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Animal behaviour

Fatal attraction: sexually cannibalistic invaders attract naive native mantids

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Overlap in the form of sexual signals such as pheromones raises the possibility of reproductive interference by invasive species on similar, yet naive native species. Here, we test the potential for reproductive interference through heterospecific mate attraction and subsequent predation of males by females of a sexually cannibalistic invasive praying mantis. *Miomantis caffra* is invasive in New Zealand, where it is widely considered to be displacing the only native mantis species, *Orthodera novaezealandiae*, and yet mechanisms behind this displacement are unknown. We demonstrate that native males are more attracted to the chemical cues of introduced females than those of conspecific females. Heterospecific pairings also resulted in a high degree of mortality for native males. This provides evidence for a mechanism behind displacement that has until now been undetected and highlights the potential for reproductive interference to greatly influence the impact of an invasive species.

1. Introduction

Invasive species pose a major threat to biodiversity, influencing native populations, communities and ecosystems [1]. Predatory insects are among the most successful and prolific of these invaders, but the specific mechanisms by which they affect native species are poorly understood [2,3]. Reproductive interference has been suggested as playing an important role in the negative impacts of invasive species via such mechanisms as signal jamming, heterospecific mating, and hybridization, leading to the displacement of native species [4]. Since its arrival in New Zealand, the invasive South African praying mantis *Miomantis caffra* has been expanding its range [5] and is widely believed to be displacing New Zealand's only native mantis, *Orthodera novaezealandiae*. Empirical evidence is however lacking and the mechanism of displacement is unknown. Females of a number of praying mantis species use airborne sex pheromones to attract males [6–8] and the attractiveness of females has been shown to vary depending on body condition [9–11] and mating history [8,12]. Heterospecific mate attraction has also been documented between praying mantids in North America (*Tenodera aridifolia sinensis* and *Mantis religiosa*) [8], suggesting a degree of overlap in the sex pheromones produced by female mantids and the potential for reproductive interference. We hypothesized that reproductive interference by *M. caffra* might severely impact *O. novaezealandiae* populations, as the sexually cannibalistic behaviour of female *M. caffra* [5] could translate to direct predation of male *O. novaezealandiae*, if these males were mistakenly attracted to heterospecific females.

Sexual cannibalism is a significant source of male mortality in *M. caffra* [5] and other species of mantis [13–16], so if male *O. novaezealandiae* are attracted to heterospecific females, the same is likely to be true for them. Thus, this research had the following objectives: (i) to determine whether mate attraction occurs between the species in question, (ii) to establish the strength of attraction to heterospecific or conspecific females by *O. novaezealandiae* males and (iii) to estimate the frequency of cannibalism or predation resulting from attraction to *M. caffra* females.

2. Material and methods

(a) Laboratory rearing

Both species were wild caught as third–fifth instar juveniles from various locations around Auckland, New Zealand, and raised to adulthood in the laboratory. Mantises were housed in inverted, 400 ml, transparent plastic cups, and fed an ad libitum mixed diet of a variety of cultured insect species and misted with water daily.

(b) Male attraction to females

In order to test whether male *O. novaezealandiae* respond to female olfactory cues, we used Y-choice experiments. The Y-maze olfactometer was constructed of glass and Perspex, with a tube diameter of 4.5 cm and length of 60 cm. The upper inside surface of the glass tube was lined with a strip of masking tape to provide a surface for the specimens to grip more easily. The apparatus and frame were placed against a plain white background, under diffuse lighting. The entrance to each terminal chamber of the maze was blocked by a sheet of white nylon gauze screen, to keep females in the appropriate chamber and to prevent males from using visual cues to locate the female. Air flow was provided by an Aqua One 7500 precision air pump, which was left running for at least 1 h between each set of tests to cycle fresh air through the apparatus and ensure that no airborne traces of previous specimens remained inside. Both target chambers and the Y tube were also cleaned with 100% ethanol and air dried between all tests.

