Sexual conflict in a sexually cannibalistic praying mantid: males prefer low-risk over high-risk females

Romina C. Scardamaglia [a, *], Sandro Fosacheca [a], Lorena Pompilio [a, b]

[a] Departamento de Ecología, Genética y Evolución & IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina
[b] Facultad de Psicología, Universidad de Buenos Aires, Argentina

Sexually cannibalistic species such as praying mantids are an ideal model in which to study sexual conflict since the interests of both sexes under a cannibalistic scenario are clearly opposed. Females gain direct material benefits of feeding on a male, which can in turn boost female reproductive output. Males, on the other hand, pay a high cost when cannibalized since they lose all chance of future reproduction. Here, we tested the hypothesis that males behave so as to reduce the risk of being cannibalized in the praying mantid *Parastagmatoptera tessellata*. Twenty-six males were tested in a choice experiment where two options were presented simultaneously: one aggressive female (signalling high risk of cannibalism) and one nonaggressive female (low risk of cannibalism). We predicted that males would prefer nonaggressive over aggressive females. We found evidence that males are sensitive to the predatory strike of a female towards a conspecific male, showing a strong preference for nonaggressive females based on the time that males spent near each type of female. In addition, the preference index we used was a predictor of mating attempts. We therefore conclude that males' behaviour is adaptive, as it serves to reduce their probability of being cannibalized by females.
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Sexual conflict, the evolutionary divergence in the interests of males and females (Parker, 1979), can drive the evolution of certain traits favourable for one sex but costly to the other. One of the most intriguing conflicts between sexes is sexual cannibalism. Defined as the predation of the male by the female during or following courtship or copulation (Elgar, 1992), this behaviour has been observed in a variety of invertebrate taxa such as spiders, scorpions and praying mantids (Andrade, 1996; Kynaston, McErlain-Ward, & Mill, 1994; Liske & Davis, 1984; Peretti, Acosta, & Benton, 1999; Roeder, 1935). The costs and benefits of sexual cannibalism for each sex depend on the timing of the female's attack relative to copulation. Females gain direct material benefits of feeding on a male, which can in turn boost female reproductive output (Barry, 2013; Barry, Holwell, & Herberstein, 2008; Birkhead, Lee, & Young, 1988). On the other hand, this behaviour portrays a potential cost to females if sperm transfer is interrupted or prevented altogether, as is the case in noncopulatory cannibalism. Males could benefit from being consumed during or after copulation if, as a result,

sperm transfer was prolonged and thereby the proportion of eggs sired by them increased. However, this benefit would apply only if the male's future mating opportunities were scarce, since death otherwise incurs the very high cost of a total loss of future reproduction (Buskirk, Frohlich, & Ross, 1984; Maxwell, 1999a).

If sexual cannibalism poses a net cost to males, then behaviours that reduce the probability of being cannibalized should be selected. Such behaviours have been described in numerous invertebrate species. Males of the nuptial gift-giving spider *Pisaura mirabilis*, for example, display a remarkable death-feigning behaviour as part of the courtship prior to mating with potentially cannibalistic females (Bilde, Tuni, Elsayed, Pekár, & Toft, 2006). Males of the autumn spider *Metellina segmentata* and the golden orb spider *Nephila fenestrata* wait for a prey item to be captured on the web of a female before initiating courtship (Fromhage & Schneider, 2004; Prenter, Elwood, & Montgomery, 1994), while male wolf spiders (*Lycosa tarantula*) approach females for mating only during the daytime, when they are less responsive to prey, instead of during the night (Moya-Laraño, Pascual, & Wise, 2004). In praying mantids, risk avoidance behaviours include trying to elude detection by females, with males ceasing movement upon sight of a female (Barry, Holwell, & Herberstein, 2009; Lawrence, 1992; Roeder, 1935), a slow rate of approach and the tendency of males to approach females from the rear rather than upfront (Barry et al., 2009; Lelito & Brown, 2006; Maxwell, 1999b). Opportunistic

* Correspondence: R. C. Scardamaglia, Laboratorio de Ecología y Comportamiento Animal, Departamento de Ecología, Genética y Evolución & IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina.
E-mail address: rscardamaglia@ege.fcen.uba.ar (R. C. Scardamaglia).

mating by males while a female is feeding has also been reported for different mantid species (Barry et al., 2009; Gemeno & Claramunt, 2006).

