

Mate location, antennal morphology, and ecology in two praying mantids (Insecta: Mantodea)

G. I. HOLWELL*, K. L. BARRY and M. E. HERBERSTEIN

Department of Biological Sciences, Macquarie University 2109 NSW Australia

Received 26 October 2005; accepted for publication 10 August 2006

The sensory systems employed by animals to locate potential mates are diverse. Among insects, chemical and acoustic signals are commonly used over long distances, with visual signals playing a role in close-range orientation and courtship. Within groups that exhibit a scramble competition mating system, selection on mate searching ability will be particularly strong. Clearly, aspects of the species ecology, such as habitat complexity and population density, will be crucial in the evolution of mate searching systems and sexual signals. Praying mantids exhibit both chemical and visual sexual signalling behaviour, and also vary in their ecology. This study employs scanning electron microscopy of antennal sensory morphology and behavioural assays to investigate the relative importance of chemical and visual signalling in two Australian praying mantid species: *Pseudomantis albofimbriata* and *Ciulfina biseriata*. As predicted, the high level of habitat complexity, low population density and strong male dispersal capability of *P. albofimbriata* corresponded to the use of airborne sex pheromones. Conversely, the open habitat, high population density, and poor dispersal of *C. biseriata* corresponded to a greater reliance on short-range visual cues for mate location. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **91**, 307–313.

ADDITIONAL KEYWORDS: *Ciulfina biseriata* – habitat complexity – mate searching – population density – *Pseudomantis albofimbriata* – sexual signals.

INTRODUCTION

Animals use diverse sensory mechanisms to locate potential mates. These sensory systems may be adapted specifically for the task of mate location, but are often used to locate other resources such as food, oviposition sites, and suitable habitats, or to detect predators (Andersson, 1994). Within the insects, potential mates are located by a diverse range of signals. However, chemical and acoustic signals appear to be most commonly used over long distances, with visual signals playing a role once individuals are within courtship range (Cade, 1985; Bailey, 1991). Species that do not rely on any sort of signal to bring the sexes together (e.g. some crab spiders; Legrand & Morse, 2000) are rarely described in the literature, perhaps due to the greater scientific interest in signalling. Sexual selection on signals and mate searching ability is predicted to be particularly strong in species

exhibiting a scramble competition mating system (Able, 1999), where male–male competition is essentially restricted to the race for females and does not involve fighting or female defence (Emlen & Oring, 1977; Thornhill & Alcock, 2000). In scrambling species, males that are more efficient in detecting and locating females are expected to achieve fertilization successfully (Parker, 1978).

The evolution of mate searching strategies, including the type and strength of signals produced, will often be under phylogenetic constraints (Bradbury & Vehrencamp, 1998), but also can be greatly influenced by ecological constraints (Cade, 1985). Daily activity patterns, population density, and the differing dispersal patterns of males and females could potentially play roles in the evolution of specific mate location/signalling systems within a species, irrespective of the patterns observed in related species. Comparative approaches permit insights to the ecological factors that may constrain mate location mechanisms and the generation of hypotheses to explain their evolutionary pathway (Emlen & Oring, 1977; Greenwood, 1980;

*Corresponding author. E-mail: gholwell@bio.mq.edu.au

Bell, 1990; Bailey, 1991; Bradbury & Vehrencamp, 1998; Shuster & Wade, 2003). In combination, a high degree of habitat complexity, low population density and high dispersal capabilities would promote the use of long-distance multidirectional signals, such as acoustic calls and airborne pheromones. Conversely, open habitats, high population density, and poor dispersal may favour close-range visual cues, or even favour the absence of signals.