To test whether male *O. novaezealandiae* were attracted to heterospecific females, laboratory raised, virgin *M. caffra* females ($n = 16$) were placed into a terminal chamber and the chamber was randomly assigned to the left- or right-hand tube. Individual lab-raised, virgin males ($n = 16$) were then introduced into the common tube. Males which moved half way or further into either terminal tube were considered to have made a choice. Specimens which failed to move at least half way into either terminal tube within 40 min were recorded as having made no choice and were removed.

To examine whether female *M. caffra* were more attractive to male *O. novaezealandiae* than conspecific females, we followed the same procedure as described earlier except that male *O. novaezealandiae* were provided with a choice between a heterospecific female *M. caffra* and a conspecific female *O. novaezealandiae* as simultaneous options. Preference for treatment over control in Y-choice experiments was tested using a binomial sign test.

(c) Cannibalism

In order to assess mortality associated with cannibalism, mating observations were carried out in the laboratory. A freshly cut, leafy branch was held in a plastic jar, inside a $1 \times 0.5 \times 0.5$ m mesh enclosure. One laboratory raised, virgin female *M. caffra* was introduced onto the top of each piece of vegetation and allowed 30 min to orientate herself naturally. One laboratory raised, virgin male (either *M. caffra* $n = 23$ or *O. novaezealandiae* $n = 16$) was then added to the branch at least 15 cm away from the female. These were observed over 16 h beginning in the evening under natural light conditions. At the end of this period, the survival of the male was recorded.

3. Results

In Y-choice tests, *O. novaezealandiae* males were significantly (binomial: $p = 0.0384$ $N = 12/16$) more attracted to the chemical cues of female *M. caffra* than an empty control chamber and when given a choice between conspecific and heterospecific

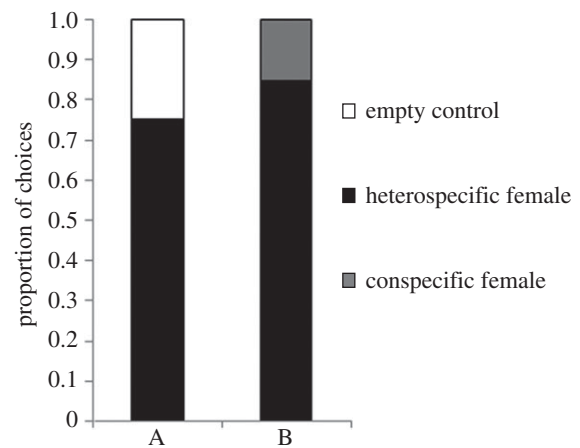


Figure 1. Proportion of male *O. novaezealandiae* to select chambers in a Y-choice maze containing females of *M. caffra*, versus control (A) or females of their own species (B). *Miomantis caffra* females were preferred in both cases.

females, moved towards the heterospecific female more frequently (binomial: $p = 0.0112$; $N = 11/13$; figure 1).

We found that 39.1% (95% CI $> 0.221 < 0.593$, $N = 9/23$) of male *M. caffra* were killed and eaten by conspecific females during pairings over 16 h. Most (68.8%, 95% CI $> 0.443 < 0.861$, $N = 11/16$) male *O. novaezealandiae* were killed and eaten by *M. caffra* females during similar pairings. During these tests, males that successfully reached the female without being killed were observed to attempt mating behaviour, suggesting that the motivation behind their approach was indeed to initiate copulation.

4. Discussion

We have demonstrated that male *O. novaezealandiae* are attracted to the sex pheromones of female *M. caffra* and in fact prefer them over those of their conspecific females. Furthermore, once attracted, male *O. novaezealandiae* suffer a high risk of predation by heterospecific females, in the context of sexual cannibalism.

