

Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a Neotropical harvestman

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Abstract Although studies classify the polygynous mating system of a given species into female defense polygyny (FDP) or resource defense polygyny (RDP), the boundary between these two categories is often slight. Males of some species may even shift between these two types of polygyny in response to temporal variation in social and environmental conditions. Here, we examine the mating system of the Neotropical harvestman *Acutisoma proximum* and, in order to assess if mate acquisition in males corresponds to FDP or RDP, we tested four contrasting predictions derived from the mating system theory. At the beginning of the reproductive season, males fight with other males for the possession of territories on the vegetation where females will later oviposit, as expected in RDP. Females present a marked preference for specific host plant species, and males establish their territories in areas where these host plants are specially abundant, which is also expected in RDP. Later in the reproductive season, males reduce their patrolling activity and focus on defending individual females that are ovipositing inside their

territories, as what occurs in FDP. This is the first described case of an arachnid that exhibits a shift in mating system over the reproductive season, revealing that we should be cautious when defining the mating system of a species based on few observations concentrated in a brief period.

Keywords Gonyleptidae · Harem · Host plant selection · Male territoriality · Opiliones · Resource holding potential · Resource value

Introduction

The evolution of animal mating systems was a central issue of Darwin's sexual selection theory (1871) and a matter of interest for evolutionary biologists ever since. Three decades ago, Emlen and Oring (1977) provided a unified theoretical framework for mating system evolution that focused on ecological constraints affecting the reproductive strategies of males and females. Emlen and Oring's (1977) central argument was that individuals from one sex (usually males) could increase their fitness by attempting to control access to the members of the other sex (usually females). According to the authors, the degree to which this monopoly is possible depends on environmental factors, such as the availability and spatial dispersal pattern of critical resources used by the limiting sex.

Polygyny is the mating system in which a minority of males control or gain access to multiple females leaving most other males without access to females (Shuster and Wade 2003). This mating system is usually favored by selection when individual males are able to monopolize a clumped group of receptive females (Emlen and Oring 1977). Polygyny can be further classified into resource defense polygyny and female defense polygyny. Resource defense polygyny occurs when

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males control females indirectly by defending territories or resources against conspecific males, whereas female defense polygyny occurs when males control females directly by defending them against conspecifics males. Thus, the spatial and temporal distribution of females and resources will determine whether males defend females or the resources that attract receptive females (Shuster and Wade 2003).

Among arthropods, resource defense polygyny is widespread (see references in Thornhill and Alcock 1983; Kelly 2008). Examples of male insects that defend resources include the hylaeine and wool-carder bees that defend the flowers that provide pollen and nectar for females (Alcock and Houston 1996; Starks and Reeve 1999), coreid bugs and grasshoppers that defend host food-plants (Mitchell 1980; Greenfield 1997; Eberhard 1998), bark beetles that defend burrows where females feed and reproduce (Reid and Stamps 1997), and carrion beetles that defend small carcasses attractive to females (Scott 1998; Suzuki et al. 2006). In pollen wasps, males may defend either water collection sites or flowers, both important reproductive resources for females (Groddeck et al. 2004). Male dragonflies, robber flies, and tephritid flies defend the oviposition sites preferred by females (Wolf et al. 1997; Hastings et al. 1994; Aluja et al. 2001).

In contrast to resource defense polygynists, males from species that engage in female defense polygyny directly defend groups of females (e.g., Poston 1997) or individual females in sequence (e.g., Robinson 1986). This kind of polygyny is fairly common among mammals, and also occurs in a small number of bird species (see Webster 1994; Poston 1997; Webster and Robinson 1999 and references within). Although female defense polygyny is not particularly common in arthropods, it has been reported for at least seven insect orders, namely Hemiptera (Fujisaki 1981), Orthoptera (Gwynne and Morris 1983), Zoraptera (Choe 1994, 1997), Thysanoptera (Crespi 1988), Coleoptera (Hamilton et al. 1976; Kirkendall 1983; Kirkendall et al. 1997), Diptera (Wilkinson and Dodson 1997), and Hymenoptera (Eberhard 1975; Alcock et al. 1977; Smith and Alcock 1980; Gwynne 1980; Lloyd 1981), and for the crustacean order Amphipoda (McCurdy et al. 2000).

Even though arachnids present a great diversity of reproductive strategies (Thomas and Zeh 1984), there is only one case of female defense polygyny among species of the group, reported for the spider mite *Stigmaeopsis miscanthi* (Saito 1990), and few cases of resource defense polygyny reported for the harvestmen *Zygopachylus albomarginis* (Mora 1990) and *Leiobunum vittatum* (Macías-Ordóñez 1997, 2000) and for the water mites of the genus *Unionicola* (see Dimock 1985). In this paper, we examine the mating system of the Neotropical harvestman *Acutisoma proximum* (Arachnida: Opiliones), whose females lay eggs mainly on the underside of leaves hanging above rivers (Buzatto et al. 2007). During the breeding season,

males have been observed fighting on the vegetation where females mate, oviposit, and guard their eggs (Buzatto et al. 2007). After copulating with several females, a male frequently patrols his mates, as previously recorded for the congeneric *A. longipes* (Machado and Oliveira 1998).

