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ARTICLE

Seasonal aspects of sexual cannibalism in the praying mantis (*Mantis religiosa*)

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Abstract According to the adaptive foraging hypothesis of sexual cannibalism, females face a trade-off between mating and consuming a courting male. Because male and prey availability can change seasonally, sexual cannibalism may change with season. However, we are not aware of any work examining how sexual cannibalism in insects relates to the time of season. Here, we examined the seasonal pattern of sexual cannibalism and reproductive behaviour in the sexually cannibalistic praying mantis (*Mantis religiosa*). We repeatedly collected the last instars of praying mantises from the field and brought them up under natural weather and photoperiod, but standardised feeding and socioecological conditions. After the females reached sexual maturity, we allowed all of the females to mate during two mating trials. In comparison to female praying mantises maturing later in the season, early-maturing females were larger but of poorer body condition on the day of a mating trial (20 days after the adult moult). During the first round of mating trials, early-maturing virgin females cannibalised males more frequently than their late-maturing counterparts. In contrast, late-maturing females that mated in the first round of mating trials were more likely than early-maturing, nonvirgin females to be cannibalistic in the second round of mating trials. The latency time until copulation was correlated with a risk of sexual cannibalism and was longer in early-maturing females. Our study suggests that the date of the last (adult) moult plays an important role in the occurrence of sexual cannibalism.

Keywords Sexual cannibalism · Season · Mating status · Foraging strategies · Praying mantis · *Mantis religiosa*

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Introduction

Sexual cannibalism is the consumption of a conspecific individual of the opposite sex before, during or after mating (Elgar and Schneider 2004). From the female perspective, consumption of a conspecific male has been reported to increase female fecundity (Birkhead et al. 1988; Elgar and Nash 1988), female body condition (Moya-Laraño et al. 2003a), and offspring hatching success (Johnson 2001). In addition, sexual cannibalism has been proposed to be an extreme form of female mate choice (Elgar and Nash 1988). While sexual cannibalism is often studied in the context of female and male phenotypes (see Prenter et al. 2006), the role of ecological factors in the occurrence of sexual cannibalism is poorly known.

Newman and Elgar (1991) used an economic model to reveal the conditions under which pre-mating sexual cannibalism could evolve. Assuming that females face a trade-off between mating and consuming a courting male, Newman and Elgar (1991) found that the most important predictors of sexual cannibalism should be the expected number of males that the female encounters during the mating season and the rate of female mass gain resulting from eating food items other than male conspecifics. Despite the fact that the availability of males (i.e., mate and prey availability) changes with season (Lawrence 1992), to our knowledge only two studies have considered the relation between the time of season and the occurrence of sexual cannibalism. Arnqvist and Henriksson (1997) failed to support the idea that the probability of sexual cannibalism in fishing spiders (*Dolomedes fimbriatus*) should be lower at the end of the mating season. Similarly, Johnson (2001) did not detect an effect of date on the likelihood of pre-copulatory cannibalistic attacks in *D. triton*. While Arnqvist and Henriksson (1997) and Johnson (2001) manipulated female condition, they did not simultaneously manipulate other factors. Also, though Arnqvist and Henriksson (1997) reared spiders under a natural photoperiod, the spiders were exposed to an unnatural, constant temperature of 20 °C. In turn, Johnson (2001) does not provide a clear description of the rearing conditions used. Therefore, it is possible that the lack of a seasonal pattern in the cannibalistic behaviour of female fishing spiders reported by Arnqvist and Henriksson (1997) and Johnson (2001) may have been due to the application of unnatural environmental conditions in the experiments.

In the present study, we examined the seasonal pattern of sexual cannibalism and reproductive behaviour in the sexually cannibalistic praying mantis (*Mantis religiosa*). We repeatedly collected the last instars of praying mantises from the field over the whole mating season and brought them up under outdoor weather and photoperiod, but standardised feeding and socioecological conditions. After the females reached sexual maturity, we allowed all of the females to mate during two mating trials. We recorded the mating and/or cannibalistic behaviour of the females during the two trials.

