Animal Behaviour 109 (2015) 23–31

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Danilo G. Muniz [a, b], Glauco Machado [b, *]

[a] *Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil*
[b] *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.

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, Requena, Lourenço, Munguía-Steyer, & Machado, 2011; Galimberti & Boitani, 1999;

---

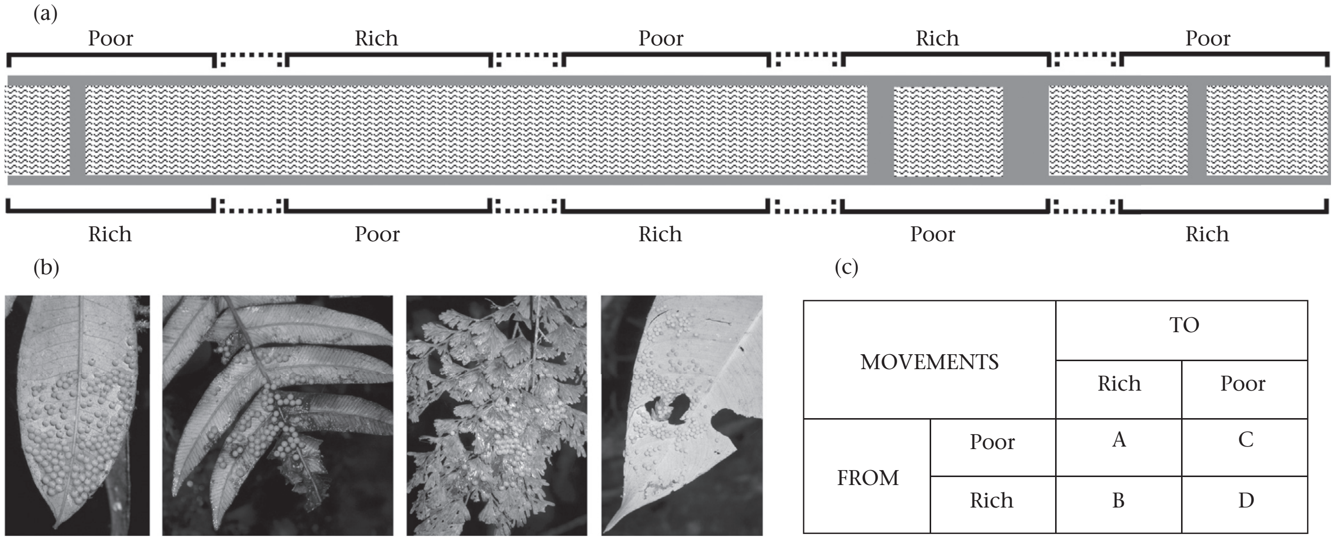
* Correspondence: G. Machado, LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP 05508-900, Brazil.
E-mail address: glaucom@ib.usp.br (G. Machado).

http://dx.doi.org/10.1016/j.anbehav.2015.08.007
0003-3472/

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, Gonser, 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



MOVEMENTS		TO	
		Rich	Poor
FROM	Poor	A	C
	Rich	B	D

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 *Vandenboschia radicans* (SPQ = 5.68), two epiphytic ferns belonging to the families Blechnaceae and Hymenophyllaceae, respectively; and *Philodendrom ochrortemon* (SPQ = 1.53), a hemi-epiphytic herb belonging to the family Araceae. (c) Notation used in the formula of the preference index β, representing all possible transitions of individuals moving between plots of high resource availability (rich) and low resource availability (poor).