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## Original Article

# Sexual cannibalism in a facultative parthenogen: the springbok mantis (*Miomantis caffra*)

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Sexual cannibalism is an extreme expression of sexual conflict, which can grant females significant fitness benefits, particularly if female fecundity depends on foraging success. However, when cannibalism is precopulatory, there is the risk that females remain unmated. Therefore, males simultaneously present the option of a meal or a mate to the females they encounter. The springbok mantis (*Miomantis caffra*) is highly aggressive, and when females cannibalize males, it is exclusively precopulatory. However, females can circumvent the risk of infertility by reproducing asexually, providing a rare opportunity to explore the interaction between sexual cannibalism and facultative parthenogenesis. We kept female mantises on high and low feeding regimes, and paired them with males, to examine how body condition and age influenced rates of cannibalism. We also investigated whether reproductive mode (sexual or asexual) influenced fecundity by measuring ootheca weight. Overall, there was an extremely high average cannibalism frequency (~62%), but no significant difference in frequencies of cannibalism between feeding regimes. Although there was a relationship between female condition and fecundity, influenced by feeding treatment, the mode of reproduction (sexual or asexual) did not result in any difference in ootheca weight. Using information-theoretic approaches, we determined that, of the variables examined, female age best accounted for cannibalistic behavior and that females became less aggressive and more likely to mate over time. This suggests that, although parthenogenesis may allow females to cannibalize males at a high frequency without incurring the cost of infertility, they may still benefit from reproducing sexually later in their lives.

**Key words:** asexual, fecundity, praying mantis, precopulatory cannibalism, sexual conflict.

## INTRODUCTION

Sexual conflict arises in a species when one sex's optimal reproductive strategy encroaches on the fitness of the other sex (Pizzari and Snook 2003; Arnqvist 2004; Chapman 2006). This conflict of interests is widespread in both the species and traits that it influences. Sexual cannibalism is one particularly extreme expression of this conflict and is relatively unique in that it is most commonly females that impose severe costs on male fitness rather than the reverse (Parker 1979; Elgar and Crespi 1992; Herberstein et al. 2002). Sexually cannibalistic females may kill and consume males before they mate (Arnqvist 1992; Fea et al. 2013) or even deceptively attract males in order to consume them (Barry 2015). In a number of species, elaborate male behaviors have evolved to minimize the likelihood of being attacked (Gaskett et al. 2004; Lelito and Brown 2006; Barry et al. 2009), and maximize male fertilization success (Andrade 1996).

One prominent theory that explains the maintenance of sexual cannibalism is the adaptive foraging hypothesis, an economic

model devised by Newman and Elgar (1991). The model predicts that, when there is a correlation between foraging success and fecundity, female starvation should result in higher rates of cannibalism. An alternative hypothesis suggests that sexual cannibalism is instead the result of aggressive spillover, a maladaptive consequence of selection for indiscriminate aggression in juvenile predators (Arnqvist and Henriksson 1997). Here, although aggressive juveniles would benefit from increased prey capture, adult females who consistently cannibalize mates, risk infertility if they remain unmated. This occurs in the fishing spider *Dolomedes fimbriatus* where a significant proportion of females die before reproducing (Arnqvist and Henriksson 1997).

The timing of sexual cannibalism is critical when determining the fitness consequences for males and females. For many species, the reality is that females may kill and consume males before they mate (Arnqvist 1992; Barry et al. 2008; Fea et al. 2013) and may even attract them for this purpose (Barry 2015). Although post-copulatory cannibalism allows a female to both mate with a male and gain a meal, precopulatory cannibalism may impose costs on females if they remain unmated and infertile. For this reason, the

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adaptive foraging hypothesis also predicts that the rate of cannibalism is likely to decrease towards the end of the season lest a female remain unmated, having consumed all available mates. Female wolf spiders (*Hogna helluo*) vary the timing of sexual cannibalism depending on their own mated state and body condition. Namely, virgin females generally tend to cannibalize males after mating and those which do cannibalize males prior to mating are of significantly poorer body condition (Wilder and Rypstra 2012). Similarly, previously mated female wolf spiders (*Pardosa pseudoannulata*) show much higher frequency of precopulatory cannibalism than virgins and the starvation of females only increases the likelihood of cannibalism for virgins (Wu et al. 2013).