The praying mantis is a suitable species for exploring seasonal patterns in female cannibalistic behaviour. First, sexual cannibalism in *M. religiosa* is common in both natural (Lawrence 1992) and laboratory conditions (Prokop and Václav 2005). Second, both the male abundance of *M. religiosa* (Lawrence 1992) and other mantids (Hurd et al. 1994; Maxwell 1998) as well as the male's interest in mating (Maxwell 1999) decreases as the season progresses (perhaps due to a temperature drop). Third, though local prey availability is expected to decline with season progression, especially for temperate populations of mantids (Eisenberg et al. 1981), females must gain about 50% of their body mass following the last ecdysis in order to successfully oviposit and increase their sexual attractiveness (Lawrence 1992). Finally, female mantids living in the temperate zone are constrained by weather conditions because most of the individuals are killed by the first frost (Hurd et al. 1995).

Methods

The study was conducted between July and September 2005. The last instars of nymph praying mantises were collected from a single abandoned field near the city of Trnava (48°21′N, 17°39′E). The nymphs were collected 3–4 times per week from mid-July to mid-August and reared individually outdoor in 0.7 l glass containers covered with a fine mesh and protected from rain and direct sunlight. The search efforts were comparable during each field visit. All nymphs were fed with small grasshoppers ad libitum. After the final moult (checked daily), the adult females were placed in 4 l jars and fed with two freshly captured grasshoppers (mean prey weight = 0.11 g) every second day for a period of 16 days, at which time praying mantises reach sexual maturity (Lawrence 1992). Subsequently, in order to increase the chance of cannibalistic attack, all females were starved for four days (Kynaston et al. 1994; Liske and Davis 1987; Prokop and Václav 2005), after which (i.e. 20 days after the adult moult) we subjected them to two mating trials. Males were fed with smaller grasshoppers ad libitum. In the first mating trials, we included females and males that had reached the ages of 20 and 12–15 days, respectively, after the final moult. Glass jars with single adults were kept together, whereas the positions of jars were randomly changed after every feed. Thus, all individuals had visual contact with individuals of both sexes prior to the experiment. The overall sex ratio of collected nymphs turned out to be roughly even (44 females and 40 males), and a similar number of male and female praying mantises moulted on the same day over the whole season. However, we needed twice as many males than females for the mating trials. Therefore, the stock of males reared by ourselves was supplemented with adult males collected from the field. It is unlikely that the use of wild males could be responsible for seasonal or intra-individual differences in the frequency of cannibalistic attacks because we used a similar proportion of hand-reared and wild males across all mating trials during the whole season (47 and 41% hand-reared males were used in early- and late-season mating trials, respectively). Moreover, *M. religiosa* females typically have dominant control over cannibalism (Lawrence 1992). After the mating trial(s), all noncannibalised praying mantises were returned to their original field habitat. Before the release, all individuals were colour-marked to avoid the same individuals being collected more than once.

On the day of a mating trial, all tested individuals were briefly anaesthetized with carbon dioxide (CO_2) and measurements of their body mass (accurate to 0.1 mg) and pronotum length (accurate to 1.0×10^{-2} mm) were taken. The index of physical condition was calculated, following Lawrence (1992), as body mass/pronotum size^3. The use of residuals from the regression between body mass and pronotum length does not change our results. Mating trials were conducted in 40 × 45 × 18 cm ventilated glass enclosures each containing 20–25 stems of chicory

(*Cichorium inthybus*). Males were introduced into the mating arena first. Each female was added 15 cm away from the male, with her back directed towards the head of the male. Subsequently, we recorded the latency time until copulation, the duration of copulation, and the occurrence of sexual cannibalism. When the male did not approach female and no sexual or cannibalistic activity had been observed by 5 h after the introduction of the female to the mating arena, such mating trials were aborted. All of the females ($n = 44$) were subjected to two rounds of mating trials with an interval of 24 h between them. Each male was used in just one mating trial. Three females failed to interact sexually or cannibalistically with a male during both rounds of mating trials, so these three females were excluded from analyses. In total, we present results for 41 females based on 82 mating trials.