In praying mantids, females cannibalize males in approximately 30% of the mating events in nature (Hurd et al., 1994; Lawrence, 1992; Maxwell, 1998; Maxwell, Gallego, & Barry, 2010). Factors known to affect the incidence of sexual cannibalism include female feeding condition ('hunger') and body condition ('fatness'; Barry, Holwell, & Herberstein, 2010). Underfed females are more likely to cannibalize males in *Tenodera aridifolia sinensis* (Liske & Davis, 1987), *Hierodula membranacea* (Birkhead et al., 1988), *Iris oratoria* (Maxwell, 2000) and *Stagmomantis limbata* (Maxwell et al., 2010). Previous work in praying mantids has been directed mainly to studying the response of males to variation in these two factors, presenting males with hungry and satiated females (Lelito & Brown, 2006, 2008) or females differing in body condition (Barry, 2010; Barry et al., 2010). Time of season has also been isolated as a factor affecting male behaviour. Mantids that mature earlier are bigger (Barry, 2013; Prokop & Václav, 2008) but are also more cannibalistic than late-maturing ones, and males approach females more cautiously at the beginning than at the end of the season (Prokop & Václav, 2008). However, the effect of female aggression per se on male behaviour has not been studied experimentally.

The aim of this work was to study male behaviour in response to the risk of cannibalism imposed by females in the praying mantid *Parastagmatoptera tessellata*, a species that occurs in the province of Buenos Aires, Argentina. Sexual cannibalism in this species has been recorded in 22% of mating events in captivity (Avigliano, 2009). Previous studies have shown that *P. tessellata* males adjust their behaviour according to female energetic state, with males preferring females that they have seen consuming a prey item over females that they have not seen consuming a prey item (Avigliano, 2009). In this study, we presented males with the choice of two different females in a laboratory-controlled experiment: one representing a low risk of sexual cannibalism and the other a high risk. Specifically, we studied whether males are sensitive to visual cues that provide information on a female's level of aggression and whether they show risk avoidance behaviour. The cue available to males in our study was the predatory strike by a female towards a conspecific male. We hypothesized that males would behave so as to reduce their risk of being cannibalized and we predicted that they would prefer nonaggressive over aggressive females.

METHODS

Collection and Rearing

The praying mantids were raised in the laboratory from oothecae collected from wild populations in Buenos Aires province, Argentina. Oothecae were incubated at 25–30 °C until egg hatching, which occurred after 32–60 days. Nymphs were reared individually in 150 ml plastic containers during the first three or four instars and then transferred to 450 ml plastic containers. Wooden sticks were placed inside the rearing containers, providing a substrate for perching. Mantids were fed *Drosophila melanogaster* ad libitum and misted with water daily, and after about 8 weeks the diet was switched to two juvenile crickets (*Acheta domesticus*) three times a week. Adult emergence occurred approximately 13 weeks after hatching. The adults ($N = 174$) were visually isolated from each other by placing sheets of paper between the rearing containers to avoid the development of any preference prior to the experiment. Both male and female adults were fed two juvenile crickets three times per week, which constitutes an abundant diet for this species (Avigliano, 2009). Room temperature (25 ± 1 °C)

and photoperiod (12:12 h light:dark) were maintained constant during rearing.

The praying mantids used in the choice experiments were all sexually mature and virgin adults. It has been reported that individuals of different species of praying mantids reach sexual maturity approximately 10–16 days after the final moult (Birkhead et al., 1988; Kynaston et al., 1994; Roeder, 1935). Because information on the reproductive biology of *P. tessellata* was lacking, we carried out exploratory sessions to determine the age at which the individuals of this species start showing sexual behaviour. We tested six males with ages ranging from 11 to 20 days post adult emergence, and six females with ages ranging from 16 to 20 days, and we found that all the individuals showed sexual behaviour. We thus determined that males older than 11 days and females older than 16 days post adult emergence are sexually mature, and thus, we used these ages as reference when selecting individuals for the experiment.

