Female predatory response to conspecific males and heterospecific prey in the praying mantis Mantis religiosa: *evidence for discrimination of conspecific males*

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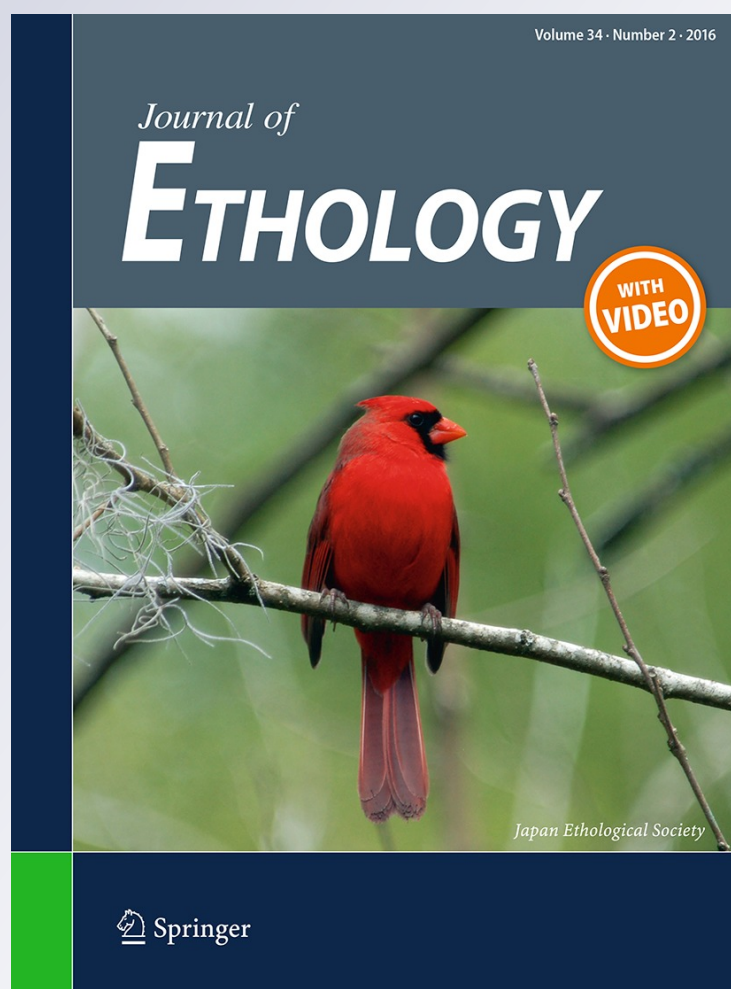
Pavol Prokop[1,2] · Michael R. Maxwell[3]

Abstract Sexual cannibalism, the attack and consumption of the opposite sex by a conspecific during courtship, copulation, or soon after copulation, is widespread among invertebrates, but the causes of this behavior are not fully understood. We examine the mistaken identity hypothesis, which posits that non-copulatory cannibalism occurs because females do not recognize conspecific males as potential mates. This hypothesis predicts indiscriminate predatory behavior by females towards conspecific males and heterospecific prey. This prediction remains largely unexamined. We tested this prediction in the praying mantis *Mantis religiosa* (Mantodea: Mantidae) through two behavioral experiments. In experiment 1, we presented targets in isolation to females: dead conspecific males or dead common prey items from the field (grasshopper *Chrysochraon dispar*). In experiment 2, we presented simultaneous live targets to females: conspecific males and grasshoppers. In both experiments, we varied female mating status (virgin vs. mated). Results indicate some degree of attack discrimination by the females. In experiment 1, the females were significantly more likely to strike at the grasshoppers, and showed a shorter latency to strike at

grasshoppers. In experiment 2, females tended to preferentially strike at the grasshoppers, although this result fell short of statistical significance. Female discrimination between the males and grasshoppers may be explained, in part, by the size difference between the males and grasshoppers. Female mating status did not affect the occurrence or latency to strike in either experiment. These results fail to strongly support the prediction of indiscriminate predatory behavior by females, while contributing to a broader taxonomic assessment of the mistaken identity hypothesis.