The temporal distribution of the dates of the last moult revealed that 13 females moulted within eight days between 9 and 16 August. The remaining 28 females moulted within ten days between 27 August and 5 September. Therefore, for simplicity we divide the two different age cohorts of female praying mantises into early- and late-maturing females. We used the McNemar test to examine whether there was a change in the cannibalistic or mating behaviour of the same female between two successive mating trials. Reported values are median ± SD.

Results

Mating patterns

We found a positive correlation between an index of female body condition on the day of the mating trial and the date of the last moult ($r_s = 0.59$, $P < 0.001$, $n = 41$). This trend can be attributed to the seasonal decrease in female body size in terms of pronotum length ($r_s = -0.51$, $P < 0.001$, $n = 41$; Fig. 1) rather than due to the seasonal increase in body mass ($r_s = 0.09$, $P = 0.44$, $n = 41$). In turn, while male pronotum length ($r_s = -0.39$, $P < 0.001$, $n = 41$) and body mass ($r_s = -0.40$, $P < 0.001$, $n = 41$) decreased with the date of the male's last moult, an index of male body condition did not significantly vary with the date of the male's last moult ($r_s = -0.13$, $P = 0.29$, $n = 41$).

We detected a nonsignificant trend for a larger proportion of late-maturing females (23/28) compared to early-maturing females (7/13) to mate in the first round of mating trials (Fisher exact test: $P = 0.073$; Table 1). After controlling for the date of the last moult, an index of body condition was not significantly different between the females that achieved and those that did not achieve copulation in the first round of mating trials (Man–Whitney *U*-test: $U = 109.0$, $P = 0.12$, $n_1 = 30$, $n_2 = 11$).

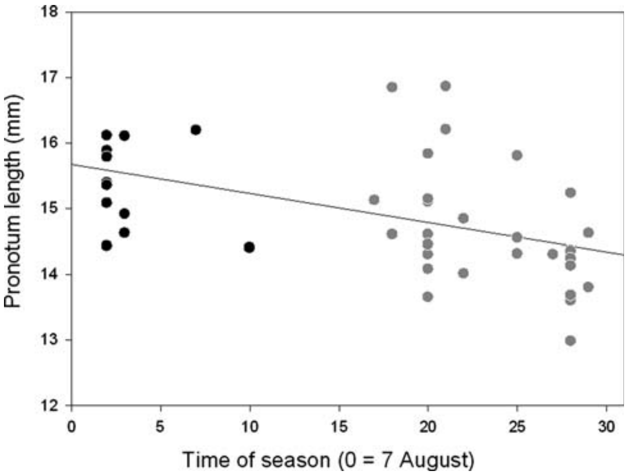

Fig. 1 Seasonal patterns of pronotum length in early- (*black circles*) and late-maturing (*grey circles*) female praying mantises. Time of season refers to the date of the last (adult) moult

Table 1 Contingency table with four types of sexual behaviour observed for early- ($n = 13$) and late- ($n = 28$) maturing female praying mantises during the first and second rounds of mating trials

Type of sexual behaviour	First round		Second round	
	Early	Late	Early	Late
Mating with cannibalism	5	5	3	7
Mating without cannibalism	2	18	7	12
Cannibalism without mating	6	5	3	8
No mating or cannibalism	0	0	0	1

The durations of copulation in early- and late-maturing females during the first mating trial were almost indistinguishable (early females: 197 ± 23.24 min, $n = 4$; late females: 182.5 ± 65.37 min, $n = 22$; $U = 32.0$, $P = 0.39$). The females that initiated mating after cannibalism ($n = 4$) were excluded from the analyses of copulation duration. In contrast, we included the females that cannibalised males after mating ($n = 8$) in the analyses of copulation duration. The latency time until copulation differed significantly depending on the date of the female's last moult. Namely, males approached early-maturing females after a significantly longer period of time (252 ± 215.98 min, $n = 4$) than late-maturing ones (64.5 ± 69.81 min, $n = 22$, $U = 16.0$, $P = 0.047$).