Praying mantids are an ideal group in which to investigate the evolution of mate location strategies. They vary considerably in their ecology, ranging from cursorial hunters to sit-and-wait predators (Svenson & Whiting, 2004) and live in a wide variety of environments. Within the Mantodea, both chemical and visual cues are important (Maxwell, 1999). Males respond to airborne pheromones in a number of genera, including *Acanthops* (Robinson & Robinson, 1979), *Sphodromantis* (Hurd *et al.*, 2004), *Hierodula* (Perez, 2005) *Mantis* and *Empusa* (Gemeno, Claramunt & Dasca, 2005). Visual cues can also be important in close-range mate-location and courtship (Roeder, 1935; Edmunds, 1975; Maxwell, 1999). Some mantids exhibit characteristic behavioural displays involving colourful patterns on the raptorial fore-legs, wings, and thorax; for example, *Oxyphilus* (Edmunds, 1979), *Paraoxyphilus*, *Gyromantis*, and *Calofulcinia* (G. I. Holwell, pers. observ.). Some emphasis has been placed on the role of visual cues to ensure that females recognize males to avoid precopulatory cannibalism (Maxwell, 1999).

We have chosen two Australian praying mantid species with marked ecological differences. *Pseudomantis albofimbriata* (Mantidae) is a medium-sized sit-and-wait predator found amongst foliage of trees, shrubs and grasses throughout Eastern Australia. *Ciulfina biseriata* (Liturgusidae) is a small cursorial predator found on the lower reaches of tree trunks, a relatively low-complexity habitat, in central Queensland, Australia.

This study tests the prediction that airborne pheromones will be important for mate location in *P. albofimbriata*, found at low densities in complex habitats, and exhibiting strong male dispersal capabilities. By contrast, we predict that *C. biseriata*, will be more reliant on short range visual cues for mate location because it is found in less complex open environments, at higher densities, and exhibits comparatively poor dispersal.

MATERIAL AND METHODS

STUDY SPECIES

The study population of *P. albofimbriata* was found entirely on the flower spikes of grassy *Lomandra* bushes (1 m × 1 m × 1 m), a relatively dense and com-

plex habitat, within parkland in suburban Sydney. The population density was relatively low, with mantids found on only 6.7% of bushes (G. I. Holwell, unpubl. data) and patchily distributed. *Pseudomantis albofimbriata* exhibits obvious sexual dimorphism in dispersal capabilities. Males are fully winged and capable of long-distance flight, whereas females are flightless (Barry, 2004). The frequency of sexual cannibalism is high (33%; Barry, 2004). *Pseudomantis albofimbriata* were housed individually in the laboratory in 10-cm diameter plastic enclosures, fed crickets (*Acheta domestica*) twice weekly, and watered daily.

In *C. biseriata*, population density was relatively high, with mantids located on 41.3% of preferred habitat trees (Hill *et al.*, 2004), and distributed evenly throughout the study site. Dispersal of both male and female *C. biseriata* is limited by lack of true flight. Individuals move between tree trunks by running across the ground, jumping between branches, or using their hindwings to glide short distances (Hill *et al.*, 2004). *Ciulfina biseriata* exhibits no sexually cannibalistic behaviour. This species was housed individually in 10-cm plastic enclosures, fed *Drosophila melanogaster* three times weekly and watered daily.

ANTENNAL MORPHOLOGY

We examined the antennae of two male and two female *P. albofimbriata* and *C. biseriata* using scanning electron microscopy (SEM) to determine whether males bear the appropriate morphological structures (basiconic sensilla) for receiving chemical signals from females (Zacharuk, 1985), and to assess general differences in antennal morphology between the sexes and between species. Mantids were immobilized with carbon dioxide vapour after which the heads (with antennae in tact) were fixed overnight in 4% paraformaldehyde 3% glutaraldehyde in 0.1 M phosphate buffer. The specimens were then washed and left overnight in 0.1 M phosphate buffer solution. Heads were then submerged in 1% osmium tetroxide for approximately 30 min. The specimens were washed several times with water, then with a graded series of ethanol baths (from 50% to 100% ethanol). Antennae were removed, critical point dried, mounted on a 10-mm stub using carbon adhesive tabs, sputter-coated with gold, and viewed with a Jeol JSM 840 scanning electron microscope (for general methods of SEM, see Bozzola & Russell, 1992). The SEM images were examined to identify the type of antennal sensilla present on male and female mantids of both species. Antennal length (*P. albofimbriata*, $N = 20$; *C. biseriata*, $N = 20$) was measured with electronic callipers and two-tailed *t*-tests were used to compare the length of antennae between the sexes.

