

## Multimodal mate assessment by male praying mantids in a sexually cannibalistic mating system

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The traditional view of sexual selection has been that of competing males and choosy females; however, more recently it has been recognized that males may exhibit mate choice when females vary in quality and when males suffer costs associated with mating. Sexually cannibalistic mating systems provide an opportunity to examine male mate choice further: the high costs potentially involved in the mating process for males, as well as variation in female quality, predict male mate choice. We used the praying mantid *Pseudomantis albofimbriata* to determine the effect of female body condition on male mate choice in a system with frequent precopulatory sexual cannibalism. Female body condition is positively correlated with fecundity and negatively correlated with the propensity to cannibalize, so we predicted males would strongly prefer females in good condition to maximize their reproductive potential. Results of our simultaneous choice tests showed that males use chemical and visual cues for mate location and assessment, and that they can use either of these sensory modalities to distinguish and choose between females differing in body condition, with a significant preference for good-condition females. However, surprisingly, males rarely rejected poor-condition females in the more ecologically relevant scenario of only one immediate potential mate and both sensory modes available to them, which may be explained by the strong scramble competition known for praying mantid systems. These results show that even when female quality varies and the cost of mating for males is substantial, male mate rejection does not always evolve.

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The classical view of sexual selection has been that of competing polygynous males and choosy monandrous females (Darwin 1871; Bateman 1948), resulting in a substantial research effort devoted to female mate choice and relatively few studies of male mate choice. This traditional dogma may, however, be too simplistic (Bonduriansky 2001). First, while it may be true that sperm are relatively cheap to produce on a gamete-for-gamete basis, they are hardly ever ejaculated as single units (Dewsbury 1982). Rather, they are transferred within ejaculates that are typically composed of millions of sperm, as well as other important substances that make up the seminal fluid. Obviously the cost of producing an ejaculate will be much greater than the cost of producing an individual spermatozoan; therefore, the difference in gametic investment between the sexes may be less than was previously thought (Wedell et al. 2002). Second, when males invest more in sexual reproduction than females, typical sex roles may be reversed and male mate choice more likely (Trivers 1972; Andersson 1994). For

example, males of many role-reversed pipefish species have been shown to prefer large females (Berglund et al. 1986; Rosenqvist 1990; Jones et al. 2001; Silva et al. 2007), and male crickets that produce spermatophylaxes exhibit 'cryptic male choice' by altering the number of sperm transferred in relation to mate competition and female size (Simmons et al. 1993; Gage & Barnard 1996; Simmons & Kvarnemo 1997; Zuk & Simmons 1997). Third, monogynous mating systems where behavioural and/or morphological traits restrict the opportunity for a male to mate with more than one female are widespread, again increasing the probability of male mate choice (Fromhage et al. 2005). Finally, if female quality is sufficiently variable, polygynous males should benefit from exhibiting some level of male mate choice (Gwynne 1991; Andersson 1994). In this case, we should expect males to choose or reject females based on traits that indicate potential reproductive success, such as body size or body condition (Gwynne 1991; Danielson-Francois et al. 2002; Hoefler 2007).

Sexually cannibalistic mating systems provide an excellent opportunity to examine and gain a better understanding of male mate choice, that is, mate choice between two or more individuals and/or the more extreme form of choice that manifests as mate rejection, including the circumstances and mechanisms by which

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males might be selective. Because of the potentially high cost involved in the mating process, that is, death, cannibalistic mating systems are partially role reversed, and males are, therefore, more likely to be choosy (Thornhill & Alcock 1983; Maxwell 1999a; Elgar & Schneider 2004). Female body condition is positively related to fecundity in many cannibalistic spiders and mantids (Rubenstein 1987; Birkhead et al. 1988; Wise 2006; Barry et al. 2008), and the high variability of female body condition in natural populations (Eisenberg et al. 1981; Lawrence 1992; Maxwell 1998) suggests males should choose females in relatively good condition to maximize their reproductive fitness (Lawrence 1992; Moya-Larano et al. 2004; Barry et al. 2008; Maxwell et al. 2010). Furthermore, males should choose females that are less likely to cannibalize them, and, in addition to female body size/condition, may use female feeding status (Liske & Davis 1987; Birkhead et al. 1988; Kynaston et al. 1994; Andrade 1998) or female mating status (Newman & Elgar 1991; Herberstein et al. 2002; Schneider & Elgar 2002) as an indication of a female's propensity to cannibalize.