In order to assess if the mode of mate acquisition in *A. proximum* is that of resource or female defense polygyny, we tested four predictions derived from the mating system theory (Table 1). In resource defense polygyny, males should be associated with a limiting resource used by females (such as oviposition sites), and should also have the same association with this limiting resource both in the presence and absence of breeding females. Consequently, if males fight for resources or territories, these fights should occur regardless of female presence. On the other hand, in female defense polygyny, critical resources used by females are not expected to be limiting, and males are expected to be attached to females rather than to resources. In these cases, if males fight, these fights should only occur in the presence of breeding females. Since males of some species may shift between two types of polygyny in response to temporal variation in social and environmental conditions (Ostfeld 1987), testing contrasting theoretical predictions is a clear-cut method to understand whether resource defense or female defense prevails in a given polygynous population.

Materials and methods

Study site

The study was conducted in an Atlantic Forest fragment at Intervalles State Park, Southern São Paulo state, southeast-

Table 1 Four predictions from the theory of mating systems that can be used to distinguish resource from female defense polygyny (modified from Ostfeld 1987)

Features	Predictions	
	Resource defense polygyny	Female defense polygyny
1. Availability of the critical resources for females	Limiting	Not limiting
2. Males are associated with the critical resources used by females	Yes	No
3. Males have the same association with a resource both in the presence and absence of breeding females	Yes	No
4. Males fight other males both in the presence and absence of breeding females	Yes	No

ern Brazil. The region has high precipitation levels, with average annual rainfall varying between 2,000 and 3,000 mm/year, and average annual temperature varying between 17°C and 19°C. The altitude in the Park ranges from 60 to 1,095 m, and the weather is mainly subtropical, with a warm-wet season lasting from October to March and a cold-dry season from April to September. The *A. proximum* population studied here was found on the vegetation at the Caçadinha Track (24°14' S; 48°04' W; 800 m a.s.l.), a trail that follows a small river inside the forest. The river is approximately 5 m wide and is flanked by abundant vegetation that sometimes partially covers the river bed.

Behavioral observations

We studied the reproductive behavior of *A. proximum* by inspecting monthly, from July 2003 to December 2005, a 200-m-long transect along the river. Each monthly sample consisted of monitoring the study site for four consecutive days, each consisting of approximately 12 h of observations, carried out between 08:00 h and 00:00 h. We conducted nocturnal observations with a flashlight covered by a red filter to avoid disturbing the harvestmen (see Buzatto et al. 2007 and references within). For the whole period of 30 months, the total duration of behavioral observations in the field was nearly 1,440 h.

We measured (to the nearest 0.01 mm) every adult of *A. proximum* ($n=484$ males; $n=547$ females) for the length of the following structures: (a) dorsal scute, (b) fourth right leg femur, and (c) second right leg. At the time of the first capture, we also recorded if the individuals had any amputated legs or pedipalps. Like all other representatives of the suborder Laniatores, *A. proximum* does not autotomize legs (Gnaspini and Hara 2007), thus any partially or totally amputated appendage indicates injury. Next, we individually marked the harvestmen applying enamel paint (Testors Co., Rockford, USA) to the dorsal scute and to the femur of the third and/or fourth pair of legs. This marking procedure has been widely used in harvestmen studies because it does not affect the behavior of these organisms (see Buzatto et al. 2007 and references within). Throughout the field observations, we continuously recorded all relevant behavioral events as suggested by Martin and Bateson (1986). The observational data obtained in this part of the study were used to test the predictions of feature 4 in Table 1.

We also conducted approximately 800 h of focal observations on 29 *A. proximum* harems between December 2006 and March 2007. These harems were composed of one territorial male and up to six egg-guarding females (see “Results”). Furthermore, we intensively monitored four of these harems, carrying out six scan samplings per day (at 08:00, 11:00, 14:00, 17:00, 20:00, and 23:00 h) for

approximately 20 consecutive days, starting when the first female of each harem began to oviposit. During each scan, we recorded how close the territorial male was to each of the egg-guarding females in his harem. The distances recorded were categorized as follows: male not present (score 0), less than 1 m from the closest female (score 1), less than 20 cm from a female (score 2), less than 5 cm from a female (score 3), or copulating with a female (score 4). Scores 2 and 3 are interpreted here as mate guarding (see Fig. 3b), whereas score 1 refers to territorial patrolling activity, when a male is walking around what we suppose to be the periphery of his territory. We later plotted the daily average of these distance categories for each female in four charts (one for each harem) in order to visualize how the territorial male divided his time among the females from his harem. Based on our scan samplings, we also calculated the frequency that territorial males were observed patrolling their territories, guarding individual females, and far away from their harems (when they were not present). We used a *G*-test to contrast the total frequency (sum of the four territorial males) of these three activities between our focal males and 12 territorial males that had no females inside their territories selected at random in the population. This analysis was used to test the prediction of feature 3 in Table 1.