CHOICE EXPERIMENTS: OLFACTORY

To determine whether *P. albofimbriata* and *C. biseriata* males respond to airborne chemicals emitted by conspecific females, we used a glass Y-maze olfactometer, which allows males to make an active choice between two stimuli. Each of the glass Y-maze had a diameter of 2.3 cm and a length of 17 cm. During choice experiments, *C. biseriata* were kept on an *ad libitum* diet of *Drosophila melanogaster* and water daily, whereas *P. albofimbriata* were kept on a diet of two small house crickets (*A. domestica*) three times per week and water daily. For both species, virgin females (*C. biseriata*: $N = 15$; *P. albofimbriata*: $N = 10$) were chosen from the laboratory population and placed into one of two Perspex boxes, whereas the alternate box remained empty. Prior to each choice experiment, females were randomly allocated to a Perspex box and boxes were randomly allocated to the left or right position. Males ($N = 10$) were subsequently placed at the bottom of the maze (A) and an air pump connected to the rear of each Perspex box via plastic tubing allowed air flow to be directed towards the male. Air was pumped past both boxes for approximately 1 min prior to the addition of the male so that any air-borne pheromones would be detectable. The anterior surface of each box was covered with an opaque cloth so that males could not use visual cues when making a choice. Males were given 1 h to move within the Y-maze and a response was recorded when they moved at least half way down tube B or C. Between each individual experiment, both Perspex boxes and the Y-maze tubing were washed with 100% ethanol so that the previous male and female scents did not affect the result of subsequent choices. Binomial statistics were used to test whether males moved towards females significantly more often than an empty box, suggesting the use of olfactory cues.

CHOICE EXPERIMENTS: VISUAL

To determine whether *C. biseriata* males ($N = 15$) respond visually to conspecific females, we first repeated the methods described above, but with the visual barriers removed from the Perspex boxes B and C. Second, we used open-arena choice tests, and allowed males ($N = 20$) to choose between a tree trunk bearing a conspecific female and an empty tree trunk. This was carried out to place males in a more realistic mate location scenario and to determine whether males can locate females on a background that would render females more cryptic. Individual males were not used in more than one experiment to avoid any effects of prior exposure or experience. Prior to these experiments, the two tree trunks used were pretested for uniformity of appeal to male mantids in a similar choice test but with females absent from both tree

trunks. The left/right position for the two tree trunks were randomly allocated in the pretest and experiment, and preference for left/right position was also tested in the pretest. Tree trunks in both the pretests and experiments were positioned 1 m apart, and 1 m from the mantid. The pretest revealed no preference for either tree trunk used in the experiment (binomial: $P > 0.7$, $N = 24$) and no preference for either the left or right trunk position in the arena (binomial: $P > 0.3$, $N = 24$). The results of the mate location experiment were therefore deemed to be unbiased by either trunk or positional preference. In all experiments, including the pretests, a male response was recorded when he alighted upon a tree trunk. Binomial statistics were used to test whether males alighted upon tree trunks bearing females significantly more often than an empty tree trunk, suggesting male ability to locate females visually.