Keywords Attack discrimination · Mistaken identity · Sexual cannibalism · Praying mantis · *Mantis religiosa*

Introduction

Sexual cannibalism, the attack and consumption of the opposite sex by a conspecific during courtship, copulation, or soon after copulation (Elgar 1992; Elgar and Schneider 2004; Wilder et al. 2009; Schneider 2014), can be considered an extreme form of sexual conflict (Schneider 2014). The occurrence of sexual cannibalism has been documented in diverse invertebrates, especially predatory species in which the female cannibalizes the male, such as spiders and praying mantises (Polis 1981; Elgar 1992; Elgar and Schneider 2004). Several adaptive and non-adaptive hypotheses have been developed to explain the occurrence of sexual cannibalism (reviewed in Wilder et al. 2009; Kralj-Fišer et al. 2013; Schneider 2014). Adaptive hypotheses include benefits to the female, such as cannibalism being part of a female's feeding strategy (Birkhead et al. 1988; Newman and Elgar 1991; Andrade 1998), or cannibalism as a mechanism of female choice (Elgar and

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Nash 1988; Prenter et al. 2006). Other hypotheses pose male benefits to cannibalism, such as increased fertilization success or increased offspring quality (Buskirk et al. 1984; Andrade 1996).

At least two non-adaptive hypotheses have been proposed for sexual cannibalism: mistaken identity and aggressive spillover (Elgar 1992; Arnqvist and Henriksson 1997). The mistaken identity hypothesis posits that females cannibalize males because of the females' failure to recognize males as conspecifics and, therefore, potential mates (Robinson 1982; Gould 1984; Elgar 1992). The aggressive spillover hypothesis posits that selection for high food consumption in the juvenile stage results in rapacious predatory behavior in the adult stage, resulting in adult females cannibalizing potential mates as part of a possible behavioral syndrome (Arnqvist and Henriksson 1997; Johnson and Sih 2005). Under both hypotheses, female attacks on conspecific males are expected to occur in the absence of copulation (i.e., non-copulatory cannibalism, variously termed "pre-copulatory," "pre-mating," or "pre-insemination" cannibalism; Elgar and Schneider 2004; Prenter et al. 2006; Wilder et al. 2009). Tests of these non-adaptive hypotheses have focused mainly on aggressive spillover in spiders, with components of this hypothesis receiving mixed support (Johnson and Sih 2005; Kralj-Fišer et al. 2012, 2013; Johnson 2013; Pruitt and Keiser 2013; Kralj-Fišer et al. 2016). The mistaken identity hypothesis has received much less scrutiny and support (Andrade 1998).

We focus on the relatively untested mistaken identity hypothesis. Under this hypothesis, females are predicted to show indiscriminate predatory behavior towards conspecific males and heterospecific prey (Andrade 1998). Andrade (1998) failed to support this prediction in an experiment with the Australian redback spider. We test the prediction of female indiscriminate predatory behavior in the praying mantis Mantis religiosa (Mantodea), thereby broadening the examination of the mistaken identity hypothesis, and of non-adaptive hypotheses for sexual cannibalism in general. We note that studies on cannibalism in two mantid species have addressed the non-adaptive aggressive spillover hypothesis but failed to support a basic prediction—that females of larger body size (i.e., pronotum length) are more likely to cannibalize males (Barry et al. 2008; Barry 2010; Maxwell et al. 2010; Maxwell and Frinchaboy 2014). Although these studies were not designed to test the aggressive spillover hypothesis *per se*, their failure to support this basic prediction calls for a broader comparative assessment of non-adaptive hypotheses.

