

# Sexual signals for the colour-blind: cryptic female mantids signal quality through brightness

Katherine L. Barry\*, Thomas E. White, Darshana N. Rathnayake, Scott A. Fabricant and Marie E. Herberstein

Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

## Summary

**1.** Cryptic coloration may evolve in response to selective pressure imposed by predators, yet effective intraspecific communication may require some level of detectability. This creates a tension between the benefits of sexually selected visual traits and the predatory costs imposed by greater conspicuousness, and little is known about how this tension may be ameliorated in highly cryptic species.

**2.** We explore these competing demands in the false garden mantid *Pseudomantis albofimbriata*, a colour-blind and seemingly cryptic insect. We use reflectance spectrometry and receptor-noise modelling to characterize the conspicuousness of mantid body regions in the visual systems of mates (mantids), as well as potential predators (birds) and prey (bees). We then use condition manipulation and conspecific choice tests to further explore the colour traits of interest.

**3.** Based on visual modelling, we find that male mantids are inconspicuous to conspecifics, prey and predators – that is, they are chromatically and achromatically cryptic. In contrast, female mantids are chromatically cryptic to all potential receivers, but their abdomens are achromatically conspicuous. Our food manipulation experiment shows that females in good condition (and therefore with more eggs) have brighter abdomens than females in poor condition. Choice assays show male mantids are consistently attracted to females bearing brighter abdomens.

**4.** Our results reveal brightness-mediated sexual signalling in a colour-blind and classically cryptic insect. By communicating in the only visual channel available to them, female mantids are conspicuously signalling their quality to mates, while potentially minimizing their conspicuousness to predators and prey. Furthermore, by signalling with only a single body region, female mantids are apparently using coincident disruptive coloration to further decrease detectability to potential eavesdroppers.

**5.** Our data reveal a novel example of the way in which the trade-off between sexual selection for conspicuousness and natural selection for crypsis may be mediated in a visual signalling system. Such signals may be common in apparently cryptic species, and this study once again demonstrates the importance of analysing visual signals beyond the capacity of human vision.

**Key-words:** camouflage, colour, crypsis, praying mantid, private communication, sexual selection

## Introduction

Camouflage via body coloration is thought to evolve through the significant selective pressure imposed by predators (Stevens & Merilaita 2009a). Furthermore, sit-and-wait predators that rely on prey to closely approach them will also benefit from concealment (Stevens & Merilaita 2009b). However, effective intersexual communication may require greater conspicuousness, leading to a

compromise between the benefits of sexually selected visual traits vs. the costs imposed by greater detection from predators. For example, in male guppies, conspicuous colour patches are important components of courtship success, but decrease in frequency and/or size in populations with increasing predator density (Endler 1983).

There are several well-documented strategies that still allow effective communication while keeping detection risk at a minimum. For instance, swordtail fish communicate via a ‘private channel’ that is not available to its main predator, the Mexican tetra. Male swordtails display UV

\*Correspondence author. E-mail: kate.barry@mq.edu.au

ornamentations that are attractive to females, but undetectable to the UV-insensitive Mexican tetra (Cummings, Rosenthal & Ryan 2003). While not entirely private, some visual signals are so restricted in their viewing angle that they can only be detected in specific signaller–receiver positioning. In the butterfly *Hypolimnas bolina*, males display structural UV spots on their dorsal wings that are presented to females flying directly above them during courtship. The restricted-view nature of this signal, coupled with a specialized behavioural display, likely minimizes broad communication to unintended viewers (White *et al.* 2014). And finally, some species limit signal display to suitable contexts only, such as using behavioural means to flash an otherwise concealed signal. For example, many lizards are cryptically coloured when viewed dorsally against a background, but their ventral throat and/or chest are conspicuously coloured. In agamid lizards, these patches are only revealed by characteristic head-bobbing and push-up behaviours. Outside this context, the signal stays concealed from predator vision (LeBas & Marshall 2000).

Not surprisingly, most examples of costly conspicuous sexual signals are found in males, while females are typically less conspicuously coloured (Andersson 1994). Nevertheless, females may be under selection for some level of conspicuousness in order to be located by potential mates. For example, in some damselflies (e.g. *Enallagma* sp.), males are unable to locate heteromorphic females that cryptically match the vegetation background (Schultz & Fincke 2013). Another classic example of cryptic females is found in the praying mantids (Mantodea), whose coloration is generally considered to match the background of the environment in which they live (Prete *et al.* 1999; O'Hanlon, Li & Norma-Rashid 2013). This is likely to reduce detection by predators, as well as allowing them to remain invisible to prey. There may, however, be selection for conspicuousness in the mating context for praying mantids. The initial mate location of female praying mantids by males is commonly based on non-visual signals, such as pheromones (Holwell, Barry & Herberstein 2007; Lelito & Brown 2008; Barry 2010; Barry, Holwell & Herberstein 2010, 2011; Maxwell, Barry & Johns 2010; Maxwell, Gallego & Barry 2010; Allen, Barry & Holwell 2012; Barry & Wilder 2012). However, at close range, males visually detect females and proceed with their approach. Therefore, we expect females to convey at least some visual information to facilitate successful copulation.

Female conspicuous traits may also serve as secondary sexual signals conveying information about female quality. For example, in the non-sex role reversed two-spotted goby, males have a preference for highly ornamented females, and ornamentation likely facilitates male evaluation of female fecundity and informs males of female quality (Amundsen & Forsgren 2001). If conspicuous female signals function as a sexual signal, we would predict a relationship between the quality/quantity of that signal and some female trait that accurately conveys quality. In blue tits, when the cost of reproduction was increased, females