In the current study, we used the false garden mantid *Pseudomantis albobimbrata* to determine the effect of female body condition on male mate choice/rejection in a mating system with frequent sexual cannibalism (about 40% of interactions, see Barry et al. 2009). The onset of cannibalism occurs prior to copulation in this species, so males potentially forfeit all present and future reproductive successes if consumed (Buskirk et al. 1984). However, approximately half of the males captured are still able to initiate copulation and transfer sperm (Barry et al. 2009). The cost of cannibalism for a male may be mitigated by increased fecundity: the consumption of a single male increases the reproductive output by up to 40% (Barry et al. 2008). Nevertheless, males are also capable of mating with and inseminating multiple females during their adult lives (Lawrence 1992; Hurd et al. 1994; Holwell et al. 2007) so sexual cannibalism is likely to represent an extreme sexual conflict in this system and males are predicted to exhibit strong mate choice and mate rejection to maximize their reproductive potential. Furthermore, female body condition is positively correlated with female fecundity (Barry et al. 2008), negatively related to the propensity of a female for sexual cannibalism (Barry et al. 2008), and is highly variable in natural populations of *P. albobimbrata* (K. L. Barry, unpublished data). This two-fold advantage of choosing females in good condition is likely to translate to a strong male preference for such females, but only if males can distinguish between females differing in body condition.

Mate choice commonly involves multiple sensory systems to obtain information and assess potential mates (Candolin 2003; Partan & Marler 2005), and this is particularly likely in cannibalistic systems because of the significant risks associated with copulation for a male. Both chemical and visual cues are assumed to be important in praying mantid communication, with chemical cues probably used as long-distance signals of female location and/or quality and visual cues more appropriate when individuals are at close range (Maxwell 1999a). In a previous study we showed that male *P. albobimbrata* use female-emitted chemical signals to locate potential mates (Holwell et al. 2007), and two recent mantid studies have shown differential male attraction to females on a high-food treatment when visual cues are obscured (Lelito & Brown 2009; Maxwell et al. 2010). It is, however, unclear whether *P. albobimbrata* males use visual and/or chemical cues for mate assessment and subsequent mate choice or rejection.

The aims of this study were (1) to confirm that *P. albobimbrata* males primarily use chemical and visual cues for mate location and assessment; (2) to determine whether males can distinguish and choose between two females differing in body condition using chemical cues only; (3) to determine whether males can

distinguish and choose between two females differing in body condition using visual cues only; (4) to determine whether male mantids reject females on the basis of body condition when presented with only one female and when both sensory modes are available to them; and (5) to place our results within an ecological context by ascertaining the likelihood of simultaneous choice between females in nature for *P. albobimbrata* males.

## METHODS

### Collection and Housing

We collected *P. albobimbrata* from various sites around Sydney, Australia, from January to February 2006 (experiment 4), 2007 (experiments 2 and 5), 2008 (experiment 1) and 2009 (experiment 3). The majority of individuals were found in *Lomandra longifolia* bushes at Kuringai Bicentennial Park, West Pymble, Sydney, Australia. Juvenile animals (usually in their antepenultimate or penultimate instar) were collected from the study sites and maintained on a diet of two small house crickets, *Acheta domestica* (mean cricket body mass  $\pm$  SE =  $0.037 \pm 0.003$  g,  $N = 50$ ) three times a week and sprayed with water daily. Animals were housed individually within well-ventilated 425 ml transparent cups in the laboratory, at a temperature of 24–26 °C and a diurnal period of 10–12 h of light per day.

### Measuring and Sexing Mantids

The pronotum length of all laboratory-reared mantids was recorded after the final moult, while body mass was measured immediately preceding experimentation. Since pronotum length remains constant throughout adulthood and can only be influenced by feeding during the juvenile stages, we used it as a measure of fixed size. Body mass is, instead, variable and depends upon size and feeding levels during adulthood (K. L. Barry & L. E. Allen, unpublished data). We used body mass divided by fixed size and the residuals of a regression of body mass over fixed size as indices of body condition (see Jakob et al. 1996 for discussion of these and other indices); however, both gave very similar results, so we report only fixed size divided by body mass throughout this paper. Measures of body condition depict an animal's 'fatness' while controlling for body size (Petrie 1983). The sex of *P. albobimbrata* individuals was determined by differences in the adult abdomen and wing morphology.

