

Predatory pollinator deception: Does the orchid mantis resemble a model species?

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Abstract Cases of imperfect or non-model mimicry are common in plants and animals and challenge intuitive assumptions about the nature of directional selection on mimics. Many non-rewarding flower species do not mimic a particular species, but attract pollinators through 'generalised food deception'. Some predatory animals also attract pollinators by resembling flowers, perhaps the most well known, yet least well understood, is the orchid mantis *Hymenopus coronatus*. This praying mantis has been hypothesised to mimic a flower corolla and we have previously shown that it attracts and captures pollinating insects as prey. Predatory pollinator deception is relatively unstudied and whether this occurs through model mimicry or generalised food deception in the orchid mantis is unknown. To test whether the orchid mantis mimics a specific model flower species we investigated similarities between its morphology and that of flowers in its natural habitat in peninsular Malaysia. Geometric morphometrics were used to compare the shape of mantis femoral lobes to flower petals. Physiological vision models were used to compare the colour of mantises and flowers from the perspective of bees, flies and birds. We did not find strong evidence for a specific model flower species for the orchid mantis. The mantis' colour and shape varied within the range of that exhibited by many flower petals rather than resembling one type in particular. We suggest that the orchid mantis resembles an average, or generalised flower-like stimulus. Thus predatory pollinator deception in the orchid mantis is likely to function as a form of generalised food deception, as opposed to model mimicry [*Current Zoology* 60 (1): 90–103, 2014].

Keywords Mimicry, Orchid mantis, *Hymenopus coronatus*, Generalised food deception, Aggressive mimicry

Mimicry theory predicts that directional selection should act upon mimics so that they match model species as closely as possible (e.g. Mappes and Alatalo, 1997). In classical Batesian mimicry organisms gain protection from predators (signal receivers) through resembling an unrelated noxious or otherwise unpalatable 'model' species (Bates, 1861). In cases such as this one might predict that selection on the ability of signal receivers to distinguish mimic from model, would drive a co-evolutionary arms race that leads to selection on the mimic to increasingly converge upon the model's signal characteristics (Dawkins and Krebs, 1979). The fact that, from a human perspective, many mimics do not precisely match models challenges this assumption and has led to extensive research into the causes of imperfect mimicry (see Pekár et al., 2011; Penney et al., 2012 and references therein). Hypotheses as to how imperfect mimicry is maintained have proposed limitations to signal receivers' sensory and cognitive systems leading to generalisation between varying signals (Dittrich et al., 1993; Kikuchi and Pfennig, 2010), high

levels of aversion towards noxious model species (Duncan and Sheppard, 1965; Sherratt, 2002), phylogenetic constraints (Holloway et al., 2002), selection for mimics to match multiple models (Edmunds, 2000; Edmunds, 2006), selection via several different predators (Pekár et al., 2011) and exploitation of signal receiver biases (Vereecken and Schiestl, 2008). Accumulating evidence for the efficacy of imperfect mimicry continues to challenge intuitive assumptions regarding how mimetic resemblances should function.

In relation to Batesian mimicry, floral mimicry has received less attention and is relatively poorly understood (Roy and Widmer, 1999). In floral mimicry the ability of pollinators to associate particular signals with a reward can be exploited by non-rewarding plant species. Many plant species are deceptive, as they attract pollinators but do not provide any nectar rewards (for reviews see Dafni, 1984; Jersákova et al., 2006). These flowers attract pollinators by presenting signals associated with pollinator resources such as mates (Gaskett, 2010) and food (Jersákova, 2009). The ability of Bate-

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sian food deceptive flowers to attract pollinators relies on animals being unable to distinguish between rewarding and non-rewarding flower types. It requires that mimics resemble model species in colour, shape and flowering phenology, and that deviation from this similarity has fitness consequences for the mimic (Schiestl, 2005).

Cases of Batesian mimicry in flowers, where a non-rewarding species mimics a specific model species, have been described (e.g. Galizia et al., 2005; Johnson, 2000; Johnson et al., 2003), however these are relatively uncommon. Most cases of food deceptive pollination do not involve mimicry of a particular model species (Jersákova et al., 2006; Schaefer and Ruxton, 2009). Many deceptive flowers present non-specific signals generally associated with rewarding flowers such as bright colours, large inflorescences and nectar guides (Dafni, 1984; Jersákova et al., 2006; Schiestl, 2005). In the absence of a model species some researchers have argued that the term mimicry is inappropriate and that this should be considered a form of generalised food deception (Jersákova et al., 2006). Herein we refer to deceptive pollination as either model mimicry, or generalised food deception.

One factor attributed to the maintenance of deceptive pollination is that the costs for pollinators visiting unrewarding flowers should be low (for discussion see Gaskett, 2010). We have found a unique case of deception that has potentially fatal consequences for pollinators. Juveniles of the praying mantis *Hymenopus coronatus* prey on pollinating insects that are attracted towards the body of the predator (O'Hanlon et al., 2014). The white/pink colouration of *H. coronatus* is unlike that of most other praying mantis species, which are typically brown or green (Fig. 1). This, in combination

with its “petal-shaped” femoral lobes and broad abdomen has led many to conclude that the orchid mantis mimics a flower (e.g. Annandale, 1900; Edmunds and Brunner, 1999; Wallace, 1889). However, there is little known about the degree of morphological similarity between orchid mantises and rewarding flower species, and to what extent this is required for orchid mantises to successfully attract prey. Whilst adult *H. coronatus* maintain their white colouration and femoral lobes, the development of long wings covering the abdomen render the adults less ‘flower-like’ (see O'Hanlon et al., 2013).

Predation upon pollinators is known to occur in ambush predators such as crab spiders (e.g. Llandres et al., 2011) and assassin bugs (Elliot and Elliot, 1991), and is believed to occur in other species of ‘flower mantises’ (Edmunds and Brunner, 1999) that can camouflage amongst inflorescences. Additionally, pollinator deception and attraction, as opposed to ambush predation, has been documented in crab spiders and orb-web spiders (Bush et al., 2008; Heiling et al., 2003; Tso et al., 2006; Tso et al., 2004). In these cases sensory exploitation using bright body colours has been suggested as the likely mechanism for pollinator attraction. By contrast, the orchid mantis is the only species for which mimicry of a complete flower has been suggested as a mechanism for prey attraction. The floral mimicry hypothesis implies that the predatory success of the orchid mantis is reliant on the presence of a model species for which the orchid mantis is misidentified. An alternative to the model species hypothesis is that the orchid mantis' predatory strategy functions analogously to generalised food deceptive pollination. The orchid mantis may present signals that are similar to flowers in general without resembling a single model species.