Oviposition sites and quality of territories

In order to test if the oviposition sites are limiting to females (feature 1, Table 1), we identified all plant species (thereafter called host plants) that were used at least once by *A. proximum* females in our 200 m transect during the reproductive season that lasted from September 2003 to April 2004. Afterwards, we sampled the relative abundance of all host plants by recording the number of individuals of each host plant in the transect. We used a *G*-test to contrast host plant abundance with their use by females.

To test if males defend territories that contain the host plants preferred by females (feature 2, Table 1), we created an index of territory quality (ITQ) based on the composition of plants inside them. To calculate the ITQ, first we ranked each host plant species, assigning the score 1 to species in which only one *A. proximum* clutch was found, and 8 to species in which the greatest number of clutches was found. Host species equally used as oviposition sites received the same score (see Electronic supplemental material S1). Secondly, we identified and counted the number of individuals of each host plant inside each one of the 29 territories studied between December 2006 and March 2007. Next, we obtained the ITQ by calculating the weighted arithmetic mean of the host plants' scores inside each male territory. Finally, we contrasted the ITQ of each male territory with the ITQ of an adjacent control area of similar size using a Wilcoxon-paired test. We measured the

size of each territory as the area of the smallest convex polygon whose vertices were defined by the exact positions where territorial males were seen during the breeding season. Given that territories were always located along the river, we positioned each control area 1.5 m upstream or downstream (directions chosen randomly by the flip of a coin) from the border of its territory counterpart.

Results

Reproductive seasonality

Between July 2003 and December 2005, we found 424 clutches of *A. proximum* in the study transect. The reproductive activity in the population is markedly seasonal: one minor peak occurs between October and November (beginning of the warm-wet season), and a major peak takes place in February (end of the warm-wet season; Fig. 1). This pattern was observed in both reproductive seasons studied (2003–2004 and 2004–2005), and the number of clutches per month was positively related to the local monthly rainfall (Spearman, $r_s=0.820$, $P=0.001$; $n=12$ for the 2003–2004 season; and $r_s=0.843$, $P<0.001$; $n=12$ for the 2004–2005 season). There was also a positive relationship between the number of clutches found each month and the monthly average local temperature (Spearman, $r_s=0.664$, $P=0.018$; $n=12$ for the 2003–2004 season; and $r_s=0.737$, $P=0.006$; $n=12$ for the 2004–2005 season).

Host plant selection

Among all females found guarding eggs, 338 (80%) had laid clutches on the underside of leaves, 73 (17%) had laid clutches on boulders, and 13 (3%) had laid clutches on the

surface of tree trunks, always close to the river margins (20–300 cm). Regarding the clutches laid on leaves, *A. proximum* females used 25 host plant species as oviposition sites, but the frequency of utilization varied among these plant species (see Electronic supplemental material S1). Three species comprised together 50% of the host plants used by the females: the ferns *Olfersia cervina* (16.4%) and *Blechnum binervatum* (10.2%), and the tree *Gomidesia schaueriana* (23.4%). Although these species were frequently used as oviposition sites, they were not the most abundant host plant species in the transect, together comprising only 9.6% of the individuals (Fig. 2a). On the other hand, some very abundant host plant species, such as *Dichorisandra thyrsiflora* and *Calathea communis*, were seldom used as oviposition sites (Fig. 2a). Thus, host plants were clearly not used according to their abundance in the study transect ($G\text{-test}=226.94$; $df=24$; $P<0.001$), further confirming that females show preference for some plant species.

Male territoriality

The beginning of the diurnal activity of males, which is associated with patrolling behavior, occurred in September (reproductive season 2003–2004) and August (reproductive season 2004–2005; Fig. 1). Individual males spent on average 61.1 days (SD=44.9 days; $n=78$) patrolling a territory on the vegetation. The areas patrolled by males and used as oviposition sites by females had higher ITQs (median 5; range 1–8; $n=29$) than the adjacent control areas (median 2; range 0–8; $n=29$; Wilcoxon, $Z=-4.065$; $P<0.001$; Fig. 2b). After April, which corresponded to the end of the reproductive season both in 2004 and 2005, males were no longer found on the vegetation during daylight (Fig. 1). From May to July, individuals of *A. proximum*