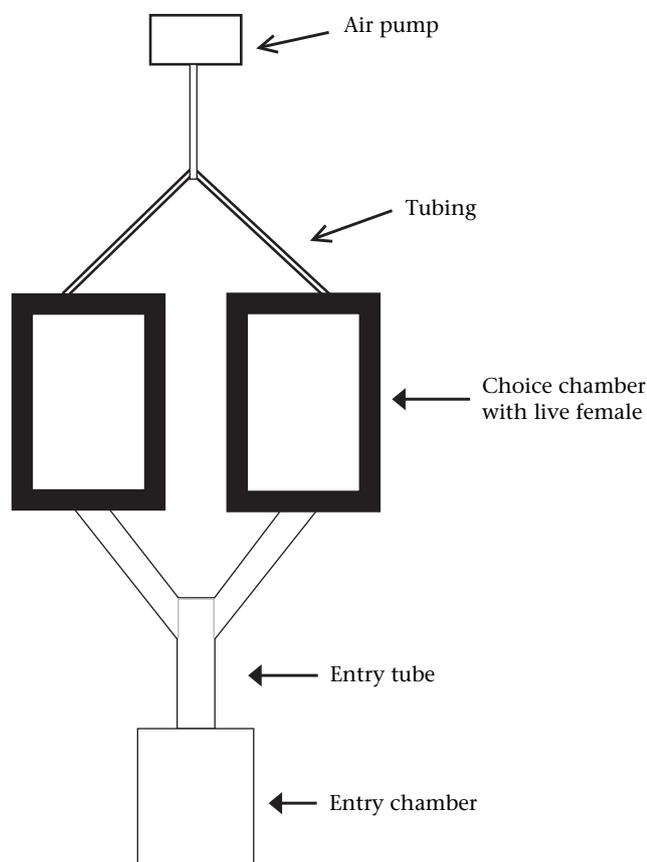
### General Data Analysis

Data were analysed using SPSS 16.0 for Mac (SPSS Inc., Chicago, IL, U.S.A.) and were checked for normal distribution (Kolmogorov–Smirnov test) before further statistical analysis. Unless otherwise stated, all values are mean  $\pm$  SE, and all statistical tests are two tailed.

### Experiment 1: Cues for Mate Location

#### Apparatus

To confirm that male *P. albobimbrata* use chemical signals to locate conspecific females (for previous results see Holwell et al. 2007) and to determine whether males use additional sensory modalities (other than chemical and visual) to locate conspecific females in a laboratory situation, we used a glass Y-maze olfactometer, which allowed males ( $N = 18$ ) to make a simultaneous choice between two chemical stimuli (Fig. 1). These tests were carried out from 26 March to 4 April 2008, from 0700 to 1000 hours each day.



**Figure 1.** Schematic of Y-maze olfactometer set-up used for experiments 1 and 2.

### Experimental treatments

Once adulthood was attained, males were randomly allocated to one of two treatments: ‘antennae snipped’ (treatment 1) or ‘antennae removed’ (treatment 2). Antennae house the chemosensory organs for most insects, including praying mantids, and we previously showed that chemosensory sensilla are found along the length of the male antennae (see Fig. 1 in Holwell et al. 2007). Males in the antennae-snipped treatment had only the very distal ends of their antennae snipped off, so the antennae were still functional. Males in the antennae-removed treatment had their antennae totally removed so that they were no longer functional. There was no significant difference in male size between the two treatments (antennae snipped:  $13.109 \pm 0.327$  mm; antennae removed:  $13.415 \pm 0.795$  mm; *t* test:  $t_{16} = -0.728$ ,  $N = 9$ ,  $P = 0.477$ ) or male body condition (antennae snipped:  $0.016 \pm 0.000$ ; antennae removed:  $0.018 \pm 0.001$ ; *t* test:  $t_{16} = -1.313$ ,  $N = 9$ ,  $P = 0.208$ ). Each male from treatment 1 was then randomly paired with a male from treatment 2, and each pair was presented with the same female during subsequent choice tests (so as to control female quality). Each male was then presented with a choice between a virgin female ( $N = 9$ ) and an empty box (see below). If males are using olfaction to locate females, antennae-snipped males should have a significant preference for the box containing a conspecific female (Holwell et al. 2007). Furthermore, if males are able to use a third sensory modality (other than olfaction and/or vision), we predicted a similar preference for females even when the antennae have been removed.

During choice tests, all mantids were kept on a diet of two small house crickets three times per week and water daily. Mature virgin females (fixed size:  $16.564 \pm 0.353$  mm; body condition:  $0.051 \pm 0.004$ ;  $N = 9$ ) were arbitrarily chosen from the laboratory

population and placed into one of two Perspex boxes ( $10 \times 7$  cm and 5 cm high), whereas the alternative box remained empty. Prior to each choice test, females were randomly allocated to a Perspex box and boxes were randomly allocated to the left or right position. Each of the glass Y-maze tubes had a diameter of 2.3 cm and a length of 17 cm. Males (antennae snipped:  $N = 9$ ; antennae removed:  $N = 9$ ) were subsequently placed at the bottom of the maze and an air pump connected to the rear of each Perspex box via plastic tubing allowed airflow 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 airborne 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 (3600 s) to move within the Y-maze and a response was recorded when they moved to the end of one of the Y-maze arms. Between tests, 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. We carried out tests during the morning hours because this is the most likely time for female pheromone emission in *P. albofimbriata* (K. L. Barry, unpublished data).