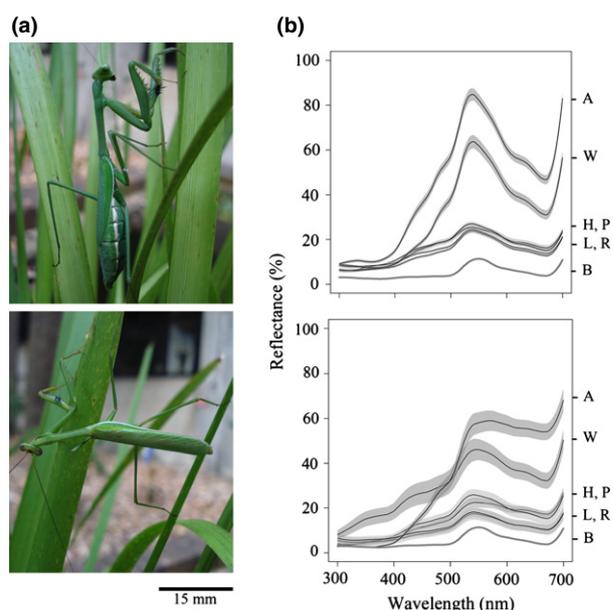
that were able to maintain their UV coloration were also able to lay more eggs, suggesting better quality females are able to invest in both reproduction and ornaments (Doutrelant *et al.* 2012). While it is broadly accepted that males prefer female phenotypes that relate to fecundity (e.g. size, condition, mating status; Bonduriansky 2001), this process assumes females are visually available for this type of assessment. In cryptic species, selection on inconspicuousness due to predation may therefore result in a complete lack of quality ornaments, a shift from one modality to another (e.g. visual to chemical) or the expression of visual ornaments via a selected channel that minimizes exposure to visual predators.

The aim of our study is to investigate the extent of crypsis in the false garden mantid *P. albofimbriata*, as perceived by mates, prey and predators. Specifically, we use reflectance spectrometry to quantify mantid colour and compare the detectability of different body parts to potential receivers using visual modelling. We further explore the colour traits of interest in relation to female body condition and carry out a series of simultaneous choice tests to determine whether males have a preference that is linked to these traits.

## Materials and methods

### COLLECTION AND HOUSING

Individual *P. albofimbriata* (Fig. 1a) were collected from various sites around Sydney, Australia, from January to February 2013



**Fig. 1.** (a) Female (above) and male (below) *Pseudomantisalbofimbriata*. (b) Aggregated reflectance spectra (mean  $\pm$  SE) of female ( $n = 27$ ) and male ( $n = 7$ ) body regions, which are identified by letters: head (H), pronotum (P), left capture arm (L), right capture arm (R), and abdomen (A), along with the mean background vegetation spectrum (B).

(visual modelling) and January to February 2014 (female brightness and condition & choice assays). The majority of individuals were found in *Lomandra longifolia* bushes at Kuringai Bicentennial Park, West Pymble, Sydney, Australia (33°45'37.76"S, 151°08'20.88"E). Juvenile animals (usually in their antepenultimate or penultimate instar) were collected from the study sites and reared on a diet of two small 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 ~26 °C and a diurnal period of 14 light hours per day.

#### REFLECTANCE SPECTROMETRY

We used an Ocean Optics USB-4000 spectrometer with a PX-2 pulsed xenon light source for reflectance measurements. The spectrometer was set to an integration time of 100 ms and to average 10 successive scans, and reflectance was measured relative to a WS-1 white standard. The light source probe was set perpendicular to the cuticular surface, with the collector at 45°. Live adult mantids were restrained on a flat mounting surface, and two spectra of the head, pronotum, left capture arm, right capture arm, wing and abdomen were recorded and averaged. To quantify the visual background where mantids were active, we measured the reflectance of three *Lomandra longifolia* leaves on each of 50 plants. Spectra were averaged within, then across, plants to generate a single 'typical' background spectrum. To test for sexual dimorphism in coloration and examine the effects of food quantity on female abdominal brightness (see below – 'Abdomen brightness and female condition'), we calculated hue as the wavelength of peak reflectance ( $\lambda R_{\max}$ ) and brightness as the mean reflectance value ( $R_{\text{avg}}$ ) for each body region in all individuals. Both metrics were restricted to the 'green' portion of the spectrum 450–600 nm.

#### VISUAL MODELLING

To assess the conspicuousness of adult mantids to potential viewers, we calculated the chromatic and achromatic contrast created by the body regions of *P. albofimbriata* against its substrate in three representative visual systems using the receptor-noise limited model (Vorobyev & Osorio 1998; Vorobyev *et al.* 2001). This model has the advantage of including a discrimination threshold based on the observation that an animal's ability to discriminate between stimuli is limited by total receptor noise. In this model, chromatic and achromatic discrimination thresholds are expressed as just noticeable differences (JND's), whereby 1 JND represents the difference between two stimuli that equal one standard deviation of receptor noise (Vorobyev *et al.* 2001). The model is limited in that it does not incorporate cognitive mechanisms that may affect colour discrimination such as spatial and temporal summation (Dyer & Neumeyer 2005; Dyer 2012). However, it has been successfully applied to predict behavioural data across several taxa (Vorobyev *et al.* 2001; Schultz & Fincke 2013).

In order to explore how mantids may appear to conspecifics, prey and predators, we modelled contrasts of individual mantid body parts in the visual system of three representative species: a mantid based on *Tenodera* spp., the honeybee *Apis mellifera* and the blue tit *Cyanistes caeruleus*, respectively. Male abdomens were excluded from these analyses as they are completely covered by their wings (Fig. 1a) and so are visible only briefly during flight. Individual analyses proceeded as below. All modelling was done using the package PAVO v. 0.5-1 (Maia *et al.* 2013) implemented in R v. 3.0 (2013).

Following Vorobyev & Osorio (1998), we calculated receptor quantum catch as the summed product of body part reflectance, the ambient illumination (here taken to be D65 standard daylight) and the absorbance spectrum of the relevant receiver's photore-

ceptors (see Appendix S1, Supporting information, for full model calculations). We log-transformed the quantum catches to ensure that differences in photoreceptor stimulation were proportional to their magnitudes, in line with the Weber–Fechner law (Vorobyev *et al.* 2001). We then calculated the contrast between mantid body parts and a typical background as a function of the log-transformed quantum catches weighted by the noise in each photoreceptor (Vorobyev & Osorio 1998).

The structure of the visual system of *P. albofimbriata* is unknown, but both physiological evidence (Sontag 1971; Rossel 1979; Towner & Gartner 1994) and indirect behavioural evidence (Prudic, Skemp & Papaj 2007; Fabricant & Herberstein 2014; but see Prete *et al.* 2012) in related species suggest that they are colour-blind. We therefore used a monochromatic model of mantid vision with peak sensitivity in a single photoreceptor at 515 nm, based on data from two related species from the Mantidae family (*Tenodera aridifolia*, Sontag 1971; *Tenodera australasiae*, Rossel 1979). Lacking precise physiological data on photoreceptor noise levels, we estimated receptor noise using the honeybee Weber fraction of 0.13 (Vorobyev & Osorio 1998), as has been successfully done in other insect systems (e.g. Schultz & Fincke 2013). Since only the achromatic channel is available to mantids (i.e. no colour vision), contrast is calculated as the difference in log-transformed quantum catch between the mantid body parts and background in the single mantid photoreceptor, weighted by photoreceptor noise (equation 7 in Siddiqi *et al.* 2004).

