

Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity

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Several hypotheses have been proposed to explain the evolution of sexual cannibalism. The foraging strategy hypothesis states that sexual cannibalism may arise as an adaptive foraging strategy, providing females with the nutrients to increase future fecundity. Yet, very few studies have found that nourishment through cannibalism translates into increased fecundity. One explanation for this may be that most of these investigations have concentrated on sexually dimorphic spider species with tiny males that do not significantly increase female body mass on consumption. The current study focuses on the praying mantid, *Pseudomantis albofimbriata*, a moderately size dimorphic species with relatively large males. Cannibalistic females of such species may be more likely to gain nutritional benefits from male consumption, which translate into increased fecundity. Here, cannibalistic females substantially improved their body condition and subsequently produced heavier egg cases than their noncannibalistic counterparts. An additional prediction of the foraging strategy hypothesis is that sexual cannibalism will increase with decreasing female condition. We found that the prevalence of sexual cannibalism in this system was indeed affected by female body condition; females in poor condition were more likely to consume their potential mates than females in good condition. Additional analysis of the data refuted the relevance of each of the remaining hypotheses for this species, providing clear evidence for the foraging strategy hypothesis as an explanation for the maintenance of sexual cannibalism in this species. **Key words:** fecundity benefit, female body condition, foraging strategy, praying mantid, *Pseudomantis albofimbriata*, sexual cannibalism, sexual conflict. [*Behav Ecol*]

Sexual cannibalism, where females consume courting males before, during, or immediately after mating, may represent the ultimate conflict of interest between the sexes (Darwin 1871; Elgar 1992). Although cannibalism during courtship/mating occurs with relatively low frequency in the majority of animal taxa, it is comparatively widespread among the arthropods (Elgar 1992; Maxwell 1999a). Several hypotheses have been proposed to explain the origin and maintenance of sexual cannibalism in various insect and arachnid groups. The costs and benefits of sexual cannibalism are typically viewed from the male or female perspective, and the timing of cannibalism in relation to insemination is also considered (Elgar and Schneider 2004). Cannibalism that occurs after insemination may be advantageous for males and/or females. The degree of conflict is minimized if a male's cannibalized soma increases female fecundity, and the paternal investment compensates for any future loss of reproductive opportunity. In contrast, precopulatory cannibalism is the most extreme form of sexual conflict; although the female may benefit from the encounter, the male forfeits all present and future reproductive successes (Buskirk et al. 1984).

There are 4 hypotheses that have been proposed to explain the evolution of precopulatory sexual cannibalism. First, it is an extreme form of female mate choice, where males of preferred phenotypes are allowed to copulate and sire offspring but inferior males are cannibalized before fertilization (Elgar and Nash 1988). Second, it occurs as a result of strong selection for female aggression in earlier life-history stages, even though there may be costs at the adult stage (Arnqvist and Henriksson 1997). Third, sexual cannibalism is the side effect of an increased foraging vigor of females that mature at

a smaller size and body mass (Schneider and Elgar 2002). And finally, precopulatory sexual cannibalism may arise strictly as an adaptive foraging strategy, providing females with nutrients that increase survival and/or fecundity (Newman and Elgar 1991).

The foraging strategy hypothesis was first proposed by Newman and Elgar (1991) to explain precopulatory cannibalism by virgin females and suggests that females adaptively assess a male's value as a mate versus his value as a meal. Therefore, the model predicts that sexually cannibalistic behavior will increase with decreasing food availability and body condition; will be more common in mated as opposed to virgin females; will increase as male size increases; and will decrease as male density decreases. Numerous studies lend support to one or more of these predictions (Liske and Davis 1987; Birkhead et al. 1988; Andrade 1996; Elgar and Fahey 1996; Maxwell 2000; Schneider and Elgar 2001; Herberstein et al. 2002; Johnson 2005a). However, contrasting evidence suggests the frequency of sexual cannibalism is not affected by female feeding condition (Herberstein et al. 2002; Johnson 2005a; Prokop and Vaclav 2005), reproductive status (Schneider et al. 2000; Schneider and Elgar 2001), or male size (Fromhage et al. 2003; Johnson 2005b; Schneider et al. 2006).

