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Complicity or Conflict over Sexual Cannibalism? Male Risk Taking in the Praying Mantis *Tenodera aridifolia sinensis*

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ABSTRACT: Male complicity versus conflict over sexual cannibalism in mantids remains extremely controversial, yet few studies have attempted to establish a causal relationship between risk of cannibalism and male reproductive behavior. We studied male risk-taking behavior in the praying mantid *Tenodera aridifolia sinensis* by altering the risk imposed by females and measuring changes in male behavior. We show that males were less likely to approach hungrier, more rapacious females, and when they did approach, they moved more slowly, courted with greater intensity, and mounted from a greater distance. Similarly, when forced to approach females head-on, within better view and better reach of females, males also approached more slowly and courted with greater intensity. Thus, males behaved in a manner clearly indicative of risk avoidance, and we support the hypothesis of sexual conflict over sexual cannibalism.

Keywords: sexual cannibalism, sexual conflict, mate choice, praying mantis, Mantidae.

Sexual cannibalism in praying mantids is legendary, and a great majority of species display sexual cannibalism at least occasionally (reviewed in Elgar 1992; Maxwell 1999*a*). Benefits of sexual cannibalism to the female are controversial in some species (Arnqvist and Henriksson 1997; Maxwell 2000), but in the Chinese mantis *Tenodera aridifolia sinensis*, the benefits are clear: females gain valuable reproductive resources through cannibalism. When females consume more prey or larger prey, they lay larger oothecae (egg cases) that contain more eggs, and they ultimately produce a greater number of offspring (Eisenberg and Hurd 1977; Eisenberg et al. 1981; see also Matsura and Mooroka 1983 for *Tenodera angustipennis*). A single ootheca may weigh 30%–50% of a female's biomass and thus represents a tremendous investment (Eisenberg et al. 1981; Hurd 1989). Yet in the field, females are often food limited (Hurd et al. 1978, 1995), making males valuable as a food source, and hungry females are more likely to cannibalize males than are satiated females (Liske and Davis 1987). Hurd et al. (1994) estimated that males in one population of *T. sinensis* made up 63% of the diet of adult females.

In contrast to these nutritional benefits to females, the possibility that males may also benefit from sexual cannibalism remains extremely controversial (see Gould 1984; Johns and Maxwell 1997). Unlike some sexually cannibalistic spiders (e.g., Sasaki and Iwahashi 1995; Knoflach and van Harten 2001; Andrade and Banta 2002; Foellmer and Fairbairn 2003), male mantids can mate repeatedly and potentially fertilize multiple females during their lifetime (Bartley 1982; Lawrence 1992; Hurd et al. 1994). Sexual cannibalism obviously eliminates the possibility of future mating for the male and thus imparts a clear cost—the total loss of future reproduction. All else being equal, this cost will generate strong sexual conflict over cannibalism. Yet male mantids can initiate copulation even after cannibalism has begun, and decapitation by cannibalism may even increase copulatory behavior (Roeder 1935; Liske 1991). Thus, precopulatory attacks by females may not diminish a male's mating success with the current female and may even increase the chance of successfully mating. One of the original theoretical models of sexual cannibalism shows that a male should be willing to sacrifice his life to an inseminated partner if he can expect little subsequent mating and if his value as a food item would allow the female to rear substantially more offspring (Buskirk et al. 1984; see also Parker 1979; Polis 1981; Birkhead et al. 1988; Maxwell 2000). More recent work on spiders has shown that males may also achieve a paternity advantage through sexual cannibalism if cannibalism can extend the period of insemination, decrease the chance of

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repeated mating by the female, or otherwise allow preferential sperm usage (Andrade 1996; Schneider and Elgar 2001).