Mantis religiosa females cannibalize males in nature and captivity, including cases where the male is cannibalized during his approach to the female (Lawrence 1992; Prokop and Václav 2005, 2008). In other mantids

(Birkhead et al. 1988; Chong 2002; Barry et al. 2008; Maxwell et al. 2010; Barry 2010), female predatory behavior, including cannibalism towards males, is influenced by feeding regime, and this is likely to be the case in *M. religiosa* (Prokop and Václav 2005, 2008). How recognition of a conspecific male might modulate a female's response, however, remains unknown for this or any mantid species. Male *M. religiosa* lack overt courtship displays (Roeder 1935, 1967; Lawrence 1992; Gemeno and Claramunt 2006; P. Prokop, personal observations), which may lead to attacks by females due to mistaken identity in nature. Indeed, the general lack of attention to the mistaken identity hypothesis seems to derive from research on spider species in which the males regularly perform conspicuous visual and vibrational displays to females, yet still may be attacked and consumed during courtship (Elgar 1992; Jackson and Pollard 1997). Attacks on overtly signaling males argue against mistaken identity by the females. In *M. religiosa*, however, such male sexual signaling appears to be absent.

In the present study, we investigate female predatory responses to conspecific males and heterospecific prey. The mistaken identity hypothesis predicts similar predatory behavior by females towards males and prey. We test this prediction in two contexts: presentation of model targets in isolation (freeze-killed males and prey; experiment 1) and simultaneous presentation of live males and prey (experiment 2). These differences in experimental design enable us to assess the sensitivity of our results to the structure of the experiments (Kralj-Fišer et al. 2013; Pruitt and Keiser 2013), as examinations of female responses to male and prey targets typically involve presentations of the targets in isolation (Andrade 1998; Wignall and Herberstein 2013). Our presentation of dead targets in isolation (experiment 1) is designed to standardize the behavior and movement of the targets. The presentation of simultaneous live targets (experiment 2) alternatively presents a paired choice to the females with more realistically moving targets. Our experiments focus on the predatory strike as the behavioral measure, rather than the occurrence of cannibalism, thereby removing the possible confounding influence of male escape and defensive abilities (Kralj-Fišer et al. 2013).

As a further examination of female predatory behavior, we varied the mating status of the females in both experiments (i.e., virgins vs. singly mated). Non-copulatory attack and consumption of a male may have greater consequences for virgin females than for mated females, as high attack rates by virgin females can put them at risk of remaining uninseminated (Newman and Elgar 1991; Elgar and Schneider 2004; Wilder et al. 2009). In a recent study, Jayaweera et al. (2015) found that virgin female mantids were less likely to attack and cannibalize males than mated

females, and similar results have been found in spiders (Herberstein et al. 2002; Wilder and Rypstra 2012). Thus, in our study, differential response towards males and prey might be seen in virgin females, but not in mated females.

Methods

Experiment 1 (one-target trials): dead conspecific male and grasshopper

Rearing conditions and pre-trial mating

Subadult female and male mantids were collected in June 2014 from abandoned old fields outside Pezinok, Slovakia (48°17′N, 17°16′E). The mantids were reared individually in 0.7-L ventilated glass vials outdoors on private property in Trnava, Slovakia (48°23′N, 17°35′E), protected from direct sunlight under the natural photoperiod and temperature. Individuals were sprayed with water daily and fed three times per week with grasshoppers freshly collected from the field (various Acrididae species; two grasshoppers per feeding). Females and males that emerged as adults were maintained on this feeding schedule.

At 20–32 days after adult emergence (i.e., sexual maturity; Lawrence 1992), females were randomly assigned to two initial treatments: virgin ($N = 32$) and mated ($N = 31$). Mated females were produced by pairing each female with a virgin adult male aged 20–25 days in a 4-L ventilated glass container. All pairings occurred during 09:00–16:00. For each pairing, the female's forelegs were lightly bound with light cloth to prevent attacks on the male. The male was then placed 10–15 cm behind the female, and the pair was subsequently observed to confirm copulation. Mean copulation duration was 198 min (SE = 12, range: 89–434 min, $N = 31$), similar to previous studies in captivity of this species (Prokop and Václav 2005, 2008). Once the male had separated from the female's genitalia, he was quickly removed to avoid attacks by the female. To standardize pre-trial handling of the females, virgin females similarly had their forelegs bound, males placed on their backs, and then the males removed. After all pairings, the females and males were returned to their home containers.

