

## Males Respond to the Risk of Sperm Competition in the Sexually Cannibalistic Praying Mantis, *Mantis religiosa*

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### Abstract

Although studies on sperm competition examined a wide range of taxa, little is known about the selection pressures on male traits in systems with simultaneous risk of sperm competition and sexual cannibalism. Here, we experimentally studied how the risk of sperm competition affects male copulatory behavior in the sexually cannibalistic praying mantis *Mantis religiosa*. We recorded the onset and duration of copulations following the introduction of virgin, adult praying mantises into mating arenas with three different sex ratio treatments: polyandrous, monogamous, and polygynous. We did not detect any female phenotypic trait predicting cannibalism. The chance of male survival was related to his condition, with males in better condition being cannibalized significantly less often. In contrast, we did not identify any male trait that would favor some males to obtain copulations. Our results on copulation duration support sperm competition theory in that the copulations in the male-biased treatment, where the perceived risk of sperm competition was greatest, were significantly longer than those in single-male treatments. Importantly, males in better condition copulated significantly longer regardless of sex ratio. Overall, our study suggests that males can adjust their copulation behavior in response to the risk of sperm competition even in a system with frequent sexual cannibalism.

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### Introduction

Sexual reproduction inevitably gives rise to an evolutionary conflict of interest between the sexes (Trivers 1972; Parker 1979). In insects, for example, the expression of various physiological, morphological, and behavioral traits like the sperm incapacitating seminal fluid (Price et al. 1999), the length/shape of intromittent male genitalia (e.g. Waage 1979; Arnqvist 1998), or sperm ejection

(Snook & Hosken 2004) indicate that the conflict over mating frequency is common (see Simmons & Siva-Jothy 1998).

Sperm competition arises whenever the ejaculates of different males compete to fertilize a female's ova (Parker 1970). When there is a risk of sperm competition, e.g. in high-density populations or in the presence of rival males, male reproductive expenditure is predicted to increase (Parker et al. 1993; Parker 1998). To fight the risk of sperm competition males were reported to increase their ejaculate size (e.g. Gage 1991), employ repeated (e.g. Dewsbury 1982) or prolonged copulations (e.g. Sillén-Tullberg 1981; Lawrence 1986), or consort with inseminated females (e.g. Radwan & Siva-Jothy 1996). In insects where copulations often last several hours and even days, copula duration may play role in physically preventing females from remating. The mate guarding hypothesis predicts copula duration to increase in the presence of rival males (see Simmons 2001). However, provided that males can inhibit female remating by transferring chemical or mechanical substances with their ejaculates (see Cordero 1995), ejaculate size or copula duration may not necessarily be affected by the number of competitors that are present at copulation.

Adult sex ratio was recognized as an effective determinant of the risk of sperm competition (e.g. Thornhill & Alcock 1983; Parker et al. 1993; Alonso-Pimentel & Papaj 1996; Simmons & Kvarnemo 1997). Recently, Schöfl & Taborsky (2002) showed experimentally that firebugs *Pyrrhocoris apterus* indeed copulate longer under a male-biased sex ratio. Likewise, male golden egg bugs *Phyllomorpha laciniata* were shown to copulate significantly longer in the presence of a rival male (García-González & Gomendio 2004).

Sexual cannibalism in a sexually promiscuous system can also depart genetic interests between the sexes (Schneider & Elgar 2001). Hereby, males seek out multiple receptive females to fertilize their eggs, but by doing so they risk losing their future mating opportunities by being cannibalized (Elgar & Nash 1988). Females, on the other hand, may accrue energetic benefits via cannibalizing males (Newman & Elgar 1991; Moya-Laraño et al. 2003), but at the same time, by killing males before mating with any of them, they run the risk of remaining unmated (Elgar 1992). The consequences of sexual cannibalism for male and female fitness depend on whether cannibalism takes place before or after mating (Parker 1979; Buskirk et al. 1984; Newman & Elgar 1991). The likelihood of cannibalism has been reported to vary according to male size (e.g. Elgar & Nash 1988), female condition (e.g. Andrade 1998; Maxwell 1998) or female mating status (e.g. Elgar 1998).