If the trade-off between mating opportunities and risk of starvation determines the likelihood of cannibalistic behavior, it is reasonable to expect that any variation in the value of males as either a meal or mate will modulate the probability of cannibalism. Numerous studies have modified male value as a meal by starving females. In both female bordered mantises (*Stagmomantis limbata*) and wolf spiders (*H. helluo*), body condition is positively related to reproductive output and correspondingly females kept on low feeding regimes cannibalize males more frequently (Wilder and Rypstra 2008a; Maxwell et al. 2010). This pattern also exists in false garden mantises (*Pseudomantis albobimbrata*) and, for this species, cannibalism has been explicitly shown to lead to improved fecundity (Barry et al. 2008).

It is more difficult to examine how the value of males as mates may vary, but we would predict that, should the value of males as mates increase, females would be less likely to cannibalize them. The adaptive foraging hypothesis (Newman and Elgar 1991) predicts that the rate of cannibalism should decrease toward the end of the season lest females remain unmated, suggesting that a male's value as a mate, rather than a meal, may increase over time, particularly as wild sex ratios become more and more female biased later in the breeding season (Lawrence 1992; Moya-Laraño et al. 2013). Conversely, if male value as a mate is in fact decreased, we might predict that females would be more likely to cannibalize them. This is the case when females have previously mated, and many studies have shown mated females to be more cannibalistic than virgins (Herberstein et al. 2002; Rabaneda-Bueno et al. 2008; Wilder and Rypstra 2008b).

A few sexually cannibalistic mantis species (e.g., *Miomantis caffra* and *Miomantis savigny*) are also facultative parthenogens (Adair 1924). In these species, as females are released from the requirement of mating in order to reproduce, we might predict that the frequency of sexual cannibalism would be particularly high and less influenced by nutritional status. Here, we examine sexual cannibalism in a facultative parthenogen, the springbok mantis *M. caffra* (Mantodea: Mantidae). This African species was introduced accidentally to New Zealand in 1978 and has since established. Females are particularly aggressive and sexual cannibalism is exclusively precopulatory (Fea et al. 2013). We tested whether manipulation of female diet influences cannibalism frequency and reproductive output, and assessed whether the likelihood of cannibalism changes with female age. We predicted that cannibalism would occur with greater frequency in the low feeding regime treatment group and that females would cannibalize males less frequently over time. However, as this species exhibits the relatively unique combination of sexual cannibalism and parthenogenesis, we also expected that well-fed females would cannibalize males more frequently compared to well-fed, nonparthenogenic mantis species. For example, Maxwell et al. (2010) found that only 1/21 well-fed

*S. limbata* females cannibalized males and well-fed female *P. albobimbrata* would not cannibalize males at all (Barry et al. 2008). Finally, we assessed the prevalence of parthenogenesis in this species and compared the weights of asexually and sexually produced oothecae. Asexuality can lead to lower fecundity in several different ways including extended preoviposition periods, reduced clutch number and size, extended hatching periods, lowered hatching rate and decreased proportion of young that reach maturity (reviewed in Meirmans et al. 2012). Therefore, we predicted that female *M. caffra* who had not mated would produce smaller oothecae.

## METHODS

### Laboratory rearing and maintenance

We established a lab population of females with known reproductive history by collecting juvenile mantises from throughout the Auckland region of New Zealand between the 19 January 2012 and 4 April 2012. We fed juveniles a combination of house flies (*Musca domestica*), mealworms (*Tenebrio molitor*), and small locusts (*Locusta migratoria*). They received 1 food item every 2 days and were misted daily with water. Mantises were raised in individual, overturned 500-mL plastic cups, each with a mesh window for ventilation. At their final molt, adult males were moved into a separate room to avoid any contact with female pheromones.

At their final molt, females were randomly assigned to high or low feeding regimes, with the former receiving 1 medium-sized locust (10–18mm) 3 times a week, whereas the latter received only 1 small locust (5–10mm) per week. These regimes are based on those used by Maxwell et al. (2010) who provided *S. limbata* the same ratio of food for their 2 treatment groups. On these treatments, poorly fed *S. limbata* females cannibalized males significantly more frequently (10/20) compared with well-fed females (1/21). We also based this on previous experience rearing *M. caffra*, where adult females rarely consumed more than this amount when provided with an ad libitum diet. Adult males were fed 1 small locust 3 times a week.