Floral resemblance in the orchid mantis may have additional benefits, including protection from predators. Animals with flower-like colouration can be concealed from predators when viewed against flowers through the process of background matching (e.g. crab spiders; Théry and Casas, 2002). This strategy relies on crypsis, where by blending in with its surroundings an organism is not detected by predators. Alternatively, organisms that share a close resemblance to a specific environmental object may benefit from camouflage through masquerade. Masquerade allows for the prey item to be detected, but cognitively misclassified as an unpalatable object, similar to Batesian mimicry (Skelhorn et al., 2010). If the orchid mantis masquerades as a flower, a predator may detect the mantis but cognitively misclas-



Fig. 1 A sub-adult female *H. coronatus* feeding on a bee

sify it as a flower due to its appearance. The response of predators to orchid mantises has not yet been studied and the degree to which an animal must match a model object to achieve masquerade is poorly understood.

Whilst early natural history accounts of the orchid mantis drew similarities between it and co-occurring flower species (e.g. *Melastoma polyanthum*; Annandale, 1900) a definitive model species for the orchid mantis has not been identified. Here we aim to identify if the orchid mantis resembles a specific model flower species for predatory and anti-predatory purposes. We do so by comparing the visual properties of flowers to those of juvenile orchid mantises. We compared the colour of mantises and flowers using predictive models of animal vision that represent the perspectives of two hypothetical pollinators (hymenopteran and dipteran) and two hypothetical predators (U and V type birds; see methods). As the femoral lobes and abdomen of the orchid mantis are believed to resemble the petals of a flower, geometric morphometric analyses were used to compare shape variation between orchid mantis femoral lobes and flower petals.

If there has been selection on the orchid mantis to resemble a model flower species, then we predict it to share close similarities with a single flower type, as in Batesian floral mimicry (e.g. Johnson, 2000). There should be low contrast in colour and strong convergence in shape between the petals of that flower and the femoral lobes and abdomen of the orchid mantis. Alternatively, if the orchid mantis does not have a specific model species then we predict colour and shape similarities with a range of flower species but no particular association with a single flower type as in generalised food deception (e.g. Gumbert and Kunze, 2001).

1 Materials and Methods

1.1 Spectral Reflectance Measurements

Orchid mantis colouration is generally uniform within an individual, yet the wing buds can reflect in the UV and differ slightly from the legs and abdomen (O'Hanlon et al., 2013). For this study orchid mantis colour was measured from juvenile female orchid mantises in captivity in Peninsular Malaysia ($n=15$). Reflectance spectra of orchid mantis femoral lobes and wing buds were obtained using a spectrometer (Ocean Optics, Jaz EL-200 with PX-2 light source) calibrated using a BaSO₄ white standard. An average spectrum for each individual orchid mantis was calculated from three randomly positioned measurements on each body part.

The flowers used for comparison here represent a sub

sample of the large diversity of flowers present across the range of *H. coronatus*. Flowers were sampled from areas where mantises are known to occur throughout Selangor region of peninsular Malaysia and where at least 4 individual plant specimens could be located. All flowers sampled were common species of understory vegetation and were in flower at the time of this study (January–February 2010). Spectral reflectance of flowers was measured *in situ* from a total of 13 flower species with varying sample sizes ($n = 4–10$). Average individual flower spectra were calculated from separate measurements of each flower petal. Where flowers did not have obvious petals (e.g. *Mimosa pudica*, *Ageratum conyzoides*) spectral measurements were taken from a bundle of their coloured filaments.

For incorporation into physiological visual models (see below) a background spectrum was calculated as the average spectra from a random sample of green leaves ($n=18$) found at the University of Malaya, Ulu Gombak Field Studies Centre; a known habitat of *H. coronatus*. Daylight illumination standard D65 was used as the ambient light spectrum.

1.2 Hymenopteran visual models

We have previously published colour contrasts between orchid mantises and the flowers used in this study using the spectral sensitivities of the honeybee (O'Hanlon et al., 2014). This analysis calculated colour contrasts between mantis femoral lobe colouration using two visual models commonly applied to assess discrimination abilities in honeybees, the colour hexagon (Chittka, 1992) and the receptor noise threshold model (Vorobyev and Osorio, 1998). These data are presented here, and we further expand our previous study by calculating colour contrast values between flower petals and orchid mantis wing buds. Individual orchid mantises were randomly paired with individual flowers and colour contrast values were calculated as a measure of colour distance between each mantis and flower pair. Colour contrasts were compared to discrimination threshold values. We predict that colour contrasts below threshold values are indistinguishable to pollinators. One sample *t*-tests were used to test whether average colour contrast between mantises and flowers differed significantly from discrimination threshold values (colour contrast = 0.62 for the colour hexagon, $\Delta S = 1$ for receptor noise threshold). We selected a conservative threshold value for the colour hexagon (see Dyer and Chittka, 2004), whereas the receptor noise threshold is based on the physiological limitations of the hymenopteran visual system (see Vorobyev and Osorio, 1998).

1.3 Dipteran visual model

Troje (1993) demonstrated that the colour discrimination abilities of the blowfly *Lucilia sp.* could be predicted by a simple model of two colour opponency channels. Blowflies appear to categorise colours into four broad groups often referred to by their closest human colour equivalents; UV, blue, yellow and purple/green. Colours falling within each of these categories are indistinguishable in behavioural trials. Between these categories very precise discrimination is possible.

Wavelengths of light, as detected by a dipteran visual system - consisting of four receptor types used for colour vision (Troje, 1993) - can be plotted as x-y coordinates in a colour space with a central origin at zero. The four quadrants of this colour space represent four possible groups defined by the flies' colour opponency-based visual system.

Receptor sensitivities are similar within a number of studied dipteran species (Hardie and Kirschfeld, 1983). Additionally only a single model for fly vision has been developed (Troje, 1993) incorporating the spectral sensitivities of *Musca sp.* (Hardie and Kirschfeld, 1983). We used this to represent the perspective of a generalised dipteran pollinator. To assess whether mantis and flower colours are distinguishable to flies the co-ordinates of each flower and mantis specimen were calculated and plotted into dipteran colour space. We infer that specimens falling into the same quadrant of this colour space should be indistinguishable to pollinating dipterans. Pairing of mantis and flower specimens as in the hymenopteran and bird vision models are not necessary here, as chromatic contrasts are not calculated.

1.4 Bird visual models

There appear to be two main arrangements of photoreceptor sensitivities in the tetrachromatic visual system of birds (Endler and Mielke, 2005; Hart, 2001b). Some birds are characterised as having very short (VS) wavelength receptors with peak receptor sensitivity in the ultraviolet region of the colour spectrum ($\lambda_{max} \sim 367$), while others have VS wavelength receptors with peak sensitivity in the violet region ($\lambda_{max} \sim 412$). These are often termed U- or V-type birds respectively. We used receptor sensitivities as published by Hart and Vorobyev (2005) to calculate colour contrasts for both U and V type birds using the noise receptor threshold model (Vorobyev and Osorio, 1998). Colour contrast values (ΔS) between mantis colour (legs and wing buds) and flower petals were calculated and one sample *t*-tests were used to test whether average colour contrast differed from the discrimination threshold of $\Delta S=1$. The

same random pairings of mantis and flower were used here as in the hymenopteran visual models to calculate contrasts.