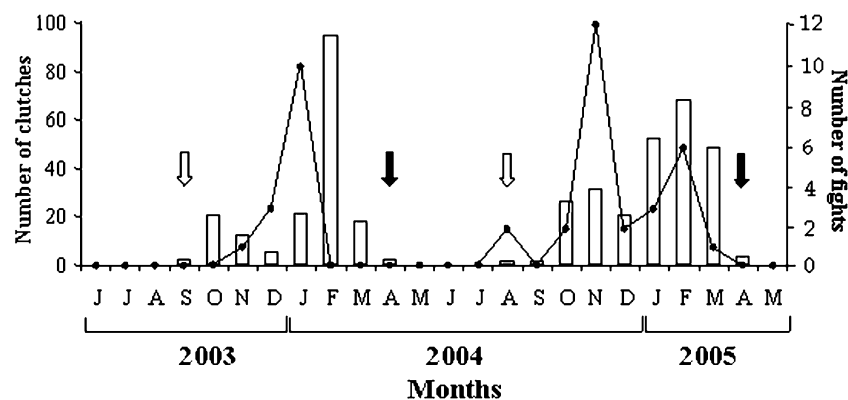
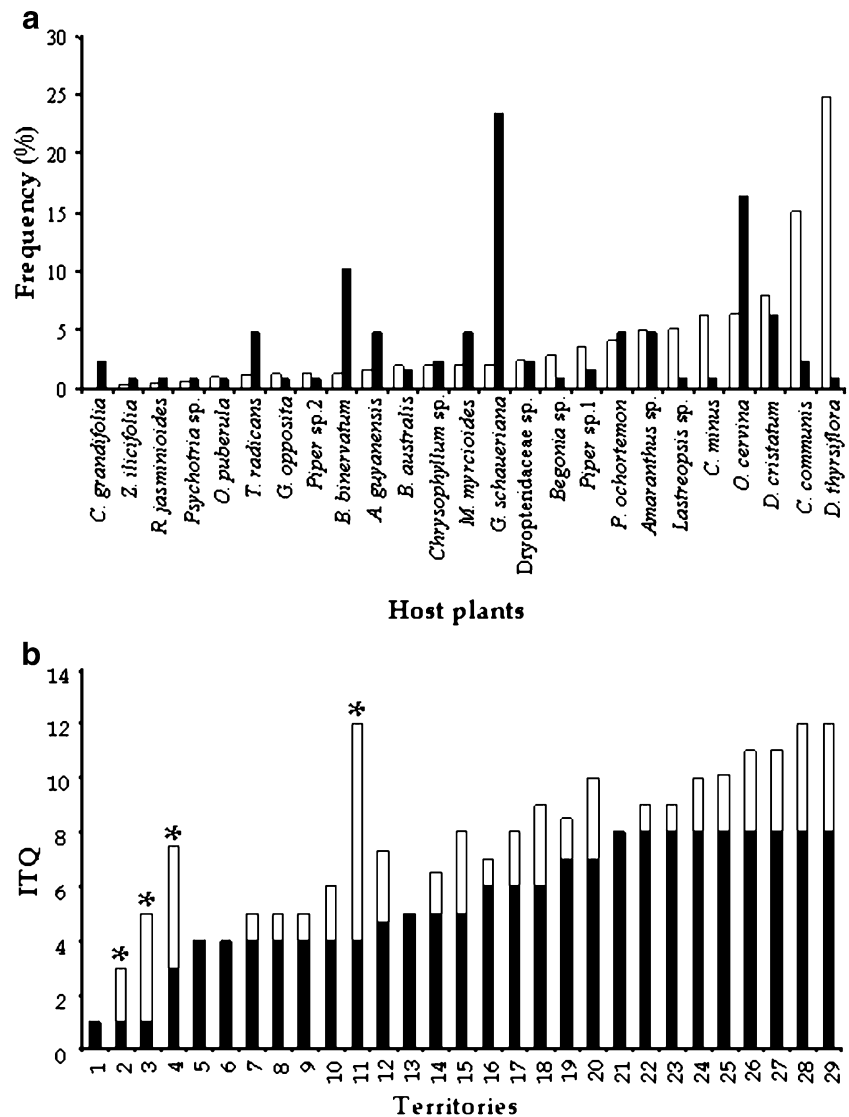


Fig. 1 Reproductive seasonality of the harvestman *Acutisoma proximum* at Intervalles State Park, southeastern Brazil. White bars represent the number of clutches found each month (from June 2003 to May 2005). The white arrows indicates when males' territorial patrolling activity began in both reproductive seasons, and the black

arrows indicates when such activity ended. The line represents the number of male territorial fights recorded for each month. Note that in both reproductive seasons fights were most common before the peak of oviposition activity in February

Fig. 2 **a** Host plant selection by ovipositing *Acutisoma proximum* females. The white bars represent the relative abundance of each host plant species, whereas the black bars represent their relative frequency of utilization by females. **b** Indexes of territory quality (ITQs) for 29 *A. proximum* males' territories (black bars) and their respective adjacent control areas (white bars). The great majority of the territories had higher ITQs than their control areas, with the exceptions of the territories marked with asterisks



(both males and females) were rarely found in the study area, and the few active individuals were only found at night.