On the previous day to the beginning of the trials, all sexually mature females from our laboratory-reared population were briefly anaesthetized (~30 s) with CO_2 following the procedure of Prokop and Vaclav (2005) and measurements of their body mass (accurate to 0.1 mg) and body length (accurate to 0.1 mm) were taken. The index of physical condition (IPC) was calculated following Lawrence (1992) as body mass/body size^3. Female body condition has been pointed out as a factor affecting mate choice in different invertebrate taxa (reviewed in: Andersson, 1994; Bonduriansky, 2001; Thornhill & Alcock, 1983) and in praying mantids in particular (Barry, 2013; Barry et al., 2008, 2010; Liske & Davis, 1984; Maxwell, 2000 Maxwell et al., 2010). Therefore, to control for any other potential confounding effects, we matched females for each trial according to their similarity in body mass (mean $\pm$ SE: 0.21 ± 0.04 g aggressive; 0.21 ± 0.04 g nonaggressive; $N = 25$), IPC (0.004 ± 0.001 aggressive; 0.003 ± 0.001 nonaggressive), body length (3.87 ± 0.05 cm aggressive; 3.88 ± 0.05 cm nonaggressive) and age (24.5 ± 1.2 days post adult emergence aggressive; 25.3 ± 1.3 days post adult emergence nonaggressive). We were not able to measure body mass for the pair of females in one of the trials; thus, we report data for 25 of the 26 females that made up each group. Each individual was used only once.

Experimental Choice Arena

We used a triangular arena ($45 \times 34 \times 12$ cm, base - $\times$ height $\times$ depth) to carry out the choice experiments (Fig. 1). The arena had a translucent cover through which the trials could be videorecorded and was divided into three sections: (1) female 1 area; (2) female 2 area; (3) focal male initial area. The areas corresponding to each female were isolated by a 13 cm long solid partition wall, so that females could not see each other. Each female was tethered to one of the corners of the arena to prevent them from approaching the focal male, ensuring that the choice was made exclusively by the focal male. The choice arena was covered with a black curtain to allow the researcher to carry out manipulations without disturbing the animals. A second arena, identical to the experimental one, was constructed in order to habituate the females separately from the male, avoiding any interactions before the experiment. Both arena surfaces were wiped with ethanol between trials to eliminate any possible olfactory cues.

Experimental Design

Each trial comprised a habituation session and an experimental session. The experimental session consisted of an attack stimulation period and a choice period. Before the beginning of each trial, the females were briefly anaesthetized with CO_2 and the tether was
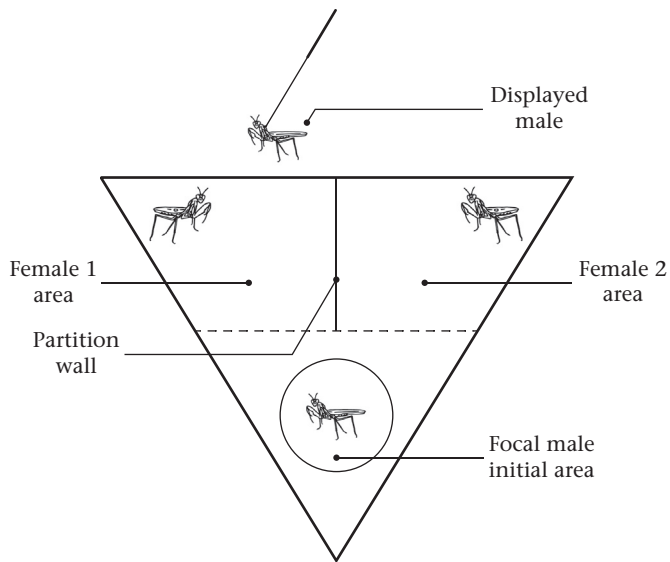
Figure 1. Experimental set-up. Focal males were presented with two options in a triangular choice arena: a female that was seen attacking a 'displayed' conspecific male (aggressive female) and a female that did not attack the conspecific male (nonaggressive female). The focal males were released from a delimited area in the arena. Female areas were also clearly delimited.

attached to them. The tether consisted of a 5 cm S-shaped piece of wire that was fastened with double-coated tape (3M, St Paul, MN, U.S.A.) to the pronotum of the mantid. The distal end of the piece of wire could be easily inserted or removed from a socket placed in each corner of the arena. Except for eliminating prothorax movements when they were tethered, mantids could groom, orient towards prey, strike, capture and eat. The use of the double-coated tape allowed releasing the animals with no harm immediately after each trial.