1.5 Geometric morphometrics

We used landmark-based geometric morphometric analysis to quantify variation in flower petal shape and in orchid mantis femoral lobe and abdomen shape. Geometric morphometric techniques assess variation in shape based on the relative position of landmarks in an arbitrary co-ordinate system (Rohlf and Marcus, 1993). These landmarks are positioned based on homologous features of the structure in question. When analysing shapes formed by outlines or surfaces of an object, homologous landmarks are often difficult to identify. In these cases the use of sliding semi-landmarks positioned along a curve using a consistent spacing rule can be used to combine shape information from both homologous landmarks and outlines (Bookstein, 1997).

One difficulty when using this method for our purposes is that we are comparing fundamentally different structures: flower petals and insect appendages. As such, we must assume that the curves we are comparing are homologous from the perspective of the signal receiver. Recently this approach has been used to investigate the potential for shape mimicry in sexually deceptive orchids (Benitez-Vieyra et al., 2009; Gaskett, 2012). In our study we hypothesize that pollinators and predatory birds cognitively misclassify the orchid mantis as a flower rather than an insect. Therefore body parts such as the femoral lobes and abdomen should constitute the individual petals of the flower-like signal. The outlines of these structures can then be considered homologous to the outlines of flower petals from the perspective of the signal receiver.

Photographs of flower petals and mantis legs (mid right and hind right legs) and abdomens were digitised using tpsDig2 software (Rohlf, 2010a). Not all flower species used in colour analyses were used here as not all have conspicuous petals (e.g. *Mimosa pudica*, *Ageratum conyzoides*). A total of 22 landmarks (2 fixed and 20 sliding semi-landmarks) were positioned evenly along the outline of each structure (see Fig. 2). The two fixed landmarks were associated with the attachment points of petals to the remainder of the flower, or of the appendages/abdomens to the insect thorax. Relative warp score values were then calculated for all specimens using tpsRelw software (Rohlf, 2010b). Relative warp scores that accounted for at least 5% of the shape variation were then subsequently analysed to investigate similarities between mantis body parts and flower petals.

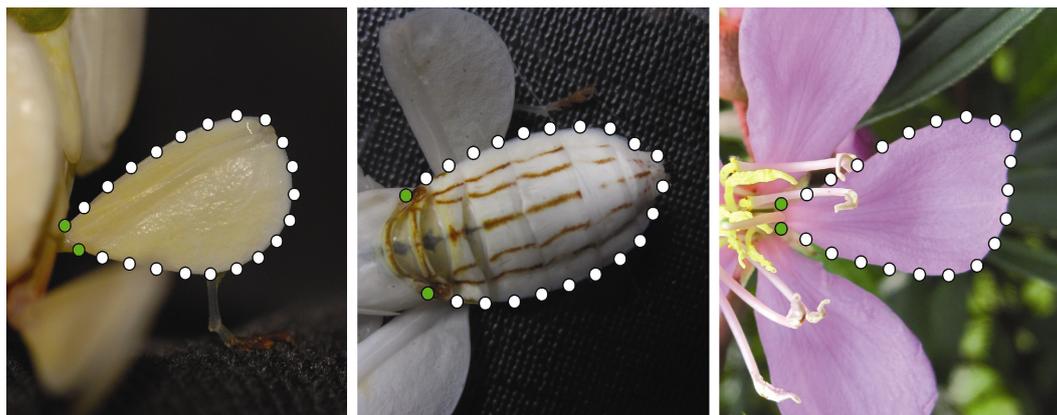


Fig. 2 Landmarks used for geometric morphometric analyses on (left to right) femoral lobes, abdomens and flower petals (e.g. *Melastoma sp. 2*)

Green dots indicate fixed landmarks white dots indicate sliding semi-landmarks.

MANOVA was used to test for significant differences between the relative warp scores describing each mantis body part (mid leg, hind leg and abdomen) and the analogous petals of each flower species. If there is strong selection for mantis appendages to resemble particular flower petal types we predict that there should be a match between mantis and flower petal shape as quantified by relative warp scores. Statistical analyses were conducted using R 2.14.1 (R Development Core Team, 2011).

Repeatability analyses were conducted on the relative warp scores obtained from repeated digitisations of specimens. Separate repeatability analyses were conducted for digitisations of flower petals, mantis legs and mantis abdomens, each using a subsample of 10 specimens. Repeatability scores were consistently high (Flowers: 0.93–0.99, Legs: 0.96–0.99, Abdomens: 0.78–0.99). For each analysis, variation between specimens was always significantly higher than within specimens (One way ANOVA - Flowers: $F_{9,20} = 15.2\text{--}228.7$, $P < 0.000001$, Legs: $F_{9,20} = 8.2\text{--}82.5$, $P < 0.0001$, Abdomens: $F_{9,20} = 3.8\text{--}245.9$, $P < 0.01$).

2 Results

2.1 Colour contrast

All mantis and flower colours sampled (Fig. 3) fall within a small area of hymenopteran colour space (Fig. 4). For both the colour hexagon and receptor noise limited models, chromatic contrast values between mantis femoral lobes and all surveyed flower species were either significantly below or not significantly different from discrimination threshold values (Figs. 5 and 6, Tables 1 and 2). Similarly, the average contrast values between mantis wing buds and flower species were all

significantly below or not significantly different from threshold values (Figs 5 and 6, Tables 1 and 2).

When plotted into dipteran colour space, all mantis and flower colours sampled fell into the fly yellow (p-y-) category (Fig. 7), indicating that all of these colours are indistinguishable to dipteran pollinators.

The colours of mantises and the 13 flower species studied cluster within a similar area when plotted into the tetrachromatic colour space of birds (Figs 8 and 9). For V type birds, contrast values between mantis legs and flower colours were generally low (Fig. 10). Contrast with most flower colours was significantly below or not significantly different from threshold values (Table 3). Three flower species were found to have colour differing from mantis legs at levels significantly above

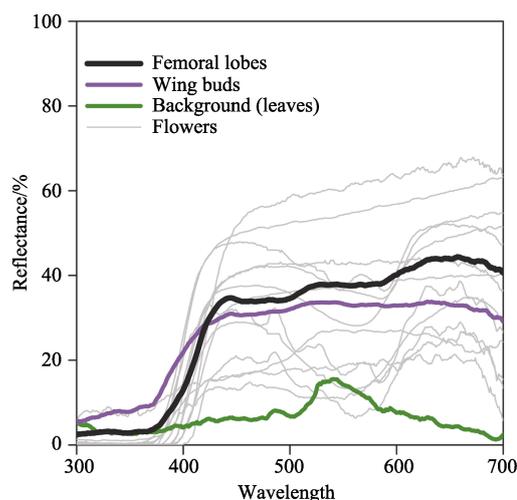


Fig. 3 Average reflectance spectra for the orchid mantis femoral lobes and wing buds, and the 13 different flower colours compared in this study

Also shown is the background spectra used for physiological visual models.