The praying mantis *Mantis religiosa* and other mantids are polygamous, sexually dimorphic insects, with frequently occurring sexual cannibalism (Elgar & Crespi 1992; Lawrence 1992; Hurd et al. 1994; Maxwell 1999a). Moreover, the results of Lawrence (1992) and Maxwell (1998, 1999a) on male mate guarding and copulation behavior indicate that sperm competition likely occurs also in this taxonomic group of insects. In this study we examined whether males of a cannibalistic insect species, the praying mantis, respond to the risk of sperm competition as determined by adult sex ratio in mating arenas. In accordance with

sperm competition theory (Parker et al. 1993; Parker 1998) and the mate guarding hypothesis (Simmons 2001), we predicted that males mating in mating arenas with a higher perceived risk of sperm competition should copulate longer than those in monogamous and female-biased arenas.

### Methods

The experiment was conducted under laboratory conditions during Jun.–Aug. 2003. The last instars of praying mantis nymphs were collected several weeks before the experiment from different meadows in Western Slovakia (48°21'N, 17°39'E). The nymphs were reared individually outdoor in 0.7 l glass covered by a fine mesh, protected from rain and direct sunlight. After the final molt, adult individuals were each replaced to 4 l ventilated jars. The jars with adults were kept together, whereas the position of jars was randomly changed after every feeding in the course of several weeks. Thus, all individuals had a visual contact with individuals of both sexes prior to the experiment. The nymphs were watered and fed daily ad libitum on grasshoppers (*Acrididae*) captured in local meadows, whereas adults received approximately one grasshopper per day. Sixteen to eighteen days after the final molt, when females reach sexual maturity (Lawrence 1992), virgin females were randomly assigned to the three different treatments, T1, T2 and T3, corresponding to the three different (male:female) sex ratio regimes, 3:1, 1:1 and 1:2, respectively. This experimental design has been chosen as a compromise between the goal of our study and natural conditions that praying mantises experience in the wild. As the situations when several fertile female praying mantises together attract males are extremely rare in the wild, and have fatal consequences for females (P. Prokop, unpubl. data), the number of females in every treatment had to be kept as low as possible. Furthermore, to simulate natural conditions, where females are usually food limited (Eisenberg et al. 1981; Lawrence 1992; Hurd et al. 1994), females from the treatments T1 and T2 ceased to receive any food 4 d prior to the experiment (cf. Liske & Davis 1987; Kynaston et al. 1994). However, starved females are highly aggressive and frequently kill one another (Birkhead et al. 1988; P. Prokop, pers. obs.). Therefore, in order to prevent the cannibalism among females, we decided to feed the females in the T3 2 d prior to the experiment. Consequently, all the trials from the T3 were excluded from the analysis on the probability of cannibalism. On experimental day, all tested individuals had been briefly anesthetized with carbon dioxide (CO<sub>2</sub>) and we subsequently took measurements of their body mass (accurate to 0.1 mg), pronotum length (accurate to  $1.0 \times 10^{-2}$  mm), and marked them onto pronotum with a glue paint. Male body size (pronotum) did not differ significantly between treatments (one-way ANOVA:  $F_{2,123} = 1.35$ ,  $p = 0.26$ ;  $p > 0.28$  for all post hoc tests). There was a slight difference in male body mass between treatments, with males from the T2 tending to be lighter than the males from the T1 (one-way ANOVA:  $F_{2,123} = 2.80$ ,  $p = 0.07$ ; post hoc Tukey HSD tests:  $p = 0.07$  for T1:T2, and  $p > 0.41$  for T2:T3 and T1:T3).

The index of physical condition was calculated following Lawrence (1992) as 'body mass/pronotum size<sup>3</sup>'. This index is a crude measure of condition reflecting the residual body mass after removing the size effect, while the linearity between body mass and size is upheld. In order to evaluate the role of condition independently of male and female biometric parameters, we performed stepwise regressions including also the condition index. Consequently, whenever our stepwise models suggested that the residual body mass plays a significant role in explaining a given dependent variable, we ran a standard regression model involving only a dependent variable, and body mass and size as predictors (see Freckleton 2002).