### Data analysis

We used binomial statistics to test whether males with antennae snipped and antennae removed preferred the female significantly more than the empty box. A Wilcoxon signed-ranks test compared results between the two treatments, which allowed us to determine whether the antennae of males, and thus olfactory cues, were being used to locate conspecific females. We also used a *t* test to compare the latency to choose between male treatments.

### Experiment 2: Chemical Signals and Mate Choice

#### Apparatus

To determine whether *P. albofimbriata* males use chemical cues to distinguish and choose between females in good and poor nutritional condition, we again used a glass Y-maze olfactometer, which allowed males ( $N = 23$ ) to make an active choice between two different chemical stimuli. These tests were carried out from 27 March to 16 April 2007, from 0700 to 1000 hours each day.

#### Experimental treatments

Once mantids attained adulthood, females were placed on one of two feeding regimes: ‘low quantity’ (treatment 1) or ‘high quantity’ (treatment 2). Females on the low-quantity feeding treatment ( $N = 19$ ) were given one small cricket three times a week, whereas females on the high-quantity treatment ( $N = 22$ ) were fed three small crickets three times a week. Adult males (male fixed size:  $13.468 \pm 0.131$  mm; male body condition:  $0.017 \pm 0.001$ ;  $N = 23$ ) remained on the normal feeding regime of two crickets three times per week. Females were weighed immediately prior to choice experiments and females in the high-quantity treatment were in significantly better nutritional condition ( $0.058 \pm 0.002$ ,  $N = 22$ ) than females in the low-quantity treatment ( $0.023 \pm 0.001$ ,  $N = 19$ ; *t* test:  $t_{24,985} = 15.296$ ,  $P < 0.001$ ). The treatment groups were, therefore, renamed ‘good condition’ and ‘poor condition’. The body condition of females raised in the laboratory was within the range of female body condition previously recorded in nature (range [mass/size] = 0.016–0.0612,  $N = 25$ ).

Choice tests were carried out as per experiment 1, except that males were given the choice between two females (one from each treatment), rather than a female and an empty box. Latency to choose a female was also recorded.

### Data analysis

We used binomial statistics to test whether males had a significant preference for females in good or poor condition.

### Experiment 3: Visual Signals and Mate Choice

To determine whether *P. albofimbriata* males use visual cues to distinguish and choose between females in good or poor nutritional condition, we carried out choice tests that allowed males ( $N = 15$ ) to inspect two females differing in body condition simultaneously. These tests were completed on the afternoons of 16 and 17 February 2009.

### Experimental treatments

As in experiment 2, adult females were placed on one of two feeding regimes: 'high quantity' or 'low quantity'. Adult males (male fixed size:  $13.953 \pm 0.184$  mm; male body condition:  $0.021 \pm 0.002$ ;  $N = 15$ ) remained on the normal feeding regime of two crickets three times per week. Females were weighed immediately prior to choice experiments and females in the high-quantity treatment were in significantly better nutritional condition ( $0.060 \pm 0.008$ ,  $N = 6$ ) than females in the low-quantity treatment ( $0.026 \pm 0.002$ ,  $N = 6$ ;  $t$  test:  $t_{5,517} = 4.189$ ,  $P = 0.007$ ). There was, however, no significant difference in female body size between the groups (high quantity:  $16.710 \pm 0.287$ ; low quantity  $16.633 \pm 0.235$ ;  $t$  test:  $t_{10} = -0.198$ ,  $N = 6$ ,  $P = 0.847$ ). The treatment groups were, therefore, renamed 'good condition' and 'poor condition'.

Tests were conducted in a seminatural laboratory environment. The open choice arena allowed males to inspect two females simultaneously, each placed on a section of tree trunk sawn in half and mounted on a Perspex board with added green foliage (this prevented mantids from moving out of the observer's range of view). Cardboard was placed between the two trunks so that females could not see each other during each trial, and all females were placed in the centre of their allocated trunk facing away from the male. The left/right position for the two tree trunks was randomly allocated during each experiment, and the trunks were positioned 1 m apart and 1 m from the male mantid. A small fan was positioned behind the male so that air was directed away from him and towards the females. This, as well as staging the tests in the afternoon (when females are unlikely to be emitting pheromones; K. L. Barry, unpublished data), ensured that males were not using chemical cues to choose between the two females. A male response was recorded when he alighted upon a tree trunk, and the latency to choose a female was also recorded.