For early-maturing females, we did not detect significant change in mating behaviour between the two mating trials (five females copulated in both rounds, two only in the first, five only in the second, and one female did not copulate in either round, McNemar test: $\chi^2 = 0.57$, $df = 1$, $P = 0.45$). Similarly, there was no significant change in mating behaviour in late-maturing females between the two rounds of mating trials (14 females copulated in both rounds, nine only in the first, five only in the second, and no female failed to copulate in one of the rounds, McNemar test: $\chi^2 = 0.64$, $df = 1$, $P = 0.42$).

Sexual cannibalism

The frequencies of sexual cannibalism performed before, after or during copulation, respectively, were similar between the first and second rounds of mating trials (15/41 vs. 16/41, 6/41 vs. 4/41, 0/41 vs. 1/41, respectively).

Early-maturing females performed sexual cannibalism in the first round of mating trials significantly more often than late-maturing females (11 of 13 early-maturing vs. 10 of 28 late-maturing females, respectively, committed sexual cannibalism, Fisher exact test, $P = 0.006$; Table 1). During the second round of mating trials, the frequency of sexual cannibalism did not differ between early- and late-maturing females (6 of 13 vs. 15 of 28 females were cannibalistic, $P = 0.52$; Table 1). However, a larger proportion of late- (15/18) than early-maturing (0/2) females that achieved copulation but did not perform cannibalism in the first round of mating trials were sexually cannibalistic in the second round of mating trials (Fisher exact test: $P = 0.05$; Table 1).

We detected a tendency towards a decrease in the number of cannibalistic attacks in early-maturing females between the two rounds of mating trials (six females cannibalised males in both rounds, five only in the first round, no females only cannibalised in the second round, and two females did not cannibalise males in either round; McNemar test: $\chi^2 = 3.20$, $df = 1$, $P = 0.074$). In turn, we did not detect significant changes in cannibalistic behaviour in late-maturing females (five females cannibalised males in both rounds, five only in the first round, ten only in the second round, and eight cannibalised males in neither round; McNemar test: $\chi^2 = 1.07$, $df = 1$, $P = 0.30$).

Discussion

In comparison to female praying mantises (*Mantis religiosa*) that matured later in the season, early-maturing females were larger but in poorer condition. During the first round of mating trials, early-maturing virgin females cannibalised males more frequently than their late-maturing counterparts. In contrast, late-maturing females that achieved mating but did not cannibalise any male in the first round of mating trials were more likely than early-maturing, nonvirgin females to be cannibalistic in the second round of mating trials. The latency time until copulation was longer for the females that were more likely to commit cannibalism (i.e. early-maturing females). This finding agrees with the idea that males are more cautious about approaching females that are likely to be more cannibalistic (Lelito and Brown 2006). Alternatively, males could have approached late-maturing females more quickly because these males were less selective or cautious about their mates toward the end of the season.

