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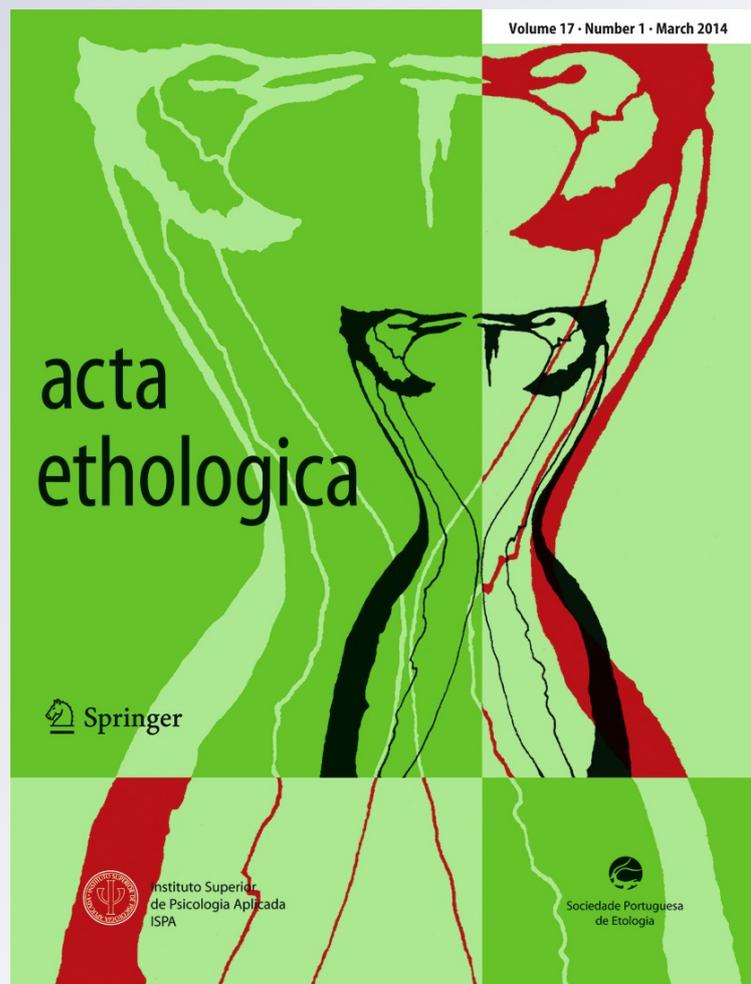
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Mating behavior of a Neotropical arachnid with exclusive paternal care

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Abstract Paternal care has independently evolved in several arthropod lineages, but mating interactions have been described in detail for only a few species. Here, we describe the mating behavior of *Iporangaia pustulosa*, a Neotropical harvestman with exclusive paternal care. We obtained the data under natural conditions, and the results are based on 51 mating interactions. Females performed mate searching exclusively, locating and approaching stationary caring males on the vegetation. Upon arrival, nearly 33 % of the visiting females were promptly attacked and repelled by the males without copulating. We did not observe pre-copulatory courtship, and males, exclusively, performed copulatory courtship. Nearly 30 % of the females that copulated with caring males left the clutches without laying any egg. Finally, several behavioral actions reported here are remarkably similar to those observed in the sex-role-reversed harvestman *Zygopachylus albomarginis*, for which there is strong evidence of both male and female mate choice. In conclusion, our results provide evidence of male aggressive rejection of mates and female abandonment of clutches without ovipositing, suggesting that individuals of both sexes may evaluate and select mating partners.