During the reproductive season, whenever two large males met, they engaged in ritualistic fights ($n=42$) during which they faced each other, holding the second pair of legs laterally extended, the first pair of legs retracted above the body, and the pedipalps raised (Fig. 3a). In this position, each male repeatedly hit the opponent with the tips of the second pair of legs, using them as whips (Fig. 3a). Males may also attack the opponent's first pair of legs with rapid pedipalp strikes ($n=14$ fights). Male fights lasted on average 31.0 ± 35.0 min ($n=22$ fights followed from the beginning), and 27 out of 42 fights were observed during daylight. There was no relationship between the quality of the territories (measured as their ITQ) and the occurrence of male fights inside them (logistic regression, $\chi^2=1.905$, $df=1$, $P=0.168$). Male fights occurred mainly in the first

months of the reproductive season, with a marked peak before the period of most intense oviposition activity (Fig. 1). Nine out of all observed fights occurred early in the reproductive season, without any reproductive female nearby.

Most fights ended with a winner ($n=25$), which usually behaved more aggressively during the interaction, i.e., striking the opponent with the pedipalps more frequently. Moreover, winner males remained in the place where the fight had occurred during the following days, and sometimes even remained there for months. Loser males left the area soon after the fight ended, sometimes ($n=14$) with the winner in pursuit for up to 3 m on the vegetation. There were no significant size differences between loser and winner males (Table 2). Although we never observed a male physically injuring another one in a territorial fight, we did find several *A. proximum* adults with amputated legs and pedipalps. If those injuries were caused by male fights,

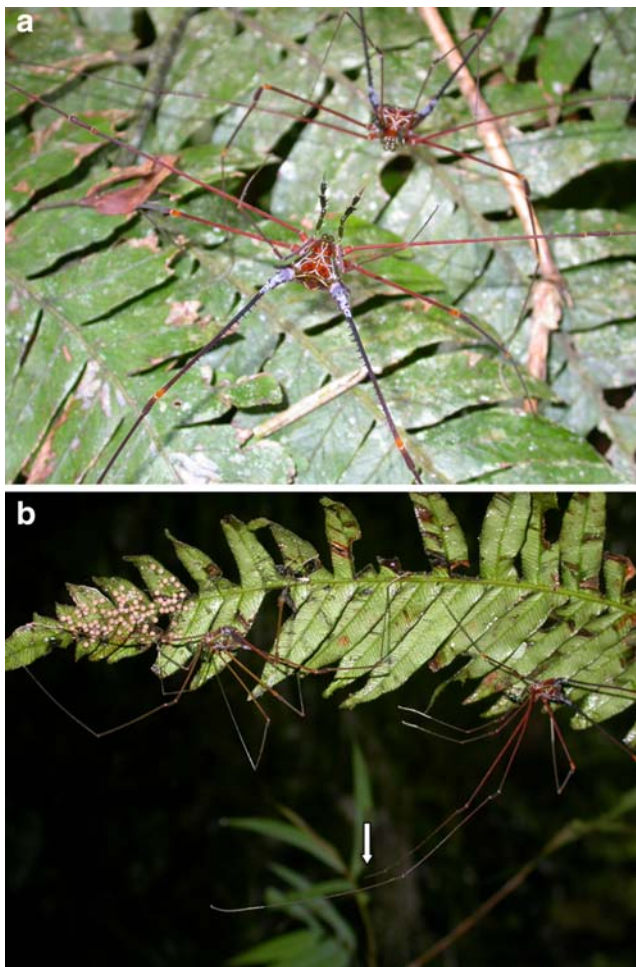


Fig. 3 **a** Two *Acutisoma proximum* males in fighting position, facing each other with the second pair of legs laterally extended, the first pair of legs retracted above the body, and the pedipalps raised. **b** A male of *A. proximum* (right) mate guarding an ovipositing female (left). The male's second pair of legs (pointed out by the arrow) is extended towards the female, and periodically touches her

we would expect to find them more frequently in males than in females. In fact, amputations were much more common in males (10.8% with amputations; $n=484$) than in females (2.7%; $n=547$; $\chi^2=22.063$, $df=1$, $P<0.001$).