Heterospecific attraction could impair *O. novaezealandiae* fitness even in the absence of predation, owing to the large numbers of exotic females in New Zealand [5], their apparently greater attractiveness to *O. novaezealandiae* males and the length of time males spend close to females during copulation attempts. Indeed, the effectiveness of competing pheromone signals in disrupting the reproduction of insects is attested to by the development of pest control methods which successfully use pheromones for this very purpose [17]. Airborne sex pheromones of insects, including those of praying mantids can operate over long distances [9] and therefore may allow a single *M. caffra* female to interfere with native male mate searching over a large area and to capture males from distant populations.

Perhaps the most insidious influence that the invasive *M. caffra* might have on native *O. novaezealandiae* populations is through the predation of males mistakenly attracted to the aggressive female *M. caffra*. The degree of sexual cannibalism and predation of heterospecific males by female *M. caffra*, as demonstrated in this study, indicates a potentially significant source of mortality for males of both species. Males may represent an important source of nutrition for those females that can attract them, as demonstrated in other species [13–16]

which would place females under strong positive selection for potent pheromone use. In such cases, males should also be under strong selection to reduce the potential for attack and consumption by females, and males of a number of mantodean species show such risk avoidance behaviour [18–20]. However, *O. novaezealandiae* has coexisted with *M. caffra* in New Zealand only since approximately 1978 and seems not to have adapted to distinguishing between the sexual cues of conspecific females and those of the more aggressive invaders. Observations of *O. novaezealandiae* mating in the field and laboratory provide no evidence for sexual cannibalism (G. Holwell 2010–2012, personal observations) so we concur with Ramsay [5] that sexual cannibalism is likely to be rare or absent in this species. As such, male-risk avoidance behaviour also appears to be absent, leading to their higher mortality compared with that of male *M. caffra*.

It is important, however, to apply caution in estimating the frequency of both sexual cannibalism in *M. caffra* and heterospecific predation of male *O. novaezealandiae* in the wild based on our observations in the laboratory. For example, the ad libitum diet provided to laboratory-reared females may have in fact led to lower hunger levels than those experienced in the wild, potentially reducing the likelihood of cannibalism and heterospecific predation in our laboratory enclosures. Caution should also be taken when inferring the attractiveness of chemical signals in the wild from the results of Y-choice tests under laboratory conditions. Behavioural

responses to close-range cues in a Y-maze may differ to responses over longer distances in the open air. Therefore, the crucial next step in understanding both heterospecific mate attraction and predation in this system is to conduct experiments in the field.

In conclusion, the impact of *M. caffra* is therefore likely to be multi-faceted, incorporating several related consequences: (i) native females' mate attraction efforts are likely to be masked by the exotics' more attractive cues; (ii) exotic females gain additional nutrition, increasing their fitness and (iii) native males are killed, reducing population size and skewing the sex ratio. This study highlights a novel mechanism behind the displacement of a native species by an invader: heterospecific mate attraction leading to predation in the context of sexual cannibalism. Given that species which evolve in different parts of the world are not likely to be selected to distinguish between each others' sexual cues, it is possible that similar heterospecific mate attraction and reproductive interference may be a common factor in the impact of numerous invasive species [4]. Our results show that for sexually cannibalistic species such as mantids and spiders, the impact of heterospecific attraction could be particularly severe.

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Data accessibility. Data used in this paper are available upon request.