Keywords Copulation · Courtship · Male aggression · Mate search · Mutual mate choice · Oviposition · Sex roles · Sexual selection

Introduction

The theoretical framework first put forth by Trivers (1972) to explain the evolution of sex roles postulates that biases in the operational sex ratio (OSR) lead to intense intrasexual competition among individuals of the over-represented sex and choosiness among individuals of the limiting sex. Although most mate choice studies (both empirical and theoretical) have focused on female preferences (Kraaijeveld et al. 2007; Clutton-Brock 2009), recent mathematical models have challenged classical foundations of behavioral ecology, highlighting alternative conditions that may determine sex roles (e.g., Kokko and Johnstone 2002; Kokko and Jennions 2008; Barry and Kokko 2010). For instance, these new models suggest that male mate choice may occur under a broader combination of conditions than previously realized, even under conventional sex roles and male-biased OSR (e.g., Houston and McNamara 2005; Kokko and Jennions 2008; South et al. 2012). In fact, mate choice is likely to be influenced not only by parental investment and potential reproductive rates, but also by the relative costs and benefits of choosiness, the mating history of the individuals, mate encounter rates, sex-specific mortalities, and variation in mate quality (Bonduriansky 2001; Kokko and Mappes 2005; Barry and Kokko 2010; Edward and Chapman 2011).

The list of species in which males heavily invest in nuptial gifts or in parental care has quickly increased in the last decades, revealing cases of female–female competition for access to males and even exclusive male mate choice (e.g., Wilson et al. 2003; Bain and Govedich 2004a; Wells 2007; Gwynne 2008). Among arthropods, exclusive paternal care

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has evolved independently in at least 17 lineages (Tallamy 2001; Machado and Macías-Ordóñez 2007; Requena et al. 2010; Proud et al. 2011; Villareal-Manzanilla and Machado 2011), but detailed descriptions of reproductive interactions between males and females are available only for a few species belonging to distantly related taxa: the harvestman *Zygopachylus albomarginis* (Mora 1990), some giant water bugs of the family Belostomatidae (Smith 1997; Kight et al. 2011), and a few sea spiders of the class Pycnogonida (Bain and Govedich 2004a). These species show different degrees of sex role reversal (sensu Vincent et al. 1992), with evidence of female exclusive initiation of courtship behavior reported for *Z. albomarginis* and the sea spider *Propallene saengeri* (Bain and Govedich 2004b). Moreover, females of these two species may engage in aggressive interactions which are supposedly over access to potential mates (Mora 1990; Bain and Govedich 2004b). From the males' perspective, mating interactions seem to always result in oviposition in sea spiders and water bugs, both groups in which males carry large clutches attached to their body (Smith 1997; Bain and Govedich 2004b). On the other hand, female rejection without oviposition has been reported for *Z. albomarginis*, in which males build and maintain mud nests used by females to lay eggs (Mora 1990).

Like most arthropods with exclusive paternal care, females of the Neotropical harvestman *Iporangaia pustulosa* (Opiliones: Gonyleptidae) undergo continuous gonadotrophic cycles, suggesting that they mature eggs relatively fast (Machado et al. 2004). Male egg-guarding behavior lasts one to four months and plays a crucial protective role in this species, since unprotected eggs suffer intense predation within a few days (Requena et al. 2009). However, females also invest in offspring protection by depositing a thick mucus coat on the eggs just after oviposition (Gnaspi and Lerche 2010), which provides physical protection to the eggs and decreases predation rates by conspecifics (Requena et al. 2009). Despite the reduction in feeding opportunities imposed by paternal care during the caring period, this foraging cost does not negatively affect survival of caring males, since their mortality rate in the field was never higher than non-caring individuals, including males and females (Requena et al. 2012). Additionally, paternal care in *I. pustulosa* does not constrain mate acquisition, so caring males can accumulate eggs from several females in multiple clutches that may have up to 400 eggs (Machado et al. 2004).

In this study, we describe male–female reproductive interactions in *I. pustulosa* as a basis for future studies on sex roles and mate choice in this arthropod species with exclusive paternal care. Our data were entirely obtained under natural conditions in the same population where previous behavioral and ecological studies of this species have been conducted. Although our study is based exclusively on observational data, which would make it difficult to definitively attribute the final mate decision to males, females, or both, we report here some

behavioral actions that are remarkably similar to those observed in the sex-role-reversed harvestman *Z. albomarginis*, for which there is stronger evidence of both male and female mate choice (Mora 1990; Table 1). The descriptive results presented here provide evidence of male aggressive rejection of mates and female abandonment of clutches without ovipositing, suggesting that individuals of both sexes may evaluate and select mating partners.