### Data analysis

We used binomial statistics to test whether males alighted upon tree trunks bearing good-condition females significantly more often than poor-condition females, indicating male ability to use vision to distinguish and choose between females differing in body condition.

### Experiment 4: Rejection of Low-quality Females

#### Experimental treatments

To determine whether males reject females on the basis of body condition when an alternative mate is absent (unlike the simultaneous choice tests from experiments 1, 2 and 3), we carried out two series of unmanipulated mating trials under seminatural conditions (experiments 4a and 4b). The first used females on the same feeding treatment, that is, two small crickets three times a week, and the second used females that had been placed on either a high-quantity or low-quantity feeding treatment during adulthood (see

experiments 2 and 3). These trials were carried out from 15 February to 16 March 2006.

The results pertaining to female body condition and its potential effect on the latency to approach and the direction of approach have been presented elsewhere (see Barry et al. 2009). Here we present the results regarding male rejection of females during the approach phase.

#### Mating trials

Virgin males and females were randomly chosen from the laboratory population and placed onto one of five potted *L. longifolia* plants in an open outdoor environment. Male approach behaviour was observed and recorded, and males were considered to have rejected a female if they stopped their stealthy approach (see Barry et al. 2009 for description) by either walking or flying away from the female. A trial was terminated if a male was still approaching a female with no interaction occurring after 3 h. For a more detailed description of mating trial methodology, see Barry et al. (2008, 2009).

#### Data analysis

We used a  $t$  test to compare female body condition between trials where males approached and mounted females and those where males actively rejected females by walking or flying away during the approach phase (experiment 4a: unmanipulated female feeding/body condition). An additional  $t$  test was used to compare the rejection rate between females in good and poor nutritional condition (experiment 4b: manipulated female feeding/body condition).

#### Mate Choice in the Field

##### Field census

To determine the likelihood a male would be presented with a simultaneous choice between two females in nature, we counted the maximum number of adult female *P. albofimbriata* per bush over a number of field seasons and also measured the population density and sex ratio of these mantids at our most commonly visited field site (Kuringai Bicentennial Park, Sydney). This population of mantids exists on a small patch of approximately 50 m<sup>2</sup> because it is situated between the many sports fields contained within the park. We recorded the maximum number of adult female mantids per bush during all collections from 2004 to 2008. We also measured population density on two separate occasions: during mid-December 2006 when the mantids are third- to fourth-instar juveniles and during late February 2007 when most mantids are mature adults. Sex ratio was calculated in the following field season: mantids were collected as juveniles throughout December 2007, reared to adulthood in the laboratory and then sexed using gender differences in the adult abdomen and wing morphology.

##### Population density and sex ratio

On each occasion, we sampled the same 50 m<sup>2</sup> area over a 6 h period. We spent about 10 min per *Lomandra* sp. bush, recording the approximate size, age and sex of each praying mantid. Density was calculated as the number of individual mantids per m<sup>2</sup>.

## RESULTS

### Experiment 1: Cues for Mate Location

Males quickly moved along the common tube of the Y-maze while oscillating the antennae (even those males with antennae cut off continuously moved the stubs without sensilla that remained). Mantids spent most of their time at the fork of the maze, and it was

not uncommon to see one antenna in each of the upper tubes. All males ( $N = 18$ ) then proceeded to move more slowly down one of the tubes, making a choice between the contents of the two Perspex boxes. Male mantids with the antennae snipped moved towards the female significantly more often than the empty box (binomial test:  $x = 8$ ,  $N = 9$ ,  $P = 0.039$ ), confirming the use of chemical signals to locate conspecific females. However, this pattern disappeared for antennae-removed males (binomial test:  $x = 3$ ,  $N = 9$ ,  $P = 0.508$ ), suggesting male mantids do not use other sensory modalities for mate location. Male mantids from treatment 1 behaved differently to males from treatment 2; while 89% (8/9) of males with snipped antennae chose the female over the empty box, only 33% (3/9) of males without antennae made the same choice (Wilcoxon signed-ranks test:  $Z = -1.890$ ,  $P = 0.059$ ). Males with snipped antennae were slower ( $1116.67 \pm 374.46$  s,  $N = 9$ ) to make a choice than males with no antennae ( $413.00 \pm 123.32$  s,  $N = 9$ ); however, the difference was not significant ( $t$  test:  $t_{9,715} = 1.785$ ,  $P = 0.105$ ).