To measure the effect of the feeding treatments on female mass, we weighed females before they were paired with males and recorded prothorax length, a fixed measure for female body size.

### Mating trials

To examine mating and sexual cannibalism, we randomly selected 1 male and 1 virgin female, placed them in an open seminatural environment (on a tree sapling *Podocarpus totara*) and observed any interactions. The trees were not enclosed so males were able to fly away or avoid interacting with the female. The female was allowed to acclimatize on a sapling for 15 min. After this, the male was placed 15 cm behind the female, facing toward her. All mantises had eclosed at least 14 days prior, and this maturation period was used because, in other mantids, male reproductive and female calling behaviors are not consistently displayed until about 10 and 14 days, respectively, after the final molt (Liske and Davis 1987; Gemeno et al. 2005).

We observed pairs until copulation or cannibalism were complete and noted the occurrence and duration of all behaviors. If an interaction did not occur within 3 h then that trial was terminated. We ran up to 4 trials (2 × high feeding regime females and 2 × low feeding regime females) simultaneously on 4 separate saplings spaced at least 1 m from each other with pairs randomly assigned to each sampling. Prior to and following trials, specimens

were weighed to determine if feeding regimes, cannibalism and/or copulation influenced female mass. We ran a total of 99 trials (47 using low feeding regime females and 42 using high feeding regime females).

### Measuring reproductive output

We monitored females daily and noted the date of oviposition whenever they laid oothecae, and we noted whether the female had copulated with a male prior to this date. When first laid, the oothecae are pale green but darken to brown-green and harden within a week. At this point, we carefully removed the oothecae from the plastic cup or off the mesh ventilation window. The height, breadth, and length of the oothecae were measured using electronic callipers accurate to 0.01 mm. The oothecae were weighed with scales accurate to 0.0001 g. We treated first ootheca mass as an index of female fecundity as first ootheca mass correlates with the number of eggs produced or the number of young that hatch in several other mantid species (e.g., *P. albofimbriata*, Barry et al. 2008; *Hierodula membranacea*, Birkhead et al. 2008; *Iris oratoria*, Maxwell 2000). Once they had been measured, we reattached the oothecae to their original cups using a glue mixture of white flour and water, applied using a small paint brush. The female remained in that cup.

### Statistical analyses

We used an analysis of covariance to verify that 2 feeding regimes produced a significant difference in female mass, treating female prothorax length as a covariate to control for body size. As cannibalism in this species is precopulatory, mating and cannibalism formed a pair of binary responses so we used a  $\chi^2$  test to determine if cannibalistic and copulatory behavior for females of each feeding regime was significantly different to an equal distribution. To investigate how different variables influenced the probability of cannibalism, we generated 11 candidate generalized linear models (GLM) with binomial errors and a logit link.

Using an information-theoretic approach outlined by Burnham et al. (2011), we ranked these models according to their AICc, a second-order Akaike information criterion for small sample sizes. The parameters were estimated using model averaging across the best models, that is, those with AICc < 2. The variables used in these models included: female condition (measured using residuals extracted from our analysis of covariance), female age (days since final molt), whether or not a female had laid an ootheca prior to the trial and relative male size (male pronotum length/female pronotum length). Pearson's correlation coefficients were calculated to examine correlations between female age and condition, and between whether the female had laid and age and condition. Our full model included female age, female condition, relative size, and an interaction term for female condition and relative male size.

We generated our candidate models using predictions from the adaptive foraging hypothesis and findings from other sexually cannibalistic species (*S. limbata*, Maxwell et al. 2010; *P. albofimbriata*, Barry et al. 2008). The adaptive foraging hypothesis suggests that female condition determines the likelihood of cannibalism but that this will be tempered toward the end of the mating season, which we treated as female age (Newman and Elgar 1991). The adaptive foraging hypothesis also predicts that mated females are more likely to be cannibalistic and this has been demonstrated in other sexually cannibalistic species such as the wolf spider, *H. helluo*, in which mated females are more likely to engage in precopulatory cannibalism than virgin females (Wilder and Rypstra 2008b). Some *M. caffra*

females laid ootheca prior to being used in trials. Therefore, it seemed likely that females that had already laid an ootheca may respond differently when presented with a male. Finally, male relative size is included as a variable to account for the possibility that females are better at capturing males of a certain size or may be practising some form of extreme mate choice.