The foraging strategy hypothesis also assumes that increased feeding and nutrition translates into increased female fecundity. To date, only 2 studies have found such a benefit from male consumption. Sexual cannibalism increased fecundity in female mantids, *Hierodula membranacea* (Birkhead et al. 1988), and increased egg sac mass in female fishing spiders, *Dolomedes triton* (Johnson 2005a). These investigations were restricted to species with relatively large, nutritious males. In contrast, the studies that found no significant increase in female reproductive output as a result of cannibalism focus on spider species that are highly sexually size dimorphic—a typical male represents less than 10% of a female's body mass (Table 1). It is, therefore, not surprising that the male soma does not substantially contribute to a female's diet in these cases.

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Table 1
Studies that examined whether sexual cannibalism affords a female fecundity benefit

Species	Measure of fecundity	Effect	Reference	Sexual dimorphism
Arachnids				
<i>Lactrodectus hasselti</i>	First egg sac mass	None	Andrade 1996	Male 1–2% of female body mass
	No. of eggs in first egg sac	None		
<i>Phonognatha graffei</i>	No. of eggs in egg sac	None	Fahey and Elgar 1997	Male 8% of female body mass
	Clutch size	None		
<i>Argiope bruennichi</i>	Hatching success	None	Fromhage et al. 2003	Male 8% of female body mass ^a
	No. of eggs	None		
<i>Argiope keyserlingi</i>	Female body mass	Positive	Elgar et al. 2000	Male 7% of female body mass
<i>Araneus diadematus</i>	Egg sac mass/offspring number	Not tested	Elgar and Nash 1988	Male 25% of female body mass
	No. of eggs in egg sac	None		
<i>Dolomedes fimbriatus</i>	Egg size	None	Arnqvist and Henriksson 1997	Male 7% of female body mass ^a
	Female body mass	None		
<i>Dolomedes triton</i>	No. of offspring	None	Spence et al. 1996	Male approximately 27% of female body mass (see Johnson 2005a)
	Egg sac mass	Positive		
Mantids				
<i>Iris oratoria</i>	First ootheca weight	None	Maxwell 2000	Male 49% of female body mass
	No. of eggs	None		
<i>Hierodula membranacea</i>	Maximum female body mass	Positive (NS)	Birkhead et al. 1988	Male 61% of female body mass
	First ootheca weight	Positive		
<i>Pseudomantis albofimbriata</i>	Female body condition	Positive (NS)	Present study	Male approximately 40% of female body mass
	First ootheca weight	Positive		

^a Personal communication with the author/s. NS, nonsignificant.

In the present study, we used the sexually cannibalistic false garden mantid, *Pseudomantis albofimbriata*, to test the assumption and first prediction of the foraging strategy hypothesis. *Pseudomantis albofimbriata* exhibits only moderate sexual size dimorphism—males are approximately 40% the body mass of females—and we predict that cannibalistic females of such species will increase body condition and fecundity as a result of male consumption. We also predict that the frequency of sexually cannibalistic attacks will increase with decreasing food availability/female condition. Because it is possible that the 4 hypotheses proposed to explain the evolution of sexual cannibalism are not mutually exclusive, we carried out further analyses to test the relevance of each remaining hypothesis for this species.

METHODS

Study species and site

Individual *P. albofimbriata* were collected from various sites around Sydney and Canberra, Australia, during the summer months of 2003/2004 and 2005/2006 (December–February). The majority of individuals were found in *Lomandra* spp. bushes at Kuringai Bicentennial Park, West Pymble, and on the Australian National University campus, Canberra. Juvenile mantids were collected from the study sites and reared to adulthood on a diet of 2 small crickets (*Acheta domestica*) 3 times a week and water daily. Animals were housed individually within well-ventilated 425-ml transparent cups in the laboratory, at a temperature of 24–26 °C. Experiments were carried out during daylight hours (typically 8 AM–8 PM) in February–April 2004 and February–April 2006.

Measuring mantids

The pronotum length of mantids was recorded after the final molt, whereas body mass was measured immediately preceding

and after each individual's mating trial. Because pronotum length remains constant throughout adulthood and can only be influenced by feeding during the juvenile stages (Barry KL, in preparation), it is used as a measure of "fixed size." Body mass is, instead, variable and depends on size and feeding levels during adulthood. Male *P. albofimbriata* represent approximately 40% the body mass of females (female body mass = 0.665 ± 0.030 g, *N* = 38; male body mass = 0.265 ± 0.006 g, *N* = 38). Finally, we used each female's mass divided by her fixed size as an index of body condition (see Jakob et al. 1996 for discussion of other indices).