RESULTS

MATE ATTRACTION AND RECOGNITION

Antennal morphology

In *C. biseriata*, there is no significant difference in antennal length between males and females (t -test: $t_5 = -1.032$, $P > 0.32$; Table 1). For *P. albofimbriata*, male antennae are significantly longer than female antennae (t -test: $t_5 = -14.545$, $P < 0.0001$; Table 1). Furthermore, male and female *P. albofimbriata* differ in the type of sensilla their antennae possess. The female antennae are primarily surfaced with large and medium trichoid sensilla (trichodea), corrugated by longitudinal ridges, and extending from relatively shallow antennal pores (Fig. 1C, D). Trichoid sensilla are generally considered to be contact chemoreceptors and as each large trichoid sensilla grows from a cuticular protuberance, a mechanosensory function is also likely (Zacharuk, 1985). By contrast, male antennae

Table 1. Antennal morphology for males and females of *Ciulfina biseriata* and *Pseudomantis albofimbriata*. The density of sensilla was assessed only qualitatively (Fig. 1)

	Mean length (mm)	Type of sensilla
<i>Ciulfina biseriata</i> male	20.14 ± 0.32 ($N = 10$)	Short trichoid Long trichoid
<i>Ciulfina biseriata</i> female	19.62 ± 0.33 ($N = 10$)	Long trichoid Short trichoid
<i>Pseudomantis</i> <i>albofimbriata</i> male	27.67 ± 0.85 ($N = 10$)	Basiconic Short trichoid
<i>Pseudomantis</i> <i>albofimbriata</i> female	12.91 ± 0.56 ($N = 10$)	Long trichoid Medium trichoid

