	1.66
<i>Philodendrom ochroritemon</i> (Araceae)	Hemi-epiphytic herb	1.53
Dryopteridaceae sp. (Dryopteridaceae)	Ground fern	1.28
<i>Amaranthus</i> sp. (Amaranthaceae)	Ground herb	1.24
<i>Bathysa australis</i> (Rubiaceae)	Treelet	1.06
<i>Chrysophyllum</i> sp. (Sapotaceae)	Tree	1.06
<i>Diplazium cristatum</i> (Atyaceae)	Epiphytic fern	1.05
<i>Ocotea puberula</i> (Lauraceae)	Tree	1.02
<i>Guapira opposita</i> (Nyctaginaceae)	Tree	0.83
<i>Piper</i> sp.2 (Piperaceae)	Shrub	0.83
<i>Piper</i> sp.1 (Piperaceae)	Shrub	0.59
<i>Begonia</i> sp. (Begoniaceae)	Ground herb	0.38
<i>Goeppertia</i> (= <i>Calathea</i> ) <i>communis</i> (Maranthaceae)	Ground herb	0.21
<i>Lastreopsis</i> sp. (Dryopteridaceae)	Ground fern	0.20
<i>Campyloneurum repens</i> (= <i>C. minus</i> ) (Polypodiaceae)	Epiphytic fern	0.17
<i>Dichorisandra thyriflora</i> (Commelinaceae)	Ground herb	0.04

SPQ is the index of standardized plant quality, which is a measure of host plant preference based on plant use and availability in the study area.

values). In poor plots, we reduced oviposition site availability by completely removing some of the preferred host plants. Using this procedure, we established our experimental plots imposing as low damage as possible to the marginal vegetation and avoiding the transplant of host plants among plots, which was not feasible for several plant species, especially trees and epiphytic ferns. Our manipulation resulted in a clear difference in host plant availability between the two experimental groups ( $t_{6,24} = 3.57, P = 0.005$ ), so that the mean  $\pm$  SD resource availability in rich plots ( $152 \pm 37$ ) was almost two times higher than in poor plots ( $83 \pm 21$ ). In the buffer areas, we removed all individuals of the preferred host plants, imposing a resource availability equal to zero. We monitored these buffer areas throughout the entire study period in order to prevent regrowth of the host plants.

We performed the manipulation in early October 2011, just before the beginning of the reproductive season. After that, we conducted six field trips, lasting 5 days each on average, summing 30 days of observations until March 2012. From these, 10 days were devoted to mark and recapture of *S. proximum* individuals and to search for females caring for eggs on the vegetation, whereas the other 20 days were devoted to focal behavioural observations (see below). Since the number of *S. proximum* clutches in the transect was unusually low between October 2011 and January 2012, we used data from the entire breeding season only to test the first prediction on individual movement among plots. For all other predictions, we used data from the period between February and March 2012 (last three field trips), which concentrated 75% of all clutches found during the 2011–2012 breeding season. In February 2013, we returned to the transect and invested 2 days searching for harems and 10 days conducting intensive focal behavioural observations on these harems (see below). The abundance of the preferred host plants at the river margins showed practically no change between 2012 and 2013, and thus the experimental plots were preserved.

#### Mark–Recapture Procedures

On each mark–recapture day we walked through the transect two or three times searching for *S. proximum* individuals. We conducted these searches especially in the afternoon and at night, when males and females are most active (Buzatto & Machado, 2008; Buzatto et al., 2011). We marked each individual using exclusive combinations of enamel colour paint applied to the dorsal scute (carapace) and to the femur of the third and/or fourth pair of legs. This marking procedure has been used in previous studies with *S. proximum* and there is no evidence that it affects the behaviour or survival of the individuals (Buzatto & Machado, 2008; Buzatto et al., 2007, 2011). For each individual we marked, we took a picture of its dorsal scute in order to later measure the length of this structure, which is a standard measure of body size in harvestmen. In the case of males, we also measured the length of the second right leg to the nearest millimetre using a ruler. We used these measurements to separate males between majors and minors following the procedure explained in Buzatto et al. (2011).

For all individuals we recaptured, we recorded their location in the transect to the nearest metre to identify the plot where they were found and to estimate movement among plots (see below). We also recorded the precise location of the harems, defined here as a female or group of females caring for their eggs on the same host plant and usually associated with a major male that patrols these females until their nymphs disperse and they leave his territory (Buzatto & Machado, 2008). We recorded the number of females per harem (harem size) and the SPQ of the host plant used as an oviposition site by each egg-guarding female. In the case of host

plants that were not used as oviposition site in previous years (see list in Table 1), we scored an SPQ equal to zero.

#### Focal Behavioural Observations

On each day devoted to behavioural observations, we visited each harem six times per day: twice in the morning (during 0900–1200 hours), twice in the afternoon (during 1400–1800 hours) and twice at night (during 2000–0000 hours). During each visit we observed each harem for 5 min, recording the presence of major and minor males in the harem, and the distance between these males and each female in the harem. We identified a harem owner as the major male that we recaptured most often in the vicinity of the same harem (i.e. at least 1 m from the closest egg-guarding female). We considered that a male (either major or minor) successfully invaded a harem when he was observed 1 m or less from at least one egg-guarding female in a harem guarded by a major (following Munguía-Steyer et al., 2012).