Female foraging strategy hypothesis: fecundity benefit

A virgin male and female were randomly chosen from the laboratory population the day after feeding had occurred, so that females were neither hungry nor satiated during mating experiments. On the day of trial, males were 24.95 ± 1.52 days postadult emergence and females were 24.25 ± 1.38 days postadult emergence. Because the majority of mantids were collected from *Lomandra* spp. bushes in the field, we placed each experimental pair onto 1 of 5 potted *Lomandra* plants, placed outdoors so as to simulate natural conditions. Approximately 10 min after the initial introduction of a female, a male was placed onto the plant at least 20 cm behind the female. If an interaction did not occur within 3 h, the trial was terminated. If copulation or cannibalism occurred, measures of female body mass and body condition were again obtained on completion of the experiment. Males that failed to mate were given at least 5 days before being paired with another female.

Although the onset of cannibalism occurs prior to copulation in this species, males are able to initiate copulation and transfer sperm while being consumed (Barry 2004). Therefore, we compared females that copulated (no cannibalism) with females that cannibalized and copulated to determine

if sexual cannibalism afforded an immediate fecundity benefit. Female fecundity was estimated using female condition (after trial) and the mass of the first ootheca (egg case). Female body condition is positively related to fecundity in many spiders and mantids (Rubenstein 1987; Birkhead et al. 1988; Wise 2006), and preliminary analyses of *P. albofimbriata* have shown that the mass of an ootheca is positively related to the number of offspring that hatch from that ootheca (Pearson's $R = 0.601$, $N = 22$, $P = 0.003$). Females were starved after copulation until ootheca production (time to first oviposition = 9.890 ± 0.900 days, $N = 27$), so that any change in fecundity was due solely to consumption of a conspecific and not subsequent consumption of another prey item. Oothecae were removed from cups 5 days after deposition to allow complete hardening and easy measurement using electronic scales.

Female foraging strategy hypothesis: female condition

In order to determine if the frequency of cannibalism increased with decreasing female condition, we first compared the body condition of cannibalistic ($N = 16$) and noncannibalistic females ($N = 19$) at the commencement of trial.

Our next experiment involved manipulating the feeding regime of a different group of virgin females ($N = 19$) immediately before a second round of mating trials. These females were starved for 10 days so as to empty their gut (see Maxwell 2000) and then randomly allocated to weeklong feeding treatments. Females on the “low-quantity” feeding treatment ($N = 9$) were given 1 small cricket (body mass = 0.037 ± 0.003 g, $N = 27$) 3 times during the week preceding experimentation, whereas females on the “high-quantity” treatment ($N = 10$) were fed 1 large cricket (body mass = 0.300 ± 0.023 g, $N = 30$) 3 times over the same week. All animals received water daily. Females were weighed prior to, and immediately after, feeding regimes, and high-quantity females were in significantly better condition (0.051 ± 0.005 g) after feeding treatments than low-quantity females (0.035 ± 0.004 g; t -test: $t_{17} = -2.593$, $P = 0.019$). The treatment groups were, therefore, renamed “good condition” and “poor condition.” Mating was then carried out as per the initial unmanipulated trials, and the frequency of sexual cannibalism was compared between treatments.

Other hypotheses

Although the primary intention of this study was to determine if the foraging strategy hypothesis explains sexual cannibalism in this system, we also wanted to test the major assumptions associated with each of the remaining 3 hypotheses. First, we compared various phenotypic characters of males that approached cannibalistic and noncannibalistic females (mate choice hypothesis: Elgar and Nash 1988). Second, we compared the fixed adult size of cannibals and noncannibals to determine whether females that consumed their mates were smaller at maturity (life-history strategy hypothesis: Schneider and Elgar 2002) or larger at maturity (aggressive spillover hypothesis: Arnqvist and Henriksson 1997).

Data analysis

Data were analyzed using SPSS 11.0 for Windows and were checked for normal distribution (Kolmogorov–Smirnov test) before further statistical analysis. The data collected during 2 different mating seasons were subsequently pooled because there was no significant difference between any of the measurements used in analyses. Unless otherwise stated, all values are mean \pm standard error, and all statistical tests are 2 tailed.