Mating and female defense by males

During the period of most intense fighting activity, but mainly later in the season, males' territories were visited by ovigerous females at night. These females visited the territories, mated with the territory owners, and subsequently oviposited inside the territories, constituting harems that ranged from one to six females (median of two females; $n=29$ harems). Males with longer legs II had a greater number of females within their harems. However, there was no correlation between the resource value of males' territories (measured as their ITQ) and the length of the owners' legs II or between the resource

value of the territories and the number of females inside them (Electronic supplemental material S2).

Within the harems, we observed 141 copulations, which lasted on average 345 ± 233 s ($n=32$ copulations followed from the beginning). After copulation, the male was generally driven away by the female, but stayed 20 cm from her apparently mate guarding for a median time of 8 h (range 4–42 h; $n=51$; Fig. 3b). During mate guarding, the male occasionally touched the female dorsum and/or legs with his second pair of legs (Fig. 3b).

Territorial males seem to divide their mate-guarding activity among the females in their harems. In the four harems in which we conducted quantitative observations, it was clear that territorial males spent most of the reproductive season very close to the females that had recently laid eggs in their territories (Fig. 4). As the days passed and the females that arrived first finished their oviposition activities, the territorial males quitted visiting these females and spent more time close to the newer females that arrived in their territories (Fig. 4). When territorial males were not mating or closely mate guarding, they were generally observed patrolling the territory (Fig. 4).

The frequency of territorial patrolling by males before the arrival of reproductive females (33.3%) was very similar to the frequency of territorial patrolling after females laid eggs in the territories (34.5%). However, after females' arrival, males left their territories less frequently (24.1%) than when females were absent (66.7%). The extra time that males spent inside their territories was invested in guarding individual females (41.6%). Therefore, the frequency of these three activities markedly differed between the beginning of the reproductive season, when males' territories had not yet received the visit of ovigerous females, and the second half of the season, when males' territories contained several breeding females ($G\text{-test}=66.679$; $df=2$; $P<0.001$).

Discussion

Reproductive seasonality and host plant selection

Reproductive seasonality seems to be fairly common in harvestmen (Curtis and Machado 2007), and the pattern

Table 2 Size features (mean \pm SD) of winner and loser males in territorial fights ($n=20$) of the harvestman *Acutisoma proximum*

Male trait (mm)	Winner	Loser	Statistics
Dorsal scute length	7.82 ± 0.34	7.80 ± 0.36	$t=0.533$, $P=0.300$
Right fourth femur length	25.87 ± 1.12	26.17 ± 1.49	$t=0.668$, $P=0.256$
Second right leg length	132.48 ± 6.98	132.50 ± 9.27	$t=0.126$, $P=0.450$

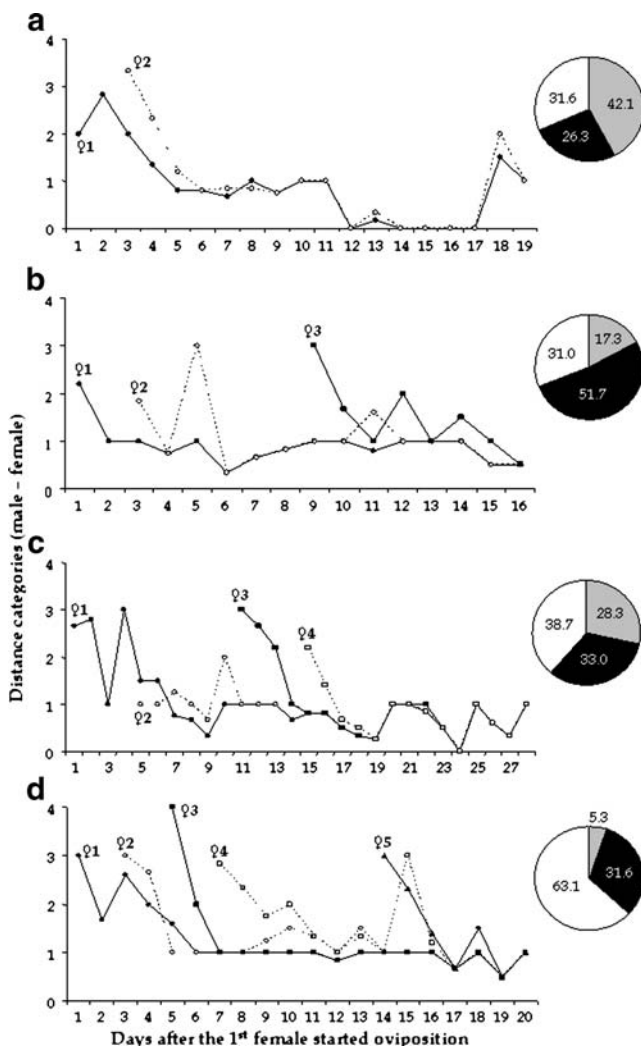


Fig. 4 The daily average distance between the territorial male and each female in his harem varies along the days of the reproductive season in the harvestman *Acutisoma proximum*. The distances were categorized as follows: male not present (score 0), less than 1 m from the closest female (score 1), less than 20 cm from a female (score 2), less than 5 cm from a female (score 3), or copulating with a female (score 4). We monitored four different harems, with respectively: **a** two, **b** three, **c** four, **d** and five egg-guarding females. Each female is represented by a different line, all of them numbered according to their arrival order in the harems. The circular charts on the right side of each graph represent the frequency (%) of observations in which the territorial males were mate guarding (white), patrolling their territories (black), and out of their territories, i.e., not present (gray)