One-target trials

Following the pairing with a male, each female was starved for 5 days to increase predatory responses to targets (e.g., Liske and Davis 1987; Kynaston et al. 1994; Prokop and Václav 2005, 2008). After this starvation period, females were randomly assigned to one of two trials: conspecific male target or grasshopper target. Thus, experiment 1

involved four treatments: (1) virgin female, male target ($N = 15$), (2) virgin female, grasshopper target ($N = 17$), (3) mated female, male target ($N = 16$), and (4) mated female, grasshopper target ($N = 15$).

On the day of the trial, body mass (to 0.0001 g) and pronotum length (to 0.01 mm) were measured for each female. Body condition was quantified as the residuals of a linear regression of body mass on pronotum length. These body measures were balanced among the treatment groups, such that no treatment group had a preponderance of large or small females; two-way ANOVA tests failed to show an effect of female mating status (virgin vs. mated) or target (male vs. grasshopper) on body mass, pronotum length, or body condition (ANOVA tests: all F values <3.7, all p values >0.05).

One-target trials took place between 16 August and 30 September 2014, during 09:00–16:00, indoors at room temperature (typically 25 °C), 1 m from a window to afford natural indirect light. At the start of each trial, the female was placed on the floor of a $30 \times 20 \times 20$ cm terrarium; the terrarium floor was covered with white absorbent paper which was replaced after each trial. An experimenter (PP) then introduced a dead conspecific male target or a dead adult grasshopper target (*Chrysochraon dispar*, collected from local field sites). Each target insect was prepared by quickly killing it via freezing and then affixing it to a 30-cm wire for manual manipulation, as in previous studies on mantids (e.g., Rilling et al. 1959; Prete et al. 1990; Scardamaglia et al. 2015). The grasshopper *C. dispar* occurs in local habitats of *M. religiosa*, thereby posing an ecologically relevant target. Experiment 1 involved five brown male *M. religiosa* ($X \pm$ SE: body length $= 51.6 \pm 0.2$ mm) and six brown *C. dispar* ($X \pm$ SE: body length $= 26.2 \pm 0.2$ mm) for use as targets. While *C. dispar* is shorter than male *M. religiosa*, it is the largest readily available local prey item.

The trial commenced with the experimenter suspending the target 5 cm in front of the female and then manually moving the target at c. 1 cm/s to repeatedly trace a 5-cm length perpendicular to the female. This target motion was maintained for a maximum of 20 min, during which a second experimenter recorded the time of the female's first predatory strike at the target to the nearest 1 min. We define a "predatory strike" or "attack" as the female moving or lunging towards the target, with the strike being a quick extension and clasping of the forelegs to seize the target. We distinguish this strike from a strike performed from a startle or deimatic posture, characterized by erection of the wings, curling of the abdomen, and spreading of the forelegs (Maldonado 1970; Edmunds 1972, 1976). After the first predatory strike, the trial was terminated and the female was returned to her home container. If the female did not strike after 20 min, the trial was terminated and the

female was tested again on the following day. Strikes occurring during a female's first or second trial are considered in the analysis. Ten trials were typically performed per day, with a minimum of 10 min between each trial. For a given day, the first trial treatment was randomly determined, and then treatments were alternated over the course of the day.

Experiment 2 (choice trials): simultaneous live conspecific male and grasshopper

Rearing conditions and pre-trial mating

Rearing conditions and pre-trial mating procedures were conducted as in experiment 1; differences are noted herein. Subadult female and male mantids were collected in June 2013 from field populations. At 21–25 days after adult emergence, females were randomly assigned to two treatments: virgin ($N = 19$) and mated ($N = 16$). Mated females were paired with a virgin adult male aged 16–20 days; mean copulation duration was 167 min (SE = 9.71, range: 93–235 min, $N = 16$).