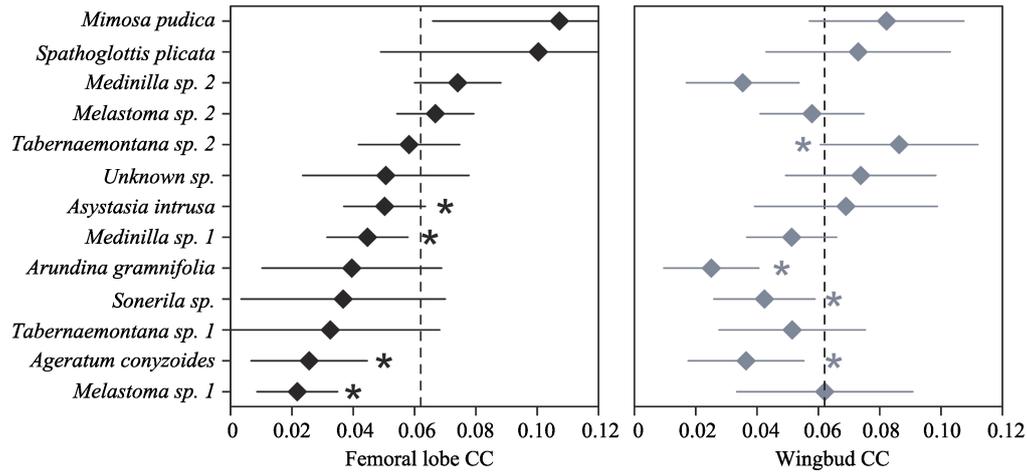


Fig. 4 Hexagonal (a) and Maxwell triangle (b) honeybee colour spaces showing the coordinates of individual orchid mantis legs (open triangles), wing buds (closed triangles) and individual flowers of 13 different species (black dots)

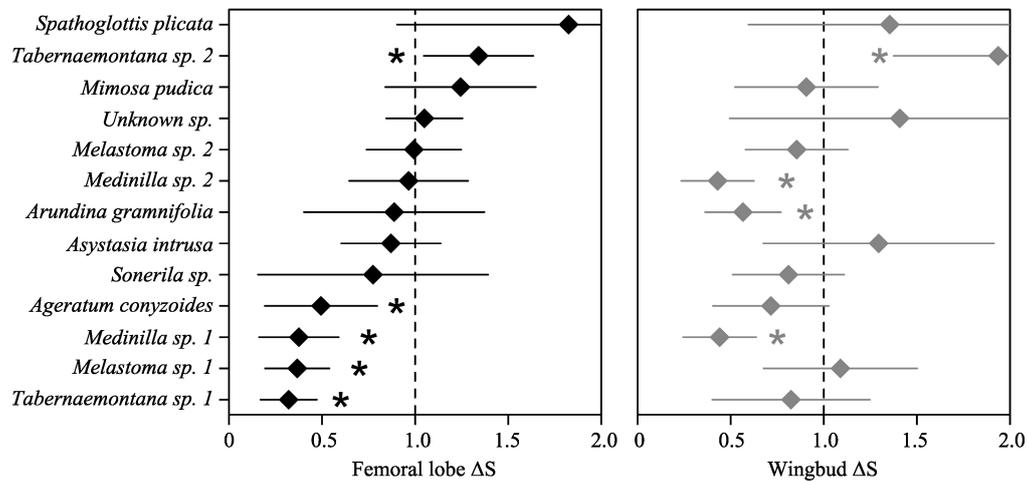


Fig. 5 Mean \pm SD chromatic contrast (CC) between flowers and orchid mantis femoral lobes and wingbuds as calculated by the colour hexagon for honeybee vision
Dashed line represents the colour discrimination threshold.

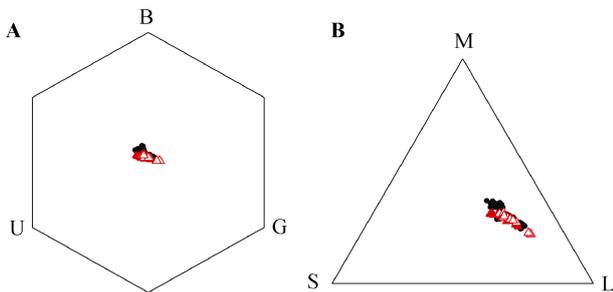


Fig. 6 Mean \pm SD chromatic contrast (ΔS) between flowers and orchid mantis femoral lobes and wingbuds as calculated by the noise receptor threshold model for honeybee vision
Dashed line represents the colour discrimination threshold.

threshold values. Similarly contrast between flower colours and mantis wing buds was generally low (Fig.

10). Three flower species yielded contrast values significantly above the threshold value. The remainder were significantly below or did not significantly differ from the threshold (Table 3).

The contrast between mantis colour and flower petals was higher overall for U type birds (Fig. 11). When examining contrast between mantis legs and flower petals five flower species yielded contrast values significantly above threshold (Table 4). The remaining flower species yielded contrast values not significantly different from threshold. Overall, contrast was even higher when comparing mantis wing buds to flowers. Only one species yielded an average contrast below threshold values, yet this was still not significantly different to the threshold. All other species had average contrast values above discrimination thresholds, eight of which reached significance levels (Table 4).

2.2 Geometric morphometrics

The first three relative warp scores explained 93.8% of the variation in shape (Singular values; RW1 = 68.29%, RW2 = 15.24%, RW3 = 10.27%). Subsequent analyses were performed on these three relative warp scores only. The results of MANOVAs comparing the shape of mantis femoral lobes and abdomens to each flower species are summarised in Table 5. Significant differences in relative warp scores were found between all pairings of mantises and flowers. The femoral lobes of mid and hind legs had similar warp scores, whereas

abdomens clearly differed in shape (Fig. 12). Within plant species flower petals varied greatly in shape in comparison to femoral lobes, which had much less variance in relative warp scores. From examination of relative warp score plots the plant species that appear to have the most similar shape to mantis femoral lobes are the two *Melastoma* species (Fig. 12). This pattern is most apparent for relative warp scores one and two. However, there were statistically significant differences in relative warp scores between femoral lobes and *Melastoma* petals (Table 5). There does not appear to be

Table 1 Chromatic contrast (CC) between flowers and orchid mantis leg colour calculated as Euclidean distances in hexagonal colour space for honeybee vision