The habituation session lasted 3–4 h. The focal male was habituated in the experimental arena (i.e. the actual arena where the choice test was carried out), while the females were habituated in a second arena, identical to the experimental one. The habituation session for females was mainly intended to habituate them to being tethered. To do this, we attached the tethers to the females immediately before the start of the habituation session and placed them in the corners of the alternative arena. Once the habituation session ended, the females were transferred to the experimental arena. The design of the tether allowed for rapid transference of the females, with minimal disturbance.

Twenty-six males were tested as focal subjects (hereafter 'focal males'). Each of them was presented with two simultaneous options: one 'aggressive female' (signalling high risk of cannibalism) and one 'nonaggressive female' (low risk of cannibalism). A second male (hereafter 'displayed male') was tethered to the end of an L-shaped piece of wire, in a similar way to the tethered females, and was drawn near each of the females alternately and repeatedly, causing an attack from the aggressive female each time but not from the nonaggressive female (Fig. 1). An attack was defined as a strike by the female towards the displayed male using her raptorial forelegs. The number of attacks in each trial varied depending on the focal male's position: an attack was considered effective only when it was performed within the focal male's visual field (i.e. the mantid's head was pointing towards the female areas). When the attack stimulation period was over (mean ± SD duration: 2.9 ± 1.9 min), the displayed male was removed from the experimental arena and the choice period of the experimental session began. The experimental session was videorecorded and lasted 4–11 h.

The aggressive and nonaggressive conditions of females were not intrinsic characteristics, but were instead manipulated. First, both females were deprived of food for 5 days prior to the experiment to stimulate attacks towards the displayed males. Aggressive condition and position (right/left) in the arena were then randomly assigned to each female. The nonaggressive condition was attained by briefly anaesthetizing the female with CO_2 approximately 5 min before the start of the attack stimulation period. Based on preliminary exploratory observations, females recover all usual activity but do not perform strikes for approximately 15 min after anaesthesia (L. Pompilio & F. Gabelli, personal communication).

For each focal male during the experimental session, we recorded the latency to first enter any of the female areas, the time spent in each female's area and any mating attempts.

Data Analysis

We evaluated male preference using two indicators: (1) preference index, which is based on the proportion of time that males spent in the nonaggressive female's area, reflecting the relative preference for one female over the other, and was calculated as total time (min) spent in the nonaggressive female area/total time (min) spent in either female area; and (2) mating attempts. We compared the proportion of time spent in each female area with a Wilcoxon test and the frequency of matings with each type of female with a binomial test. We also analysed the consistency between the female area first entered by the male and the preference index, and between the preference index and mating attempts. Side preference was tested using a logistic regression, with nonaggressive female position (left/ right) as the independent variable and preference for this type of female (yes/no) as the dependent variable.

All tests were two tailed and differences considered significant at $P < 0.05$. Values are reported as means ± SD.

Ethical Note

We did not observe any harmful effects associated with food deprivation in females: none of the females died and all appeared to be in good condition when we carried out the experiment. Females were returned to their normal feeding regime (two juvenile crickets three times per week) immediately after the end of each trial.

RESULTS

Female Attacks

The presentation of the displayed male caused the aggressive female to attack each time. The mean number of attacks by aggressive females towards the displayed males was 4.0 ± 0.8 per trial ($N = 26$, range 2–5). Female attacks were always unsuccessful (the females were not able to grab the males). In two cases the female was able to grab one of the male's antennae, but she released it few seconds later, causing no further damage to the male. Nonaggressive females did not attack the displayed males.

Female Area First Entered

Males entered female areas and approached females in every trial. They advanced towards females very slowly, with a latency to enter a female area for the first time of 109.0 ± 187.3 min ($N = 26$). We found a marked consistency between the area first entered and male preference (see below). Only in 15% (4/26) of the trials did the male first enter one female area and then switch to the other one, where he spent the rest of the time slowly approaching the female.

In these four cases the switch to the second female area was made within 31.4 ± 35.4 min of the first entrance (i.e. before 14% of the time spent at any area had elapsed).

Preference Index

The preference index exhibited extreme values in all the cases, showing a marked male preference for one of the females in every trial. Males spent a greater proportion of time in the nonaggressive females' areas ($Z = 2.55$, $N = 26$, $P = 0.01$; Fig. 2). We did not find any preference for either the left or right corner of the arena in association with male preference for nonaggressive females (number of choices to each side: left $= 12$, right $= 14$; $\chi^2_{25} = 0.05$, $P = 0.83$).