Our goal here is to distinguish between the alternative hypotheses of male complicity versus sexual conflict over sexual cannibalism in *T. sinensis* by testing how male behavior may change depending on the likelihood of being eaten. As Gould (1984) pointed out, the model of male complicity "makes good sense, but nature will match it only if we can show that such males actively promote their own consumption" (p. 14). Gould went on to argue that he found "little persuasive evidence" (p. 16) based on the descriptive accounts of male behavior (Roeder 1935; for more recent accounts, see Liske and Davis 1987; Lawrence 1992; Kynaston et al. 1994; reviewed in Maxwell 1999*a*). But remarkably, this question of whether male mantids are complicit has never been experimentally resolved. Only one study has attempted to test the causal relationship between risk and male behavior (Maxwell 1999*b*). None has focused on female hunger, possibly the most important risk factor for males, given that hungry female mantids are significantly more rapacious than satiated females in *T. sinensis* (Liske and Davis 1987), *Hierodula membranacea* (Birkhead et al. 1988), and *Sphodromantis lineola* (Kynaston et al. 1994).

Most previous attempts to resolve the question of complicity versus conflict in mantids have attempted to measure the costs and/or benefits of cannibalism on male reproductive success, with the clear prediction that if the costs of cannibalism exceed the benefits, there is conflict, but if the benefits are somehow greater, there is complicity (e.g., Birkhead et al. 1988; Maxwell 1998). The difficulty of this approach, however, is that it has proven exceptionally difficult to collect reliable data on the reproductive opportunities of male mantids in wild populations, making it very difficult to measure the costs. Moreover, low mate encounter rates for males may be the consequence of an evolutionary history of sexual cannibalism rather than its causal precursor (Andrade 2003; Fromhage et al. 2005). Thus, the cost/benefit approach has been unable to resolve the controversy over male complicity in sexual cannibalism in mantids.

We address the question of complicity versus conflict by studying the adaptive design of male mating behavior in an experimental context that tests the causal relationship between variable risk of cannibalism and male behavior. We ask whether males switch their mating behavior according to variation in the risk of being cannibalized. The male complicity hypothesis predicts that males will engage in behavior that actively facilitates, or at least passively fails to avoid, acts of sexual cannibalism during and after copulation. To the contrary, our results show that males assess risk of cannibalism and that, given this risk, they behave in a manner to reduce the likelihood of cannibalism. Thus, male mantids are not complicit in cannibalism, and we support the hypothesis of sexual conflict.

Material and Methods

Mantid Rearing

We reared mantids from oothecae, which were either purchased from Carolina Biological Supply (Burlington, NC) or collected from a wild population in Fredonia, New York. We reared oothecae initially at room temperature and later under an incandescent bulb that increased ambient temperature and developmental rate. We misted the oothecae with water daily.

Mantids hatched after 4–6 weeks. Nymphs were reared individually in 500-mL plastic containers, fed an ad lib. supply of *Drosophila hydei*, and misted daily. Malformed or unusually inactive mantids were discarded. Rearing containers were lined on the inside with fiberglass screening as a substrate for moving and perching. We also added a slice of apple for moisture and to feed the flies until the mantids consumed them. Diet was switched to juvenile crickets, *Acheta domesticus*, after about 5 weeks, when mantids reached their fourth instar. Mantids eclosed as adults approximately 8 weeks after hatching.

Manipulating the Risk of Sexual Cannibalism

We used a two-by-two factorial experiment to test male response to altered risk of sexual cannibalism. All mantids were virgins at the beginning of the experiment. Treatments included female hunger level and orientation of male approach. To control female size and fecundity between hunger levels, all females in the experiment were first fed ad lib. crickets for 24 days after adult eclosion. Female body mass (measured to 0.01 mg on an A & D HR-202 balance; A & D Engineering, Milpitas, CA) showed a negative exponential increase over time ($y = 2.81x^{0.101}$, where y = body mass and x = age from adult emergence; $t = 5.90$, $N = 16$, $P < .001$), with mass slowing toward an asymptote after about 20 days. Thus, by 24 days, females were near their maximum size, possessing visibly distended abdomens, and body mass was independent of subsequent experimental treatments (diet treatment: $F = 0.58$, $\mathrm{df} = 1, 16$, $P = .46$; orientation: $F = 0.19$, $\mathrm{df} = 1, 16$, $P = .67$). Females were then randomly divided into either "satiated" treatment of ad lib. crickets or "hungry" treatment of 4–5 days without food to begin the experiment. All females that laid oothecae before the experiment were returned to an ad lib. diet for another 24 days to regain fecundity. Males were fed ad lib. throughout the experiment.