For honeybees, we used a trichromatic model (equation 4 in Vorobyev & Osorio 1998) with sensitivity peaks at 344, 436 and 556 nm (Peitsch *et al.* 1992). The Weber fraction assigned to each receptor class was 0.13 (Vorobyev & Osorio 1998). In the honeybee eye, the distribution of photoreceptors within ommatidia and the distribution of ommatidia classes across the eye are highly heterogeneous (Spaethe & Briscoe 2005; Wakakuwa *et al.* 2005). Accordingly, we used a ratio of 1 : 0.471 : 4.412 for the relative density UV, B and G receptors as per Defrize, Théry & Casas (2010). Achromatic contrast in the honeybee eye is simply the green receptor contrast and was calculated as above.

For the blue tit, we used a tetrachromatic visual model (equation 5 in Vorobyev & Osorio 1998). We used the spectral sensitivities of Hart *et al.* (2000), which take into account the influence of visual pigments, oil droplets and ocular media transmittance. Relative densities of the ultraviolet-sensitive, short-wavelength-sensitive, medium-wavelength-sensitive and long-wavelength-sensitive photoreceptors were 1 : 2 : 2 : 4, respectively (Schaefer, Schaefer & Vorobyev 2007). We use the behaviourally derived Weber fraction value of 0.1 (Maier & Bowmaker 1993), which corresponds to a threshold value of 1 JND, while acknowledging that our understanding of photoreceptor noise in avian systems remains unclear (Lind & Kelber 2009). Birds are thought to use achromatic vision at long range through the use of double cones (Osorio, Miklósi & Gonda 1999). Achromatic contrast was calculated as above, using the spectral sensitivity function of the blue tit double cone.

#### ABDOMEN BRIGHTNESS AND FEMALE CONDITION

Here we tested whether visual traits in females correlate with aspects of female quality. Once female mantids reached maturity, the body size (pronotum length) and body mass of all individuals were recorded. A subset of the laboratory population was then placed onto one of two feeding regimes: high quantity or low quantity. The high-quantity females ( $n$  = 43) received three small crickets *Acheta domestica* three times per week, and the low-quantity females ( $n$  = 52) received one small cricket three times per week. These regimes are commonly used in praying mantid studies as they consistently result in adults from each end of the natural body condition spectrum (Barry 2010, 2013, Barry, in press Holwell & Herberstein 2010). Feeding regimes continued for

a period of 3 weeks, after which body mass was again recorded. Body condition was calculated as body mass over fixed size and is a good indicator of female quality in this species (Barry 2010). To examine the effects of food quantity/body condition on female abdominal brightness, we calculated brightness as the mean reflectance value ( $R_{\text{avg}}$ ) in all individuals (see above – ‘Reflectance spectrometry’).

#### CHOICE ASSAYS

Females (a separate subset to those above) were paired by size and condition for the choice assays to test whether males show a preference for females displaying particular visual traits. The dorsal surface of the manipulated female was painted with non-toxic poster paint (Tim & Tess poster colour paint), while the control females had a patch of the ventral surface painted (but not visible to the males). As mantids are assumed to be colour-blind (Sontag 1971; Rossel 1979; Towner & Gartner 1994), we considered only the achromatic effects of paint manipulations for the choice experiments among conspecifics (Fig. S1). As such, the paint used to artificially dull female abdomens, when contrasted against the average background in the mantid visual model, falls below the achromatic threshold of 1 JND (mean  $\pm$  SE contrast =  $0.834 \pm 0.086$  JND's; Wilcoxon signed-rank test,  $V = 0$ ,  $P = 1$ ). The paint used to brighten females falls above 1 JND when contrasted with unmanipulated female abdomens (mean  $\pm$  SE contrast =  $1.56 \pm 0.23$  JND's; Wilcoxon signed-rank test,  $V = 271$ ,  $P = 0.025$ ). We thus predict that artificially dulled females would be difficult to discriminate from a typical background (in line with their other body parts), and brightened females would likely be distinguishable from naturally occurring, unmanipulated females.

The experimental arena consisted of two wooden logs cut in half (500 mm tall, 180 mm wide, 90 mm radius), covered in freshly cut *Lomandra* sp. leaves and placed 300 mm apart on a table. A female mantid was placed at the base of each of the logs and allowed to ascend freely. An adult male was placed 300 mm from the middle of the two logs in an opaque enclosure. A small fan was placed approximately 1 m behind the male, blowing towards the females, to reduce the possible influence of scent. After waiting five minutes for females to settle, the opaque cover was lifted, and the male was free to approach the logs. A male was given 1 h to choose a female, as demonstrated by alighting on a particular log and orienting towards the resident female. If the male did not choose within 1 h, the trial was stopped and the individual was omitted from the analysis. A particular pair of females was reused for four consecutive trials, and the left/right location of treatments was alternated between trials. All experiments were conducted in a temperature-controlled (25 °C) glasshouse.

In the first experiment, we gave males the choice between a naturally coloured female and an artificially dulled female. ‘Dull’ mantids were painted to closely match their *Lomandra* sp. leaf background – a mixture of ‘Forest Green’ and ‘Auburn’ paints in a ratio of approximately 3 : 1. Eight pairs of females and 32 individual males were used, although two males were omitted from the analysis for not making a selection within the observation period. In the second experiment, we tested whether males could detect ‘dull’ females from the *Lomandra* sp. background by using four dorsal-painted females on a log against a vacant log. Sixteen males from the prior experiment were randomly chosen to take part in this follow-up test. One was excluded for no selection within the observation period.

In the third experiment, we tested whether males preferred artificially brighter females compared to naturally bright females. Female pairs from previous experiments were shuffled to eliminate the possible effects of specific pairs, but new pairs were also matched for size and condition. Females that had previously been painted with dull paint were cleaned with water and repainted

with white poster paint, which had bright broadband reflectance between 400 and 700 nm (Fig. S1). We used eight female pairs along with 32 individual males. Most males had not been used in prior experiments, but eight males from experiment one were reused to reach the full sample size. To avoid pseudoreplication, these males are removed entirely from analyses that jointly examine experiment one and three.