#### Experiment 2: Chemical Signals and Mate Choice

Male mantids moved within the Y-maze in a similar manner as was described for experiment 1. Males moved towards the female in good condition significantly more often than the female in poor condition (binomial test:  $x = 20$ ,  $N = 23$ ,  $P < 0.001$ ; Fig. 2), confirming the differential attraction of males to conspecific females in good nutritional condition. The latency to choose a female was  $596.84 \pm 100.16$  s ( $N = 23$ ).

#### Experiment 3: Visual Signals and Mate Choice

After being placed at the rear of the open choice arena, most males began swaying from side to side, a behaviour typically associated with depth perception in praying mantids (see Kral 1999). Before moving forwards, each male peered in the direction of both females, and there was minimal antennal oscillation during the approach phase. There was also no evidence that acoustic cues

were being used; however, we cannot completely rule out their use in this system. Although all females slightly swayed from side to side during each choice test, they generally maintained the position in which they were originally placed on the trunk and none of the females ever detected the approaching male and turned to face him. Males alighted upon tree trunks bearing females in good condition significantly more often than tree trunks with females in poor condition (binomial test:  $x = 12$ ,  $N = 15$ ,  $P = 0.035$ ; Fig. 2), confirming the use of visual cues to distinguish and choose between conspecific females differing in body condition. The latency to choose a female was  $1541.73 \pm 360.50$  s ( $N = 15$ ).

#### Experiment 4: Low-quality Females

In experiment 4a (where all females were on the same feeding treatment), there was no physical interaction between the male and female in 37 of 75 trials. However, most of these males (35/37) were still interested in the female, and slowly approached her throughout the experimentation period, but did not reach the female within the 3 h timeframe. Only two males (about 3%) actively ran/flew from the female, making the sample size too small to analyse statistically, but showing that males are generally unlikely to reject a female, irrespective of her body condition, when presented with only one option.

There was a physical interaction between the male and female in all trials of experiment 4b ( $N = 19$ ). None of the males paired with good-condition females ( $N = 10$ ) ran/flew away during the approach phase, and all males (10/10) successfully mated without being cannibalized. Furthermore, none of the males paired with poor-condition females ( $N = 9$ ) ran/flew away during the approach phase; however, 89% (8/9) were cannibalized and only 44% (4/9) mated successfully. The proportion of males that successfully mated, irrespective of cannibalism, was significantly greater when paired with good-condition females than with poor-condition females ( $t$  test between proportions:  $t_8 = 3.354$ ,  $P = 0.01$ ).

#### Mate choice in the Field

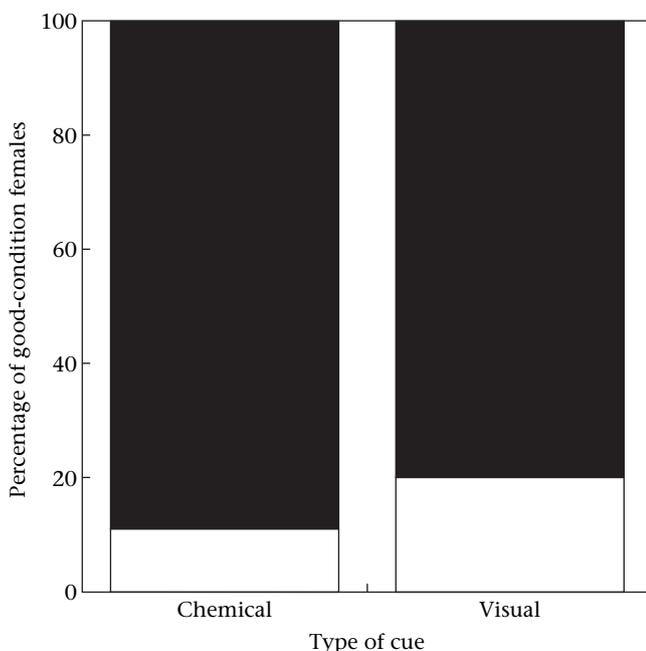
We recorded the maximum number of adult female mantids per bush on at least two occasions during each of the field seasons between 2004 and 2008, and on no occasion did we observe more than one female per bush.

During the search for mantids in mid-December 2006, we found a total of 54 juvenile mantids on 33 *Lomandra* sp. bushes (range 1–4 individuals per bush) on an area of approximately 50 m<sup>2</sup>. The total juvenile population density was, therefore, 1.08 individuals/m<sup>2</sup>. In the following year's searches (December 2007), we collected a total of 48 juveniles on 32 *Lomandra* sp. bushes from the same 50 m<sup>2</sup> area: 26 were female and 22 were male, making the sex ratio of this population approximately 6:5 (female:male).