#### Statistical Approach

We tested our predictions using the randomization procedures of Monte Carlo simulation and permutation tests (Manly, 2006). Randomization procedures are especially adequate for the analysis of animal behaviour when data do not fit distribution assumptions (Adams & Anthony, 1996). Moreover, these procedures allow the construction of customized null scenarios in nonstandard situations, such as when observations are not statistically independent (Adams & Anthony, 1996). The rationale behind all randomization tests is to calculate a descriptive test statistic from the observed data, compare it with a null distribution generated via repeated randomizations, and estimate the probability that the observed test statistic value (i.e. the *P* value) was generated randomly (Crowley, 1992; Manly, 2006). We performed all statistical procedures described below in the software R 3.1.1 (R Development Team, 2014).

#### Prediction 1: Movement among Plots

To test whether individuals move preferentially from poor to rich plots, we used an index of preference derived from the Bateman's index of constancy (Bateman, 1951; Waser, 1986). If there is a preference for rich plots, individuals in rich plots should remain where they are, whereas individuals in poor plots should move to rich plots. Therefore, movements from rich to poor plots should be rare. According to this rationale, a sequence of recaptures can be described as a Markov process in which individuals can remain in their state or switch to another state (Straw, 1972; Waser, 1986). After an individual was marked, we considered all recaptures as transitions, so that four transitions were possible (Fig. 1c). In our case, we were interested in the tendency of individuals to remain in or move to rich plots. Thus, transitions to rich plots (Fig. 1c, transitions A and B) should be more frequent than those to poor plots (transitions C and D). By modifying Bateman's constancy index, we derived the index of preference

$$\beta = \frac{(A \times B)^{\frac{1}{2}} - (C \times D)^{\frac{1}{2}}}{(A \times B)^{\frac{1}{2}} + (C \times D)^{\frac{1}{2}}},$$

which varies from  $-1$  to  $1$ . A value of  $\beta = 1$  represents total preference for rich plots,  $\beta = -1$  represents total preference for poor plots, and  $\beta = 0$  represents no preference. We calculated  $\beta$  separately for females, majors and minors using only the information

gathered in the 2011–2012 breeding season because we had no data on individual movement for the 2012–2013 breeding season.

We compared the  $\beta$  value (test statistic) obtained in the field for females, majors and minors with  $\beta$  values estimated from a null model. This null model is a Monte Carlo simulation based on the recapture history of the individuals in the field. According to this simulation, each individual kept the number of times it was recaptured, so that the overall rate of recaptures remained the same. We also kept the original plot (either rich or poor) where each individual was first marked in order to retain their initial distribution in the transect. At each recapture, however, the individual could switch to a plot of the other experimental group (transitions B and C in Fig. 1c) with a probability  $m$ , or remain in a plot of the same experimental group (transitions A and D in Fig. 1c) with probability  $1 - m$ . We calculated the probability  $m$  as the actual frequency of plot switching, so that the null model retained, on average, the observed frequency of movements between plots. Each replication of the simulation generated a new history of recaptures from which we calculated a  $\beta$  value. We ran 5000 replications of the null model for females, majors and minors separately, generating a null distribution of  $\beta$  values for each of them. Finally, we estimated the  $P$  values as the proportion of  $\beta$  values in the simulated distributions that were equal to or higher than the  $\beta$  values we observed in the field.

#### Predictions 2 and 3: Harems per Plot and Mean Harem Size

To test whether the mean number of harems was higher in rich plots than in poor plots (prediction 2), we built a null scenario in which the observed number of harems was randomly distributed between all experimental plots. The test statistic was the difference in the mean number of harems between rich and poor plots, and it was calculated by pooling data from both breeding seasons (2011–2012 and 2012–2013), but each season was randomized separately in the simulations, so that seasons were considered as separate experimental blocks (following Manly, 2006).

To test whether the mean harem size was higher in poor plots than in rich plots (prediction 3), we built the null scenario using a simulation in which we maintained the number of harems per plot recorded in the field in each season, thus retaining the spatial distribution and total number of harems in the study area. Then, we considered that each harem had at least one female, and randomly distributed the remaining number of observed egg-guarding females through all harems, regardless of the experimental group. As in the previous simulation, we performed this randomization separately for each breeding season, considering each of them as a separate experimental block. In this case, however, our test statistic was the difference in the mean harem size between rich and poor plots.

In both tests, we ran 5000 randomizations to build a null distribution of the test statistics under the scenario of no difference between rich and poor plots. In each test, we estimated the  $P$  values as the proportion of values of the test statistics in the null distribution that were equal to or higher than the values observed in the field.