In the orientation treatment, males approached females either head-on, the more risky treatment, or from behind, the less risky treatment. Both Liske and Davis (1987) and Maxwell (1999*b*) suggest that males in front of and within the visual field of females are at greater risk. Our experiment differs from these two studies in that male orientation was manipulated so that males could not alter their direction of approach throughout the experiment. We varied the orientation of male approach by placing the female at the end of a wooden plank (80 cm long × 6 cm wide) that was marked in 1-cm increments and then introducing the male from the desired orientation. Once in place, a female did not turn around until either she leapt aggressively at the male or the male attempted to mount. The initial distance of 80 cm is within the visual and chemosensory range of the mantids (Liske and Davis 1987). Following Liske and Davis (1987), we illuminated the mating arena in an otherwise darkened room, allowing us to observe without being seen by the mantids.

Mantids are difficult to rear, which restricts sample sizes. To increase our data set on male risk taking, we tested 25 males under each of the four different treatment combinations, for a total of 100 trials. Males were paired to the same female for each of the four trials, and we randomly determined the order of treatments experienced by each male. Pairs were given 5–9 days between trials. To reduce the risk of cannibalism and subsequent loss of data, the three initial trials for each pair were terminated immediately after the male mounted the female. Thus, we do not report actual rates of sexual cannibalism. On the fourth trial, pairs were allowed to mate.

Male Approach and Courtship Behavior

Tenodera sinensis courtship is described in detail by Liske and Davis (1984, 1987). We recorded total approach speed as the distance that the male traveled on foot toward the female from the point of release, divided by the time taken to travel this distance. Leap distance was the distance between the male and the female from which the male leapt onto the back of the female to mount. The hypothesis of sexual conflict over sexual cannibalism predicts that males will approach more slowly and leap from a greater distance when the risk of attack is greater. In 10 cases, males flew away from the female rather than mounting them, and this behavior is analyzed separately. Following Liske and Davis (1987), we predicted that if males are risk avoiders, they will increase courtship when the risk of cannibalism is greater in order to better differentiate themselves from other prey and pacify the females. Courtship by male *T. sinensis* involves an upward thrusting of the forewing and hindwings and a rhythmic bending motion of the abdomen at an angle of 0°–90° (Liske and Davis 1987). We judged variation in the degree, that is, the angle of abdominal bending to represent differences in the intensity of male courtship.

We recorded instances of aggressive behavior directed at males by females. We judged a leap at the male and strikes with the raptorial forelegs to be aggressive. We judged lowering of the tibial claws to be submissive behavior (following Liske and Davis 1987); claw lowering may be an indication of responsiveness to courtship. During two trials, females responded to males with defensive deimatic displays—flashing the colored eyespots on the inside of their forelimbs—but this behavior was too infrequent for analysis. Finally, for the trials in which pairs were allowed to mate, we also recorded precopulatory mounting duration as the time from mounting to genital linkage, copulation duration as the time from linkage to separation of the genitalia, and postcopulation duration as the time from the end of intromission until the male leapt off the female. Given the experimental design, the sample size for mating behavior was small ($N = 25$), and nonsignificant results should thus be viewed with caution.

Female Hunger Level

Subsequent to the experiment, we tested the assumption that our treatment successfully altered female hunger. We provided eight females from each diet treatment an ad lib. supply of crickets and recorded the number eaten over 24 h.

Analyses

Individual males experienced each treatment combination with a single female, and thus we analyzed the results on approach speed, leap distance, and courtship using a within-subjects ANOVA with $N = 25$ pairs. The data for approach speed and durations of the three stages of mating (precopulation, copulation, and postcopulation) were normalized by natural-log transformation before analysis. Female behavior and male flight away from females were recorded as binary (yes/no) data and were analyzed using McNemar tests for significant changes in behavior within individuals (Sokal and Rohlf 1995). Each pair contributed only a single set of measures of the durations of the three stages of mating, and we analyzed these data by multivariate ANOVA.