Materials and methods

We conducted the study in an Atlantic Forest fragment at the Intervales State Park (24°14' S; 48°04' W), in the state of São Paulo, southeastern Brazil. Between February and March 2009, which corresponds to the peak of the reproductive season of this species (Requena et al. 2012), we inspected the vegetation up to 1 m from both margins of a forest stream (approximately 5 m wide) along a transect of 200 m. The marginal vegetation along this transect concentrates almost all clutches and individuals in the studied population (Requena et al. 2012). We located 56 *I. pustulosa* clutches and individually marked each male observed guarding a clutch using enamel color paint applied to their dorsum and hind legs. This marking procedure has been previously used in other studies with the species and has the advantages of not affecting egg-guarding behavior (Requena et al. 2009).

After marking the caring males, we monitored their clutches daily during 30 days, conducting intensive focal observations at night (between 19:00 h and 02:00 h) using a flashlight covered with a red filter to minimize the disturbance to the individuals. In each survey, we spent at least 1 min observing each clutch and looking for females within its vicinity (ca. 50 cm). If we did not find any female approaching the clutch during this 1 min period, we moved to another clutch and started a new observation. When we found a female in the vicinity of a clutch, we conducted focal observations. If the female approached the clutch and interacted with the caring male, we followed their behavioral interactions until she walked away (>1 m from the clutch). In these cases, we classified the interaction as a *complete observation* because we were able to follow the female approach from the beginning. In contrast, when we found a male and a female already interacting at the time we started our observation, we classified it as a *partial observation*. During each night, we inspected every caring male present in the transect in regular intervals of 2 h, and the number of inspections per male in a given night ranged from two to four.

For both complete and partial observations, we also noted the behaviors exhibited by males and females using the sequence sampling method (Altmann 1974). This method consists of observations focused on the description and quantification of behavioral sequences composed of easily

Table 1 Behavioral actions observed during male–female interactions in the harvestman *Iporangaia pustulosa*. The symbol ‘X’ indicates whether members of one sex or both were observed to perform an action pattern

Action pattern	Sex		Definition
	Male	Female	
Pre-copulatory			
Approaching partner		X	The female orients toward the male and walks directly toward him (following Mora 1990).
Attacking	X	X	The individual grabs the front legs of its partner with its spiny pedipalps and bites them on the tarsi and/or leg articulations (following Mora 1990).
Retreat		X	The female does not aggressively respond to the attacks of the male and just moves back, leaving the area.
Soliciting copulation	X		The male grasps the female's pedipalps using his own pedipalps and raises the anterior portion of the female's body, putting their ventral sides in close contact (<i>grasping</i> sensu Macías-Ordóñez 1993).
Copulatory			
Copulation	X	X	Male and female face each other, with pedipalps intertwined and their bodies raised. In this position, the male introduces his penis into the female's genital opening (following Mora 1990).
Tapping genitalia	X		The male intensely and repeatedly touches the base of his penis using the first pair of legs during intromission.
Tapping partner	X		Similar to <i>tapping genitalia</i> , but the touches are directed to the female's leg.
Terminating copulation		X	The female pushes back its body, promoting the removal of the penis from her genital opening.
Post-copulatory			
Quiescent		X	Pauses in which the female remains in the same position for more than 10 s (following Mora 1990; Fig. 2b).
Manipulating ovipositor		X	The female everts the ovipositor and manipulates it using her chelicerae.
Walking around		X	The female walks around the clutch, on the same leaf or nearby (ca. 50 cm).
Directing female	X		The male uses his second pair of legs to hold some of the female's legs and directs her to the leaf apex (Fig. 2a).
Inspecting clutch	X	X	The individual touches the eggs at the border of the clutch using its front legs, pedipalps, and chelicerae after (in the case of males) or just before oviposition (in the case of females) (Fig. 2c).
Mate guarding	X		The male remains close to the partner, constantly keeping leg contact, usually using the curled tip of his second pair of legs to hold one of the female's leg (following Macías-Ordóñez 1993; Fig. 2b, c).
Ovipositing		X	The female everts the ovipositor, releases an egg that is held at the tip of the ovipositor, lowers the body so that her ventral surface is close to the border of the clutch, and inserts the egg at that position (modified from Macías-Ordóñez 1993).
Abandoning clutch		X	The female leaves the caring male, walking a distance further than 1 m from the leaf containing the clutch.