We conducted a 1-way analysis of variance (Anova) to compare the average change in mass for females that mated, females that cannibalized, and females who did not interact with males. We used a 2-way Anova to compare the average weights of first oothecae produced by mated and virgin females of high or low feeding regimes. All statistical analyses were conducted in R 3.03 including use of the AICcmodavg package (R Core Team 2014; Mazerolle 2015).

## RESULTS

### Female cannibalistic behavior

Females from the well-fed treatment group had an average ( $\pm$  standard error [SE]) mass of  $0.707 \text{ g} \pm 0.0527$ , whereas poorly fed females had an average mass of  $0.489 \text{ g} \pm 0.0142$ . Controlling for differences in body size, the analysis of covariance produced evidence that the 2 feeding regimes produced a significant difference in female mass ( $F_{2,17} = 4.67$ ,  $P = 0.0242$ ).

When males and females interacted ( $n = 29/99$ ; 14 poorly fed females, 15 well-fed females), females cannibalized males 62.1% of the time (17/29). All cannibalism was precopulatory. Poorly fed females cannibalized males 9/14 times (64.3%) and well-fed females cannibalized males 8/15 times (53.3%). There was no significant difference in the frequency of cannibalism or mating between the 2 feeding regimes ( $\chi^2 = 0.0489$ , degrees of freedom [df] = 3,  $P = 0.825$ ).

Female condition and whether a female had laid an ootheca were moderately positively correlated (Pearson's  $\rho = 0.39$ ,  $P = 0.047$ ). Therefore, we could not include candidate models containing both variables. There were no other significant correlations between our variables. When our 11 candidate models were ranked by AICc (Table 1), the model of female age and whether females had laid oothecae produced the lowest AICc although female age alone produced a very similar result ( $\Delta\text{AICc} = 0.01$ ). Due to this small difference, we opted for the more parsimonious model with a linear predictor: probability of cannibalism =  $3.15 - 0.067 \times$  female age (Figure 1). The Pearson's residuals for this model raised no concerns. Multimodel averaging across these 2 models estimated that  $\beta_{\text{age}} = -0.06$  (SE = 0.03; 95% confidence interval [CI] [-0.12, -0.01]). This indicates that the probability of cannibalism decreased with female age and conversely the probability of copulation, given any interaction between the male and female, increased with female age.

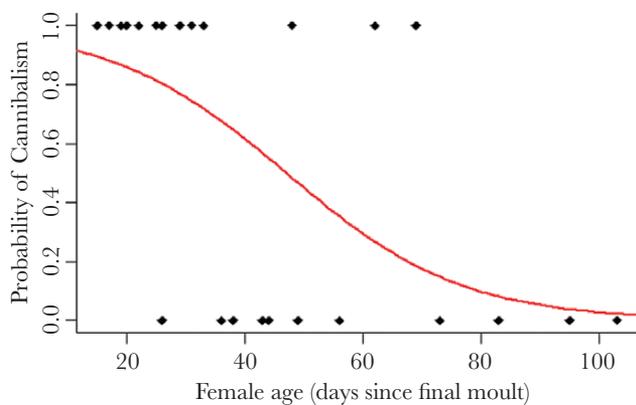
### Condition, fecundity, and parthenogenesis

Females that cannibalized males increased their mass, whereas females that copulated did not (Figure 2). We found a significant difference in the change in mass of females who either cannibalized, mated, or did not interact with males (Anova:  $F = 86.972$ ,  $\text{df} = 31$  and 2,  $P < 0.00001$ ). Post hoc Tukey Honestly Significant Difference tests showed difference in how female mass changed following cannibalism compared with following copulation or no interaction (estimated difference = 0.165 g, 95% CI [-0.200, -0.130],  $P < 0.00001$ ; estimated difference = 0.146 g, 95% CI