#### STATISTICAL ANALYSES

All data were analysed in R v3.0 (2013), and means are reported  $\pm$  standard error throughout. The hue and brightness of individual body parts were compared between sexes using Wilcoxon two-sample tests with Bonferroni correction. Values of chromatic ( $\Delta S$ ) and achromatic ( $\Delta L$ ) contrast between mantid body parts and the average background, expressed as JND's, were contrasted against a threshold of 1 JND using Wilcoxon rank-sum tests with Bonferroni correction.

For choice assays, analyses were performed using generalized estimating equations (GEE) as implemented in GEEPACK v1.1-6 (Halekoh, Hojsgaard & Yan 2006) in R v3.0. Choice of female (painted vs. control, or female vs. nothing) was treated as a binary response variable with binomial distribution and pair ID as the clustering variable. Experiments were analysed independently, unless otherwise stated. To determine whether any confounds other than the paint manipulation had a significant impact on male choice, a number of additional parameters were measured and included in a full model. This was measured by pooling experiments one and three (response: brighter vs. duller) to maximize power. These parameters included residual intrapair differences in female age, size (pronotum length) and body condition; male age and weight; and binary observations of which female moved more during a trial and which female was closer to the male as he made a choice. Subset model averaging, as ranked by QIC, was performed in package MUMIN v1.10 (Bartoń 2013) in R v3.1.0 to determine whether any factor was highly weighted or significant in an averaged model. Finally, to determine whether paint treatment influenced time required for males to make a choice, a GEE were performed on the pooled data using time as the response variable (log-transformed for normality) and paint treatment as a dependent variable, with male age as a covariate to account for possible alterations in male vision or preference as a function of age.

## Results

#### MANTID SPECTRA

The reflectance spectra of all body parts of both male and female *P. albofimbriata* show Gaussian peaks between 535 and 565 nm (Fig. 1b). Male and female wings and abdomens showed peak reflectance 30–60% greater than other body regions, as well as the average background (Fig. 1b). Our analyses revealed a significant hue difference between sexes for all body regions, characterized by a very slight long-wavelength hue ( $\lambda R_{\text{max}}$ ) shift in males relative to females (Table 1; Fig. 1b). Female abdomens were significantly brighter than male abdomens (Table 1).

#### VISUAL MODELLING

Our visual modelling showed a disparity in conspicuousness between the sexes and between body regions within

**Table 1.** Summary of Wilcoxon two-sample tests ( $W$  and  $P$  values) contrasting the hue ( $\lambda R_{\max}$ ) and brightness ( $R_{\text{avg}}$ ) of body segments between male ( $n = 7$ ) and female ( $n = 27$ ) *P. albofimbriata*

Region	Hue		Brightness	
	$W$	$P$	$W$	$P$
Head	174.5	<0.001*	64	0.206
Pronotum	172	<0.001*	72	0.357
Left arm	161.5	0.004*	41	0.021
Right arm	157	0.007*	46	0.039
Wing	164	0.003*	62	0.017
Abdomen	266	<0.001*	27	<0.001*

\*Significance following Bonferroni correction.

the sexes (Figs 2 and 3). Both male and female *P. albofimbriata* are chromatically cryptic in the blue tit and honeybee visual models, with contrasts of all body regions against the typical viewing background falling below threshold levels (Table S2). The achromatic contrasts of all male body regions fall below the threshold of 1 JND in the mantid, honeybee and blue tit visual systems (Fig. 3b). The head, thorax, capture arms and wings of females also fall below 1 JND in all visual systems (Fig. 3a). Female abdomens, however, create significant achromatic contrast with a typical background in the visual systems of mantids ( $V = 372.00$ ,  $P < 0.001$ ), blue tits ( $V = 372.00$ ,  $P < 0.001$ ) and honeybees ( $V = 371.00$ ,  $P < 0.001$ ).

#### ABDOMEN BRIGHTNESS AND FEMALE CONDITION

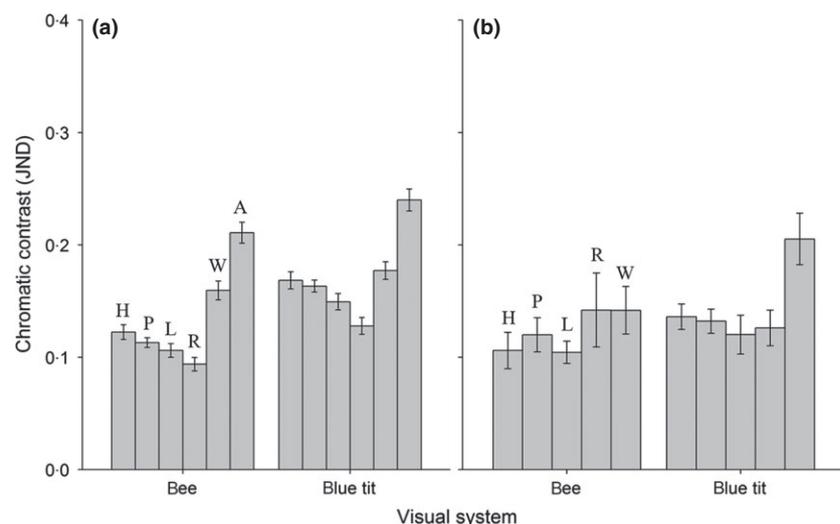
There was no significant difference in female body size ( $W = 2035$ ,  $Z = -0.217$ ,  $P = 0.828$ ,  $r = 0.022$ ) or body condition ( $W = 2343$ ,  $Z = -1.144$ ,  $P = 0.253$ ,  $r = 0.117$ ) at maturity (i.e. prior to the feeding treatment). However, a significant difference in body condition was created as a result of feeding treatments ( $W = 1434$ ,  $Z = -7.94$ ,  $P < 0.001$ ,  $r = 0.815$ ), so that females on the high-quantity

feeding regime were better condition (condition =  $0.070 \pm 0.001 \text{ g mm}^{-1}$ ) than females on the low-quantity treatment (condition =  $0.036 \pm 0.001 \text{ g mm}^{-1}$ ). Food quantity had a significant effect on female abdominal brightness ( $W = 1708$ ,  $Z = -4.255$ ,  $P < 0.001$ ,  $r = 0.437$ ), so that females in good condition had brighter abdomens (brightness =  $32 \pm 1.10\%$ ) than those in poor condition (brightness =  $25.98 \pm 0.73\%$ ).