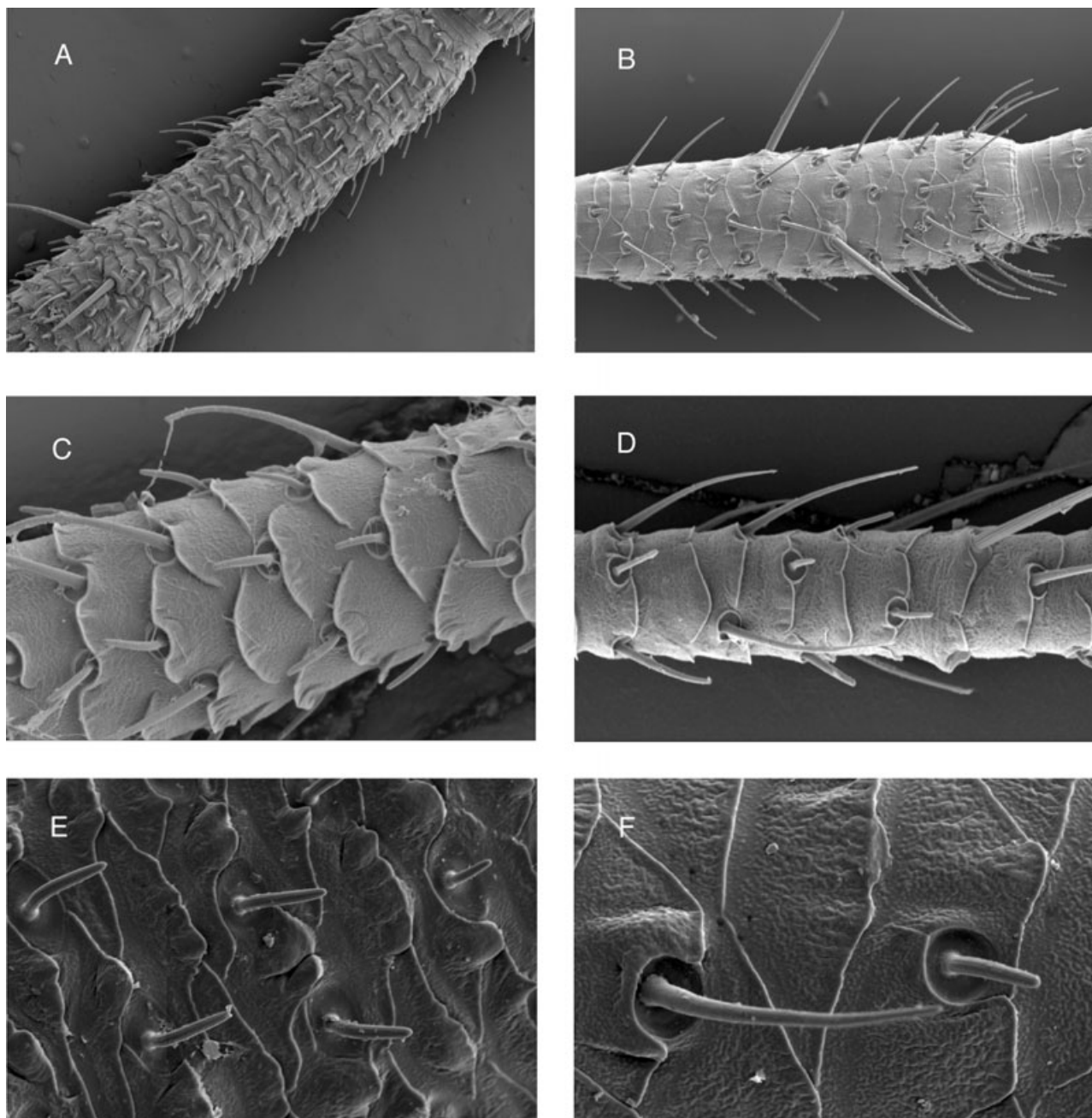


Figure 1. Scanning electron micrographs showing median segments of male (A) and female (B) *Pseudomantis albofimbriata* antennae, male (C) and female (D) *Ciulfina biseriata* antennae, and higher magnification images of basiconic (E) and trichoid (F) sensilla of *P. albofimbriata* antennae.

are covered in relatively small basiconic sensilla with grooves down their length and extend directly from the antennal cuticle, rather than from a pore (Fig. 1E, F). Grooved basiconic sensilla are olfactory receptors with a variety of functions in insects, including long distance pheromone reception (Zacharuk, 1985). Male antennae also have a small number of large trichodea.

The type of sensilla found on the antennae of male and female *C. biseriata* does not greatly differ, except that females appear to have more long trichoid sensilla, and males bear more short trichoid sensilla. In addition, female antennae of both species were much cleaner than male antennae, probably as a result of more frequent grooming performed by females (G. I. Holwell and K. L. Barry, pers. observ.).

Choice experiments

Pseudomantis albofimbriata males quickly moved along the common tube of the Y-maze while oscillating the antennae. Mantids spent the majority of their time at the fork of the maze, and it was not uncommon to see one antenna in each of the upper tubes. Males then proceeded to move more slowly down one of the tubes, making a choice between the contents of the two Perspex boxes. Ten of the 12 male *P. albofimbriata* chose the box containing the female significantly more often than the empty box (binomial test: $P = 0.019$).

Ciulfina biseriata males did not make any clear choice between the empty box and that containing a female, with the majority of males remaining in the entry arm of the Y-maze (nine of 15) and only half of those making a choice, chose the box containing a female (binomial: $x = 4$, $N = 8$, $P = 0.6367$). When the visual barrier was removed from the entrances to the boxes, this significantly altered the choice behaviour of the male mantids. All males subsequently chose between test boxes, and they significantly chose boxes containing females over empty boxes (binomial: $x = 12$, $N = 15$, $P = 0.0176$). In the open arena choice tests, given the choice between a tree trunk bearing a female and an empty tree trunk, male *C. biseriata* chose tree trunks bearing females significantly more often (binomial: $x = 18$, $N = 20$, $P = 0.0002$).