#### Prediction 4: Host Plant Quality

To test whether clutches in rich plots are established on the preferred host plants when compared with poor plots, we performed a permutation test using the difference between the mean SPQ of the host plants used by females as oviposition site in rich and poor plots as test statistic. Clutches on rocks and tree trunks, which comprised only 7% of all clutches in the two breeding seasons, were ignored in this analysis because we cannot attribute an

index of quality to these sites and because it was impossible to manipulate their natural availability in the transect. As described for predictions 2 and 3 above, we calculated the test statistic by pooling data from both seasons, but each season was randomized separately in the simulations. We ran 5000 randomizations and estimated the  $P$  values as the proportion of values of the test statistic in the null distribution that were equal to or higher than the value observed in the field.

#### Prediction 5: Intensity of Sexual Selection

We quantified sexual selection using the  $I_{\text{mates}}$  metric (Shuster & Wade, 2003). This is a standardized measure of variation in the reproductive success, in which male reproductive success can be calculated either as the number of copulations or the number of sired offspring. Although we do not have paternity data, behavioural data on the study system suggests that the second male to mate with a female (generally a minor) can inseminate up to 20% of her eggs. In general, females lay 80–90% of their eggs immediately after copulating with the territorial owner (major), but remain receptive for nearly 15 days. During this period, invader males (generally minors) can sneak copulations to fertilize the eggs retained by the females in their reproductive tract (Buzatto & Machado, 2014; Buzatto et al., 2011). We took this behavioural data into account to estimate  $I_{\text{mates}}$  by considering that any copulation during a harem invasion adds a value  $s$  to a male's reproductive success, which is discounted from the reproductive success of the harem-holding male. For the harem-holding males, a female in his harem represents a reproductive success of 1 if she has never been observed copulating with an invader, and  $1 - s$  if she has. Males that we never observed copulating were scored as having a reproductive success equal to zero. Based on these assumptions, we estimated the reproductive success of each male observed in each experimental plot separately for each of our last three field trips in the 2011–2012 breeding season, and used this estimated success to calculate  $I_{\text{mates}}$  values. We calculated the  $I_{\text{mates}}$  metric considering four possible  $s$  values (0.05, 0.1, 0.15 and 0.2) to test the sensitivity of our results.

To test the prediction that sexual selection would be more intense in poor plots, we calculated an  $I_{\text{mates}}$  value for each plot in each observation period (field trip), and used the difference in the mean  $I_{\text{mates}}$  between poor and rich plots as the test statistic. We built the null distribution by shuffling the reproductive success of all males (calculated as explained above) from rich and poor plots within each observation period (field trip), so that each period was considered a separate experimental block. Finally, we recalculated the test statistic 5000 times and estimated the  $P$  value as the proportion of values of the test statistic in the null distributions that were equal to or higher than the value observed in the field.

#### Prediction 6: Harem Ownership

To test whether harem-holder majors have longer second legs in poor plots than in rich plots as a result of more intense competition for harems, we used a logistic regression in which  $P$  values were calculated via permutation (following Manly, 2006). We included in the analysis all major males (with and without harems) captured or recaptured between February and March 2012, a period of the breeding season when all harems are already settled down and turnovers in their ownership are very rare (Buzatto & Machado, 2008; Muniz et al., 2015). We used the experimental groups (rich or poor), the second leg length (weapon size), and the interaction between these two variables as predictors of harem ownership. The model coefficients (slopes) were used as our test statistics, and to build a null distribution of these test statistics, we shuffled the

observed predictor variables among all major males in our sample. Then, we recalculated the value of the coefficients 5000 times and estimated  $P$  values as the proportion of values of the test statistics in the null distributions that were equal to or higher than the value observed in the field.

#### Prediction 7: Harem Invasion

To test whether harem invasion is higher in poor plots than in rich plots, we quantified harem invasion in two complementary ways: frequency of invasion and number of invaders. Frequency of invasion was calculated as the number of times we observed an invader in a harem divided by the total number of visits we made to that harem. The number of invaders was the total number of different invader males observed per harem. We only used data from the 2011–2012 breeding season for this test because the number of invasions observed in the 2012–2013 season was too low. We considered each harem as an observation and used as test statistics the difference between rich and poor plots both in the mean frequency of invasions and in the mean number of invaders per harem. We built null distributions of the test statistics by shuffling the observed values of frequency of invasions and number of invaders among all plots (both rich and poor). Finally, we recalculated the test statistics 5000 times and estimated the  $P$  values as the proportion of values of the test statistics in the null distributions that were equal to or higher than the values observed in the field.

## RESULTS

### General Description of the Data

In the 2011–2012 breeding season, we marked a total of 139 females, 99 major males and 45 minor males in the study area. In the peak of this breeding season, between February and March 2012, we observed 33 harems with a total of 64 egg-guarding females. During this period, 70% of the clutches were laid in rich plots and 30% in poor plots. Eleven clutches were laid in buffer areas, all of them in rocks or plants with SPQ = 0. These clutches were not included in the analyses reported in the following topics. Of all majors captured in this season, the percentage of harem-holder males was 34% in rich plots and 21% in poor plots.