Choice trials

Following the pairing with a male, each female was starved for 5 days, after which she was placed in a choice trial. On the day of the trial, body mass, pronotum length, and body condition were measured for each female. These body measures were balanced between virgin and mated females; t-tests failed to show a significant difference in any measure (t-tests: all t_{33} values <1.92, all p values >0.05).

Choice trials took place between 19 August and 3 September 2013, during 09:00–16:00, indoors at room temperature (typically 25 °C), 1 m from a window to afford natural indirect light. Each trial involved two glass terraria. In one (30 × 20 cm, 20 cm high), the female mantid was placed on the terrarium floor. In the other (30 × 20 cm, 20 cm high), an opaque barrier created two compartments that separated a live male mantis *M. religiosa* from a live adult grasshopper *C. dispar*. For use as targets, experiment 2 involved 3 male *M. religiosa* ($X \pm$ SE: body mass = 0.42 ± 0.01 g, body length = 54.0 ± 0.3 mm, range = 53.4–54.5 mm) and 3 *C. dispar* grasshoppers ($X \pm$ SE body mass = 0.42 ± 0.01 g, body length = 26.5 ± 0.1 mm, range = 26.4–26.6 mm). The male *M. religiosa* and adult *C. dispar* were kept physically and visually separated by the opaque barrier (Fig. 1). The terrarium side that faced the female was fitted with a glass plane with a film that allowed one-way visibility. Thus, the female could view both the conspecific male and the grasshopper, but the male and the grasshopper
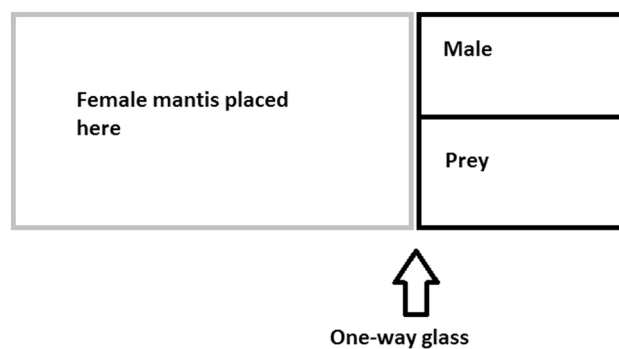

Fig. 1 Design of experiment 2. The positions of male and prey were alternated from one trial to the next

could not view each other or the mantid female. The one-way glass removed the possible effects of the targets' responses to the females' presence (Kralj-Fišer et al. 2013). Male mantids, including *M. religiosa*, are responsive to female behavior and movements at a distance (Lawrence 1992; Maxwell 1999a, b; Prokop and Václav 2005; Lelito and Brown 2006; Gemeno and Claramunt 2006; Barry et al. 2009; Scardamaglia et al. 2015), and most likely behave differently than heterospecific prey when able to view the females.

Once the female was placed in her terrarium, the trial commenced when the experimenter placed the male mantis and the grasshopper targets simultaneously in their compartments. The male and grasshopper were simultaneously tapped with a slim wooden dowel to stimulate initial movement. Once either target stopped, it was gently tapped to stimulate movement. The time of the female's first predatory strike was recorded to the nearest 1 min. After this strike, the trial was terminated and the female was returned to her home container. If the female did not strike after 20 min, the trial was terminated and the female was tested again on the following day. Strikes occurring during a female's first or second trial are considered in analysis. Five trials were typically performed per day, with a minimum of 30 min between each trial. For a given day, the placement of the male was randomly determined (i.e., left or right), and then placement was alternated over the course of the day (17 trials with male on left, 18 trials with male on right).