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References

- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz F. 2000 Biotic invasions: causes, epidemiology, global consequences and control. *Ecol. Appl.* **10**, 689–710. (doi:10.1890/1051-0761)
- Wagner DL, Van Driesche RG. 2010 Threats posed to rare or endangered insects by nonnative species. *Ann. Rev. Entomol.* **55**, 547–568. (doi:10.1146/annurev-ento-112408-085516)
- Snyder WE, Evans EW. 2006 Ecological effects of invasive arthropod generalist predators. *Ann. Rev. Ecol. Evol. Syst.* **37**, 95–122. (doi:10.1146/annurev.ecolsys.37.091305.110107)
- Gröning J, Hochkirch A. 2008 Reproductive interference between animal species. *Q. Rev. Biol.* **83**, 257–282. (doi:10.1086/590510)
- Ramsay G. 1990 Mantodea (Insecta) with a review of aspects of functional morphology and biology. *Fauna NZ* **19**, 1–96.
- Hurd LE, Prete FR, Jones TH, Singh TB, Co JE, Portman RT. 2004 First identification of a putative sex pheromone in a praying mantid. *J. Chem. Ecol.* **30**, 155–166. (doi:10.1023/B:JOEC.0000013188.79411.18)
- Holwell GI, Barry KL, Herberstein ME. 2007 Mate location, antennal morphology, and ecology in two praying mantids (Insecta: Mantodea). *Biol. J. Linn. Soc.* **91**, 307–313. (doi:10.1111/j.1095-8312.2007.00788.x)
- Lelito JP, Brown WD. 2008 Mate attraction by females in a sexually cannibalistic praying mantis. *Behav. Ecol. Sociobiol.* **63**, 313–320. (doi:10.1007/s00265-008-0663-8)
- Maxwell MR, Barry KL, Johns PR. 2010 Examination of female pheromone use in two praying mantids, *Stagmomantis limbata* and *Tenodera aridifolia sinensis* (Mantodea: Mantidae). *Ann. Entomol. Soc. Am.* **103**, 120–127. (doi:10.1603/008.103.0115)
- Barry KL, Holwell GI, Herberstein ME. 2010 Multimodal mate assessment by male praying mantids in a sexually cannibalistic mating system. *Anim. Behav.* **79**, 1165–1172. (doi:10.1016/j.anbehav.2010.02.025)
- Maxwell MR, Gallego KM, Barry KL. 2010 Effects of female feeding regime in a sexually cannibalistic mantid: fecundity, cannibalism, and male response in *Stagmomantis limbata* (Mantodea). *Ecol. Entomol.* **35**, 775–787. (doi:10.1111/j.1365-2311.2010.01239.x)
- Barry KL, Holwell GI, Herberstein ME. 2011 A paternity advantage for speedy males? Sperm precedence patterns and female re-mating frequencies in a sexually cannibalistic praying mantid. *Evol. Ecol.* **25**, 107–119. (doi:10.1007/s10682-010-9384-3)
- Lawrence SE. 1992 Sexual cannibalism in the praying mantid, *Mantis religiosa*: a field study. *Anim. Behav.* **43**, 569–583. (doi:10.1016/S0003-3472(05)81017-6)
- Hurd LE, Eisenberg RM, Fagan WF, Tilmon KJ, Snyder WE, Vandersall KS, Datz SG, Welch JD. 1994 Cannibalism reverses male-biased sex-ratio in adult mantids—female strategy against food limitation. *Oikos* **69**, 193–198. (doi:10.2307/3546137)
- Maxwell MR. 1998 Lifetime mating opportunities and male mating behaviour in sexually cannibalistic praying mantids. *Anim. Behav.* **55**, 1011–1028. (doi:10.1006/anbe.1997.0671)
- Barry KL, Holwell GI, Herberstein ME. 2008 Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity. *Behav. Ecol.* **19**, 710–715. (doi:10.1093/beheco/arm156)
- Witzgall P, Kirsch P, Cork A. 2010 Sex pheromones and their impact on pest management. *J. Chem. Ecol.* **36**, 80–100. (doi:10.1007/s10886-009-9737-y)
- Lelito JP, Brown WD. 2006 Complicity or conflict over sexual cannibalism? Male risk taking in the praying mantis *Tenodera aridifolia sinensis*. *Am. Nat.* **168**, 263–269. (doi:10.1086/505757)
- Barry KL, Holwell GI, Herberstein ME. 2009 Male mating behaviour reduces the risk of sexual cannibalism in an Australian praying mantid. *J. Ethol.* **27**, 277–283. (doi:10.1007/s10164-008-0130-z)
- Brown WD, Muntz GA, Ladowski AJ. 2012 Low mate encounter rate increases male risk taking in a sexually cannibalistic praying mantis. *PLoS ONE* **7**, e35377. (doi:10.1371/journal.pone.0035377)