In the 2012–2013 breeding season, we marked a total of 60 females, 45 majors and 11 minors. In February 2013, we observed 29 harems with a total of 54 egg-guarding females in the experimental plots; 57% of these females laid eggs in rich plots and 43% in poor plots. Only six clutches were laid in buffer areas in plants with SPQ = 0, and again they were not included in the analyses below. Since our behavioural observations were focused exclusively on harems, we do not have the percentage of harem-holder males in rich and poor plots for this breeding season.

#### Prediction 1: Movement among Plots

Only 7% of the recaptured females moved among plots, but they showed a marked preference for rich plots ( $\beta = 0.43$ ,  $P = 0.002$ ). The percentage of recaptured majors that moved among plots was also low (13%) and they showed no preference pattern ( $\beta = 0.19$ ,  $P = 0.07$ ). Finally, 31% of the recaptured minors moved among plots, and showed a significant preference for rich plots ( $\beta = 0.38$ ,  $P = 0.001$ ).

#### Predictions 2 and 3: Harems per Plot and Mean Harem Size

Rich plots had, on average, almost 60% more harems than poor plots ( $N = 10$  plots  $\times$  2 breeding seasons,  $P = 0.03$ ; Fig. 2a). Mean

harem size, however, was similar between poor and rich plots ( $N = 62$  harems,  $P = 0.21$ ; Fig. 2b).

#### Prediction 4: Host Plant Quality

Although females used plants with high SPQ in poor plots, they also used many plants on which *S. proximum* females have never been observed to lay eggs before (SPQ = 0). Females in rich plots occasionally used plants with low SPQ, but they concentrated their clutches mostly on plants with high SPQ. Thus, the mean SPQ of the oviposition sites was higher in rich plots than in poor plots ( $N = 109$  clutches,  $P < 0.001$ ; Fig. 2d).

#### Prediction 5: Intensity of Sexual Selection

The  $I_{\text{mates}}$  values showed great variation between sampling periods and within experimental groups (Fig. 3). Considering a value of  $s = 0.2$ , the  $I_{\text{mates}}$  in rich plots varied from 0 to 9.85 (mean = 3.29; Fig. 3), whereas in poor plots it varied from 0 to 8 (mean = 2.30). We did not observe a difference in  $I_{\text{mates}}$  between experimental groups ( $P > 0.83$ ). This result was qualitatively the same for  $s = 0.05$ , 0.10 and 0.15 (data not shown).

#### Prediction 6: Harem Ownership

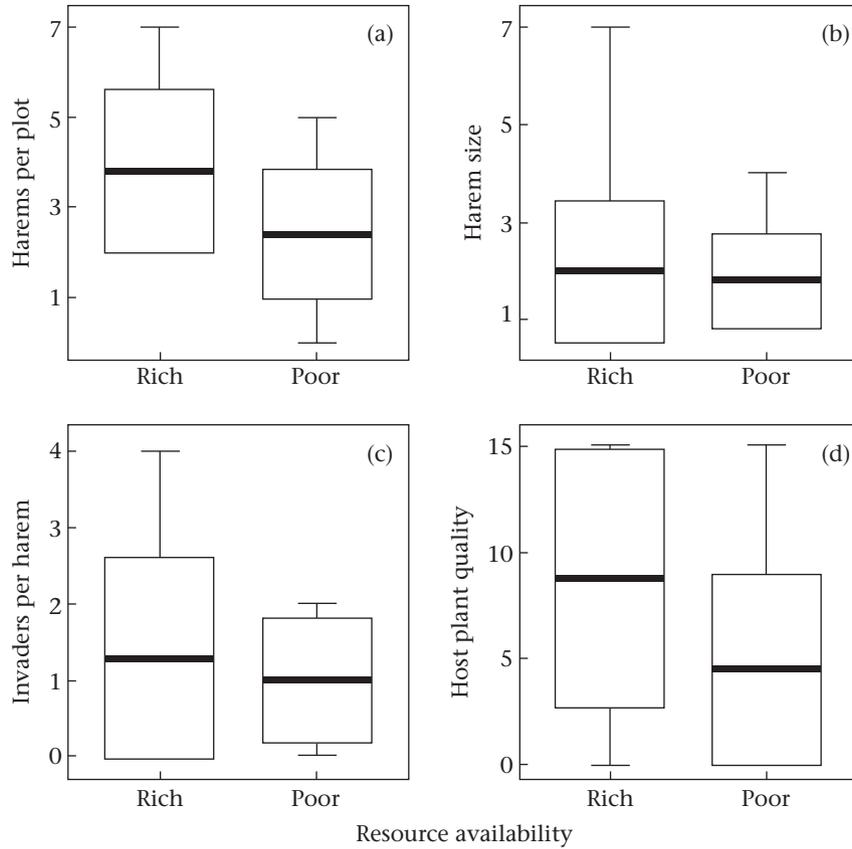
The mean  $\pm$  SD second leg length of majors with and without harems was  $13.61 \pm 0.77$  cm and  $13.47 \pm 0.66$  cm, respectively. The experimental groups (coefficient = 7.39,  $P = 0.25$ ), the second leg length (coefficient =  $-0.04$ ,  $P = 0.46$ ), and the interaction between these two variables (coefficient =  $-0.56$ ,  $P = 0.24$ ) did not predict harem ownership ( $N = 62$  males; Fig. 4). Thus, an increase in second leg length did not increase a male's probability of holding a harem, either in rich plots or in poor plots.