recorded here for *A. proximum* is similar to what was previously described for *A. longipes* (Machado and Oliveira 1998), *Goniosoma spelaeum* (Gnaspini 1995), and *G. albicriptum* (Willemart and Gnaspini 2004), three closely related species of the subfamily Goniosomatinae (Gonyleptidae). These species have two peaks of reproductive activity throughout the year: a minor one in the beginning of the warm-wet season and a major one at the end of the

same season. Furthermore, similar to what was observed for *A. longipes* (Machado and Oliveira 1998), the number of clutches of *A. proximum* found in each month at the study site was strongly correlated with specific environmental conditions, such as local monthly rainfall and temperature. However, when compared to the other goniosomatine mentioned above, *A. proximum* had the shortest reproductive period, lasting from October to March. Given that *A. proximum* is the only species in the group known to regularly reproduce outside caves in relatively exposed microhabitats, females of this species are probably more exposed to the climatic harshness of the cold-dry season, and hence can only reproduce during a narrower period.

Leaves were the most frequent oviposition site used by *A. proximum* females, which showed a marked preference for certain host plant species (Fig. 2a). Females of the Neotropical *Bourguyia hamata* also choose very specific oviposition sites, using almost exclusively the leaf-tube of the bromeliad *Aechmea nudicaulis* (Machado and Oliveira 2002). Additionally, females prefer bromeliads with longer rosettes, which accumulate more water and have small amounts of debris inside them. These features probably promote a better microhabitat for egg development and may increase offspring survival (Osses et al. 2008). The reasons for the preference for some host plants exhibited by *A. proximum* females, however, is not that obvious. The three most often used host plants are not closely related (two ferns and one tree), nor do they possess similar leaf morphology (including shape, surface texture, and pilosity). Moreover, the preferred host plants have also completely different habits: *Olfersia cervina* grows in soil, *Blechnum binervatum* is epiphytic, and *Gomidesia schaueriana* is woody. Consequently, it is unlikely that females choose the host plants according to some conspicuous morphological trait they possess. An alternative hypothesis is that preferred host plants are the ones with more long-lived leaves, a feature that would minimize the risks of losing a clutch due to the abscission of the leaf on which the eggs were laid. Indeed, *O. servina* and *G. schaueriana* seem to have quite long-lived leaves. Nevertheless, several abundant host plants in the study site, including *Calathea communis* and *Philodendrum ochrorhemon*, also possess long-lived leaves, but were rarely used by females. Thus, this hypothesis is also incapable of satisfactorily explaining the females' preference for certain host plants. The reasons why they prefer some host plants over others remain unknown and deserve further investigation.

Nonetheless, assuming that host plant selection evolved before male territoriality in *A. proximum*, female preference for certain plants has important implications for the mating system of this harvestman species. Given that the preferred host plants are used much more frequently than it would be expected by their availability in our study transect, they are

likely to be critical resources that limit females' reproduction, as predicted in a resource defense mating system (feature 1, Table 1). Moreover, preferred host plants probably represent predictable resources where females will aggregate at the time of breeding, so that males benefit from defending and monopolizing these plants as a means of securing mates (Emlen and Oring 1977; Thornhill and Alcock 1983). Perhaps by aggregating, females also intensify male competition and indirectly select the best males capable of succeeding in a harem-like mating system (Wiley and Poston 1996).

Mating system

In opposition to the strictly nocturnal activity of most gonyleptid harvestmen, *A. proximum* males are also active during the day. Especially between November and January, males spend most of the day patrolling and fighting for territories on the vegetation. Territorial behavior has been previously described for *A. longipes*, whose males defend small areas on cave walls where females lay their eggs (Machado and Oliveira 1998). Although *A. longipes* males have been observed patrolling their territories, detailed descriptions of male fights in species of *Acutisoma* were not available until the present study. In spite of apparently being ritualized fights that normally consist of mutual assessment of the opponents' condition by each contestant, the fights of *A. proximum* may also result in physical damage to contestants judging from the fact that males were more frequently found with amputations than females. This sexual bias in the frequency of amputations could also be caused by the increased exposure of males to predators due to their territorial activities during daylight. However, all known harvestmen predators at the study site, including opossums, wandering spiders, and toads (Cokendolpher and Mitov 2007), are active at night, when both territorial males and females are found exposed on the vegetation. Moreover, males placed together in the same vial generally end up with leg amputations (BA Buzatto unpublished data).