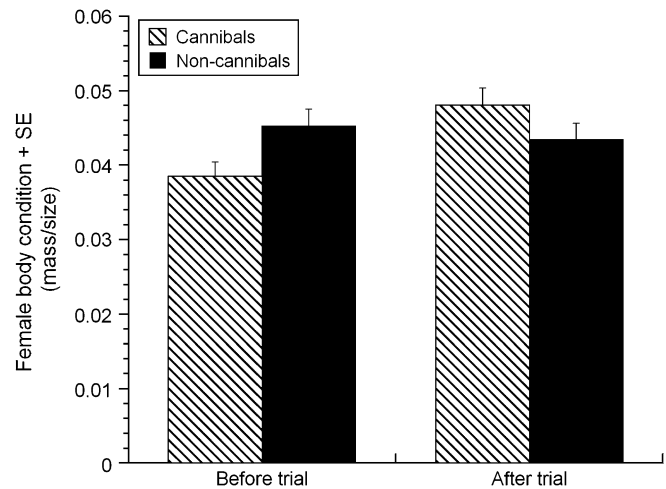


Figure 1
Female body condition before and after mating trials, compared between cannibals ($N = 8$) and noncannibals ($N = 19$). Cannibalistic females were in significantly poorer condition at the start of trial, but this difference disappeared when condition was compared after trial.

RESULTS

Female foraging strategy hypothesis: fecundity benefit

There was a significant difference in condition change (before and after trial) between the cannibalistic and noncannibalistic females (t -test: $t_{16,924} = 11.883$, $P < 0.001$; Figure 1); all females that consumed male conspecifics substantially improved their condition, whereas all noncannibalistic females saw a decrease in body condition. Furthermore, female body condition significantly predicted ootheca mass (linear regression: $r^2 = 0.437$, $F_{1,26} = 4.405$, $P < 0.001$; Figure 2), and cannibalistic females tended to be in better condition after trial than their noncannibalistic counterparts (t -test: $t_{36} = 1.418$, $P = 0.165$; Figure 1).

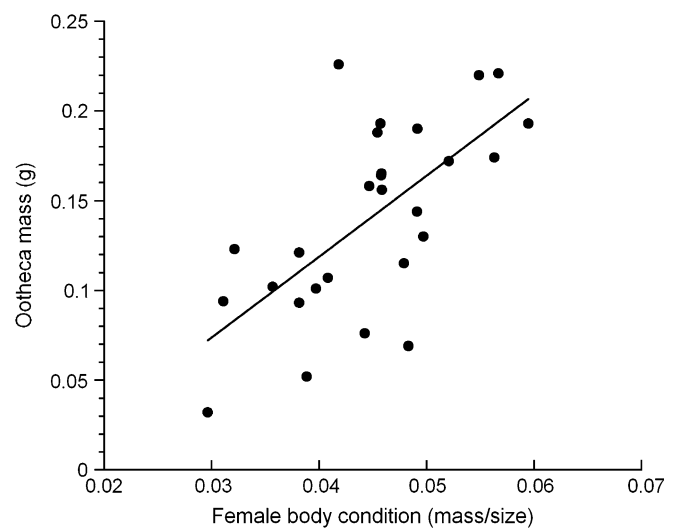


Figure 2
Female body condition had a significant positive effect on ootheca mass in *Pseudomantis albofimbriata* (regression equation = $-0.06 + 4.51 \times$ female body condition after trial).

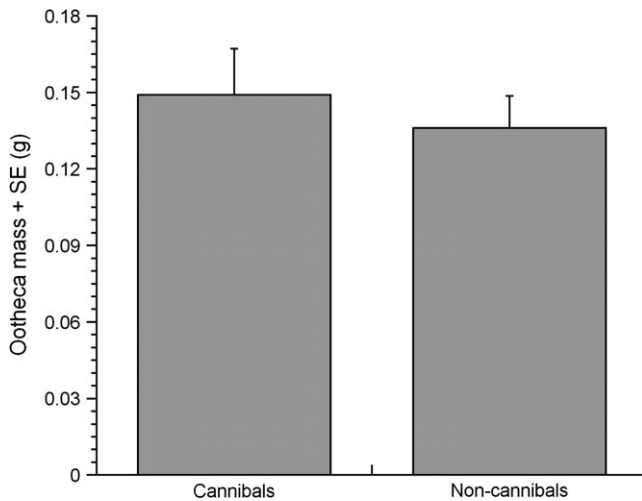


Figure 3

Mass of the first ootheca compared between cannibalistic ($N = 8$) and noncannibalistic ($N = 19$) females. Sexual cannibalism had a significant effect on mean ootheca mass, so that the oothecae of cannibalistic females were heavier than those of noncannibalistic females.