We corrected the problem of elevated Type I statistical error due to multiple testing by adjusting P values to control the false discovery rate (Benjamini and Hochberg 1995), as described by Verhoeven et al. (2005). As recommended by Neuhäuser (2004), when uncorrected $P <$ .05, we report both uncorrected and adjusted P values. We report back-transformed means and 95% confidence in-

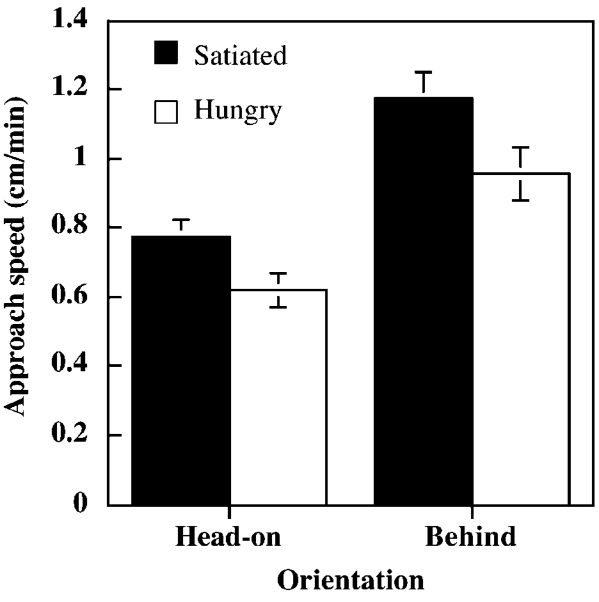

Figure 1: Relationship between female hunger treatment, male orientation of approach, and speed at which males approached females. Means are back transformed with back-transformed SE.

tervals (CIs). The effect of diet treatment on cricket consumption by females was analyzed by *t*-test.

Results

Our tests confirmed that food-restricted, "hungry" females were indeed significantly hungrier than "satiated" females given an ad lib. diet of crickets. Hungry females consumed an average of 6.0 ± 0.33 crickets within 24 h after the experiment, whereas satiated females consumed only 2.7 ± 0.42 crickets ($t = 6.2$, df = 14, $P < .001$). Thus, hungry females were more rapacious.

Male Approach to the Female

Both female hunger and the orientation of approach had significant effects on male approach to the female. First, some males chose to fly away from the female rather than mount. Males flew away from hungry females more often than they flew from satiated females, though the effect was not significant after correcting for false discovery rate (8 of 50 [16%] trials vs. 2 of 50 trials [4%], respectively; McNemar test: $G_{\text{adj}} = 3.85$, df = 1, $P = .049$, $P_{\text{adj}} = .077$). Orientation of approach had no significant effect on the frequency of male flight (head-on: 7 of 50 [14%]; behind: 3 of 50 [6%]; $G_{\text{adj}} = 1.57$, df = 1, $P = .20$).

Second, when males approached females, they approached hungry females significantly more slowly than satiated females (within-subjects ANOVA: $F = 25.76$, df = 1, 24, $P < .0001$, $P_{\text{adj}} < .00055$; fig. 1). They also approached females more slowly head-on than from behind ($F = 8.85$, df = 1, 24, $P = .007$, $P_{\text{adj}} = .018$). There was no significant interaction effect ($F = 0.98$, df = 1, 24, $P = .33$).

Third, males leapt from their perches onto the backs of hungry females from a significantly greater distance than that from which they leapt onto satiated females ($F = 13.48$, df = 1, 24, $P = .001$, $P_{\text{adj}} = .0044$; fig. 2). Orientation of approach had no significant effect on leap distance ($F = 2.64$, df = 1, 24, $P = .12$), nor was there a significant interaction effect ($F = 2.61$, df = 1, 24, $P = .12$).

Male Courtship Behavior

Female hunger and the orientation of approach also had a significant effect on male courtship behavior. Males showed greater abdominal bends when approaching females head-on (52.8° ± 3.2°) than when approaching them from behind (10.8° ± 0.2°; $F = 117.60$, df = 1, 24, $P < .0001$, $P_{\text{adj}} < .0011$). Similarly, abdominal bends of male courtship were greater when directed at hungry females (36.6° ± 3.1°) than at satiated females (27.0° ± 2.3°; $F = 5.89$, df = 1, 24, $P = .023$, $P_{\text{adj}} = .042$). There was a significant interaction between hunger level and male orientation of approach ($F = 6.51$, df = 1, 24, $P = .018$,