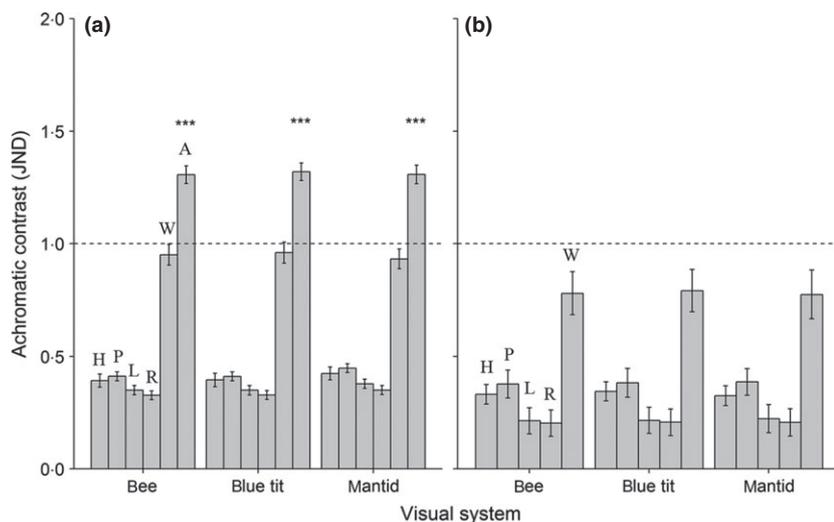
#### CHOICE ASSAYS

In the pooled analysis of experiments one (artificially dull vs. normal female) and three (artificially bright vs. normal female), we found that no cofactor was significant (all  $P > 0.2$  in the subset average and  $P > 0.4$  in the full average). Furthermore, no individual subset model had a greater weight than 0.016, and all models were within a  $\Delta\text{QIC}$  of 4.33. Therefore, we assume that the parsimonious intercept-only model is sufficient to explain variance in male choice. However, as a precautionary measure, intra-pair difference in size and condition, *a priori* chosen as the most likely confounds on male choice, was tested separately when analysing the results of each experiment. These factors were not significant in explaining male choice in experiment one (size:  $P = 0.89$ ; condition:  $P = 0.27$ ) or experiment three (size:  $P = 0.64$ ; condition:  $P = 0.06$ ).

In experiment one, males significantly preferred control (naturally bright) females compared to dull-painted females. Twenty-two out of 30 males chose the naturally bright female, which when controlling for differences between pairs of females meant the odds of choosing a naturally bright female were 3 : 1 (log-odds  $\pm$  SE =  $1.097 \pm 0.251$ , Wald  $Z = 19.2$ ,  $P < 0.001$ ). To determine whether this result was due to male preference or a lack of ability to detect dull-painted females, experiment two pitted dull-painted females against an unoccupied log with *Lomandra* leaves. Males were clearly able to detect females: 14 out of 15 males chose the dull-painted female, an odds ratio of 12.2 when accounting



**Fig. 2.** Mean ( $\pm$  SE) chromatic discriminability (in just noticeable differences) against a typical viewing background, for female (a) and male (b) *Pseudomantisal bofimbriata* in the honeybee and blue tit visual models. Body regions are identified by letters above bars: head (H), pronotum (P), left capture arm (L), right capture arm (R), and abdomen (A, absent in males).



**Fig. 3.** Mean ( $\pm$  SE) achromatic discriminability (in just noticeable differences) against a typical viewing background for female (a) and male (b) *Pseudomantis albobombriata* in the honeybee, blue tit, and mantid visual models. Body regions are identified by letters above bars: head (H), pronotum (P), left capture arm (L), right capture arm (R), and abdomen (A, absent in males). Significance of Z (Wilcoxon signed-rank test): \*\*\* $P < 0.001$ .

for repeat use of females (log-odds  $\pm$  SE =  $2.503 \pm 0.876$ , Wald  $Z = 8.16$ ,  $P = 0.004$ ). However, males in experiment two ( $24 \pm 3.43$  min) took significantly longer to make their choice than in experiment one ( $13.59 \pm 2.08$  min:  $V = 25$ ,  $P = 0.05$ ).

In experiment three, naturally bright females were compared to artificially bright females to determine whether brightness alone could act as a supernormal stimulus for male attraction. Twenty out of 30 males chose the artificially bright female over the unpainted naturally bright female. When controlling for differences between pairs of females, the odds of choosing an artificially bright female were 1.88 : 1 (log-odds  $\pm$  SE =  $0.633 \pm 0.225$ , Wald  $Z = 7.92$ ,  $P = 0.005$ ).

The odds of choosing the brighter female were statistically indistinguishable between experiments one and three ( $P = 0.25$ ), with an overall odds ratio of 2.3 (log-odds  $\pm$  SE =  $0.835 \pm 0.194$ , Wald  $Z = 18.6$ ,  $P < 0.001$ ). However, the time taken by males choosing between natural and bright females (mean trial length =  $27.42 \pm 3.38$  min) was greater than the time taken by males choosing between natural and dull females (mean trial length =  $13.59 \pm 2.08$  min; estimate log-difference =  $0.868 \pm 0.222$ , Wald  $Z = 15.3$ ,  $P < 0.001$ ).

## Discussion

We discovered a novel form of visual conspicuousness in an otherwise highly cryptic animal. In the praying mantid *P. albobombriata*, conspicuousness is purely achromatic and sex specific. Females are chromatically cryptic to potential receivers (Fig. 2a), but their abdomens are achromatically conspicuous to prey, predators and conspecifics (Fig. 3a). In this way, female mantids use the only visual channel available to them for conspecific communication (assuming *P. albobombriata* are indeed colour-blind; Sontag 1971; Rossel 1979; Towner & Gartner 1994; Prudic, Skemp & Papaj 2007; Fabricant & Herberstein 2014), while also minimizing the risk that predators and prey will detect them (see below). Male mantids, on the other hand, are

inconspicuous to prey, predators and conspecifics – that is, they are chromatically and achromatically cryptic (Figs 2b, and 3b).