Our experiments were conducted in  $40 \times 45 \times 18$  cm ventilated glass-enclosures each containing 25–30 stems of the chicory *Cichorium intybus*. The experiments were carried out between 1000 and 1600 h as this time corresponds to the peak copulation activity in the praying mantis (Lawrence 1992). Males were introduced to the mating arena as first. Then females were added 15 cm away from males, with their back directed to the head of the male because male mantises are more likely to mate with females from the rear (away from their raptorial legs) rather than from the front side (Roeder 1935; Birkhead et al. 1988; Maxwell 1999b). We then recorded the latency time until copulation, copulation duration, and the occurrence of cannibalism. When males did not approach females and no activity was recorded in the course of 5 h after the introduction of females to the mating arena, such mating trials were aborted. Overall, we carried out 28, 26, and 16 trials, respectively, for the treatments T1, T2, and T3, respectively, involving 126 different males and 86 different females. For the analyses on the probability of cannibalism, we used data from the treatments T1 and T2 (see above for reasoning), which corresponded to 110 males and 54 females. After excluding the trials where no copulation was observed within 5 h after the start of experiment, the sample size was reduced to 57 trials (22, 19, and 16), including 101 and 73 different males and females, respectively. After the experiment, we released all the individuals that were not cannibalized to their original habitat. The data were inspected for normal distribution and square-root or log-transformed when necessary. Unless the differences between the groups that were to be pooled were significant, we used planned comparisons to test our hypotheses (see Rosenthal & Rosnow 1985). All statistical tests are two-tailed and, except for G tests, calculated with Statistica (StatSoft, Inc. 2001).

## Results

### The Patterns of Sexual Cannibalism

Cannibalism occurred in 17 of 19 cases after males had drawn near to a motionless female or shortly after they dismounted her. In two cases, males were cannibalized while mounted on the female's back trying to copulate with her. Classifying the instances of cannibalism according to whether they occurred

before or after copulation, 8 and 1, 6 and 2, and 0 and 2 cases of cannibalism, respectively, occurred in polyandrous, monogamous, and polygynous treatments, respectively ( $G_2 = 6.64$ ,  $p = 0.036$ ). Of all the tested individuals from the trials in which females were not fed, cannibalism was committed by 28% (15/54) of females on 16% (17/110) of males. We found that the probability that a male would be cannibalized was related to the sex ratio in the mating arena (Fig. 1a). Namely, males in the monogamous treatment were more likely than males in the polyandrous treatment to be cannibalized by females (Fig. 1a). In contrast, we found no difference in the rate of cannibalistic females with respect to the sex ratio in mating arenas (Fig. 1b).

Cannibalism occurred more frequently on the males that were in worse condition (a backward stepwise logistic multiple regression with nine predictors – male, female, and female/male condition, pronotum size, and body mass – only male condition remained in the model: likelihood ratio  $\chi^2 = 5.78$ ,  $p = 0.016$ ,  $n = 70$  trials). Including into a model only male body mass and the male pronotum size raised to the third power, a standard logistic regression confirms that the variation in the occurrence of cannibalism is significantly explained by male body mass (male body mass: likelihood ratio  $\chi^2 = 6.13$ ,  $p = 0.013$ ; male pronotum size<sup>3</sup>: likelihood ratio  $\chi^2 = 0.01$ ,  $p = 0.94$ ). In the latter two tests, when several males were cannibalized and/or when more individuals of the same sex appeared in one trial, respectively, their biometric data were averaged.