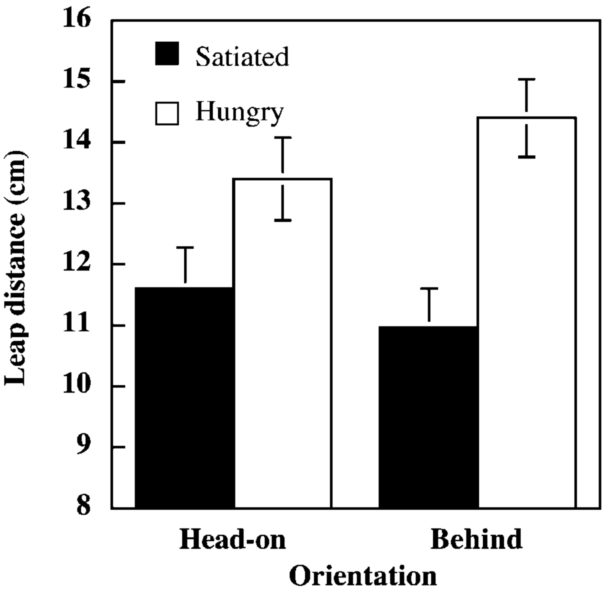

Figure 2: Relationship between female hunger treatment, male orientation of approach, and distance from which males leaped onto the backs of females. Means are shown ±SE.

$P_{adj} = .040$), with males providing uniformly low courtship when approaching from behind (hungry females: 10.8° ± 2.9°; satiated females: 10.8° ± 3.1°) but differentiating between hungry and satiated females when approaching head-on (hungry females: 62.4° ± 4.9°; satiated females: 43.2° ± 3.9°).

Female Behavior

Hungry females made predatory strikes at males significantly more often than did satiated females (16 of 50 [32%] times vs. 5 of 50 [10%] times, respectively; McNemar test: $G_{adj} = 8.72$, df = 1, $P = .003$, $P_{adj} = .018$). Orientation of approach had no significant effect (head-on: 12 of 50 [24%] times; behind: 9 of 50 [18%] times; $G_{adj} = 2.89$, df = 1, $P = .09$). In contrast, aggressive leaps by females were affected more by the orientation of approach, though this effect was not significant after correcting for false discovery rate (head-on: 14 of 50 [28%] trials; behind: 4 of 50 [8%] trials; $G_{adj} = 3.85$, df = 1, $P = .049$, $P_{adj} = .15$). Diet treatment had no significant effect ($G_{adj} = 0.11$, df = 1, $P = .75$). There was no significant effect of either treatment on the claw-lowering display of females (diet: $G_{adj} = 0.48$, df = 1, $P = .49$; orientation: $G_{adj} = 0.38$, df = 1, $P = .54$).

Mating

Males that mated with hungry females had significantly greater overall mounting duration than those that mated with satiated females (multivariate ANOVA: Wilks's $\lambda = 0.65$, $F = 3.45$, df = 3, 19, $P = .037$). This was due to a difference in postcopulatory mounting by males. Males remained on the backs of hungry females for (back-transformed mean) 86.06 min (95% CI = 52.61–140.75 min) before dismounting but remained on satiated females for only 28.62 min (95% CI = 17.18–47.70 min; $F = 10.42$, df = 1, 25, $P = .004$). The duration of neither precopulatory mounting (mean = 5.44 min, 95% CI = 0.96–30.66 min; $F = 0.28$, df = 1, 25, $P = .61$) nor copulation (mean = 207.00 min, 95% CI = 107.22–399.63 min; $F = 0.003$, df = 1, 25, $P = .96$) differed significantly between diet treatments. There were no significant correlations between the durations of precopulatory, copulatory, and postcopulatory mounting (Pearson correlations, all $P \geq .64$). Upon mounting, the male aligns its body to that of the female; therefore, it is not surprising that orientation of initial approach had no effect on mating duration (Wilks's $\lambda = 0.99$, $F = 0.08$, df = 3, 19, $P = .97$).