#### Prediction 7: Harem Invasion

Harem invasions were accomplished by minors (50% in poor plots and 37% in rich plots), majors without territories (42% in poor plots and 37% in rich plots), and neighbouring harem-holder majors (8% in poor plots and 26% in rich plots). The mean frequency of invasions in poor and rich plots was similar, being 19.3% and 20.8%, respectively ( $N = 32$  harems,  $P = 0.42$ ). The number of invaders per harem varied from zero to four, and we observed no difference in the mean number of invaders between rich and poor plots ( $N = 32$  harems,  $P = 0.63$ ; Fig. 2c).

## DISCUSSION

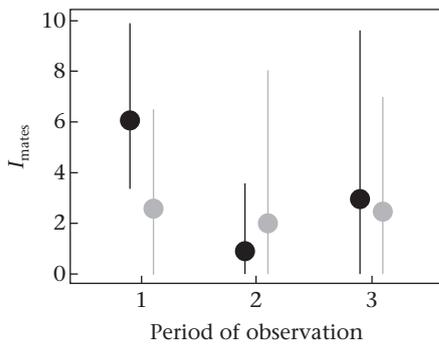
Here we experimentally manipulated the natural availability of the plants used by *S. proximum* females as oviposition sites, and investigated how it affected the mating system and the intensity of sexual selection in this harvestman over two consecutive breeding seasons. We found that females and minor males moved preferentially to plots with high host plant availability, while no directional movement pattern was detected for major males, which is partially consistent with prediction 1. We also found more harems in plots with high host plant availability, supporting prediction 2. In contrast to prediction 3, we found no difference in mean harem size between areas of high and low host plant availability. The quality of the plants used as oviposition sites, however, was higher in plots with high host plant availability, supporting prediction 4. Finally, the intensity of sexual selection, the size of harem-holder majors, the frequency of harem invasions and the number of invader males per harem were not influenced by host plant availability, refuting predictions 5–7.



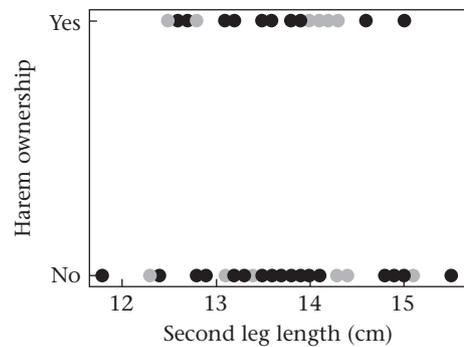
**Figure 2.** Comparison between high- (rich) and low- (poor) resource-availability plots in a field experiment of manipulation of host plant availability with the harvestman *Serracutisoma proximum*. In each graph, the bold line represents the mean, the box represents the standard deviation and the whiskers indicate the range. (a) Number of harems per plot. (b) Harem size. (c) Number of invader males per harem. (d) Standardized plant quality of host plants used as oviposition sites (each observation is a clutch). Panels (a), (b) and (d) present pooled data from two breeding seasons, and panel (c) presents data from only one breeding season.

The seminal work by [Emlen and Oring \(1977\)](#) predicts that females should adjust their distribution to the availability and distribution of reproductive resources, and that males should follow female distribution to acquire mates. However, such demographic effect in terms of individual movement has been poorly explored, either because conditions of low and high resource availability are established in isolated cages or pools (e.g. [Reichard et al., 2009](#);

[Singer et al., 2006](#)) or because study areas are distant from each other and migration between them is unlikely (e.g. [Bessert et al., 2007](#); [Forsgren et al., 1996](#)). Even when studies are conducted in contiguous areas with different resource availability, individual movement among areas has rarely been reported (e.g. [Borg et al., 2002](#); [Jacot et al., 2009](#); [Lehtonen & Lindström, 2008](#)). An exception is a study with the frog *Mantella laevis*, which showed an increase in population density when oviposition sites (water-filled tree holes) were experimentally increased, but no information on sex-specific movements was provided ([Heying, 2004](#)). Here we



**Figure 3.** Intensity of sexual selection (measured as the standardized variance in mating success,  $I_{mates}$ ) in a field experiment of manipulation of host plant availability with the harvestman *Serracutisoma proximum*. In this figure we show the result considering that invader males fertilize 20% of a female’s eggs ( $s = 0.2$ ). Measures were taken in three different periods (field trips) within the same breeding season (1 = early February; 2 = late February; 3 = mid-March). Circles represent the mean of five experimental plots and bars indicate the range. Grey: low-resource-availability plots; black: high-resource-availability plots.