Despite their aggressiveness, winning *A. proximum* males were not statistically larger than losers (at least for three measures of size, see Table 2) and it is likely that, as previously observed for the harvestman *Leiobunum vittatum*, whose males defend mating territories on rocks (Macías-Ordóñez 1997), residency is more important than the physical attributes of both contestants. Because winning males usually return to the original area where the fight begun, we conclude that males of *A. proximum* possess well-defined territories on the vegetation during the reproductive season. Males began patrolling and fighting for these territories on the vegetation at the beginning of the reproductive season, before females arrived to reproduce on these areas. Some fights even occurred between males with

no females in their territories, which would be expected only in a resource defense polygynous mating system (feature 4, Table 1). Moreover, males' territories had higher ITQs than adjacent control areas, which indicates that males establish their territories in patches of the vegetation where the host plants preferred by females are more abundant. Thus, as in a typical resource defense polygyny mating system, *A. proximum* males are clearly associated with a critical resource used by females, i.e., oviposition sites (feature 2, Table 1). By defending territories that contain the preferred host plants, males may monopolize later mating access to ovigerous females.

Recently, Kelly (2008) conducted a quantitative review of resource defense polygyny, in which he proposed three scenarios with possible mechanisms driving either a positive, negative, or no correlation between resource value and resource holding potential. Our findings indicate that there is no correlation between the resource value of males' territories (measured as their ITQ) and their resource holding potential (measured as the length of males' legs II) in *A. proximum*. However, the longer the sexually dimorphic leg II of the males, the more egg-guarding females were found in their harems (an indirect measure of the males' reproductive success). These findings suggest that, in *A. proximum*, male phenotype is more important for female choice than the value of the defended resource. Males with longer legs II may be preferred by ovigerous females that visit different territories, either because leg size is an indicative of male quality or because males with longer legs II perform copulatory and post-copulatory courtship more effectively.

After females arrived and copulated, *A. proximum* males concentrated their patrolling activity on that part of the host plant where individual females had laid their eggs. We observed the same host plant (a large *Gomidesia* tree) being occupied by three distinct territorial males, each of them defending a different harem in a different part of the host plant (BA Buzatto unpublished data). At this stage, male behavior seems to shift to a female defense polygynous mating system, like that described for the coreid *Acanthocoris sordidus*, whose males defend the small portions of the host plant where females aggregate (Fujisaki 1981). A rigorous test of this shift to female defense polygyny in *A. proximum* would require the experimental removal of females from the male territory. The prediction from a female defense polygyny is that males would leave their territories following the experimental removal of females. Although we did not formally test this hypothesis, we did show that the association of *A. proximum* males with the reproductive resources used by females is affected by the presence of females because, after females' arrival, males leave their territories less frequently and spend more time inside them guarding individual females (Fig. 4). If males

adjust their position and attachment to the territory in response to the presence of females, then female defense probably plays an important role in the species' mating system (feature 3, Table 1).

Given that *A. proximum* females may take several days to complete oviposition (Buzatto et al. 2007) and that some males furtively invade the harems and sneak copulations with egg-guarding females during the oviposition period (Buzatto et al. in preparation), mate guarding in the species is probably an adaptive trait that functions to secure the paternity over all the eggs laid by the female. In fact, our intensive scan samplings on four different harems revealed that mate guarding by territorial males is focused on those females that have most recently arrived in their territories and were still laying eggs (Fig. 4). This male strategy is analogous to defending individual females in sequence, as in some other animals that present female defense polygyny (e.g., Robinson 1986). Moreover, this strategy also indicates that, at this point, males of *A. proximum* are more attached to females than to the reproductive resources used by them.

Concluding remarks

Although many studies classify the mating system of arthropod species as female defense or resource defense polygyny, the boundary between these two categories is slight and most species do not fall neatly into either of them or fall in both (see examples in Ostfeld 1987). Here, we described the mating system of the Neotropical harvestman *A. proximum*, for which the dichotomy between female defense and resource defense polygyny can be particularly misleading. Our results indicate that the *A. proximum* mating system can only be precisely described as follows: in the beginning of the reproductive season, males defend territories on the vegetation where females lay their eggs, resembling a resource defense polygyny. Over the course of the reproductive season, however, the mating system shifts to female defense polygyny after females arrive and aggregate on small parts of the host plants. At this point, males start guarding sequentially individual females inside their territories. Although shifts between different types of polygynous mating system are known to occur in some insects (examples in Thornhill and Alcock 1983), to the best of our knowledge, this is the first time that this phenomenon is described for arachnids. Our findings reveal that we should be cautious when defining the mating system of a species based on few observations concentrated in a brief period.

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