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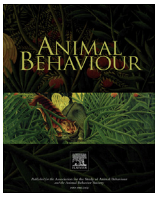

Sexual conflict in a sexually cannibalistic praying mantid: males prefer low-risk over high-risk females

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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.

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

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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 ± 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 × 34 × 12 cm, base × height × 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