DISCUSSION

MATE LOCATION AND THE ECOLOGY OF *C. BISERIATA* AND *P. ALBOFIMBRIATA*

We have uncovered distinct differences in the way that male praying mantids locate females. *Pseudomantis albofimbriata* appears to use olfaction during mate searching, whereas the mechanisms used by male *C. biseriata* appear to be entirely visual, and very acute. The ability of males to visually detect motionless and cryptic females from a considerable distance demonstrates an impressive level of visual acuity (Prete, 1999), supporting the results of previous studies on the ability of *C. biseriata* to visually discriminate between bark-types of trees (Hill *et al.*, 2004). Interpretation of the antennal morphology of both species using SEM provides us with a proximate explanation for the different sensory systems used by the two species. Basiconic sensilla, which were only found on male *P. albofimbriata* in the present study, are generally associated with olfaction in insects, whereas trichodea, identified from all individuals in this study, are associated with a mechanosensory or gustatory function (Zacharuk, 1985; Keil, 1999). The lack of basiconic sensilla in male *C. biseriata* makes chemoreception of airborne pheromones unlikely. Sexual dimorphism in antennal length was also detected for *P. albofimbriata* but not for *C. biseriata* (Table 1).

Such dimorphism in antennal length or structure is prevalent in species that use airborne pheromones for mate location (Keil, 1999). These data help to explain why *C. biseriata* did not respond to females in the Y-choice olfactometer test when vision was excluded. A more ultimate explanation for the difference in mate location mechanisms between these two species comes from a comparison of their ecology. In this regard, our initial predictions were supported by the results.

HABITAT COMPLEXITY

Habitat is markedly different between the two species studied. In the relatively complex environment of *Lomandra* shrubs, male *P. albofimbriata* cannot rely on visual cues to locate females because they may be visually obscured by vegetation in all directions. The use of airborne pheromones to attract males in *P. albofimbriata* may therefore be adaptive to their environment. *Ciulfina biseriata* is found in open eucalypt woodlands on the bark of tree trunks. Despite being cryptically coloured, *C. biseriata* can effectively use visual cues when locating preferred habitat trees (Hill *et al.*, 2004) or mates (present study) without obstruction from vegetation. Chemical signals may be unnecessary in this environment, or more difficult to locate due to differences in ambient air movement.

POPULATION DENSITY AND DISPERSAL

The density and patchiness of the two study populations also relate to the observed results. For *P. albofimbriata*, which exhibits a low-density, patchy distribution, signals would be advantageous for locating mates (Bell, 1990). *Ciulfina biseriata* is found evenly distributed throughout its woodland at relatively high density where the location of females by males would not require a mate-attracting signal. Visual searching of a small number of trees would be likely to yield some success for an active male *C. biseriata*. Chemical signals would not only be unnecessary in this environment, but also may oversaturate the receiver in a high density of close-proximity signallers (Wyatt, 2003). *Pseudomantis albofimbriata* and *C. biseriata* differ in dispersal capability. Male *P. albofimbriata* are fully winged and capable of long-distance flight, whereas females are flightless. The use of airborne pheromones has been linked to long-distance dispersal, and insects producing airborne sex pheromones can attract mates from large distances (Cade, 1985). Conversely, the dispersal capabilities of both male and female *C. biseriata* are limited by a lack of flight. In species lacking long-distance dispersal, such as *C. biseriata*, we might intuitively expect that populations would exist at relatively high densities, reducing mate-searching time

and negating the requirement for long-distance signals to locate mates.

CANNIBALISM

Pseudomantis albofimbriata and *C. biseriata* differ in mating behaviour with *P. albofimbriata* exhibiting a high frequency of sexual cannibalism (Barry, 2004) and *C. biseriata* exhibiting no cannibalistic behaviour (Holwell, 2006). This is potentially important for the results of the present study. Cannibalistic *P. albofimbriata* females, which produce airborne pheromones, could attract mates and gain substantial nutrition from each mating encounter. An effective long-distance sexual signal may be particularly advantageous for sexually cannibalistic species and it has been suggested that food-limited female mantids may attract males as a foraging strategy (Hurd *et al.*, 1994). The early detection and location of females through chemical stimuli may also be particularly beneficial to males of sexually cannibalistic species due to the risk of being cannibalized before mating (Maxwell, 1999). Precopulatory cannibalism occurs frequently in *P. albofimbriata* (Barry, 2004), demonstrating a real advantage for males that can detect females using nonvisual cues.