Statistical analysis

We analyzed the influence of various variables on female propensity to strike (strike or not strike) through logistic regression and on latency to strike (in minutes) through linear models. Primary variables of interest were target type (male vs. grasshopper) and female mating status (virgin vs. mated). The trial in which the strike occurred was included (first vs. second trial), as were female

pronotum length and body condition. While female pronotum length and body condition were balanced among treatment groups in experiments 1 and 2, we include these measures as covariates to test for biometric effects across all females. Previous studies indicate that, within a species, longer mantids are found with larger prey in the field, and are more likely to strike at larger targets than are shorter mantids in captive studies (Hurd 1988; Iwasaki 1991; Whitman and Vincent 2008; Maxwell and Frinchaboy 2014). Thus, in the present study, an effect of size may be seen, such as longer females being more likely to strike at a target of a standardized size, regardless of treatment. Similarly, females of relatively low body condition, reflecting differences in individual feeding behavior, may be more likely to strike at the target, as indicated by manipulations of female feeding regime in mantids (Birkhead et al. 1988; Chong 2002; Barry et al. 2008; Maxwell et al. 2010; Barry 2010). For both experiments, correlations between female pronotum length and body condition were low (Pearson correlation: $r < 0.1$, $p > 0.9$ for both experiments), so these two variables were analyzed simultaneously in multivariable tests.

Mean ± standard error are reported for descriptive statistics. Statistical tests were performed with the software Statistica (version 8, StatSoft 2007, Tulsa, OK, USA, http://www.statsoft.com). All tests are two-tailed. Normality of data was assessed via the Shapiro–Wilk test. Variables that significantly departed from normality (i.e., Shapiro–Wilk p value <0.05) were subjected to data transformation. Standard data transformations did not normalize the latency to strike data, so generalized linear models (GLMs) with gamma distributions were used in the analysis (Zuur et al. 2009).

Results

Experiment 1 (one-target trials): dead conspecific male and grasshopper

Overall, 33 females attacked the target with a predatory strike. No strike occurred from a startle or deimatic posture. Grasshoppers were more likely to be attacked (24/32 females, 75 %) than conspecific male targets (9/31, 29 %; Fig. 2). Target type (grasshopper vs. male) showed a significant effect on the occurrence of a predatory strike when analyzed with the variables mating status (virgin vs. mated), trial in which the strike occurred (first vs. second), female pronotum length, and female body condition (logistic regression: target type $p < 0.001$, all other variables $p > 0.05$). Target type showed a significant effect on latency to strike, with strikes at the male target occurring later than strikes at the grasshopper target (Fig. 3), and
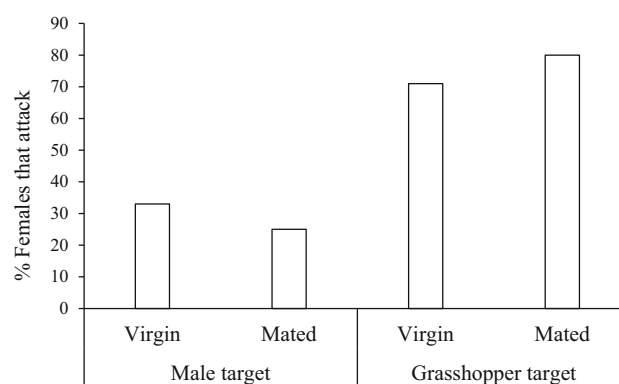

Fig. 2 Experiment 1 (one-target trials): dead conspecific male and dead prey (grasshopper) targets. Occurrence of predatory strikes by females (virgin vs. mated) on different targets (male vs. grasshopper); % females that strike shown. For the four groups, sample size per group = 15–17 females
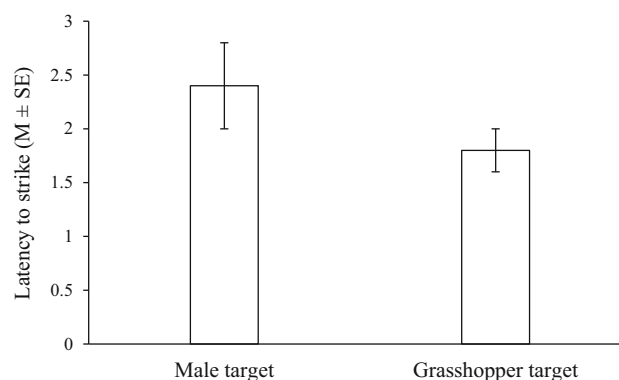

Fig. 3 Experiment 1 (one-target trials): latency to strike (in minutes) by females on male targets ($N = 9$) and grasshopper targets ($N = 24$)

longer females showed longer latencies to strike (generalized linear model, gamma distribution: target type $p < 0.05$, female pronotum length $p < 0.05$, all other variables $p > 0.3$).