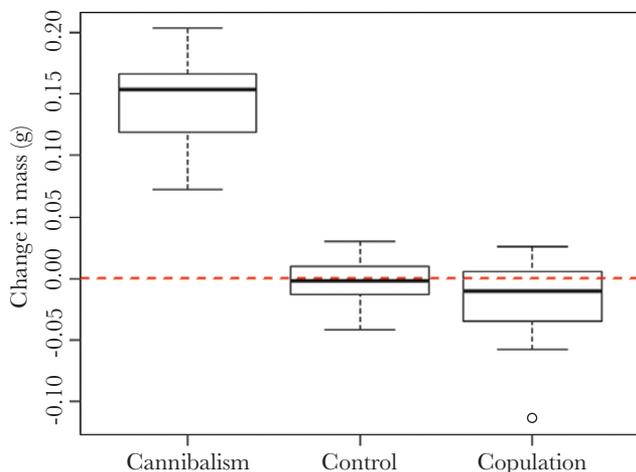
**Table 1**

**Summary of candidate models ranked by AICc including number of parameters estimated ( $K$ ), model weight (AICc weight), and ratio of model likelihoods (evidence ratio)**

Rank	Model	$K$	AICc	$\Delta$ AICc	AICc weight	Evidence ratio
1	Age + ootheca laid	3	30.68	0	0.34	—
2	Age only	2	30.69	0.01	0.34	1
3	Full additive model	5	32.75	2.07	0.11	3.09
4	Age + condition	3	32.91	2.23	0.1	3.4
5	Age $\times$ ootheca laid	4	33.45	2.77	0.8	0.425
6	Condition + relative male size	3	34.89	4.21	0.04	8.5
7	Full model	6	36.41	5.74	0.3	1.13
8	Age + relative male size	2	36.55	5.87	0.02	17
9	Condition + relative male size	4	37.39	6.71	0.01	34
10	Condition only	2	38.63	7.95	0.01	34
11	Intercept only	1	38.66	7.98	0.01	34

**Figure 1**

The probability of sexual cannibalism decreases with female age in *Miomantis caffra*.

**Figure 2**

Mass change of females (medians, quartiles, and range) following trials in which they cannibalized a male (cannibalism), copulated (copulation) or did not interact with the male (control). Dashed line indicates no change in mass. Open circle indicates outliers at least 1.5 times the interquartile range above or below upper and lower quartiles.

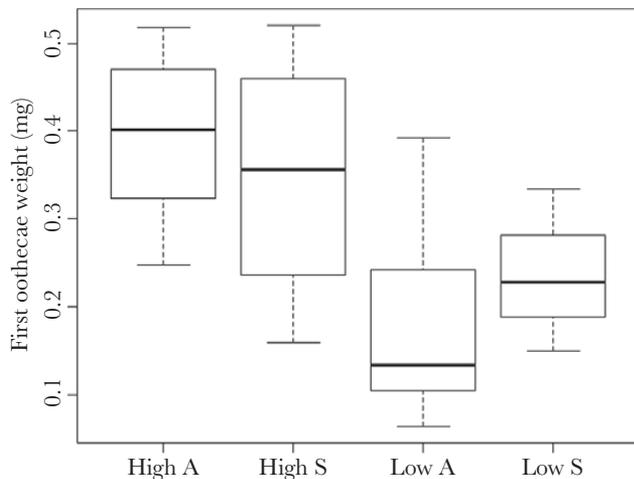
$[-0.180, -0.112]$ ,  $P < 0.00001$ , respectively). There was no significant difference in the change in mass following copulation or no interaction (estimated difference = 0.019g, 95% CI  $[-0.055, 0.0.170]$ ,  $P = 0.405$ ).

Twenty females oviposited (12 well-fed females and 8 poorly fed females). Of these first oothecae, 8 females were produced asexually (4 well-fed females and 4 poorly fed females). Among these first oothecae that were produced either sexually or asexually by females from the 2 feeding treatments, there was a difference in mean ootheca weights (Figure 3; Anova:  $F_{2,19} = 4.794$ ,  $P = 0.02336$ ,  $n = 19$ ). Although there was a significant difference between the ootheca mass of poorly and well-fed females (Figure 3;  $F = 9.58$ ,  $P = 0.00695$ ,  $n = 19$ ,  $df = 1$ ), we found no evidence that parthenogenesis significantly affected first ootheca mass (Figure 3;  $F = 0.0083$ ,  $P = 0.929$ ,  $n = 19$ ,  $df = 1$ ). We found no evidence that parthenogenesis occurred more or less frequently for high or low feeding treatments (Fisher's exact test:  $P = 0.179$ ;  $df = 19$ ).