PRAYING MANTIDS AND SCRAMBLE-COMPETITION

Ecological factors are important in the evolution of different mating systems (Emlen & Oring, 1977). The dispersal capabilities of males, as well as the spatial and temporal distribution of females and resources, will all interplay to determine the strategies males will use to maximize their reproductive output (Emlen & Oring, 1977; Thornhill & Alcock, 2000). Praying mantids exhibit the characteristics of a scramble competition mating system. High male mate-searching efficiency, low possibility of female defence, low operational sex ratio, and long periods of female receptivity would benefit 'roaming' males (Sandell & Liberg, 1992). In such a scramble mating system, indirect sexual selection may strongly influence male mate searching ability and their perception of female signals (Wiley & Poston, 1996; Legrand & Morse, 2000). For mantids, sexual cannibalism would further negate the possibility of a defence-based mating system in some species.

In the present study, we have revealed two distinct mechanisms of scramble competition within the Mantodea: (1) scrambling by males in response to the sexual advertisement of a female and (2) scramble competition between males through their efficiency in searching for females at likely encounter-sites. These two mechanisms have been highlighted previously for insect scramble competitors (Thornhill & Alcock, 2000).

Also related to this study is the role of indirect mate choice in scramble competition mating systems. We have shown that female *C. biseriata* do not advertise themselves to roaming males with chemical signals (present study) and actively evade males when they become aware of them (Holwell, 2006), which may indirectly select for good visual acuity, efficient searching behaviour, and stealth in male approach. For *C. biseriata*, which is a cursorial predator, any heritable component of these traits would provide advantages to offspring of both sexes through improved predatory efficiency. Praying mantids may therefore be useful models for the investigation of indirect sexual selection on male mate searching.

CONCLUSIONS

Although single-species studies are required to deduce the relative importance of various ecological influences, the comparison of *P. albofimbriata* and *C. biseriata* that we have presented highlights components of species' ecology that may influence whether females produce sexual signals, and also the modality of those signals. We suggest that long-distance chemical signalling would be favoured in species with: (1) high-complexity habitats; (2) sparse and patchy distributions and; (3) high dispersal capabilities in the searching sex. Among praying mantids, sexually cannibalistic species would also favour such signals. Praying mantids as a group exhibit both scramble strategies and may prove to be ideal for the study of scramble competition in insects. The differences in dispersal abilities of males, dispersion of females, range of feeding modes (cursorial through to sit-and-wait predation), and the differing sensory systems used to locate mates (chemical and visual) within the Mantodea, provide a unique opportunity in which to study the effects of these factors on the scramble competition mating system.

ACKNOWLEDGEMENTS

We thank Anne Gaskett for designing the Y-choice olfactometer and for assistance with the choice tests. Debra Birch and Nicole Vella assisted greatly with scanning electron microscopy. Anne Gaskett, Matthew Bruce, Katie Robinson, Kim Shaddick, and Phoebe Hill assisted with collection of mantids in the field. We also thank David Briscoe for helpful comments on the manuscript.

REFERENCES

- Able DJ. 1999.** Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioral Ecology and Sociobiology* **46**: 423–428.