Flower type	n	Contrast with mantis leg					Contrast with mantis wing bud				
		Mean CC	SD	t	df	P	Mean CC	SD	t	df	P
<i>Melastoma sp. 1</i>	4	0.0218	0.0131	-6.127	3	0.009	0.0621	0.0287	0.005	3	0.996
<i>Ageratum conyzoides</i>	10	0.0256	0.0189	-6.079	9	<0.001	0.0364	0.0189	-4.293	9	0.002
<i>Tabernaemontana sp. 1</i>	5	0.0325	0.0356	-1.851	4	0.138	0.0514	0.0239	-0.989	4	0.379
<i>Sonerila sp.</i>	9	0.0367	0.0333	-2.279	8	0.052	0.0424	0.0165	-3.568	8	0.007
<i>Arundina graminifolia</i>	5	0.0395	0.0293	-1.717	4	0.161	0.0251	0.0155	-5.333	4	0.006
<i>Medinilla sp. 1</i>	5	0.0446	0.0132	-2.947	4	0.042	0.0513	0.0146	-1.637	4	0.177
<i>Asystasia intrusa</i>	10	0.0502	0.0133	-2.805	9	0.021	0.0690	0.0298	0.742	9	0.477
Unknown sp.	4	0.0506	0.0271	-0.840	3	0.463	0.0738	0.0245	0.965	3	0.406
<i>Tabernaemontana sp. 2</i>	8	0.0582	0.0165	-0.650	7	0.536	0.0863	0.0257	2.682	7	0.031
<i>Melastoma sp. 2</i>	4	0.0668	0.0125	0.765	3	0.499	0.0579	0.0169	-0.487	3	0.660
<i>Medinilla sp. 2</i>	4	0.0741	0.0140	1.721	3	0.184	0.0353	0.0184	-2.905	3	0.062
<i>Spathoglottis plicata</i>	4	0.1004	0.0514	1.494	3	0.232	0.0730	0.0300	0.732	3	0.517
<i>Mimosa pudica</i>	5	0.1073	0.0413	2.450	4	0.070	0.0822	0.0252	1.799	4	0.147

Significance values are two-tailed.

Table 2 ΔS values of chromatic contrast between flowers and orchid mantis leg colour as calculated by the receptor noise threshold model for honeybee vision

Flower type	n	Contrast with mantis leg					Contrast with mantis wing bud				
		Mean ΔS	SD	t	df	P	Mean ΔS	SD	t	df	P
<i>Tabernaemontana sp. 1</i>	5	0.3207	0.1513	-10.042	4	0.001	0.8242	0.4234	-0.929	4	0.406
<i>Melastoma sp. 1</i>	4	0.3667	0.1727	-7.335	3	0.005	1.0892	0.4125	-0.433	3	0.695
<i>Medinilla sp. 1</i>	5	0.3754	0.2136	-6.538	4	0.003	0.4406	0.1962	-6.374	4	0.003
<i>Ageratum conyzoides</i>	10	0.4943	0.3017	-5.310	9	<0.001	0.7158	0.3116	-2.885	9	0.318
<i>Sonerila sp.</i>	9	0.7739	0.6180	-1.098	8	0.304	0.8105	0.2994	-1.899	8	0.094
<i>Asystasia intrusa</i>	10	0.8700	0.2667	-1.541	9	0.158	1.2947	0.6196	1.504	9	0.167
<i>Arundina graminifolia</i>	5	0.8875	0.4846	-0.519	4	0.631	0.5661	0.2040	-4.757	4	0.009
<i>Medinilla sp. 2</i>	4	0.9650	0.3192	-0.219	3	0.841	0.4297	0.1955	-5.836	3	0.010
<i>Melastoma sp. 2</i>	4	0.9932	0.2540	-0.053	3	0.961	0.8542	0.2749	-1.060	3	0.367
Unknown sp.	4	1.0497	0.2048	-0.486	3	0.661	1.4083	0.9142	0.893	3	0.438
<i>Mimosa pudica</i>	5	1.2442	0.4042	1.351	4	0.248	0.9064	0.3839	-0.545	4	0.614
<i>Tabernaemontana sp. 2</i>	8	1.3408	0.2939	3.280	7	0.013	1.9371	0.5616	4.720	7	0.002
<i>Spathoglottis plicata</i>	4	1.8246	0.9217	1.789	3	0.172	1.3542	0.7590	0.933	3	0.420

Significance values are two-tailed.

any obvious similarities between femoral lobes and petal shape for relative warp score three.

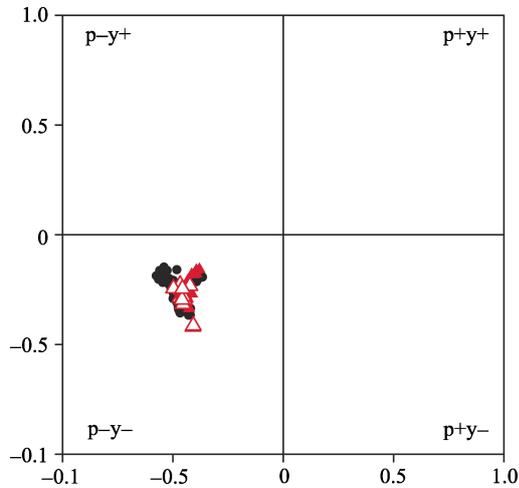


Fig. 7 Colour coordinates of orchid mantis wing buds (closed triangles), legs (open triangles) and flowers (black dots) in dipteran colour space

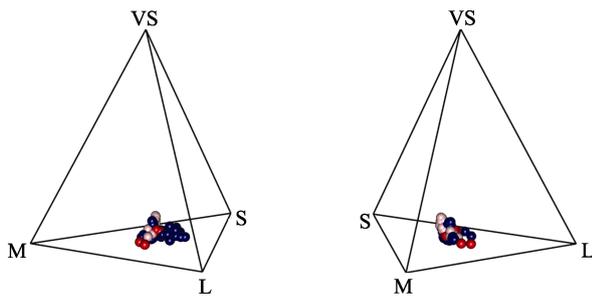


Fig. 8 Tetrachromatic bird visual space (V type bird) showing the colour coordinates of orchid mantis wing buds (pink), legs (red) and individual flowers (blue)

3 Discussion

All mantis and flower colours occupy a similar niche in the colour spaces of pollinators and predators (Figs 4, 7–9). Similarly, the shape of mantis femoral lobes and abdomens fit within the range of variation in morphospace exhibited by flower petals (Fig. 12). We have no strong evidence to suggest that any of the flower species sampled here are exceptionally similar to the orchid mantis so as to warrant considering it as a model species. This supports the prediction that orchid mantises mimic a generalised or average flower type, indicating that mimicry of a model flower species is not necessary for the deception of prey.