The demonstrated sexual dimorphism in brightness (Fig. 1b) and achromatic conspicuousness (Fig. 3) suggests that female abdominal colour may be under sexual selection, a process that often produces significant differences between the sexes within a species (Darwin 1871). One obvious consequence of sexually selected ornamentation is the divergence of male and female appearance, where the elaboration of traits is suppressed in one sex by the naturally selected benefit of crypsis (Andersson 1994). In praying mantids, males are generally the more mobile/searching sex (Maxwell 1999), so being conspicuous to females is presumably of little advantage. There might be further selective pressure on males to remain entirely cryptic because female mantids (Mantodea) are often highly aggressive, with sexual cannibalism occurring in ~40% of interactions in this species (Barry, Holwell & Herberstein 2008). Females, however, must be at least somewhat detectable so that males can visually identify them during mate search. Since males generally prefer to approach females from the rear so as to remain undetected (Barry, Holwell & Herberstein 2009), it makes intuitive sense that the abdomen and not one of the other more anterior body parts is conspicuous.

The function of visual communication in these mantids may be related to simple mate location or to the more complex mate choice. Male mantids are initially attracted to a female via long distance airborne sex pheromones, but then once in close range, they need to visually orient in order to more precisely locate and approach (Maxwell 1999). The constant threat of sexual cannibalism makes it even more important that this orientation is accurate. Therefore, it is possible that the sole purpose of the bright signal is detectability of females during mate location. While the mate location and mate choice mechanisms are not necessarily mutually exclusive, three lines of evidence suggest that female abdominal brightness conveys

additional information about female quality for male *P. albofimbriata*. First, we found that high-condition females are brighter than poor condition females (independent of size). Female body condition is positively related to fecundity (Birkhead, Lee & Young 1988; Barry 2010; Maxwell, Gallego & Barry 2010) and negatively related to the propensity to cannibalize in praying mantids (Kynaston, McErlain-Ward & Mill 1994; Barry, Holwell & Herberstein 2008; Maxwell, Gallego & Barry 2010), suggesting a twofold advantage for males that choose high-condition females. Secondly, previous simultaneous choice experiments showed that males have a strong visual preference for good condition females as opposed to poor condition females (Barry, Holwell & Herberstein 2010). Thirdly, simultaneous choice tests in the current study showed that males have a significant preference for brighter females even though dull females were detectable. We therefore suggest that males are likely to use female abdominal brightness for both mate location and mate choice. It is also worth noting that males in experiment two (normal female vs. empty log) and three (normal vs. bright female) of the choice assays took significantly longer to make a choice than males in experiment one (dull vs. normal female). We suspect this may be because males had trouble detecting dull females in experiment two, and that males in experiment three were particularly cautious when choosing and approaching a super-normal, and therefore unnatural, stimulus.

The use of signal brightness to communicate information in the mating context without any underlying chromatic contrast is seemingly rare. Achromatic information is notoriously unreliable because even slight variation in illumination (such as passing clouds or patchy forest canopy cover) can have dramatic impacts on the appearance of objects (Endler 1993). This can, in part, be ameliorated through the use of colour vision and, hence, colour signals (Lovell *et al.* 2005). In species that do use signal brightness to indicate mate quality, for example the coliadine butterflies *Eurema hecabe* (Kemp 2008) and *Colias eurytheme* (Kemp, Vukusic & Rutowski 2006), the structural UV sexual signals of males coincide with underlying pigment-based coloration to amplify and enhance the chromaticity of the sexual signal (Rutowski *et al.* 2005). In contrast, the chromatic matching of female mantids to their background (Fig. 2a), and the putative colour-blindness of mantids (Sontag 1971; Rossel 1979; Towner & Gartner 1994), shows that visual sexual signalling in this species is entirely achromatic. It is unclear then how males are able to make reliable discriminations between females on the basis of signal brightness alone, especially given the achromatically noisy habitats that females are almost exclusively found in (*Lomandra* spp.; Barry, Holwell & Herberstein 2008). The significant time taken by males to choose between potential mates (~20 min on average) poses the working hypothesis that *P. albofimbriata* uses cognitive mechanisms, such as the temporal and spatial summation of light (as in other insects: Warrant, Porombka & Kirchner 1996; Warrant 2008), to improve discrimination in noisy environments. As previously

mentioned, cognitive components of colour discrimination are not captured by the receptor-noise model (Dyer & Neumeier 2005; Dyer 2012), so the discriminatory capabilities of mantids may be underestimated in our visual model. We may also predict that females should bias their detectability by preferentially signalling in open habitats and under sunny skies (i.e. in relatively constant environments), though this too stands to be tested.

Males are not the only viewers in the achromatic channel – both prey and predators can also detect female mantids in this way. However, being detectable in this manner may not be overly costly, because the use of achromatic vision in prey and predators is strongly context dependent in a way that may diminish the detectability of the female's signal. Honeybees, for example, primarily use achromatic vision for detecting small targets (or targets at a distance; Giurfa *et al.* 1997; Giurfa & Vorobyev 1998), so it may be difficult for them to detect female mantids at close range (which is where they are most at risk of being captured). Avian predators should also have difficulty detecting and recognizing the brighter female abdomen, as birds are thought to predominantly use achromatic vision for assessing general features of visual stimuli – such as textures and motion – rather than specific features, such as biological signals (Osorio, Miklósi & Gonda 1999). Indeed, evidence from budgerigars and pigeons (albeit non-insectivorous taxa) suggests that brightness discrimination in birds is relatively poor (Hodos *et al.* 1985; Lind, Karlsson & Kelber 2013). Finally, the classic mantid features (i.e. head and forelegs) are always highly cryptic to both bees and birds (Figs 2 and 3), so they are unlikely to recognize mantids as predators even if the abdomen is achromatically conspicuous. Such concealment of highly recognizable body regions suggests camouflage via coincident disruptive coloration, which may affect both prey and predators alike (Cott 1940; Stevens *et al.* 2006; Cuthill & Székely 2009). There is thus clear potential for the purely achromatic signals of female *P. albofimbriata* to offer a degree of privacy from both predators and prey, while simultaneously signalling individual quality to prospective mates. Given that our study was not designed to bear squarely on the question of signal privacy, our evidence here is limited, and it stands as an intriguing direction for future research.