Experiment 2 (choice trials): simultaneous live conspecific male and grasshopper

All females struck at a target; all first strikes were predatory in form. Females tended to direct their first strikes at grasshoppers (23/35 females, 66 %) rather than at conspecific males (12/35 females, 34 %), although this difference fell short of statistical significance (binomial test: $p = 0.090$). Female mating status, pronotum length, and body condition failed to affect whether grasshoppers or males were attacked, although females that struck in the first trial were more likely to strike at males than those females that required a second trial to elicit a strike (logistic regression: trial $p < 0.05$, all other variables

$p > 0.2$). Females struck earlier in the first trial than in the second trial, while latency to strike was not significantly affected by the actual target attacked, female mating status, pronotum length, or body condition (generalized linear model, gamma distribution: trial $p < 0.05$, all other variables $p > 0.05$).

Discussion

The present study indicates some degree of attack discrimination by female *Mantis religiosa* towards conspecific males and heterospecific prey. When presented with dead male and grasshopper targets in isolation (experiment 1), females were significantly more likely to strike at the grasshoppers, and with a shorter latency to strike at grasshoppers. When presented with live males and grasshoppers simultaneously (experiment 2), females tended to preferentially strike at the grasshoppers, but this result fell short of statistical significance. Latency to strike did not differ between male and grasshopper targets in experiment 2. Given this empirical indication of attack discrimination by females in the present study, a basic prediction of the mistaken identity hypotheses—that females show indiscriminate predatory behavior towards conspecific males and heterospecific prey—is not strongly supported (Robinson 1982; Gould 1984; Elgar 1992).

We note that the present study represents the first explicit test of the mistaken identity hypothesis in mantids, and in a species without overt sexual displays. It adds to Andrade's (1998) failure to support this hypothesis in the Australian redback spider, thereby contributing to a broader comparative assessment of this idea. The lack of attention to this hypothesis in spiders stems from the notion that females of species with overt sexual signals are not expected to misidentify conspecific males as heterospecific prey (Elgar 1992; Jackson and Pollard 1997). Why this hypothesis has been ignored in mantids is not quite clear, but reasons for this neglect are most likely rooted in descriptions of visual courtship displays by males of several species (Edmunds 1975; Loxton 1979; Liske and Davis 1987; Kynaston et al. 1994; Maxwell 1999a). The present study does not strongly support the inverse notion, that the lack of courtship displays results in attacks due to mistaken identity.

While the present study indicates some degree of attack discrimination by female mantids, the basis for this discrimination is unclear. On the one hand, females may have indeed recognized the males as conspecifics, and were less likely to attack them so as to not jeopardize insemination (Newman and Elgar 1991; Elgar and Schneider 2004; Wilder et al. 2009). According to this "economic" hypothesis of female foraging and reproductive concerns, virgin females are expected to be less likely to attack males

than mated females. This prediction was not supported in the present study, however, as mating status (i.e., virgin vs. singly mated) did not influence the occurrence or latency to strike in either experiment. Interestingly, *M. religiosa* females show anatomical indications of multiple matings in nature (i.e., volume of stored sperm, Lawrence 1992), so perhaps singly-mated females do not show increased aggression as part of a strategy to gain multiple inseminations. We note that Jayaweera et al. (2015) found that virgin female mantids were less likely to attack and cannibalize males than singly-mated females in the mantid *Pseudomantis albofimbriata*, but the mating histories in nature for females of this species are not known.