Mating Attempts

Mating attempts were observed in 31% (8/26) of the trials. All mating attempts were successful and ended in a mating event, with no females rejecting males. The mean latency to a mating attempt was 298.4 ± 254.8 min ($N = 8$). Males tended to mate with nonaggressive females more frequently than with aggressive ones, but the difference was not statistically significant (binomial test: $P = 0.07$). In addition, the single case in which a male mated with the aggressive female also showed the shortest choice latency. Males spent a greater proportion of time in the area of the female they mated with ($Z = 2.52$, $N = 8$, $P = 0.01$). The median preference index associated with copulations with nonaggressive females was 1.00 (range 0.99−1.00, $N = 7$) and 0 for aggressive females ($N = 1$).

DISCUSSION

Male *P. tessellata* showed a preference for nonaggressive over aggressive females in choice tests carried out under controlled laboratory conditions. The behaviours observed (i.e. avoidance of females that were seen attacking a conspecific male and cautious approach towards the females) are in line with risk avoidance behaviours described in other praying mantids (Barry et al., 2009; Lelito & Brown, 2006; Maxwell, 1999a). Our results show that males are sensitive to the predatory strike of a female at a conspecific male. By preferring nonaggressive females, males are able to reduce the probability of being cannibalized.
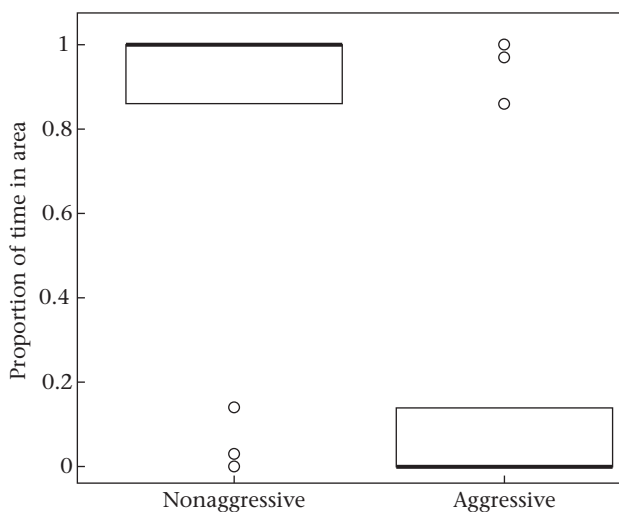
Figure 2. Box plots indicate the proportion of time spent by *P. tessellata* males in the area of each type of female. The thick line represents the median, the box represents the upper and lower percentiles and the dots are outliers.

To our knowledge this is the first study that addresses male preference in praying mantids by manipulating a visual cue signalling female level of aggression. Previous studies that found evidence of risk avoidance behaviour in mantids examined the response of males to altered risk of sexual cannibalism by manipulating female feeding condition (Lelito & Brown, 2006, 2008), body condition (Barry et al., 2010) or the initial position of males relative to females (Lelito & Brown, 2006; Maxwell, 1999b).

In our experiment, only about one-third of the approaches resulted in a mating attempt, while in the remaining trials the male had not reached the female by the time the experimental session ended. As we consider the mating attempt to be the most informative variable when analysing mate choice, we extended the duration of the experimental session from 4 h (initial trials) to a maximum of 11 h to try to record a higher number of mating attempts. Additional mating attempts with latencies greater than 7 h were then recorded. A possible explanation for recording so few mating attempts despite the long duration of experimental sessions is the initial position of the males relative to the females in our experiments. Males were placed frontally to both females, remaining this way for most of the approach phase. Maxwell (1999b) found that the males' initial positions relative to the females influenced their mating behaviour in the praying mantid *Iris oratoria*. He reported that the latency to the mating attempt was longer for males that were placed frontally to a female and that attempted to mount frontally than for males that were placed behind the female and that attempted to mount from behind. Furthermore, Lelito and Brown (2006) found that males approached females more slowly head-on than from behind in *Tenodera aridifolia sinensis*. Therefore, it is possible that the slow approach speed observed in this experiment was related to the risk associated with a frontal approach, and thereby with the impossibility of the male making contact undetected by the females, a tactic that has been suggested for some praying mantids (Birkhead et al., 1988; Maxwell, 1995; Roeder, 1935). Nevertheless, since mating attempts were associated with the proportion of time that males spent in a female area, we think the preference index can be considered a reliable predictor of mating attempt. Furthermore, in previous choice experiments in *P. tessellata* males also spent a greater proportion of time in the area of the female that they mated with ($Z = 2.52$, $N = 8$, $P = 0.01$: Avigliano, 2009; $Z = 2.55$, $N = 9$, $P = 0.01$: Zelzman, 2013), further supporting the reliability of the preference index as a predictor of mating attempt.