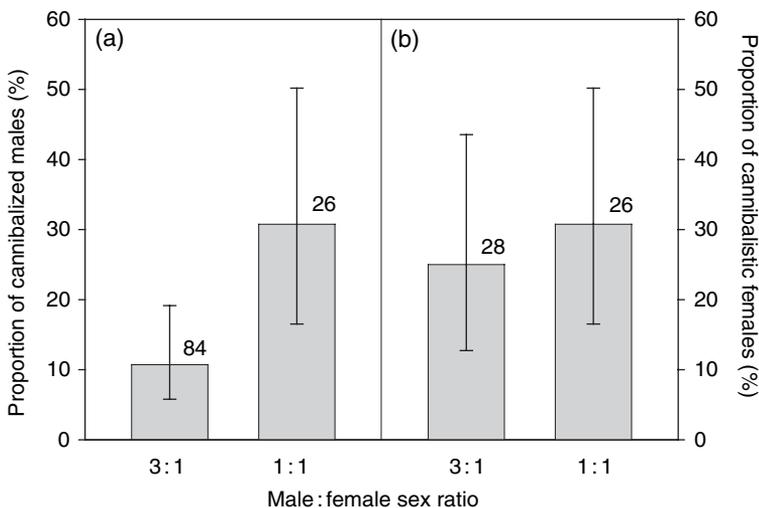


Fig. 1. The probability a male was cannibalized and a female became cannibalistic in relation to sex ratio. (a) Nine of 84 and eight of 26 males, respectively, were cannibalized in male-biased and sex-unbiased treatments, respectively;  $G_1 = 5.41$ ,  $p = 0.020$ . (b) Seven of 28 and eight of 26 females, respectively, became cannibalistic in male-biased and sex-unbiased treatments, respectively;  $G_1 = 0.22$ ,  $p = 0.64$ . Error bars are 95% confidence intervals for proportions (Agresti & Coull 1998) and numbers over boxes are sample sizes

Examining the same predictors as in the previous analysis, a backward stepwise linear multiple regression revealed that larger males were more likely to be attacked by cannibalistic females (only male pronotum size remained in the model:  $r^2 = 0.24$ ,  $\beta = -0.49$ ,  $p = 0.044$ ,  $n = 17$  cannibalistic females). As for the latter analysis, when a female cannibalized more than one male, only the first cannibalized males were involved in the analysis.

### The Sperm Competition Experiment

The male probability of mating in the female-biased treatment was higher than in the monogamous treatment. In particular, in the course of 5 h, 16 of 16, and 19 of 26 males, respectively, succeeded in mating in polygynous and monogamous conditions, respectively ( $G_1 = 7.56$ ,  $p < 0.01$ ). We excluded the polyandrous treatment from this analysis as the experiment was aborted after females had finished copulating with one of the three males. It was common, however, that after or before one of the males in the male-biased treatment had finished copulation, the other males attempted to copulate with the mated female as well. In contrast, the males in the female-biased treatment that had finished copulating with one of the two females did not attempt to copulate with the unmated female, but instead tried to escape from the mating arena.

Confining the analysis to the 22 trials where females were introduced into mating arenas containing three males, we found no significant morphological differences between males that obtained and those that did not obtain copulation (paired t-tests for male body mass, size and condition index:  $0.20 > t > 0.01$ ,  $0.84 > p > 0.96$ ,  $n = 22$ ). In this analysis, the biometric data of the males that did not obtain copulation were averaged within each trial.

We found a significant difference in copulation duration as well as the latency time until copulation between the three treatments (Table 1; Fig. 2). Only the trials where cannibalism did not occur before or during copulation were included

*Table 1:* The univariate results for MANCOVA analyzing the effect of sex ratio on male sexual behavior while controlling for the effect of male and female condition. Multivariate tests: male condition Wilks'  $\lambda = 0.91$ ,  $p = 0.11$ , female condition Wilks'  $\lambda = 0.99$ ,  $p = 0.89$ ; fixed effect – sex ratio Wilks'  $\lambda = 0.62$ ,  $p < 0.001$

	Beta (slope)	$t_{46}$	p
<b>Male condition</b>			
Time till copulation	0.02	0.14	0.89
Copulation time	0.29	2.14	0.04
<b>Female condition</b>			
Time till copulation	0.07	0.50	0.62
Copulation time	-0.01	0.03	0.98
<i>Fixed effects</i>			
<b>Sex treatment</b>			
Time till copulation		3.73	< 0.001
Copulation time		3.11	< 0.01