- Andersson M. 1994.** *Sexual selection*. Princeton, NJ: Princeton University Press.
- Bailey WJ. 1991.** Mate finding: selection on sensory cues. In: Bailey WJ, Ridsdill-Smith J, eds. *Reproductive behaviour of insects: individuals and populations*. Melbourne: Chapman & Hall.
- Barry KL. 2004.** Mating behaviour of the sexually cannibalistic praying mantid, *Pseudomantis albobimbriata*. Honours Thesis. Department of Biological Sciences, Macquarie University.
- Bell W. 1990.** Searching behavior patterns in insects. *Annual Review of Entomology* **35**: 447–467.
- Bozzola JJ, Russell LD. 1992.** *Electron microscopy: principles and techniques for biologists*. Boston, MA: Jones and Bartlett.
- Bradbury JW, Vehrencamp SL. 1998.** *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Cade WH. 1985.** Insect mating and courtship behaviour. In: Kerkut GA, Gilbert LI, eds. *Comprehensive insect physiology, biochemistry and pharmacology*. Oxford: Pergamon Press.
- Edmunds M. 1975.** Courtship, mating, and possible sex pheromones in three species of Mantodea. *Entomologists Monthly Magazine* **111**: 53–57.
- Emlen ST, Oring LW. 1977.** Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Gemeno C, Claramunt J, Dasca J. 2005.** Nocturnal calling behavior in mantids. *Journal of Insect Behavior* **18**: 389–403.
- Greenwood P. 1980.** Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* **28**: 1140–1162.
- Hill PJB, Holwell GI, Goth A, Herberstein ME. 2004.** Preference for habitats with low structural complexity in the praying mantid *Ciulfina* sp (Mantidae). *Acta Oecologica – International Journal of Ecologica* **26**: 1–7.
- Holwell GI. 2006.** Mating behaviour and genital morphology of *Ciulfina* praying mantids. PhD Thesis. Department of Biological Sciences, Macquarie University.
- 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.
- Hurd LE, Prete FR, Jones TH, Singh TB, Co JE, Portman RT. 2004.** First identification of a putative sex pheromone in a praying mantid. *Journal of Chemical Ecology* **30**: 155–166.
- Keil TA. 1999.** Morphology and development of the peripheral olfactory organs. In: Hansson BS, ed. *Insect olfaction*. Berlin: Springer-Verlag, 5–47.
- Legrand R, Morse D. 2000.** Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society* **71**: 643–664.
- Maxwell MR. 1999.** Mating behavior. In: Prete FR, Wells H, Wells PH, Hurd LE, eds. *The praying mantids*. Baltimore, MD: John Hopkins University Press.
- Parker GA. 1978.** Evolution of competitive mate searching. *Annual Review of Entomology* **23**: 173–196.
- Perez B. 2005.** Calling behaviour in the female praying mantis, *Hierodula patellifera*. *Physiological Entomology* **30**: 42–47.
- Prete FR. 1999.** Prey recognition. In: Prete FR, Wells H, Wells PH, Hurd LE, eds. *The praying mantids*. Baltimore, MD: John Hopkins University Press.
- Robinson MH, Robinson B. 1979.** By dawn's early light: Matutinal mating and sex attractants in a neotropical mantid. *Science* **205**: 825–827.
- Roeder KD. 1935.** An experimental analysis of the sexual behavior of the praying mantis (*Mantis religiosa*, L.). *Biological Bulletin* **69**: 203–220.
- Sandell M, Liberg O. 1992.** Roamers and stayers: a model on male mating tactics and mating systems. *American Naturalist* **139**: 177–189.
- Shuster SM, Wade MJ. 2003.** *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
- Svenson GJ, Whiting MF. 2004.** Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator. *Systematic Entomology* **29**: 359–370.
- Thornhill R, Alcock J. 2000.** *The evolution of insect mating systems*. Lincoln, NE: Universe.com, Inc.
- Wiley R, Poston J. 1996.** Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**: 1371–1381.
- Wyatt TD. 2003.** *Pheromones and animal behaviour: communication by smell and taste*. Cambridge: Cambridge University Press.
- Zacharuk RY. 1985.** Antennae and sensilla. In: Kerkut GA, Gilbert LI, eds. *Comprehensive insect physiology, biochemistry and pharmacology*. Oxford: Pergamon Press.