The use of chemical and visual cues in mate location and assessment has been investigated in different mantid species. Empirical evidence suggests that chemical cues work for signalling over long distances, attracting males to the vicinity of females, while visual cues play a role in female location and assessment in close range (Barry, 2010; Lawrence, 1992; Maxwell, 1999a, 1999b). Males in the present experiment were continuously in very close range of the females (<34 cm), and thus, visual cues probably guided their preferences. Therefore, it is unlikely that male choices were the result of chemical changes in the females due to their previous exposure to CO_2. Colinet and Renault (2012) found that a 7 min exposure to CO_2 temporally altered the concentration of a few metabolites during the following 14 h of recovery in *Drosophila melanogaster*. In the present experiment, both the aggressive and nonaggressive females were exposed to CO_2 for a maximum of 30 s between 3 and 4 h before the beginning of the experiment (when the tether was attached). However, since the nonaggressive females were additionally treated with CO_2 for a maximum of 30 s just before the attack stimulation period, the possibility that males were responding to subtle cues or behaviours by the nonaggressive females, rather than avoiding the aggressive females per se, cannot be completely discarded. It is uncertain, however, whether such

brief exposures to CO_2 are enough to cause undesirable effects in females.

In our study, the visual cue available to males was the predatory strike by a female towards a conspecific male. Thus, males could have cued on the strike itself or, instead, on the strike towards the conspecific male. However, we find no reason whereby the selection of a mechanism to discriminate between a strike performed towards a male and a strike performed towards an interspecific prey would be advantageous, since a hungry female should attack either an interspecific prey or a male (which can become simultaneously a source of food and of sperm). We thus hypothesize that the visual cue used by males is the observation of a female performing a strike (regardless of whether it is directed at a male or an interspecific prey). To test this idea, future experiments should examine male mantis' response to females attacking a prey and females attacking a male. If the cue used by males is the strike itself, we would expect a similar response in both cases. Visual cues other than the manipulated one, such as abdominal girth or fatness, are unlikely to have played a role here since we controlled for female feeding and body condition, as well as reproductive status.

Related experiments studied the response of males to females that were seen attacking and subsequently consuming an interspecific prey versus females that were observed attacking but not consuming a prey (analogous to our unsuccessful strike). The results showed that males behaved differently based on the consumption or not of a prey by the female, being more cautious towards females that attacked but did not consume the prey (Gemeno & Claramunt, 2006). In agreement with this evidence, males of our study species exposed to a simultaneous choice situation (in which they could choose among a female consuming a prey, a female without a prey and a male eating a prey), preferred females that were observed consuming an interspecific prey (Avigliano, 2009). The evolution of such a mate choice mechanism can be explained by its high payoff: the consumption of a prey may reduce the chances of the female showing sexual cannibalism.

Taken together, these results suggest that males react based on the level of aggression shown by females: avoiding those that they have observed performing unsuccessful strikes and choosing those that they have observed consuming a prey.

The evolution of such a mate choice mechanism may suppose that males regularly have opportunities to observe females interacting with other individuals (either conspecific or interspecific). Empirical evidence shows that males of at least some species of praying mantid may aggregate during mating. Maxwell et al. (2010) and Barry (2010), for example, found that groups of males arrive during the night to cages containing females, suggesting that females use chemical cues to attract males from a distance. Therefore, it seems plausible that, under natural conditions, males arrive at a female location simultaneously, thus regularly having opportunities to observe a female interacting with other males. Under such an ecological scenario, a mate choice mechanism that allows males to respond differently towards aggressive and nonaggressive females would be selected because of its adaptive advantage.

In conclusion, male preference for nonaggressive, less risky females is consistent with other risk-reducing behaviours observed in sexually cannibalistic praying mantids. The high cost of being cannibalized, with the loss of all future mating opportunities as a consequence, would have selected for male behaviours that reduce the probability of being cannibalized during mating events, resulting in sexual conflict over sexual cannibalism.

Acknowledgments

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