**Figure 4.** Relationship between harem ownership and the length of the second pair of legs (weapon size) of *Serracutisoma proximum* major males in a field experiment of manipulation of host plant availability. Black circles represent majors in high-resource-availability plots; grey circles represent majors in low-resource-availability plots.

showed that rich plots attracted individuals from poor plots and that this directional movement was performed predominantly by females and minor males. Selection of adequate oviposition sites has important fitness consequences for females of several animal groups (Resetarits, 1996), which may explain why some females moved to areas where the abundance of the preferred host plants was high.

From the males' perspective, the movement by minors to rich plots cannot be explained by the possible benefit minors may get from increasing mating success when invading large harems (Munguía-Steyer et al., 2012) because mean harem size did not differ between rich and poor plots. In a previous work conducted in the same population studied here, we showed that minors concentrate their invasions on neighbouring harems, so that the higher the density of harems, the greater the risk of invasions (Muniz et al., 2015). Considering that minors are more vagile than majors and rely on the invasion of harems (Buzatto et al., 2011), we suggest that minors adjust their distribution mostly to the density of harems, which we showed to be higher in rich plots. Previous papers on fish have already shown that nest site availability influences the success of alternative mating tactics (e.g. Borg et al., 2002; Reichard, Jurajda, & Smith, 2004), but our study is perhaps the first empirical demonstration that minor males rearrange their spatial distribution in the population, probably in response to the availability of potential mates.

Although the shortage of oviposition sites has a positive effect on the frequency of sneaking attempts in some fish species (e.g. Borg et al., 2002; Reichard et al., 2004), the frequency of invasions and the number of invaders per harem were similar between experimental groups in our study. We suggest that these results are related to the plasticity in the mating tactics exhibited by *S. proximum* males. As should be expected, minors accomplished most of the harem invasions. However, majors without harems also accounted for a large percentage of all invasions, especially in poor plots, where the percentage of unsuccessful males was higher than in rich plots. Thus, majors are able to switch from territorial defence to invasion, which may increase their reproductive opportunities (Muniz et al., 2015). Curiously, harem-holder majors also accomplished invasions in neighbouring harems. These invasions were more frequent in rich plots, where the density of harems was higher and their distribution was more clumped than in poor plots. These results reinforce the notion that male mating tactics show great behavioural plasticity in response to reproductive resource availability (e.g. Borg et al., 2002; Jones, Walker, Kvarnemo, Lindström, & Avise, 2001; Reichard et al., 2004).

In species in which the offspring feeds on the host plant where they hatch, the use of alternative host plants can incur high fitness costs (e.g. Greenfield, Choe, & Crespi, 1997; McLain, 1986). Nymphs of *S. proximum*, however, do not feed on plants (Buzatto et al., 2007), and the fitness loss associated with the use alternative host plants is probably low. Thus, some plasticity in oviposition site selection should be expected. During our field experiment, we indeed found clutches in plants that have never been used before by *S. proximum* females, and small harems were found even in buffer areas where we removed all host plants. The plasticity in host plant use, however, does not mean that the identity of the plants used as oviposition site is irrelevant. As we stated before, females moved preferentially to rich plots, where they laid eggs on plants with higher SPQ when compared with poor plots. These results suggest that the distribution and availability of the preferred oviposition sites are important drivers of female distribution in the field.

Plasticity in host plant use may have important consequences for the mating system of *S. proximum*. First, it may explain the low frequency of female movement from poor to rich plots. Rather than

moving to plots with high host plant availability, many females laid eggs on low-quality plants in poor plots. Since mortality is positively correlated with movement rates in some arthropods, including Neotropical harvestmen (e.g. McCauley & Lawson, 1986; Polis, Barnes, & Seely, 1998; Requena et al., 2012; Requena & Machado, 2014), females may face a trade-off between the benefit of selecting high-quality oviposition sites and the cost associated with predation risk while searching for these sites. Second, the use of alternative oviposition sites may also attenuate intrasexual competition (e.g. Wong, Munday, Buston, & Jones, 2008). In our experiment, several majors defending territories on low-quality host plants achieved copulation in poor plots, which may explain why sexual selection intensity did not vary between experimental groups, and also why harem ownership was not influenced by the majors' weapon size. Under this scenario, the benefits of moving to rich plots are decreased for majors, which may explain why major movements showed no directional pattern among experimental plots.

In conclusion, our findings show that oviposition site limitation affects females in two different ways: while most females relax their preferences for certain host plants and lay eggs on alternative plant species in areas of low host plant availability, some females move to areas where the availability of the preferred host plants is high. The long-term consequences of these two tactics for females' reproductive success are still unknown, but we argue that plasticity in host plant use attenuates competition among majors. Thus, even majors with poorly developed weaponry may achieve copulations. Minors, on the other hand, seem to adjust their distribution mostly in response to the density of harems, moving preferentially to areas of high host plant availability. The income of minors does not increase the frequency and number of harem invaders in areas with high host plant availability, probably because majors (with and without harems) have plastic mating tactics and can also invade harems as a means of increasing their reproductive success. We argue that behavioural plasticity of both females and males may have profound implications for our ability to make predictions about the effects of oviposition site limitation on the organization of mating systems and the intensity of sexual selection in species exhibiting resource defence polygyny.