3.1 Pollinator perspectives

In the absence of any evidence for a specific model species we suggest that the orchid mantis' prey attraction strategy is more analogous to 'generalised food deception' in plants than classical Batesian mimicry. Whilst mantises share certain similarities with some of

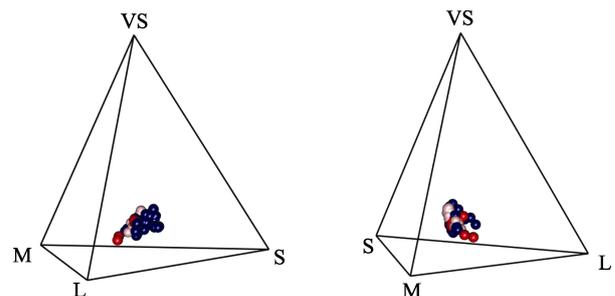


Fig. 9 Tetrachromatic bird visual space (U type bird) showing the colour coordinates of orchid mantis wing buds (turquoise), legs (blue) and individual flower (brown)

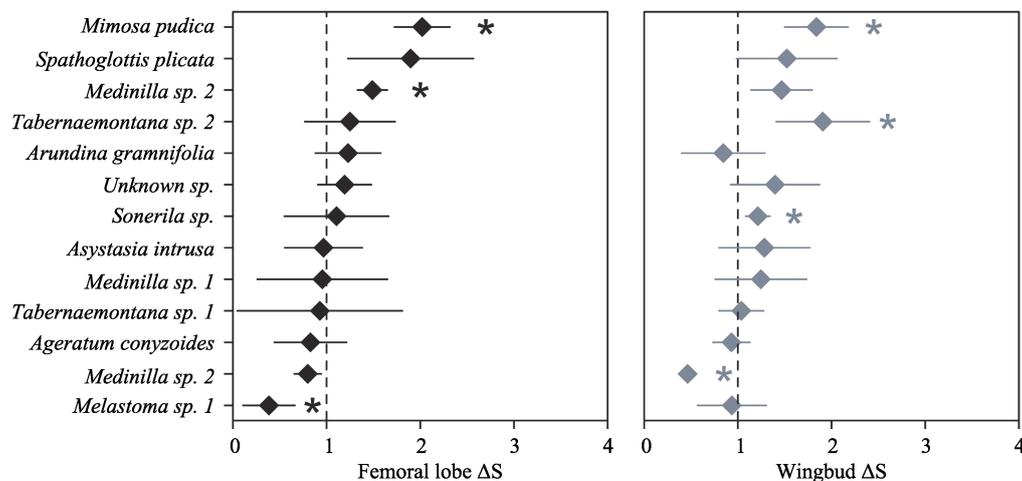


Fig. 10 Mean \pm SD chromatic contrast (ΔS) between flowers and orchid mantis femoral lobes and wingbuds as calculated by the noise receptor threshold model for a V-type bird. Dashed line represents the colour discrimination threshold

Table 3 ΔS values of chromatic contrast between flowers and orchid mantis colour as calculated by the receptor noise threshold model for a V type bird

Flower type	n	Contrast with mantis leg					Contrast with mantis wing bud				
		Mean CC	SD	t	df	P	Mean CC	SD	t	df	P
<i>Melastoma sp. 1</i>	4	0.3845	0.2771	-4.433	3	0.021	0.9360	0.3673	-0.349	3	0.750
<i>Medinilla sp. 2</i>	4	0.7989	0.1437	-2.800	3	0.067	0.4638	0.0485	-22.094	3	<0.001
<i>Ageratum conyzoides</i>	10	0.8275	0.3858	-1.414	9	0.191	0.9316	0.1978	-1.093	9	0.303
<i>Tabernaemontana sp. 1</i>	5	0.9278	0.8809	-0.183	4	0.863	1.0367	0.2380	0.344	4	0.748
<i>Medinilla sp. 1</i>	5	0.9546	0.6948	-0.1461	4	0.891	1.2457	0.4878	1.127	4	0.323
<i>Asystasia intrusa</i>	10	0.9668	0.4139	-0.254	9	0.805	1.2830	0.4847	1.846	9	0.098
<i>Sonerila sp.</i>	9	1.1057	0.5562	0.570	8	0.584	1.2136	0.1294	4.953	8	0.001
Unknown sp.	4	1.1926	0.2856	1.347	3	0.270	1.3973	0.4756	1.671	3	0.193
<i>Arundina graminifolia</i>	5	1.2291	0.3487	1.469	4	0.216	0.8446	0.4430	-0.784	4	0.477
<i>Tabernaemontana sp. 2</i>	8	1.2494	0.4826	1.462	7	0.187	1.9068	0.4977	5.154	7	0.001
<i>Melastoma sp. 2</i>	4	1.4885	0.1593	6.134	3	0.009	1.4665	0.3273	2.851	3	0.065
<i>Spathoglottis plicata</i>	4	1.8971	0.6698	2.679	3	0.075	1.5229	0.5362	1.9504	3	0.146
<i>Mimosa pudica</i>	5	2.0204	0.2961	7.707	4	0.002	1.8387	0.3388	5.535	4	0.005

Significance values are two tailed.

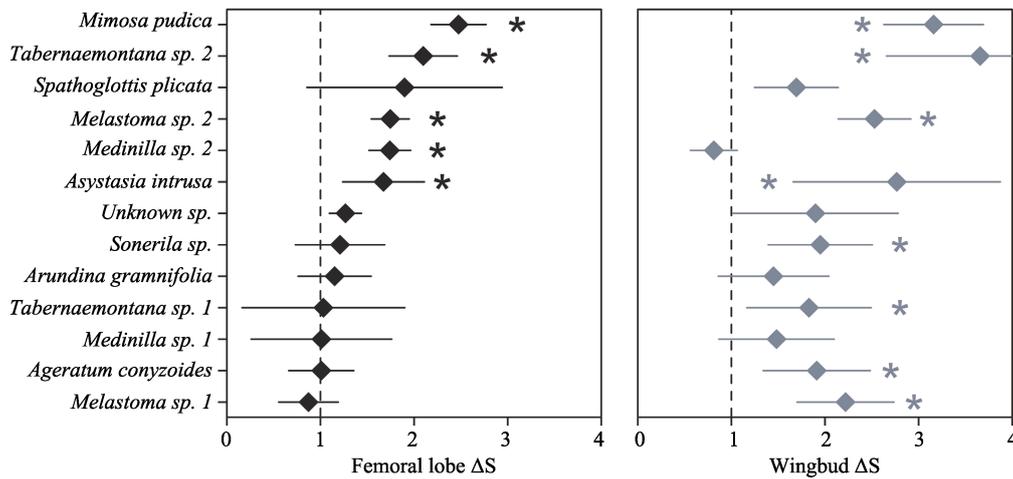


Fig. 11 Mean \pm SD chromatic contrast (ΔS) between flowers and orchid mantis femoral lobes and wingbuds as calculated by the noise receptor threshold model for a U-type bird

Dashed line represents the colour discrimination threshold

Table 4 ΔS values of chromatic contrast between flowers and orchid mantis colour as calculated by the receptor noise threshold model for a U type bird