On the other hand, females may have been less likely to attack the male targets simply because the male targets were longer than the grasshopper targets. Ethological studies of three mantid species demonstrate that a mantid of a given size becomes less likely to attack as relative prey size increases (Rilling et al. 1959; Iwasaki 1990). In the present study, part of our motivation was to ground the experiment in an ecological context, so the size difference between conspecific males and the grasshopper targets (*C. dispar*) reflects size differences that are relevant to natural populations. *C. dispar* is the largest commonly found prey item in local populations of *M. religiosa*. Such a size difference between conspecific males and captured heterospecific prey appears to be the norm in temperate populations of mantids, as conspecifics are the largest prey items reported in field studies on four species (Hurd et al. 1994; Maxwell and Eitan 1998; Maxwell and Frinchaboy 2014). Thus, while target size and species identity were admittedly confounded in the present study, they are likely to be confounded in nature as well.

We caution that target size or length alone may not explain female discriminatory attack behavior. When live targets were presented in the present study (experiment 2), the females' preference for grasshoppers was weakened, suggesting an effect of experimental design. Behaviors performed by the live targets, such as subtle body movements and postures, may have influenced the females' attacks, possibly making the males more likely to be attacked or the grasshoppers less likely to be attacked. Conversely, we note that our experimental design focused on visual information as the females' main modality to assess the targets. Any pheromonal communication between the sexes was reduced, if not eliminated, between the sexes. It is possible that male responses to female pheromones, or male-emitted pheromones, would decrease female aggression towards males (Robinson and Robinson 1979; Lawrence 1992). Given that these two considerations suggest opposite effects on female attacks on males, further investigations should involve comparisons of female responses under the full suite of sensory cues and signals between the sexes.

As an additional note, the frequency of attacks on conspecific males by females in the present study (29 % of females in experiment 1, 34 % of females in experiment 2) are comparable to other frequencies of cannibalism in similar mating trials in *M. religiosa*. Lawrence (1992) reports cannibalism by 31 % of females in matings in nature, and captive work reports cannibalism in 23–32 % of staged pairings (Lawrence 1992; Prokop and Václav 2005, 2008). This battery of studies suggests that a certain proportion of female *M. religiosa* can be expected to cannibalize males during intersexual encounters. Given the present study's lack of strong support for the mistaken identity hypothesis, the "economic" consideration of female foraging and reproductive interests may explain cannibalistic attacks in *M. religiosa*, where starved or food-limited females are predicted to become more likely to attack (Birkhead et al. 1988; Newman and Elgar 1991; Andrade 1998). Attacks by the starved females in the present study and in Prokop and Václav (2005, 2008) seem to align with this prediction, but it must be noted that none of these studies included a satiated control group, and that the females in Lawrence's (1992) study do not appear to have been starved or greatly food-limited. Other explanations for female-on-male cannibalism include cannibalism as a mechanism of female choice (Elgar and Nash 1988; Prenter et al. 2006) and the aggressive spillover hypothesis (Arnqvist and Henriksson 1997; Johnson and Sih 2005). With regard aggressive spillover, we caution that the present study failed to detect an effect of female pronotum length on the occurrence of attacks on males, just as previous studies on mantids have failed to support the basic prediction of larger females being more likely to cannibalize males (Barry et al. 2008, 2010; Maxwell et al. 2010; Maxwell and Frinchaboy 2014). A more rigorous comparative assessment of aggressive spillover, as well as mate choice, is warranted.

To conclude, the present study's indication of attack discrimination by female mantids towards conspecific males and heterospecific prey does not strongly support the mistaken identity hypothesis for the occurrence of noncopulatory cannibalism. Additionally, a prediction drawn from the "economic" consideration of female foraging and reproductive concerns, that virgin females are less cannibalistic than mated females, was not supported. The present study points to continued examination of the hypotheses surrounding the evolution of sexual cannibalism in a wider taxonomic context, thereby contributing to a much fuller understanding of the causes of this phenomenon.

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