## Acknowledgments

We are grateful to the staff of Intervalles State Park for logistic support, to Pedro P. Bueno and Louise Alissa for helping in the fieldwork, to Sara Mortara for helping in the identification of some fern species, to Bruno A. Buzatto for helping in the analysis of male morph discrimination and for revising a previous version of the manuscript, to Ayana B. Martins for revising the methods section, and to two anonymous referees who made useful comments on the manuscript. The authors are supported by research grants from São Paulo Research Foundation (FAPESP 2011/12675-2 and 2012/50229-1) and National Council of Technological and Scientific Development (CNPq).

## References

- Adams, D. C., & Anthony, C. D. (1996). Using randomization techniques to analyse behavioural data. *Animal Behaviour*, *51*, 733–738.
- Almada, V. C., Gonçalves, E. J., Oliveira, R. U. I. F., & Santos, A. J. (1995). Courting females: ecological constraints affect sex roles in a natural population of the blennioid fish *Salaria pavo*. *Animal Behaviour*, *49*, 1125–1127.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Bateman, A. J. (1951). The taxonomic discrimination of bees. *Heredity*, *5*, 271–278.
- Bessert, M. L., Brozek, J., & Ortí, G. (2007). Impact of nest substrate limitations on patterns of illegitimacy in the fathead minnow, *Pimephales promelas* (Cypriniformes: Cyprinidae). *Journal of Heredity*, *98*, 716–722.