Flower type	n	Contrast with mantis leg					Contrast with mantis wing bud				
		Mean ΔS	SD	t	df	P	Mean ΔS	SD	t	df	P
<i>Melastoma sp. 1</i>	4	0.8718	0.3175	-0.808	3	0.478	2.2192	0.5171	4.716	3	0.018
<i>Ageratum conyzoides</i>	10	1.0087	0.3475	0.079	9	0.938	1.9113	0.5719	5.040	9	<0.001
<i>Medinilla sp. 1</i>	5	1.0100	0.7506	0.030	4	0.977	1.4826	0.6152	1.754	4	0.154
<i>Tabernaemontana sp. 1</i>	5	1.0316	0.8688	0.081	4	0.939	1.8291	0.6642	2.791	4	0.049
<i>Arundina graminifolia</i>	5	1.1511	0.3898	0.866	4	0.435	1.4497	0.5906	1.706	4	0.164
<i>Sonerila sp.</i>	9	1.2088	0.4759	1.317	8	0.225	1.9496	0.5550	5.133	8	<0.001
Unknown sp.	4	1.2666	0.1712	3.115	3	0.053	1.8984	0.8833	2.034	3	0.135
<i>Asystasia intrusa</i>	10	1.6732	0.4360	4.883	9	<0.001	2.7667	1.1061	5.051	9	<0.001
<i>Medinilla sp. 2</i>	4	1.7409	0.2221	6.671	3	0.007	0.8123	0.2496	-1.504	3	0.230
<i>Melastoma sp. 2</i>	4	1.7456	0.2022	7.374	3	0.005	2.5291	0.3880	7.881	3	0.004
<i>Spathoglottis plicata</i>	4	1.8984	1.0430	1.723	3	0.183	1.6943	0.4473	3.104	3	0.053
<i>Tabernaemontana sp. 2</i>	8	2.0978	0.3636	8.540	7	<0.001	3.6574	1.0001	7.513	7	<0.001
<i>Mimosa pudica</i>	5	2.4749	0.2944	11.203	4	<0.001	3.1605	0.5316	9.088	4	<0.001

Significance values are two tailed.

the flowers analysed in this study, there are also apparent differences between them. For example, while *Melastoma sp.* have petals of a somewhat similar shape to orchid mantises (see below), unlike mantises they lack nectar guides and exhibit radial symmetry. Other flower types, such as *Mimosa pudica* and *Ageratum conyzoides*, have similar colouration to orchid mantises yet lack large petals and are characterised by long coloured styles and/or filaments. It should also be noted that orchid mantises do not require pollinators to land upon them as flowers do. Their attractive appearance only needs to elicit pollinator inspections within striking range of the mantis. This may relax selection pressures on mantises to mimic a specific model flower type.

Flower colours do not exhibit variation across all potential spectra perceivable to pollinators. Rather, flower

colours fall into a small number of colour 'categories' that may represent spectra particularly conspicuous to pollinators (Chittka et al., 1994). All flowers sampled in this study clustered in the same region of pollinator colour space (Figs 4 and 5). Just as colour similarity to rewarding plants has a strong effect on pollination success in both Batesian flower mimics (Jersákova et al., 2012; Johnson et al., 2003) and generalised food deceptive plants (Gumbert and Kunze, 2001; Internicola et al., 2007; Peter and Johnson, 2008) the attractiveness of orchid mantises to pollinators is likely a result of their colour converging upon this region in pollinator colour space. All flowers sampled in this study were similar to orchid mantis colouration from a human perspective in that they varied between white and pink hues. This is likely a result of the limited region and single season

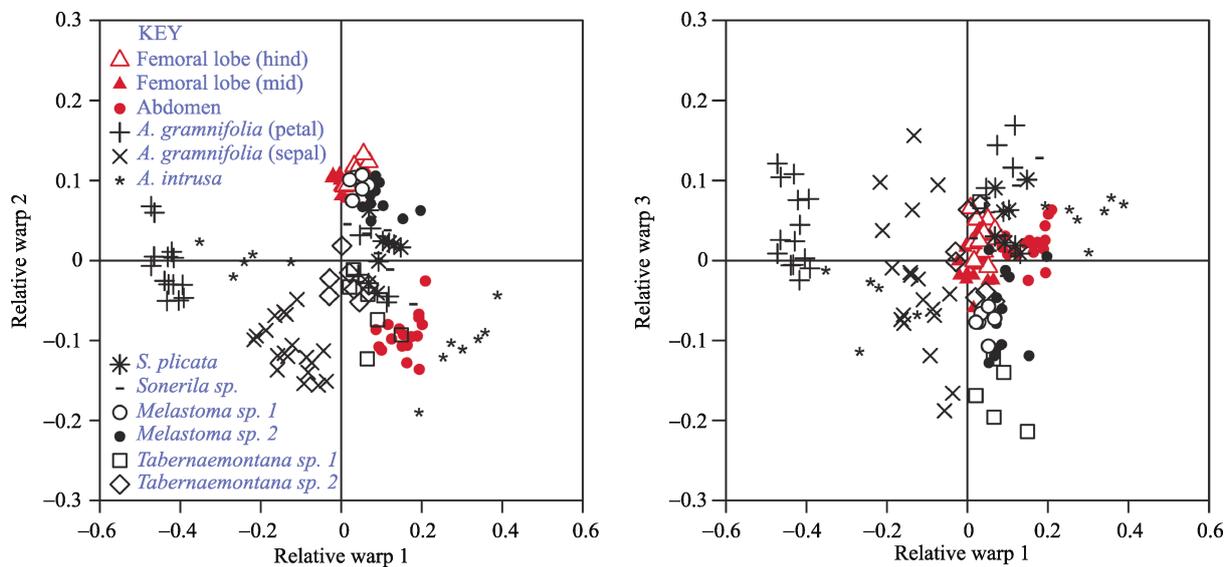


Fig. 12 Morphospace showing variation in petal, abdomen and femoral lobe shape as quantified by relative warp scores. Origin represents the consensus configuration or average shape of all specimens.

Table 5 MANOVA summaries comparing the first three relative warp scores of mantis legs and abdomens to those of each flower petal type

	Mid leg			Hind leg			Abdomen		
	<i>Wilk's λ</i>	<i>df</i>	<i>P</i>	<i>Wilk's λ</i>	<i>df</i>	<i>P</i>	<i>Wilk's λ</i>	<i>df</i>	<i>P</i>
<i>Arundina grammifolia</i> (sepal)	0.0259	3,31	<0.001	0.0279	3,31	<0.001	0.0784	3,31	<0.001
<i>Arundina grammifolia</i> (petal)	0.0692	3,31	<0.001	0.0533	3,31	<0.001	0.1910	3,31	<0.001
<i>Asystasia intrusa</i>	0.1040	3,24	<0.001	0.1206	3,24	<0.001	0.8899	3,24	<0.001
<i>Melastoma sp.1</i>	0.1178	3,18	<0.001	0.2560	3,18	<0.001	0.0433	3,18	<0.001
<i>Melastoma sp.2</i>	0.2190	3,26	<0.001	0.2960	3,26	<0.001	0.0200	3,26	<0.001
<i>Sonerila sp.</i>	0.1101	3,21	<0.001	0.1564	3,21	<0.001	0.1899	3,21	<0.001
<i>Spathoglottis plicata</i>	0.0729	3,20	<0.001	0.0604	3,20	<0.001	0.1716	3,20	<0.001
<i>Tabernaemontana sp.1</i>	0.0773	3,18	<0.001	0.0771	3,18	<0.001	0.1779	3,18	<0.001
<i>Tabernaemontana sp.2</i>	0.0563	3,19	<0.001	0.0450	3,19	<0.001	0.1211	3,19	<0.001

from which flowers were sampled. As this represents a small sample of the flowers within the orchid mantises range there are likely to be flowers co-occurring with mantises that do not fall into this same region of colour space and are easily distinguishable from orchid mantises.