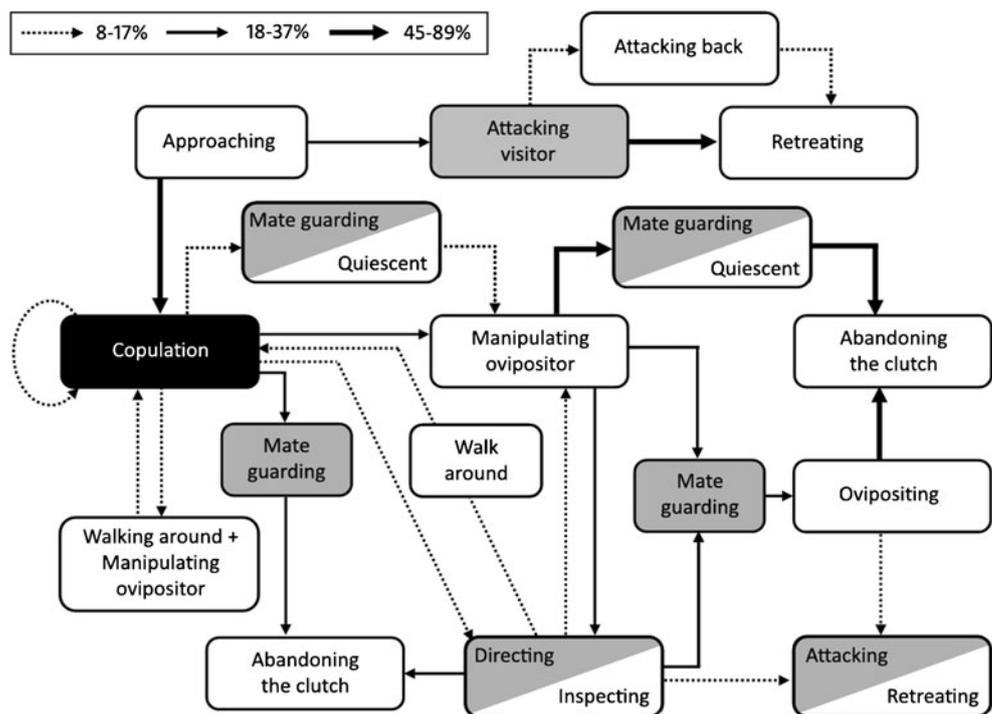
recognizable behavioral actions, which are described in detail in Table 1. Following Mora (1990), we created a flow chart to describe male–female interactions based on all behavioral sequences observed in the field. During male–female interactions, we also quantified the duration of copulation, the period between copulation and oviposition, and the oviposition. Finally, in order to improve our quantitative dataset, we also report the results obtained by sporadic observations during fieldwork conducted for other projects for five previous breeding seasons (between 2003 and 2007).

Results

We observed a total of 51 mating interactions, of which 21 were complete (seven in 2009 and 14 in previous breeding

seasons) and 30 were partial observations. During the systematic inspections conducted in 2009, we observed sexual interactions at least once for 21 of the 56 caring males marked at the beginning of our study. For a subset of these males ($n=6$), we observed them interacting with different females more than once (range=2 to 5 females for each male). Based on these observations, we characterized 16 action patterns, which are defined in Table 1. Only three of these action patterns were performed by both males and females, namely *attacking*, *copulating*, and *inspecting clutch* (Table 1; Fig. 1). The behaviors performed exclusively by females include *approaching partner*, *retreating*, *terminating copulation*, *quiescent*, *ovipositor manipulation*, *walking around*, *ovipositing*, and *abandoning clutch* (Table 1; Fig. 1). On the other hand, *soliciting copulation*, *penis tapping*, *tapping partner*, and *mate guarding* were exclusive to males (Table 1; Fig. 1).