Discussion

Despite the notoriety of sexual cannibalism in mantids, there has been no strong experimental evidence to demonstrate either the complicity of males or active male risk avoidance. Most inference comes from purely descriptive accounts of male mating behavior (Roeder 1935; Liske and Davis 1987; Lawrence 1992; Kynaston et al. 1994; Maxwell 1998). Our results show that males alter their approach, mounting behavior, and courtship depending on the risk imposed by their prospective mate. These results clarify two major issues surrounding the controversy over male complicity versus conflict during sexual cannibalism. First, the change in male behavior with the experimental manipulations shows that male mantids are assessing variation in the risk imposed by the females. Thus, males appear to be cueing in on some aspect of female phenotype or behavior indicative of risk. Orientation itself is one obvious cue, but even at the same orientation, males appear to judge the risk of a hungry versus a satiated female when female fecundity is controlled. Courting males may alter their behavior in response to visual or olfactory cues given by the female, but this warrants further study.

Second, male response to female hunger and orientation is clearly not consistent with male complicity in sexual cannibalism. Males do not facilitate being grasped by the raptorial front legs of their mate; instead, as risk increases, they become more cautious in their approach of females, in a manner clearly indicative of risk avoidance and male-female conflict over sexual cannibalism.

Male Responses to Female Hunger

Hungry female *Tenodera sinensis* are more rapacious, make more predatory strikes at males, and impose a greater risk of sexual cannibalism than satiated females (Liske and Davis 1987). Males were more likely to fly away from hungry females than satiated females. When males approached hungry females, they moved more slowly and mounted from a greater distance. This "cautious" approach by males matches our a priori expectations of an effective risk avoidance tactic. Maxwell (1999*b*) found that male *Iris oratoria* mantids were less likely to mount females in poor condition (i.e., relatively low body mass), though it was not clear how condition related to hunger, fecundity, or some other factor contributing to the state of the female. For example, in contrast to our results, female *I. oratoria* in poor condition were less likely to attack males; however, all females were maintained on the same diet regime, and thus the lower attack rate and poor condition might both be related to the overall lower rapacity of these females.

Male *T. sinensis* also displayed more intense courtship toward hungry females than satiated females. We predicted that if males were risk avoiders, they would increase courtship when the risk of cannibalism was greater in order to better differentiate themselves from other prey and pacify the females (Liske and Davis 1987). This prediction is supported. To our knowledge, the only similar example of a change in male behavior in response to experimentally altered risk is the study by Elgar and Fahey (1996) demonstrating that male orb-weaving spiders increase their attempts to copulate after females are presented with substitute prey. Fromhage and Schneider (2005) subsequently showed that this behavior by males significantly reduced the risk of sexual cannibalism. We note that for both the spider and the mantid, these changes in male behavior are indicative of a direct trade-off between a male's motivation to reproduce and his motivation to escape death.

Male Responses to the Orientation of Approach

Males were also more cautious when approaching females head-on versus from behind. A head-on approach puts males well within the visual field of the female and in the most convenient position for an attack. When approaching females head-on, males moved more slowly and courted with greater intensity. These results match Liske and Davis's (1987) correlative data showing that male *T. sinensis* slowed down as they approached females head-on but sped up as they approached females from behind. Maxwell (1999*b*) experimentally set the initial orientation approach by male *I. oratoria* but allowed males to adjust their orientation after release. He found that those mantids that started from the risky head-on position typically switched to approach from behind. This switch in orientation could be interpreted as either risk avoidance or simply facilitation of proper alignment for mounting.

Mating

After mating, males remained with hungry females for a substantially longer period compared to well-fed females. This behavior also matches our prediction based on risk avoidance. Lawrence (1992) pointed out that "dismounting is more dangerous to a male than remaining on the back of a female" (p. 576), and when they do dismount, males invariably drop or fly away quickly from the female, acts that quickly get them out of reach of the female. Prolonged postcopulatory mounting suggests that males with hungry females are more selective of proper situation for a safe dismount. Thus, each component of male mating behavior—approach, courtship, and mounting—becomes more cautious as the risk of sexual cannibalism increases. Males employ a tactic of risk avoidance, and these results on the functional design of male mating behavior strongly support the hypothesis of sexual conflict over sexual cannibalism in mantids.

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