During the search in late February 2007, we found nine adult mantids ( $N = 7$  females,  $N = 2$  males) on 35 *Lomandra* sp. bushes (range 0–1 individuals per bush) on the same 50 m<sup>2</sup> area. The adult population density was, therefore, 0.18 individuals/m<sup>2</sup> and the sex ratio 7:2 (female:male).

## DISCUSSION

Male *P. albofimbriata* primarily used two sensory channels, chemical and visual, for mate location and mate assessment, and they could use either of these sensory modalities to distinguish and simultaneously choose between females differing in body condition, with a significant preference for good-condition females. However, surprisingly, males rarely rejected poor-condition females in the more ecologically relevant scenario of only one



**Figure 2.** Preference of males for good-condition females when using chemical cues ( $N = 23$ ) and visual cues ( $N = 15$ ). Black: % chosen; white: % not chosen.

immediate mating opportunity and both sensory modes available to them. These results show that even when both of the conditions theoretically required for the evolution of male choosiness are satisfied, that is, female quality varies and the cost of mating for males is substantial, strong male mate choice in the form of mate rejection does not always evolve.

#### *Male Mate Choice Using Chemical and Visual Cues*

As predicted, we showed that males can use both chemical and visual cues to distinguish and choose between females in good condition and poor condition, with significantly more males preferring females in good nutritional condition. These results support our hypothesis: female body condition is positively correlated with female fecundity and negatively correlated with the propensity of a female to cannibalize in many praying mantids (Birkhead et al. 1988; reviewed in Maxwell 1999a), including *P. albofimbriata* (Barry et al. 2008). Thus, females in good condition provide a two-fold advantage to males. A preference for large females over smaller ones is common for many male arthropods (reviewed in Andersson 1994), because larger, fatter females are generally more likely to be gravid (Bonduriansky 2001). Abdominal girth or 'fatness' (Bonduriansky 2001; M. R. Maxwell, K. M. Gallego & K. L. Barry, unpublished data) may be the visual cue used to distinguish and choose between females in the current study, and pheromonal quantity or quality is likely to be the chemical indicator of size or condition (Wyatt 2003).

This study confirmed the previous finding (Holwell et al. 2007) that male *P. albofimbriata* are able to locate conspecific females when visual cues are obscured, indicating the use of airborne sex pheromones in mantid mate location. More importantly, we showed that when vision was obscured and the antennae were removed, male mantids were no longer able to locate conspecific females in a controlled laboratory situation. These results suggest that *P. albofimbriata* males are unable to use other sensory channels such as sound or vibration for mate location; however, further experiments directly establishing the presence or absence of such cues are required to confirm this proposal. The combination of only chemical and visual communication is widespread in insects, with chemical cues commonly used over long distances and visual cues playing a role in close-range orientation, assessment and courtship (Cade 1985; Bailey 1991).

We also found that the percentage of males that preferred fat females when using either visual or olfactory information was very similar: 80% of males chose good-condition females when using visual cues and 87% of males chose good-condition females when using chemical cues. These results suggest that both sensory modes are important for simultaneous male mate choice in praying mantids, and are probably used to reiterate the same message and/or to increase signal accuracy (Wyatt 2003). However, there may be some differences in efficiency of the sensory modes: males responded more quickly when using chemical cues than when using visual cues. This variation in male response to certain sexual signals should be approached with caution, however, as the differences mentioned could be related to the differences in experimental regime, that is, Y-maze versus tree trunks. We would also argue that in *P. albofimbriata*, female body condition communicated via both visual and chemical pathways is an honest indicator of fecundity and potentially the propensity of a female to cannibalize. Abdominal girth and body condition ('fatness') are tightly linked to the number of eggs produced by a female in many invertebrate species (Bonduriansky 2001; for mantid examples see Maxwell 1999b; K. L. Barry unpublished data; M. R. Maxwell, K. M. Gallego & K. L. Barry, unpublished data), and female praying mantids are unable to alter the visual appearance of body size to