Most importantly, sexual cannibalism had a significant positive effect on the mass of oothecae (analysis of covariance: $F_{1,26} = 6.631$, $P = 0.017$; Figure 3), as did the covariates of female condition before the mating trial ($F_{1,26} = 19.934$, $P < 0.001$) and copulation duration ($F_{1,26} = 7.639$, $P = 0.011$; whole-model test: $r^2 = 0.540$, $F_{3,26} = 9.000$, $P < 0.001$). Using the regression equation given in Figure 2, the difference in ootheca mass between the groups indicates that sexual cannibalism could increase female reproductive output by up to 40%. Interestingly, sexual cannibalism no longer influences the mass of oothecae if female body condition after trial replaces body condition before trial as a covariate (body condition before trial: $F_{1,26} = 28.247$, $P < 0.001$; sexual cannibalism: $F_{1,26} = 0.25$, $P = 0.877$; whole-model test: $r^2 = 0.615$, $F_{3,26} = 12.227$, $P < 0.001$).

Female foraging strategy hypothesis: female condition

As predicted, females that cannibalized males during unmanipulated mating trials were in significantly poorer condition at the start of trial than their noncannibalistic counterparts (t -test: $t_{36} = -2.090$, $P = 0.044$; Figure 1). Furthermore, there was a significant difference in the frequency of sexual cannibalism between feeding treatments during the second experiment (Fisher's Exact test: $N = 19$, $P = 0.0001$): 89% (8/9) of females in the poor-condition treatment attacked and subsequently cannibalized the male; however, none (0/10) of the females in good condition attempted to strike at a male conspecific.

Other hypotheses

There was no significant difference in the characteristics of males that were cannibalized and males that were not cannibalized (latency to approach, $P = 0.082$; male mass, $P = 0.953$; fixed male size, $P = 0.546$; male condition, $P = 0.706$; relative mass, $P = 0.184$; relative size, $P = 0.067$; relative condition, $P = 0.273$). Furthermore, there was no significant difference in fixed adult size between cannibalistic (15.720 ± 0.233 mm) and noncannibalistic females (15.482 ± 0.276 mm; $t_{36} = 0.624$, $P = 0.537$).

DISCUSSION

Foraging strategy hypothesis: fecundity benefit

As predicted, sexual cannibalism had a significant positive effect on both female body condition and the mass of the first ootheca. Furthermore, a female's body condition after trial was a significant predictor of her subsequent reproductive output, suggesting that females gain an immediate fecundity benefit as a direct result of male consumption. *Pseudomantis albobimbrata* males represent a relatively large proportion of a conspecific female's body mass, so it is not surprising that sexual cannibalism can boost the reproductive output of a female by up to 40%. A similar increase in body condition and/or fecundity has been shown for other cannibalistic species with relatively large males (see Table 1). For example, male garden spiders, *Araneus diadematus*, represent approximately 25% a female's body mass, and cannibalistic females increase their body mass as a result of consuming a male (Elgar and Nash 1988). Birkhead et al. (1988) found that cannibalistic *H. membranacea* female mantids achieved a greater maximum weight and a significantly greater ootheca weight than females that were prevented from eating a male. There are, however, species that exhibit a similar degree of moderate sexual size dimorphism but have shown little benefit to female fecundity as a result of sexual cannibalism (Spence et al. 1996; Maxwell 2000). For example, Maxwell (2000) showed that female *Iris oratoria* maintained on a high-quantity feeding regime were more fecund; however, a single cannibalistic event did not have the same significant impact. It may be that the rate of resource utilization is different for this species, so that male consumption has a delayed effect on reproductive output. Perhaps, eggs contained in the first egg case are manufactured during the weeks prior to copulation, and those derived from the male soma are laid in subsequent egg cases (see Johnson 2001, e.g., in fishing spiders).