We now discuss whether male availability, female body condition, and environmental conditions in early life could explain the seasonal differences in the occurrence of sexual cannibalism. First, although hatchling sex ratio in a related mantid *Tenodera sinensis* was found to be 1:1 (Moran and Hurd 1994), the sex ratios of adult *M. reliogiosa* (Lawrence 1992) and other closely related mantids (Hurd et al. 1994; Maxwell 1998) typically become female-biased as the season progresses. This change in sex ratio could be due to a higher mobility of males (Matsura and Inoue 1999), which may result in higher predation rates (Lawrence 1992). Also, male insects have been found to show shorter physiological longevity than females (Matsura and Inoue 1999). Finally, sexual cannibalism of males also contributes to a seasonal decrease in male numbers (Hurd et al. 1994), thus making males a limited resource for late-maturing females (Moya-Laraño et al. 2003b). Therefore, unlike in other sexually cannibalistic systems, such as that of fishing spiders, where adult sex ratio was not found to vary with season (Zimmerman and Spence 1992), the propensity of female praying mantises to adjust their cannibalistic behaviour to the time of season may be genetically based. This genetic trait could regulate the rate of cannibalism according to changes in male availability. Nevertheless, our previous work on the same species, where females did not adjust their cannibalistic behaviour according to operational sex ratio (Prokop and Václav 2005), does not support the idea that female praying mantises reduce their cannibalistic attacks in response to low perceived male availability.

Second, female size and condition affect female fitness through fecundity (Lawrence 1992; Matsura and Mooroka 1983) and physical attractiveness (Lawrence 1992). Moreover, female praying mantids in good condition were also reported to be less cannibalistic than hungry females (Birkhead et al. 1988; Kynaston et al. 1994; Liske and Davis 1987). We found that on the day of a mating trial, late-maturing females were significantly smaller but had a better body condition index than early-maturing females. Therefore, late-maturing females may have been less likely than early-maturing females to cannibalise their potential mates because they were either in better condition or less attractive (i.e. smaller). However, it is unlikely that body condition alone could explain cannibalistic behaviour of late-maturing females because females changed their cannibalistic behaviour between trials according to their mating status. Specifically, while virgin, late-maturing females were less likely than virgin, early-maturing females to cannibalise males in the first round of mating trials, this trend was reversed in the second round of mating trials. Here, considering only the females that copulated but did not cannibalise males in the first round of mating trials, non-virgin, late-maturing females cannibalised males significantly more often than nonvirgin, early-maturing females. Thus, our results are compatible with the idea that late-maturing females postpone their cannibalistic behaviour so that insemination is not jeopardised.

Third, although female praying mantises were kept under standardised food conditions, it is likely that they experienced different environmental conditions during their juvenile life stages (it takes ~3 months from hatching until the last moult; Prokop and Václav, unpublished results). Small body size may be the result of unfavourable environmental conditions, such as food deprivation during juvenile stages (mantids: Eisenberg et al. 1981; spiders: Moya-Laraño et al. 2003a). Therefore, our finding that late-maturing females had a smaller body size than early-maturing females indicates that the early-maturing group had a greater food intake. This idea is supported by our observation that body size decreased with season in both sexes of male praying mantises. According to Arnqvist and Henriksson (1997), pre-mating sexual cannibalism by adult females may be the result of high and indiscriminate aggressiveness during early life stages, which leads to the prediction that large females (i.e. those with higher juvenile food consumption) will be cannibalistic more often than smaller females. Our results are in apparent agreement with the ''aggressive spillover'' hypothesis because cannibalistic attacks were more frequently committed by larger, early-maturing females. However, we found that late-maturing females committed significantly more attacks than early-maturing females as soon as they achieved mating, suggesting that there is a strong physiological component (i.e. insemination) to sexual cannibalism in *M. religiosa*. Moreover, in contrast to Arnqvist and Henriksson's hypothesis, the cannibalistic behaviour was not consistent between mating trials even for early-maturing female praying mantises because the number of females that cannibalised males only in the first mating trial tended to be greater than that of females cannibalising males only in the second mating trial.

To conclude, although we cannot exclude the possibility that photoperiod could have been used by females as a cue for male availability, weather conditions, or their lifespan, our results suggest that the need for insemination influences the propensity of virgin females to cannibalise males in praying mantises. In turn, once the female has mated, the female's hunger level and/or perceived food availability may be more important factors in the occurrence of cannibalism.

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