attract more males. An example of females dishonestly signalling their body size occurs in long-tailed dance flies, *Rhizophomyia longicauda*, where females swallow air to inflate expandable abdominal pouches and deceptively signal a larger body size to attract more mates (Funk & Tallamy 2000). Chemical cues might similarly depend on egg development, which is in turn influenced by feeding status. For example, females of the armyworm moth, *Pseudaletia unipuncta*, do not release pheromones until they have produced a certain number of oocytes (Cusson & McNeil 1989). Alternatively, pheromone production could be influenced by feeding condition per se if these signals are energetically expensive to produce (see Johansson et al. 2005). If the production/release of chemical signals is not state dependent, then we expect to find poor-condition females using this sensory mode to lure males in with the intent of cannibalizing them (see Maxwell 1999a; Lelito & Brown 2009), thereby improving their body condition and subsequent reproductive output (see Birkhead et al. 1988; Barry et al. 2008). However, the results of this and two other recent studies (Lelito & Brown 2009; Maxwell et al. 2010) provide no evidence that food-deprived female mantids deceptively signal to males. Further mate choice experiments, as well as direct measurement of pheromone titres using gas chromatography and mass spectrometry, are required to understand how female nutritional condition affects pheromone production and subsequent male attraction.

#### *Male Mate Choice/Rejection Using a Multimodal Cue*

Our prediction that mate rejection should be more likely by males paired with poor-condition females was not supported. Instead, we found a very low incidence of mate rejection by males during both parts of experiment 4: only two of 75 males actively ran/flew away from the female when feeding status and subsequent female body condition was not manipulated, and none of the 10 males rejected a poor-condition female when body condition was manipulated. This result was unexpected because of the potential costs associated with approaching and mating with a poor-condition female. For example, poor-condition females produce very few (if any) viable eggs (K. L. Barry, unpublished data; M. R. Maxwell, K. M. Gallego & K. L. Barry, unpublished data), they are much more likely to attack and consume a male (Barry et al. 2008), and males that are cannibalized successfully mate in only 44% of cases (present study). This lack of male mate choice in the form of mate rejection may be partially explained by the strong/intense scramble competition selecting for efficient mate location proposed for praying mantid mating systems (Jones 1997 in Bonduriansky 2001; Holwell et al. 2007); the cost of not finding a virgin female may exceed the cost of not being choosy. First-male sperm precedence or low female remating in *P. albofimbriata* may be responsible for this intense sperm competition scenario; however, further study is required to determine this. An example of first-male sperm precedence in a scrambling species occurs in the Australian redback spider, *Lactrodectus hasselti*. Male redbacks compete by trying to outrace rivals to receptive females because the first male to locate a female will copulate and deposit a sperm plug that ensures a high level of paternity (Snow et al. 2006). Alternatively, males may scramble for virgin females if females are unlikely to remate, which might occur if females stop emitting pheromones after they have copulated, as in the praying mantids *Acanthops falcata* (Robinson & Robinson 1979) and *Mantis religiosa* (Lawrence 1992).

Another possible explanation for the lack of mate rejection by males is that the frequency of sexual cannibalism is not as high in nature as in laboratory experiments (Maxwell 1999a), which would mean less of a selective advantage to being choosy for males. It has been suggested that the enclosed conditions created by captivity

may increase the natural frequency of cannibalism because there is nothing to distract females and to hide the movements of males (Roeder 1935; Lawrence 1992). However, we carried out all mating trials (experiment 4) in an open outdoor environment so as to simulate natural conditions and allow males a means of escape; so this is unlikely to be the case in our study. Nevertheless, the natural frequency of sexual cannibalism for *P. albofimbriata* needs to be confirmed by field observations before its role in male mate choice can be understood.

We calculated adult population density to be very low, with only 0.18 adult individuals per m<sup>2</sup>, and never found more than one adult female on a bush at any one time. This thin dispersal of individuals is typical of praying mantid populations, with adult densities of less than one adult per m<sup>2</sup> reported for numerous species (see Maxwell 1999a). It is, therefore, unlikely that males will come across two females at the same time in nature, suggesting males will rarely have the opportunity to exhibit simultaneous visual choice. Because of the nature of chemical signals, it is, however, possible that males will have to make a choice based on chemical signals produced by two or more females differing in body condition, even though the pheromone plumes may come from females that are metres away from each other. If pheromone production is state dependent, males will rarely come across poor-condition females in nature, which may explain why males responded equally favourably to poor-condition and good-condition females when they could see them. The ability to choose good-condition females by sight, although seemingly unnecessary in nature, might indicate the ability of *P. albofimbriata* to respond to a potentially changing environment. For example, a seasonal increase in temperature might mean more food is available, increasing the mantid population density, and thereby creating an advantage for choosy males. Alternatively, a preference for large females may be a plesiomorphic trait in insects, even though the ecologies of some species mean they rarely get to inspect two or more females at the same time. These findings remind us that laboratory studies placed in a more natural context have greater relevance and ecological meaning when conducting sexual selection research.

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