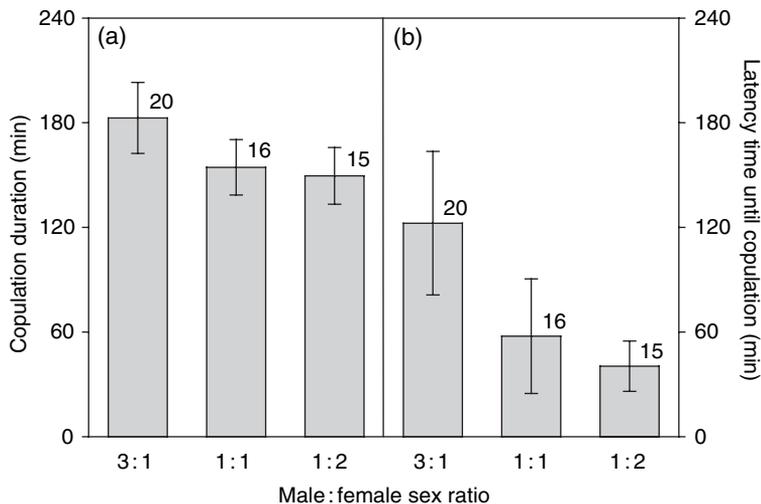


Fig. 2: The effect of sex ratio on (a) copulation duration and (b) the time until copulation. For informative purposes, the graph displays the means of untransformed and unadjusted copulation duration, and the time until copulation. Error bars are 95% confidence intervals and numbers over boxes are sample sizes

in this analysis ( $n = 51$  trials). Importantly, the analysis revealed a covariance between male condition and copulation duration (Table 1), and this finding is also supported by a linear regression model involving only copulation duration, male body mass, and cubed pronotum size (male mass:  $\beta = 0.28$ ,  $p = 0.07$ ; pronotum size:  $\beta = -0.15$ ,  $p = 0.36$ ). A contrast analysis revealed that the males in the multi-male treatment copulated longer than those in single-male treatments ( $p < 0.01$ ), thus supporting the sperm competition hypothesis. Moreover, copulations under polyandrous conditions were initiated later than in single-male treatments ( $p < 0.001$ ; see Fig. 2). As for the female density effect, the copulations in the multi-female treatment were significantly shorter than those in single-female treatments ( $p = 0.036$ ; see Fig. 2).

In 45% (9/20) of the trials in the male-biased sex ratio treatment, in which cannibalism did not occur before or during copulation, we observed at least one rival male simultaneously mounting a female along with a male succeeding in copulating with such a female. Importantly, when two males were mounted on the female, copulation duration was significantly longer compared to the cases when only one male was in the physical contact with the female (copulation duration with and without the presence of a rival male on the female's back, respectively:  $\bar{x} = 212$  and 160 min, respectively; median test:  $\chi^2 = 5.05$ ,  $p = 0.025$ ,  $n_1 = 9$ ,  $n_2 = 11$ ).

## Discussion

The results of our study are consistent with the predictions of the sperm competition hypothesis. Male praying mantises copulated for longer time when

the perceived sex ratio in mating arenas was male-biased and when more males were in physical contact with a female. Moreover, we show that male condition is an important predictor for both male mating behavior and sexual cannibalism. Although the probability of mating was not related to male condition, the males in better condition were less likely to be cannibalized and copulated with females for longer time irrespective of sex ratio in the mating arena.

### Male Sexual Behavior

Our study implies that copulation behavior can be coupled with the risk of sperm competition also in a system with frequent sexual cannibalism. Apart from the between-treatment differences in copulation duration, a strong evidence for this assertion is also provided if one focuses on the males within the male-biased sex ratio treatment. When multiple males mounted a female, the males in such cases copulated for longer than when only one male was in physical contact with the female. Interestingly, males in better condition copulated consistently longer regardless of the risk of sperm competition (cf. Engqvist & Sauer 2003). This is contrary to the results of Simmons & Kotiaho (2002) who found that male dung beetles *Onthophagus tauris* in poor condition copulated for longer. As of yet, we do not know whether this variation in copula duration in the praying mantis is driven by males (e.g. effect of male condition per se; see Simmons 2001) or females (cryptic female mate choice; see Eberhard 1996).

Contrast analyses revealed that both the differences in male and female density between mating arenas resulted in significant differences in copulation duration. While the effect of male density on copulation duration is consistent with the perceived risk of sperm competition, the female density effect indicates that the perceived availability of females might also have some influence on copulation duration (see Alonso-Pimentel & Papaj 1996). For example, males could to some extent adjust their copula duration according to the risk of cannibalism. There are grounds for this to happen because, although it is rare that a male would be attacked by the female with which he mates, the pair in copula can be attacked by an adjoining female (P. Prokop & R. Václav, unpubl. data). Alternatively, provided that male praying mantises are sperm limited and/or physical mate guarding is costly, the female density effect on copulation duration could indicate that males perceived female availability as an opportunity to reduce their reproductive effort for each female (cf. Archer & Elgar 1999; Bateman & MacFadyen 1999).