- Borg, A. A., Fosgren, E., & Magnhagen, C. (2002). Plastic sex-roles in the common goby: the effect of nest availability. *Oikos*, 98, 105–115.
- Buzatto, B. A., & Machado, G. (2008). Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a Neotropical harvestman. *Behavioral Ecology and Sociobiology*, 63, 85–94.
- Buzatto, B. A., & Machado, G. (2014). Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behavioural Processes*, 109, 2–13.
- Buzatto, B. A., Requena, G. S., Lourenço, R. S., Munguia-Steyer, R., & Machado, G. (2011). Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones). *Evolutionary Ecology*, 25, 331–349.
- Buzatto, B. A., Requena, G. S., Martins, E. G., & Machado, G. (2007). Effects of maternal care on the lifetime reproductive success of females in a Neotropical harvestman. *Journal of Animal Ecology*, 76, 937–945.
- Buzatto, B. A., Tomkins, J. L., & Simmons, L. W. (2013). Alternative phenotypes within mating systems. In D. M. Shuker, & L. W. Simmons (Eds.), *The evolution of insect mating systems* (pp. 106–128). Oxford, U.K.: Oxford University Press.
- Byers, J., & Kitchen, D. (1988). Mating system shift in a pronghorn population. *Behavioral Ecology and Sociobiology*, 22, 355–360.
- Campbell, P., Akbar, Z., Adnan, A. M., & Kunz, T. H. (2006). Resource distribution and social structure in harem-forming Old World fruit bats: variations on a polygynous theme. *Animal Behaviour*, 72, 687–698.
- Crowley, P. H. (1992). Resampling methods for data analysis in ecology and evolution. *Annual Review of Ecology and Systematics*, 23, 405–447.
- Emlen, S., & Oring, L. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215–223.
- Formica, V., Gonsler, R., Ramsay, S., & Tuttle, E. (2004). Spatial dynamics of alternative reproductive strategies: the role of neighbors. *Ecology*, 85, 1125–1136.
- Forsgren, E., Kvarnemo, C., & Lindström, K. (1996). Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution*, 50, 646–654.
- Gadgil, M. (1972). Male dimorphism as a consequence of sexual selection. *American Naturalist*, 106, 574–580.
- Galimberti, F., & Boitani, L. (1999). Demography and breeding biology of a small, localized population of southern elephant seals (*Mounga leonina*). *Marine Mammal Science*, 15, 159–178.
- Greenfield, M. D., Choe, J. C., & Crespi, B. J. (1997). Sexual selection in resource defense polygyny: lessons from territorial grasshoppers. In J. C. Choe, & B. J. Crespi (Eds.), *The evolution of mating systems in insects and arachnids* (pp. 75–88). Cambridge, U.K.: Cambridge University Press.
- Gross, M. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution*, 11, 92–98.
- Gustafsson, L., & Sutherland, W. (1988). The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature*, 335, 813–815.
- Heying, H. E. (2004). *Reproductive limitation by oviposition site in a treehole breeding Madagascan poison frog (Mantella laevisgata)*, 193 pp. 23–30. Miscellaneous Publications of the Museum of Zoology University of Michigan.
- Jacot, A., Valcu, M., van Oers, K., & Kempenaers, B. (2009). Experimental nest site limitation affects reproductive strategies and parental investment in a hole-nesting passerine. *Animal Behaviour*, 77, 1075–1083.
- Jones, A. G., Walker, D., Kvarnemo, C., Lindström, K., & Avise, J. C. (2001). How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 9151–9156.
- Kelly, C. D. (2006). Fighting for harems: assessment strategies during male–male contests in the sexually dimorphic Wellington tree weta. *Animal Behaviour*, 72, 727–736.
- Kunz, T., August, P., & Burnett, C. (1983). Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica*, 15, 133–138.
- Lehtonen, T. K., & Lindström, K. (2008). Density-dependent sexual selection in the monogamous fish *Archocentrus nigrofasciatus*. *Oikos*, 117, 867–874.
- Leonard, M. L. (1990). Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. *American Naturalist*, 136, 446–458.
- Manly, B. F. J. (2006). *Randomization, bootstrap and Monte Carlo methods in biology* (2nd ed.). Chicago, IL: Chapman & Hall.
- McCauley, D., & Lawson, E. (1986). Mating reduces predation on male milkweed beetles. *The American Naturalist*, 127, 112–117.
- McLain, D. K. (1986). Resource patchiness and variation in the intensity of sexual selection in a resource defending polygynous insect species. *Oikos*, 47, 19–25.
- Mousseau, T., & Collins, N. (1987). Polygyny and nest site abundance in the slimy sculpin (*Cottus cognatus*). *Canadian Journal of Zoology*, 65, 2827–2829.
- Munguia-Steyer, R., Buzatto, B. A., & Machado, G. (2012). Male dimorphism of a Neotropical arachnid: harem size, sneaker opportunities, and gonadal investment. *Behavioral Ecology*, 23, 827–835.
- Muniz, D. G., Guimarães, P. R., Jr., Buzatto, B. A., & Machado, G. (2015). A sexual network approach to sperm competition in a species with alternative mating tactics. *Behavioral Ecology*, 26, 121–129.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation*, 70, 265–276.
- Oliveira, R. F., Taborsky, M., & Brockmann, H. J. (2008). In *Alternative reproductive tactics: an integrative approach*. Cambridge, U.K.: Cambridge University Press.
- Polis, G., Barnes, J., & Seely, M. (1998). Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. *Ecology*, 79, 2560–2566.
- R Development Team. (2014). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Reavis, R., & Barlow, G. (1998). Why is the coral-reef fish *Valenciennea strigata* (Gobiidae) monogamous? *Behavioral Ecology and Sociobiology*, 43, 229–237.
- Reichard, M., Jurajda, P., & Smith, C. (2004). Male–male interference competition decreases spawning rate in the European bitterling (*Rhodeus sericeus*). *Behavioral Ecology and Sociobiology*, 56, 34–41.
- Reichard, M., Ondracková, M., Bryjová, A., Smith, C., & Bryja, J. (2009). Breeding resource distribution affects selection gradients on male phenotypic traits: experimental study on lifetime reproductive success in the bitterling fish (*Rhodeus amarus*). *Evolution*, 63, 377–390.
- Requena, G. S., Buzatto, B. A., Martins, E. G., & Machado, G. (2012). Paternal care decreases foraging activity and body condition, but does not impose survival costs to caring males in a Neotropical arachnid. *PLoS One*, 7, e46701.
- Requena, G. S., & Machado, G. (2014). Lack of costs associated with nest-related behaviors in an arachnid with exclusive paternal care. *Oikos*, 124, 372–380.
- Requena, G. S., & Machado, G. (2015). Effects of egg attendance on male mating success in a harvestman with exclusive paternal care. *Behavioral Ecology*, 26, 926–935.
- Resetarits, W. J. (1996). Oviposition site choice and life history evolution. *American Zoologist*, 36, 205–215.
- Robertson, R. J., & Stutchbury, B. J. (1988). Experimental evidence for sexually selected infanticide in tree swallows. *Animal Behaviour*, 36, 749–753.
- Shuster, S. (1987). Alternative reproductive behaviors: three discrete male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. *Journal of Crustacean Biology*, 7, 318–327.
- Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton, Princeton University Press: NJ.
- Singer, A., Kvarnemo, C., Lindström, K., & Svensson, O. (2006). Genetic mating patterns studied in pools with manipulated nest site availability in two populations of *Pomatoschistus minutus*. *Journal of Evolutionary Biology*, 19, 1641–1650.
- Straw, R. M. (1972). A Markov model for pollinator constancy and competition. *American Naturalist*, 106, 597–620.
- Thornhill, R., & Alcock, J. (1983). *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press.
- Village, A. (1983). The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. *Journal of Animal Ecology*, 52, 635–645.
- Wade, M. (1995). The ecology of sexual selection: mean crowding of females and resource-defence polygyny. *Evolutionary Ecology*, 7, 118–124.
- Waser, N. M. (1986). Flower constancy: definition, cause, and measurement. *American Naturalist*, 127, 593–603.
- Wong, M., Munday, P., Buston, P., & Jones, G. (2008). Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. *Behavioral Ecology*, 19, 353–361.