Colour vision research has advanced to the stage where predictive models of vision, supported by behavioural and physiological data, can be utilised to understand animal perception (Chittka, 1992; Troje 1993; Vorobyev and Osorio, 1998). Equivalent tools to model shape perception have not yet been developed, as such our ability to make inferences on shape distinction in pollinators is relatively limited. Pollinators can distinguish floral stimuli based on spatial parameters such as size (e.g. Martin, 2004), symmetry (e.g. Giurfa et al., 1996; Rodríguez et al., 2004), orientation (Giurfa et al., 1995; Lamb and Wells, 1995), patterning (Dyer and Chittka, 2004; Lehrer et al., 1995) and complexity of the corolla outline (e.g. Herrera, 1993; Kaczorowski et al., 2012). Bees are also able to learn to recognise stimuli based on complex spatial parameters of patterns including configuration (Avarguès-Weber et al., 2010), relative positioning (Avarguès-Weber et al., 2011) and feature assemblages (Stach et al., 2004). There is little evidence to suggest that variations in the shape of individual petals are important cues for pollinators (but see Gómez et al., 2008). As such there may not be selection on orchid mantis femoral lobes to converge upon a particular petal shape but to display overall 'flower-like' spatial characteristics such as a symmetrical and dissected outline. In this study, femoral lobe and abdomen shape were significantly different to all flower petal types (Table 5). Whilst relative warp scores for *Melastoma spp.* petals and mantis femoral lobes appear to occupy a similar region in the morphospace (Fig. 12), we have little evidence that this is due to any selective pressure upon the orchid mantis to resemble *Melastoma*. There are many other morphological differences that suggest *Melastoma* is an unlikely model. For example, the orchid mantis exhibits bilateral symmetry whereas *Melastoma spp.* present a radial stimulus to pollinators. Whereas variation in colour is limited for both mantises and flowers, there is considerable variation and overlap in femoral lobe, abdomen and petal shape. We suggest that the orchid mantis femoral lobes and abdomen present general 'petal-like' stimuli to pollinators, rather than mimicking a particular species' petals.

Praying mantises are generalist predators (Hurd, 1999) and the same holds true for the orchid mantis.

Orchid mantises have been observed preying upon a diversity of insects including bees, flies, butterflies and crickets (pers. obs.). Thus generalised food deception may be a more effective predatory strategy than model mimicry. Model mimicry may limit the prey types available to those that have past experience with the model. A generalised food deceptive predatory strategy that exploits the innate and learned preferences of a range of pollinators, and the tendency of pollinators to explore novel stimuli, may provide greater returns than model mimicry. It may allow orchid mantises to exploit a large and diverse array of prey and occupy a wide range of habitats, as they are not limited to the range of a single model species, as has been suggested for imperfect mimicry (Edmunds, 2006; Pekár et al., 2011). Very little is known about the distribution of *H. coronatus*, however collection records cover a wide distribution throughout South East Asia (Delfosse, 2007a; Delfosse, 2007b) and there is no evidence to suggest that they are restricted to the range of a particular plant model species.

3.2 Predator perspectives

Mantis and flower colours occupy a similar region within the colour space of both U and V type birds (Figs 8 and 9), however the contrast between mantises and flowers often reached above discrimination threshold levels (Figs 10 and 11). In particular, the mantis' UV-reflecting wing buds contrasted highly with most flower colours.

Variation in spectral sensitivities of birds can reflect differences in ecology, such as feeding behaviour, diet and habitat type, rather than phylogeny (Hart, 2001a). The two visual systems modelled here (U-type birds and V-type birds) are classed as being generally characteristic of either open canopy inhabiting birds (U-type) or closed canopy inhabiting birds (V-type) (Endler and Mielke, 2005). Thus one might predict that birds inhabiting closed canopy forests should be better at discriminating between orchid mantises and flowers. However, chromatic contrasts between mantises and flowers, although generally above threshold for U-type birds, were still relatively low. The highest average contrast obtained for U-type birds was $\Delta S = 3.657$ when comparing orchid mantis wing buds against *Tabernaemontana sp. 2* flowers (see Table 4). The threshold value of 1 used in this study is based upon the physiological limitations of photoreceptor cells and represents the point at which colours should be indistinguishable under ideal viewing conditions (Kelber et al., 2003; Vorobyev and Osorio, 1998). However, when predicting animal behaviour

from models, researchers often use much higher threshold values (e.g. $\Delta S = 4$; Siddiqi et al., 2004) to define colours that should be difficult to discriminate depending on viewing conditions. Thus mantis colours are likely to be indistinguishable from flower colours from the perspective of predators as well as pollinators.

In resembling a flower blossom, the orchid mantis may be able to avoid predators through either masquerade or through cryptically camouflaging amongst flowers. In both cases the degree of colour similarity between orchid mantises and flowers may influence their susceptibility to predation. Orchid mantises vary in colour between pink and white hues, and this has been tentatively linked to the timing of ecdysis (see O'Hanlon et al., 2013). The mechanism and function of this colour change are unknown. Whether this and other factors such as rearing conditions can alter their colour to an extent that influences their predatory and camouflage strategies requires further investigation.

Furthermore there is little known about the micro-habitat use of orchid mantises, hence there is little known about the light conditions they may be observed under by predators. We have observed orchid mantises inhabiting a range of light environments including beneath rainforest canopies, forest edges and in low shrubs under full sunlight (*pers. obs.*). Whether variation in the spectral sensitivities of predators and viewing conditions can further influence the likelihood that orchid mantises are preyed upon requires further investigation.

To sum up, by exhibiting characteristics typical of rewarding flowers - such as UV-absorbing white/pink colouration, bilateral symmetry, large size, radiating petal-like structures and 'nectar-guide' lines - the juvenile orchid mantis provides a generic flower-like stimulus to pollinators. The orchid mantis shares similar colour and shape characteristics with a range of rewarding flowers and there is little evidence to suggest it mimics a specific model. The predatory strategy of the orchid mantis, often described as 'floral mimicry' (O'Hanlon et al., 2013; 2014), is likely to function analogously to generalised food deceptive pollination in flowers, as opposed to specific model mimicry. We have investigated adaptive resemblances from a purely visual angle, though there are likely to be many more unknown factors, such as, behaviour, signal context and olfaction, underlying the cognitive misclassification of orchid mantises as flowers. Whether a resemblance to flowers can function as a form of camouflage remains to be established.

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