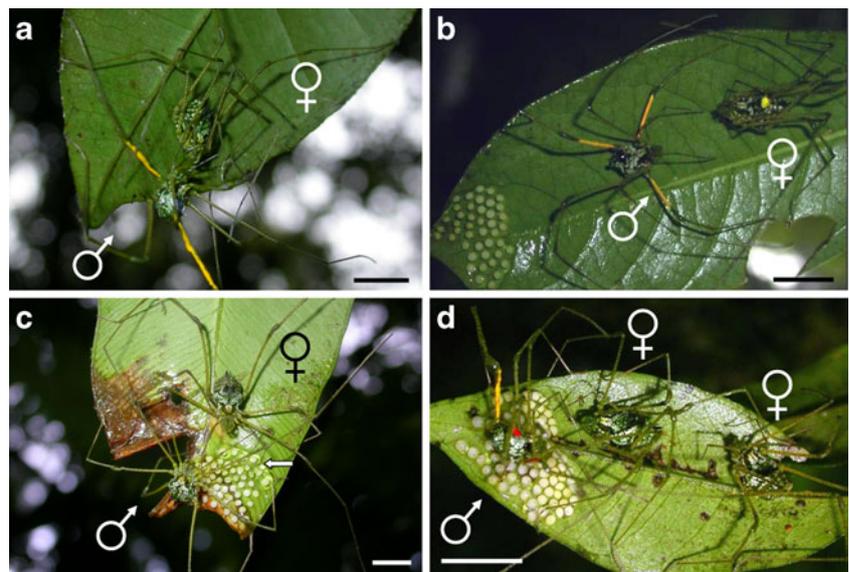
Fig. 1 Flow diagram showing the sequence of mating interactions in the harvestman *Iporangaia pustulosa*. Behaviors exhibited exclusively by females are indicated in white boxes, behaviors exhibited exclusively by males are indicated in gray boxes, and behaviors exhibited by the pair are indicated in black boxes. When more than one behavior is described in the same box, the white part refers to the female and the gray part, to the male behavior. The same behavior (e.g., mate guarding and abandoning the clutch) may appear in more than one box to avoid crossing lines and also to highlight that they can be exhibited at different moments of the mating interaction



In only one occasion, we observed a female approaching a non-caring male that was stationary on the vegetation (Fig. 2a); in all other cases, females approached males that were caring for clutches ($n=50$). The mating interaction between the female and the non-caring male was very similar to those observed between females and caring males (compare, for instance, Fig. 2a, c), and they will be all described in detail in what follows. Every time a female approached a leaf (approaching partner: $n=21$ complete observations; Fig. 1), the male quickly moved toward her. This pre-mating stage was always fast, never lasting more than 30 s, and resulted either in the immediate attack by males ($n=7$ observations,

33.3 % of the total) or in prompt copulation ($n=14$ observations, including the non-caring male; 66.7 % of the total), without any noticeable pre-copulatory courtship (Fig. 1). Caring males aggressively attacked females with their spiny pedipalps, in an apparent attempt to grab and bite the females' legs. As a possible response to male aggressive behavior, females generally moved away from the clutches (retreating: $n=6$ observations), except once when the female exhibited the same attack behavior against the caring male, but quickly retreated (Fig. 1). After repelled females left the surrounding area, all males returned to their clutches and resumed defensive position.

Fig. 2 Mating behavior of the harvestman *Iporangaia pustulosa*. **a** Non-caring male directing a female to the leaf apex after copulation. **b** After copulation, the pair may stay quiescent for a while close to the clutch, when the male exhibits mate guarding behavior, gently touching the female's legs with his second pair of legs. **c** In cases when the female does not abandon the clutch, she may be directed to the leaf apex, touching the previous eggs and the mucus coat with her first pair of legs (white arrow) and mouthparts. **d** In some occasions, caring males may interact with more than one female simultaneously. Scale bars ca. 1 cm



In the other complete observations in which females approached males but were not immediately attacked by them ($n=14$), copulation always succeeded and followed a rigid behavioral sequence. First, the male *solicited copulation*, which led to the male everting his penis and inserting it into the female's genital opening (*copulating*; Fig. 1). Intromissions lasted up to 180 s (mean \pm SD=139.8 \pm 30.2 s, $n=10$ complete observations). During this period, males held females using their long and spiny pedipalps, occasionally also holding females' legs using the tip of their second pair of legs. In addition, males intensely and repeatedly touched the base of their penis (*penis tapping*: $n=20$, including complete and partial observations) and the first pair of females' legs using their own first pair of legs (*tapping partner*: $n=20$, including complete and partial observations). Females always *terminated copulation* by pushing back their bodies and, consequently, removing the penis from their genital opening ($n=20$, including complete and partial observations). In three occasions, the couple stayed *quiescent* for a short period after the female terminated the copulation (ranging from 60 to 130 s), and then, they started the entire sequence of copulation over again (Fig. 1).