Although the fecundity of *P. albobimbrata* females is improved as a direct result of sexual cannibalism, the possibility of remaining unmated prevails. It, therefore, seems extraordinary that a behavior with such detrimental possibilities for both males and females has not been selected against. One explanation for the maintenance of sexual cannibalism is the evolution of alternative male strategies that substantially reduce the risk of attack; the safety precautions undertaken by most male mantids, such as mounting females from low-risk positions (Maxwell 1998, 1999b, 2000; Barry et al. forthcoming) and maintaining a copulatory posture out of female reach (Roeder 1935; Robinson MH and Robinson B 1979; Liske and Davis 1984, 1987; Maxwell 1998, 1999b; Barry et al. forthcoming), are evidence of such. The ability to inseminate a female even when cannibalism precedes genital contact may be an additional method of combating highly aggressive females—all *P. albobimbrata* males that are cannibalized attempt to copulate with their female attacker, and approximately half are successful (Barry et al. forthcoming).

Foraging strategy hypothesis: female body condition

In addition to increased fecundity, the foraging strategy hypothesis suggests that the likelihood of sexual cannibalism will be influenced by female body condition. As predicted, cannibalistic females were in significantly poorer condition at the commencement of unmanipulated mating trials than noncannibalistic females but had a marginally better body condition after the completion of trial (Figure 1). *Pseudomantis* females in poor condition seem to use sexual cannibalism as a means of improving their condition, which positively influences their subsequent reproductive output. Furthermore, all females in

the good-condition treatment copulated without consuming their mate, whereas all but one poor-condition female attacked and subsequently cannibalized the male. Numerous studies have similarly shown that sexually cannibalistic behavior increases with decreasing food availability and/or female body condition (Liske and Davis 1984; Birkhead et al. 1988; Kynaston et al. 1994; Andrade 1998; Maxwell 1998; Maxwell 2000; Schneider and Elgar 2001). Again, the majority of these studies involve cannibalistic species with moderate sexual size dimorphism.

Although sexual cannibalism occurs frequently in many laboratory studies, it may be relatively uncommon in natural populations. If alternative prey types are readily available, wild females may never be food limited and cannibalism might be infrequent. Further studies outlining female body size/condition, the availability of prey, and the frequency of sexual cannibalism in natural populations are required before the evolutionary significance of this behavior can be totally understood.

Other hypotheses

Because the hypotheses proposed to explain precopulatory sexual cannibalism are not necessarily mutually exclusive, we also tested the major assumptions associated with the mate choice, aggressive spillover, and life-history strategy hypotheses. The mate choice hypothesis suggests that sexual cannibalism is an extreme form of female mate choice, where males of preferred phenotypes are allowed to copulate and sire offspring but inferior males are cannibalized before fertilization (Elgar and Nash 1988). However, we found no evidence of morphological or behavioral differences in males that were cannibalized versus males that were not cannibalized. The aggressive spillover hypothesis suggests that sexual cannibalism occurs as a result of strong selection for female aggressiveness in earlier life-history stages; therefore cannibalistic females tend to be larger at maturity than females that do not consume their mates (Arnqvist and Henriksson 1997). Finally, the life-history strategy hypothesis suggests that sexual cannibalism is the side effect of an increased foraging vigor of females that mature at a smaller size and body mass (Schneider and Elgar 2002). However, our study suggests that there is no significant difference in the fixed size of cannibalistic and noncannibalistic *P. albofimbriata* females, making neither of the latter hypotheses relevant as an explanation for sexual cannibalism in this system.

Summary

Our results support the foraging strategy hypothesis as a primary explanation for the maintenance of sexual cannibalism in this system. We found that sexual cannibalism had a significant positive effect on both female body condition and ootheca mass and that female body condition was a significant predictor of ootheca mass. Finally, we found that females in poor condition were significantly more likely to attack and cannibalize a male than females in good condition.

In conclusion, our results confirm the lack of a general rationalization for the evolution and/or maintenance of sexual cannibalism. Many factors, such as the timing of cannibalism in relation to insemination and the degree of sexual size dimorphism, vary between and within the mantids and arachnids, suggesting that sexual cannibalism has evolved multiple times and is maintained in numerous species for many different reasons. The female foraging strategy hypothesis is more likely to explain sexual cannibalism in moderately sexually size dimorphic species (i.e., most praying mantids), as the relatively large males make for bigger and more nutritious meals.

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