## DISCUSSION

Female *M. caffra* cannibalized males at a very high overall frequency with ~62% of interactions resulting in the male being killed and eaten by the female with no males managing to mate once a female attack had commenced. What is more surprising is that the frequency of cannibalism was very similar between feeding treatments and, therefore, the frequency of cannibalism amongst well-fed females was very high compared to mantids under similar conditions. This is unexpected given the behavior of other cannibalistic species. Female wolf spiders (*H. helluo*) are more likely to cannibalize without mating if they are poorly fed (Wilder and Rypstra 2008a), and although 50% of poorly fed *S. limbata* females cannibalized males, only 10% of well-fed ones were cannibalistic (Maxwell et al. 2010). Even more strikingly, female *P. albofimbriata* in good condition did not cannibalize males at all, whereas females in poor condition did so in almost 90% of interactions (Barry et al. 2008). The absence of any effect of feeding treatment on rate of cannibalism in our study is therefore surprising and suggests that for *M. caffra*, sexual cannibalism is not as closely linked to hunger as demonstrated for other mantis species.

We found that female age was the most important factor determining probability of sexual cannibalism. As females grew older, they were less likely to cannibalize males and more likely to mate. However, as females did not show any evidence of reduced appetite and continued to consume all prey provided (Walker L, personal observation), this reduction in sexual cannibalism with age is unlikely to be the result of a general decrease in aggression over a female's lifespan. Age is also shown to influence the female decision to mate with or consume a male in empirical studies on wolf spiders



**Figure 3**

First oothecae mass (medians, quartiles, and range) depending on whether they were produced asexually or sexually by a well-fed female (“High A” and “High S,” respectively) and asexually or sexually by a poorly fed female (“Low A” and “Low S,” respectively).

(Uetz and Norton 2007; Wilgers and Hebets 2012). This pattern is predicted under the adaptive foraging hypothesis (Newman and Elgar 1991) which reasons that females may benefit most from eating males earlier in the season but, in order to reproduce, will mate with males toward the end of the mating season. This reasoning is appropriate for species where females that do not mate forego all chance of reproduction. Yet for *M. caffra*, we have determined that this is not the case; parthenogenesis was common. Therefore, the reasons behind the higher likelihood of mating among older female *M. caffra* are unlikely to be solely to prevent infertility. Instead, perhaps asexual reproduction incurs costs, such as reduced offspring viability, or lower long-term fitness of asexual offspring, and females may be choosing to mate with males later in the season due to the benefits of reproducing sexually (Engelstädter 2008; Meirmans et al. 2012). Although we found that feeding treatment influenced ootheca mass, asexually produced oothecae did not differ in mass from those produced by mated females and females on both feeding regimes were capable of laying viable oothecae without mating. However, we cannot rule out any later effects of parthenogenesis on offspring viability and fitness.

Traditionally, all of the costs associated with sexually cannibalistic behavior have been assumed to be paid by males, except the potential cost to females of remaining unmated and therefore infertile. However, facultative parthenogens may be exempt from such costs. As far as we are aware, this is the first study of sexual cannibalism in a facultative parthenogen. It is tempting to connect the 2 phenomena and suggest that facultative parthenogenesis frees females of the costs associated with remaining unmated, leading to a high cannibalism rate. If there are indeed more species that share these traits, and if data on such species were to accumulate, a formal assessment using comparative methods could test this hypothesis. Regardless, this study demonstrates that sexual cannibalism is not always driven by variation in female hunger and condition. That parthenogenesis has potentially allowed females to cannibalize males at such a high rate emphasizes that in other species, the risk of remaining infertile may be a significant cost, constraining the level of aggression females impose on males. It is highly likely that for most sexually cannibalistic species, the value of males to females incorporates both their value as mates, as well as meals.

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