After copulation, males always stayed with their second pair of legs extended frontward, gently touching the female's legs (*mate guarding*: $n=42$, including complete and partial observations; Figs. 1 and 2a–c), except once when the female *abandoned the clutch* as soon as she had terminated *copulation*. Caring males usually held their partners while exhibiting *mate guarding*, but this behavior prevented females from leaving the clutch in only two occasions. Females exhibited a more diverse set of behaviors after copulation (Fig. 1). In most of the observations ($n=30$), they stayed *quiescent* close to the male for a period that lasted up to 5 h (range=0.5–5 h; Figs. 1 and 2b). In four occasions, females moved away from the clutch to another leaf in the close vicinity (*walking around*) and stayed there for a short period (ranging from 10 to 100 min), but always returned to the clutch area, *approached* the caring males, and they *copulated* again (Fig. 1). Females also *manipulated their ovipositor* ($n=13$, including complete and partial observations; Fig. 1) in different moments: right after *copulation* ($n=4$), after a *quiescent* period while males were *mate guarding* them ($n=3$), after *walking around* ($n=2$), or during oviposition ($n=4$).

Females never touched the eggs until the moment that caring males directed them to the clutches' border, after they had copulated (*directing female*: $n=11$, including complete and partial observations; Fig. 1). Upon contact with the clutch, females always manipulated the mucus coat around the eggs using their front legs, pedipalps, and chelicerae (*inspecting clutch*: $n=11$, including complete and partial observations; Figs. 1 and 2c). Consecutively, females started *ovipositing* ($n=6$ observations following female inspection of the clutch and $n=3$ partial observations; Fig. 1). Given

that inspecting females remained close to the clutch, it was difficult to quantify the number of eggs laid and the total time that they actually invested in each oviposition event because we were not sure whether the female was *ovipositing* or just *quiescent*. Therefore, considering only the cases in which we were sure about the female behavior, we were able to time three ovipositions that lasted nearly 8 min per egg.

After copulation, we observed females *abandoning the clutch* ($n=21$, including complete and partial observations; Fig. 1) at different moments of the sexual interactions: right after copulation ($n=5$; 23.8 % of the total); after they had copulated and manipulated their ovipositor ($n=3$; 14.3 % of the total); after they had copulated, manipulated their ovipositor, and inspected the clutch ($n=5$; 23.8 % of the total); or after they had copulated, manipulated their ovipositor, inspected the clutch, and oviposited at least one egg ($n=8$; 38.1 % of the total). In four occasions, after females had touched the eggs and left the leaves containing the clutches, caring males approached the eggs and inspected them (*inspecting clutch*). In two of these occasions, females had also laid eggs and males specifically inspected the newly oviposited eggs for a period that reached 3 h. In the other two occasions, females left without ovipositing, and males inspected the area in the clutch that females had also inspected.

In 17 occasions, we observed more than one female within the vicinity (ca. 30 cm) of a clutch (Fig. 2d). However, we never observed females fighting each other for access to caring males, either close to the clutches or in their vicinity. In 14 of those occasions, the caring male copulated with two females sequentially, and in two observations, the male interacted with three females. In one occasion, six different females surrounded the male at the same time. After copulating with the first female, the male mated a second female, while the first one was observed quiescent or manipulating her ovipositor. In two occasions, we observed the unattended female manipulating one egg in the clutch and, finally, consuming it while the caring male was interacting with another female.