Although the time interval between the introduction of females into the mating arena and copulation initiation differed significantly in relation to sex ratio, the difference in the latency time until copulation is hard to interpret. Apparently, the result is in line with the 'last-male precedence' in that the males under a higher risk of sperm competition started to copulate later than males from single-male treatments (see Simmons 2001). To date, nothing is known about the 'second- or last-male precedence' in the praying mantis, however, there are three

behavioral lines of evidence against fertilization advantage of last males to copulate with the female in our model species. First, after one of the courting males engaged in mounting a female in the male-biased treatment, usually following several hours of courtship, other males did not wait until their competitors finished copulation but instead hastened to substitute them and insert their copulatory organ in the female first in order. Second, in the cases when females attacked one of the courting males – usually the one that approached them prematurely, the two unassaulted males both immediately began to mount the female, apparently taking advantage of the female being occupied with handling her prey (see also Birkhead et al. 1988; Moya-Laraño et al. 2004). Third, female mantises seem to become unreceptive right after copulation (Lawrence 1992), so later copulating males may run a risk of being rejected, or even killed, by the female. Future experiments are necessary to distinguish whether male praying mantises in male-biased mating conditions delay mating in order to increase their chance of survival or fertilization.

### **Sexual Cannibalism**

The proportion of female praying mantises practicing cannibalism did not differ with respect to sex ratio and was comparable to the results reported by Lawrence (1992). However, after distinguishing whether cannibalism took place before or after female mating, it appears that females committed cannibalism in line with the risk of remaining unmated. From the male perspective, the probability that a male would be killed by a female conspecific was significantly lower in the polyandrous compared to the monogamous treatment.

We showed that sexual cannibalism in the praying mantis was committed more frequently on males in poor condition. The hunger level is likely to determine whether a male remains in front of a receptive female, waiting for the right moment to mount her, or whether he moves on (e.g. to approach female or forage). Because the prey capture in the praying mantis is based on the perception of movement (e.g. Kral 2003), the most parsimonious explanation for the higher rate of cannibalistic attacks on the males in poor condition might be their higher locomotory activity (see Lima 1998; cf. the ‘mistaken identity’ hypothesis; Elgar 1992; see Arnqvist & Henriksson 1997). Our result could also suggest that the risk of injury (Schneider & Lubin 1997) or the cost of prey subduing (Johnson 2001) moderate the rapaciousness of adult females, making physically poor males the most innocuous prey. Also, given the fitness of female mantids increases with their size and/or body condition (Matsura & Mooroka 1983; Birkhead et al. 1988; Hurd et al. 1994; Maxwell 2000), sexual cannibalism could reflect a female strategy to postpone her reproduction and instead improve her condition, particularly when courted by poor quality males (Buskirk et al. 1984; Newman & Elgar 1991). Finally, killing males in poor condition could be the strategy of females to prevent such males from fertilizing their eggs independent of the males’ nutritional value (Elgar & Nash 1988; Persons & Uetz 2005).

We found that cannibalistic female praying mantises more readily attacked larger than smaller males (cf. Elgar 1991). This result appears to give support for the nutritional cause of cannibalism (Newman & Elgar 1991). Yet, larger males could have been killed also because they (1) were less agile than smaller males to escape the female capture (Ghiselin 1974; Vollrath & Parker 1992) or (2) presented larger targets for voracious females (Elgar & Fahey 1996). It is important to note that in our study the cannibalistic females were not in worse condition than non-cannibalistic females, so their motivation to kill males cannot be linked to their immediate hunger level. Overall, our study does not provide unequivocal evidence of the causes of cannibalism in the praying mantis. However, as cannibalism is common within the taxonomic group Mantodea, sexual cannibalism in *Mantis religiosa* may reflect phylogenetic constraints on female sexual behavior (see Morse 2004).

In conclusion, we showed that male praying mantises adjust their copulation behavior according to the perceived risk of sperm competition. Our study suggests that both sperm competition and sexual cannibalism yield males in superior condition to be in a selective advantage.

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