In summary, our study uncovered a sex-specific visual signal in a species highly cryptic to humans. This example once again demonstrates the importance of analysing visual signals beyond the capacity of human vision (*sensu* Heiling, Herberstein & Chittka 2003). We reveal a novel compromise in the trade-off between sexual and natural selection that allows rapid and selectively advantageous mate choice for males, while apparently minimizing conspicuousness to predators and prey.

## Acknowledgements

We would like to thank Kaytlyn Davis and Anu Jayaweera for help with species collection and laboratory husbandry. To Darrell Kemp for his

helpful comments on the experimental design, and to the Department of Biological Sciences at Macquarie University for funding this project.

## Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.gq716> (Barry et al. 2014).

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Received 23 June 2014; accepted 21 October 2014

Handling Editor: Sara Lewis

## Supporting Information

Additional Supporting information may be found in the online version of this article:

**Appendix S1.** Materials and methods.

**Fig. S1.** Reflectance spectra of paints used to dull (solid line) and brighten (dashed line) the abdomens of female *Pseudomantis albobombriata* in conspecific choice experiments.

**Table S1.** Summary of Wilcoxon rank-sum tests ( $V$  and  $p$  values) comparing chromatic and achromatic contrasts of male ( $n = 7$ ) and female ( $n = 27$ ) *P. albobombriata* body segments, calculated against a typical background, with a threshold of 1 JND in hymenopteran, avian, and mantid visual systems.

Online supporting information for

**Sexual signals for the colour-blind: cryptic female mantids signal quality through  
brightness**

*KL Barry<sup>1\*</sup>, TE White<sup>1</sup>, DA Rathnayake<sup>1</sup>, SE Fabricant<sup>1</sup>, ME Herberstein<sup>1</sup>*

<sup>1</sup> Department of Biological Sciences, Macquarie University NSW 2109, Australia

\* Corresponding author

Email: [kate.barry@mq.edu.au](mailto:kate.barry@mq.edu.au)

**This file includes:**

Supplementary materials and methods

Supplementary figure S1

Supplementary table S1

## Supplementary Materials and Methods

### VISUAL MODELLING

For all observers quantum catch  $Q$ , corrected for background adaptation  $k$ , for a given spectrum in photoreceptor  $i$  is:

$$Q_i = k_i \int_{300}^{700} R_i(\lambda) S(\lambda) I(\lambda) d\lambda \quad (1)$$

where  $R(\lambda)$  is the reflectance spectrum of the mantid body part or background,  $S(\lambda)$  is the sensitivity function of the photoreceptor  $i$  in the visual system, and  $I(\lambda)$  is the irradiance spectrum, here taken to be D65 standard daylight. The constant  $k$  describes the von Kries transformation that accounts for receptor adaptation by normalising receptor quantum catches to the background:

$$k_i = \frac{1}{\int_{300}^{700} R_i(\lambda) S(\lambda) I(\lambda) d\lambda} \quad (2)$$

In the trichromatic eyes of honeybees, chromatic contrast in JND units ( $\Delta S$ ) between each mantid body part and the background is calculated as:

$$\Delta S = \sqrt{\frac{e_{UV}^2 (\Delta f_G - \Delta f_B)^2 + e_B^2 (\Delta f_G - \Delta f_{UV})^2 + e_G^2 (\Delta f_{UV} - \Delta f_B)^2}{(e_{UV} e_B)^2 + (e_{UV} e_G)^2 + (e_B e_G)^2}} \quad (3)$$

where  $e_i$  is the internal receptor noise for each receptor class of bees (with sensitivity peaks at 344 nm, 436 nm, 556 nm; Peitsch *et al.* 1992) and  $\Delta f_i$  is the log of quantum catches for receptor  $i$  between mantids and the background. Internal receptor noise is calculated as:

$$e_i = \omega / \sqrt{n_i} \quad (4)$$

where  $\omega$  is the Weber fraction assigned to each receptor class (0.13 for honeybees; Vorobyev & Osorio 1998) and  $n_i$  is the relative density of the receptor class  $i$ . In the honeybee eye, the distribution of photoreceptors within ommatidia and the distribution of ommatidia classes across the eye is highly heterogeneous (Spaethe & Briscoe 2005; Wakakuwa *et al.* 2005). Accordingly, we used a ratio of 1:0.471:4.412 for the relative density UV, B, and G, receptors as per Defrize *et al.* (2010).

Achromatic contrast in the honeybee is simply the green contrast, and is calculated as:

$$\Delta L = \left| \frac{\Delta f_i}{e_i} \right| = \left| \ln \left( \frac{Q_{i-M}}{Q_{i-B}} \right) / e_i \right| \quad (5)$$

where  $\Delta f_i$  is the log of quantum catch (Q) for the relevant photoreceptor  $i$  between mantid body part (M) and background (B).

For the tetrachromatic visual system of the blue tit we calculated quantum catch (Eqn. 1) using the spectral sensitivities of Hart *et al.* (2000) which take into account the influence of visual pigments, oil droplets and ocular media transmittance. Relative densities of the ultraviolet sensitive (uvs), short wavelength sensitive (sws), medium-wavelength sensitive (mws), and long-wavelength sensitive (lws) photoreceptors were 1:2:2:4, respectively (Schaefer, Schaefer & Vorobyev 2007). Chromatic contrast in this system is given by:

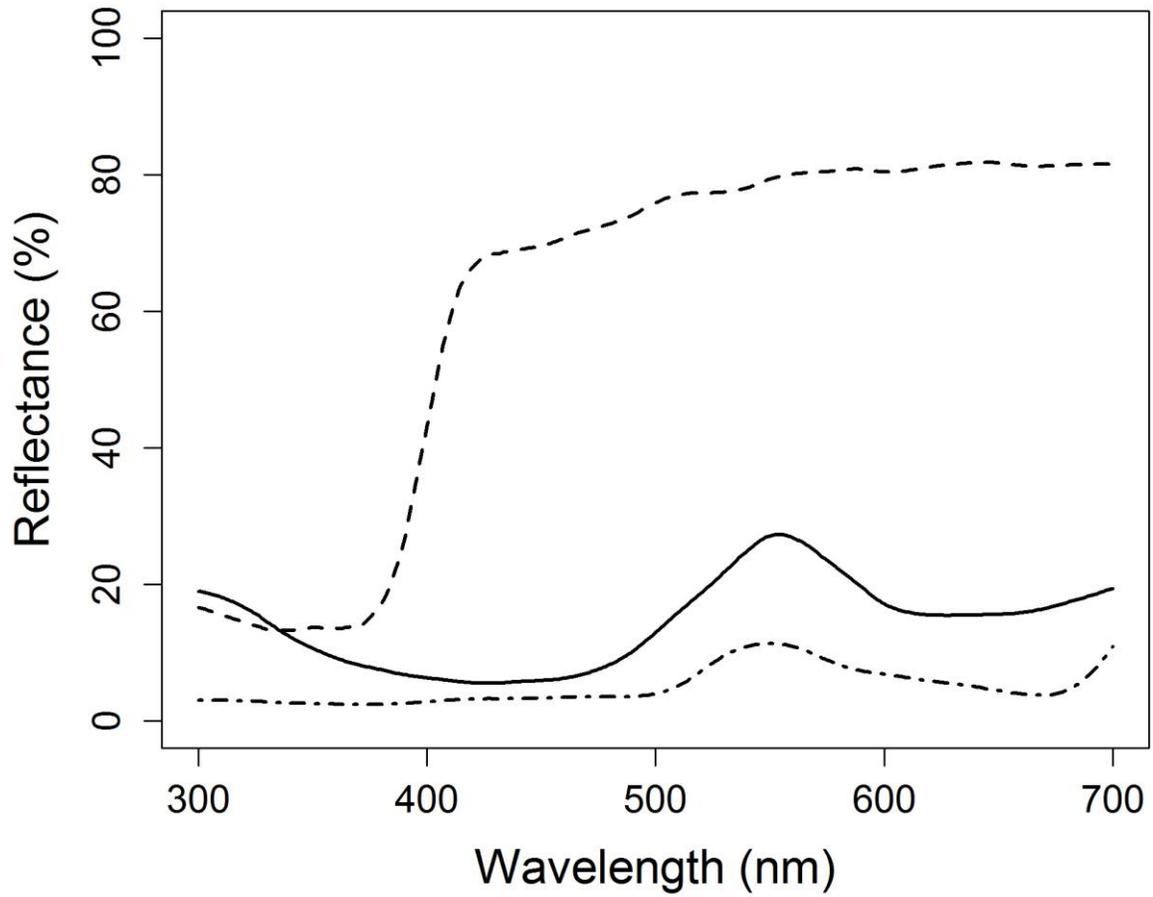
$$\begin{aligned}
(\Delta S)^2 = & ((e_{UVS}e_{SWS})^2(\Delta f_{LWS} - \Delta f_{MWS})^2 + (e_{UVS}e_{MWS})^2(\Delta f_{LWS} - \Delta f_{SWS})^2 \\
& + (e_{UVS}e_{LWS})^2(\Delta f_{SWS} - \Delta f_{MWS})^2 + (e_{SWS}e_{MWS})^2(\Delta f_{LWS} - \Delta f_{UVS}) \\
& + (e_{SWS}e_{LWS})^2(\Delta f_{MWS} - \Delta f_{UVS})^2 \\
& + (e_{MWS}e_{LWS})^2(\Delta f_{SWS} - \Delta f_{UVS})^2) / ((e_{UVS}e_{SWS}e_{MWS})^2) \\
& + (e_{UVS}e_{SWS}e_{LWS})^2 + (e_{UVS}e_{MWS}e_{LWS})^2 + (e_{SWS}e_{MWS}e_{LWS})^2
\end{aligned} \tag{6}$$

where  $e_i$  is the internal receptor noise for each receptor class  $i$  of birds (Eqn. 4). We use the behaviourally derived Weber fraction value of 0.1 (Maier & Bowmaker 1993), which corresponds to a threshold value of 1 JND, while acknowledging that our understanding of photoreceptor noise in avian systems remains unclear (Lind & Kelber 2009). Birds are thought to use achromatic vision at long range through the use of double cones (Osorio, Miklósi & Gonda 1999). Achromatic contrast is calculated as per equation 5, where  $i$  is the spectral sensitivity function of the blue tit double cone.

The structure of the visual system of *P. albofimbriata* is unknown. We therefore used a monochromatic model of mantid vision with peak sensitivity in a single photoreceptor at 515 nm, based on data from two related species from the Mantidae family (*Tenodera aridifolia*, Sontag 1971; *Tenodera australasiae*, Rossel 1979). Lacking precise physiological data on photoreceptor noise levels, we estimated receptor noise using the honeybee Weber fraction of 0.13 (Vorobyev & Osorio 1998), as has been successfully done in other insect systems (e.g. Schultz & Fincke 2013). Since only the achromatic channel is available to mantids (i.e. no colour vision), contrast is calculated by equation 5, where  $i$  is the spectral sensitivity function of the single mantid photoreceptor.

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**Figure S1:** Reflectance spectra of paints used to dull (solid line) and brighten (dashed line) the abdomens of female *Pseudomantis albofimbriata* in conspecific choice experiments. For clarity, the mean spectrum of background vegetation is included (dot-dash).

**Table S1:** Summary of Wilcoxon rank-sum tests (V and p values) comparing chromatic and achromatic contrasts of male (n = 7) and female (n = 27) *P. albobimbrata* body segments, calculated against a typical background, with a threshold of 1 JND in hymenopteran, avian, and mantid visual systems. Stars indicate significance following Bonferroni correction.

Sex	Region	Honeybee		Blue tit		Mantid	
		V	p	V	p	V	p
Female	<i>Head</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
	<i>Pronotum</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
	<i>Left arm</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
	<i>Right arm</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
	<i>Wing</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	150.00	0.826	158.00	0.772	128	0.929
	<i>Abdomen</i>						
Chromatic	0.00	1.00	0.00	1.00	NA	NA	
Achromatic	371.00	< 0.001*	372.00	< 0.001*	372	< 0.001*	
Male	<i>All</i>						
	Chromatic	0.00	1.00	0.00	1.00	NA	NA
	Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
	<i>Pronotum</i>						

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Chromatic	0.00	1.00	0.00	1.00	NA	NA
Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
<i>Left arm</i>						
Chromatic	0.00	1.00	0.00	1.00	NA	NA
Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
<i>Right arm</i>						
Chromatic	0.00	1.00	0.00	1.00	NA	NA
Achromatic	0.00	1.00	0.00	1.00	0.00	1.00
<i>Wing</i>						
Chromatic	0.00	1.00	0.00	1.00	NA	NA
Achromatic	6.00	0.922	6.00	0.922	6.00	0.922

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