Discussion

Our observations of the mating behavior of the harvestman *I. pustulosa* suggest that both males and females may evaluate and select their partners. Given that caring males remain stationary on the vegetation and usually move within the immediate vicinity (0–2 m) around their clutches (Requena et al. 2012), females are the sex that actively search for mates. The single observation of a female approaching and copulating with a non-caring male reinforces the notion that mate search is accomplished exclusively by females. Moreover, given that females can walk up to 15 m during the breeding season, they are likely to access and copulate with several stationary males in this period (Requena et al. 2012). In the sex-role-reversed

harvestman *Z. albomarginis*, mate searching is also accomplished exclusively by females, which may visit several mud nests built by males (Mora 1990). Both in *I. pustulosa* and *Z. albomarginis*, there are many vagrant non-caring males in the population, but females were never observed copulating with them (Mora 1990; this study).

Upon arrival, nearly 33 % of the *I. pustulosa* visiting females were promptly attacked and repelled by the caring males without copulating. Some of the visiting females were clearly bearing eggs because they showed free tergites spaced out with the intersegmental membrane visible, which is typical of ovigerous females (Machado and Macías-Ordóñez 2007). Therefore, it is reasonable to suppose that at least some of these visiting females were ready to copulate and oviposit. In all cases, rejection occurred very fast and it was not preceded by any behavioral act performed by either the caring males or the visiting females. In fact, the attacking behavior observed for *I. pustulosa* males was similar to that previously reported against potential egg predators that approach the clutch (Requena et al. 2009), and we suggest that this aggressive response is a form of mate selection in caring males. In *Z. albomarginis*, approximately 14 % of the visiting females are also aggressively rejected by males upon arrival in the mud nest. Attacked females never respond to the male's bites (Mora 1990), a passive behavior similar to that reported here for *I. pustulosa* in almost 90 % of the attacks we witnessed (Table 1).

The reasons why some females are attacked in paternally caring harvestman species remain unknown, but it is possible that males evaluate visiting females through close-range volatile chemicals or through contact with tegumentary hydrocarbons (e.g., Weddle et al. 2013), even during brief pre-copulatory interactions, as previously recorded for other arachnids (e.g., Aisenberg et al. 2011). In *Z. albomarginis*, nearly 90 % of the females visit only one or two nests during the breeding season, and some of them may even care for the eggs if the caring male is experimentally removed (Mora 1990). Thus, *Z. albomarginis* males could base their mate decisions on the specific identity of females, recognizing their frequent partners and repelling newcomer females, which probably represent a high risk of sperm competition. For *I. pustulosa*, the risk of sperm competition is likely to be as high as in *Z. albomarginis* because females are able to store sperm from previous copulations in their multiple spermathecae (Moya et al. 2007). Therefore, future studies are necessary to investigate whether repelled females are more likely to have sperm from rival males stored in their spermathecae compared to accepted females.

A second non-exclusive explanation for the aggressive male behavior observed in *I. pustulosa* is related to sperm depletion. In internally fertilizing species, such as insects and harvestmen, the most attractive males in the population can be sperm limited if they monopolize the great majority of the

copulations (e.g., Warner et al. 1995; Preston et al. 2001; see also Kvarnemo and Simmons 2013). Therefore, even though the sperm produced by harvestmen is probably of low energy cost (see discussion in Macías-Ordóñez et al. 2010), we argue that the high mating frequency reported here and the low food intake while caring (Requena et al. 2012) may act together in compromising sperm number of highly attractive caring males. In this sense, the benefits of being choosy are expected to increase (Edward and Chapman 2011), since the indiscriminate mating behavior of males would compromise future mating opportunities with high-quality females (e.g., Härdling et al. 2008). To test this hypothesis, future studies should compare sperm load in the seminal vesicle of males that accept and reject visiting females.

Finally, the aggressive male behavior in *I. pustulosa* may also be related to egg defense, and it has already been proposed to explain why *Z. albomarginis* caring males repel ovigerous females from their nests (Mora 1990). According to this hypothesis, the observed aggression toward visiting females in *I. pustulosa* would represent a protective behavior, since cannibalistic females are one of the most important sources of egg loss (Requena et al. 2009). In fact, although rare, we have observed females consuming eggs while the caring males were interacting with additional females. We also observed some caring males attacking females after they have mated and females were close to the clutch, touching the eggs with their legs and mouthparts. Therefore, male aggression against potential mates could be related to the cannibalistic tendency of females, and rejection would be more likely toward hunger females. Unfortunately, we do not have field data on body condition for the females we sampled in this study, and thus we are unable to test this hypothesis.

Contrary to *Z. albomarginis*, in which females exclusively exhibit pre-copulatory courtship (Mora 1990), in *I. pustulosa* there is no evident behavioral interaction between males and females before copulation. This difference suggests that sex role reversal in *Z. albomarginis* is more evident than in *I. pustulosa*. In both species, however, copulatory courtship is performed exclusively by males, which intensively tap different parts of the partners' body (Mora 1990; this study). Regarding the post-copulatory behavior, there is a marked difference between the two harvestman species: while *Z. albomarginis* males do not touch their partners and remain quiescent (Mora 1990), *I. pustulosa* males always perform what we called mate guarding (Table 1). This behavior does not prevent females from abandoning the clutches, and in 31 % of the cases in which we observed copulation, females indeed left the place without laying any egg. An alternative explanation for the behavior exhibited by males after copulation would be therefore post-copulatory courtship, as has already been suggested for other harvestman species (e.g., Nazareth and Machado 2009). Regardless of the role of the post-copulatory behaviors exhibited by males, our observations show that

copulation is not immediately or necessarily followed by oviposition (Fig. 1), suggesting that females are somehow selecting their partners. The factors that influence oviposition decision in *I. pustulosa* remain unknown, but previous studies of other arthropod species with paternal care suggest that females may base their oviposition decision on different features, including male size, ownership of a nest, presence of eggs in the nest, or the intensity of potentially stimulatory behaviors (e.g., Mora 1990; Gilbert et al. 2010; Nazareth and Machado 2009, 2010).

Given that females seem to be responsible for terminating the copulation, we argue that they may control the duration of copulation and, consequently, the duration of sperm transference. Duration of copulation, in turn, may have severe implications for sperm competition and the number of eggs sired by the males (Simmons 2001), but such information is not available for *I. pustulosa*. Furthermore, there can be a long period during which females manipulate the ovipositor until abandoning the caring male without adding eggs to the clutch (Fig. 1). It has been demonstrated for several arthropods that females can increase longevity or fecundity by acquiring nutrients directly from male seminal fluids (Wagner Jr. 2011; Gwynne 2008). Moreover, there is empirical evidence for a close relationship between the quantity and quality of seminal fluids and male body condition (e.g., Jia et al. 2000; Blanco et al. 2009; Perry and Rowe 2010). We argue that two possible explanations for *I. pustulosa* females manipulating their ovipositor using their mouthparts are the following: (1) they may use substances transferred by the males during copulation to gather direct benefits, as has been suggested for other harvestman species in which males provide nuptial secretions secreted by glands located in the penis (Macías-Ordóñez et al. 2010), and (2) they may acquire information on male quality through substances transferred in the ejaculate, which may be subject to cryptic female choice (Eberhard 1996). Given that the high foraging costs paid by *I. pustulosa* caring males may negatively affect the prospective quality of parental care that they can provide (Requena et al. 2012), females would be selected to accurately evaluate body condition and genetic quality of the caring males before leaving their eggs under their guard.

In conclusion, our qualitative results based on the exhibition of stereotyped behavioral patterns suggest that both males and females show some degree of choosiness in the harvestman *I. pustulosa*. Given that the front legs in this species are known to have sensory organs responsible for the detection of tactile and chemical stimuli (Willemart and Chelini 2007), we argue that these types of cues probably play a decisive role in mutual evaluation during and after mating. These chemical cues may come from the mating partner, signaling body condition or fecundity, as well as from the clutch, indicating the presence or the quantity of eggs. Understanding the mechanisms through which sexual selection works in *I. pustulosa*, however, requires

a more detailed fine-scale quantification of sexual behavior, focusing on how the variation among individuals affects mating interaction outcomes. In this way, the results presented here provide an important baseline for future studies designed to experimentally test theoretical predictions derived from the recent models about sex role evolution using *I. pustulosa* as model system.

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