



## RESEARCH PAPER

# The Roles of Colour and Shape in Pollinator Deception in the Orchid Mantis *Hymenopus coronatus*

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**Abstract**

The orchid mantis *Hymenopus coronatus* (Insecta: Mantodea) is a deceptive predator that attracts pollinators as prey. Their resemblance to a flower has given rise to the hypothesis that they are flower mimics. However, floral mimicry as a predatory strategy, and in particular, how predatory floral mimicry functions at a mechanistic level is poorly understood. Two main morphological characteristics are thought to make orchid mantises appear similar to flowers and thus attractive to pollinators: (1) their 'flower-like' white colouration and (2) their 'petal-shaped' expansions of exoskeleton on their mid-femur and hind femur (femoral lobes). I investigated the contribution of these colour and shape characteristics to pollinator attraction using artificial orchid mantis models. Models with the 'flower-like' white colouration of the orchid mantis had higher rates of pollinator inspection than brown models. Manipulating overall body shape by removing or changing the orientation of the 'petal-shaped' femoral lobes did not affect the attractiveness of models. As certain flower-like characteristics (symmetry and petals) did not affect the attractiveness of models, pollinators may not necessarily cognitively misclassify orchid mantises as flowers. Rather, mantises may be exploiting sensory biases of their pollinator prey, and their UV-absorbing white colouration may be sufficient to lure pollinators. The effectiveness of using artificial models established here provides a basis for future research into orchid mantis morphology and the fine-scale interactions between orchid mantises and pollinators.

**Introduction**

Being in close proximity to prey is a first step towards successful prey capture. Many predators achieve this by stalking, chasing or ambushing prey, whilst others deceive prey into approaching them. Deceptive predation requires the predator to emit signals that resemble characteristics associated with prey resources, such as food (e.g. caudal luring in snakes; Nelson et al. 2010) or mates (e.g. fireflies; Lloyd 1965). These signals can be visual, such as in the anglerfish (*Antennarius* spp.) whose modified dorsal fin simulates a small fish (Pietsch & Grobecker 1978), chemical, as in the bolas spiders that attract male moths as prey by emitting chemicals that mimic female moth pheromones (Eberhard 1977), or tactile, as in *Stenolemus*

assassin bugs that lure spiders by plucking the prey capture silks of their webs (Wignall & Taylor 2011).

Deceptive predation is often interpreted as a form of aggressive mimicry, where the effectiveness of a predator's signal is related to its overall resemblance to a model species. However, signals can be complex and consist of a number of components. Visual signals for example can convey information using shape, size, pattern, colour and movement. Often, only particular characteristics of the overall signal are salient to receivers and influence their behaviour (e.g. Fan et al. 2009; Nelson et al. 2010). Receivers' apparent biases towards a subset of available information suggest that deceptive predation need not rely on accurate mimicry of a model species. Predators may only need to produce salient signal characteristics that

exploit the sensory biases of their prey (Cheng et al. 2010; Nelson et al. 2010).

Juvenile orchid mantis *Hymenopus coronatus* (Fig. 1) prey upon pollinating insects that are attracted towards the body of the mantis. The rate at which pollinators inspect mantises can even be higher than the rate at which pollinators inspect nearby rewarding flowers (O'Hanlon et al. 2014a). Pollinator deception is a strategy used by a number of predators including crab spiders (Heiling et al. 2003), orb-web spiders (Fan et al. 2009) and carnivorous plants (Schaefer & Ruxton 2008). By displaying bright colour patches, these predators exploit the sensory biases of pollinators. However, the orchid mantis is the only predator that appears to resemble a complete flower corolla and is believed to be a flower mimic. This implies that there is a cognitive dimension to pollinator deception in that orchid mantises are misclassified as an actual flower, as opposed to an abstract, innately attractive stimulus. To understand the mechanisms behind this case of pollinator deception, it is necessary to tease apart the signal components and examine their effect on pollinator behaviour.

From the perception of pollinating insects, the orchid mantis' colouration is indistinguishable from that of many sympatric rewarding flowers based on physiological models of animal vision (O'Hanlon et al. 2014a,b). Also, the femoral lobes of the orchid mantis' mid-leg and hind leg may present pollinators with stimuli similar to flower petals (O'Hanlon et al. 2013, 2014b; Fig. 1). By exhibiting characteristics generally associated with rewarding flowers, the orchid mantis may be attracting prey by exploiting the same sensory biases used by flowers to attract pollinators.

Pollinators such as bees show innate preferences for visual cues characterised by bilateral and radial symmetry (Lehrer et al. 1995; Rodríguez et al. 2004), colours with high chroma (spectral purity) (Lunau 1992) and hues such as UV-blue and green (Giurfa et al. 1995b). The presence of these features in the phenotypes of many pollinators' preferred host plants (e.g. White et al. 1994) is evidence that flowers exploit the sensory biases of pollinators (Chittka 1996).

Flowers also rely on the ability of pollinators to learn to associate food rewards with a range of visual cues such as colour (e.g. Giurfa et al. 1996b), pattern (Dyer & Chittka 2004), shape (Anderson 1977), height (Wiegmann et al. 2000) and two-dimensional and three-dimensional orientation (Giurfa et al. 1995a; Lamb & Wells 1995). This can lead to bees exhibiting flower constancy – a tendency to only forage on a small number of available flower types – thus increasing the plant's chances of successful pollen transfer (Waser 1986; Chittka et al. 1999). Not only do bees respond to the raw information contained in visual cues, they can also recognise visual characteristics, such as symmetry (Giurfa et al. 1996a) and iridescence (Whitney et al. 2009), and respond to relational properties of objects such as height (Wiegmann et al. 2000).

The body of an orchid mantis presents pollinators with a complex stimulus comprised of visual cues similar to flowers including radiating patterns, UV-absorbing white/pink colouration and bilateral symmetry. Precisely which aspects of orchid mantis morphology elicit responses from pollinators is unknown. Here, I aim to investigate the functional contributions of colour and shape towards pollinator deception by juvenile orchid mantises. In particular,



**Fig. 1:** Juvenile female *Hymenopus coronatus* (left) and scale model of *H. coronatus* used in experiments (right).

I investigate how the overall body colouration – including the presence/absence of UV reflectance – and the presence and orientation of the femoral lobes may contribute to the attractiveness of orchid mantises to pollinators. Manipulating the colour of orchid mantises should affect their attractiveness to pollinators and allow the identification of the colour components that contribute to pollinator attraction. If the presence and orientation of the femoral lobes are important in attracting pollinators, then removing or realigning the femoral lobes into an asymmetrical pattern should negatively affect the attractiveness of mantises to pollinators. To test these predictions, I examined the behaviour of sympatric wild pollinators towards artificial models of orchid mantises with which I could manipulate their visual and structural characteristics.

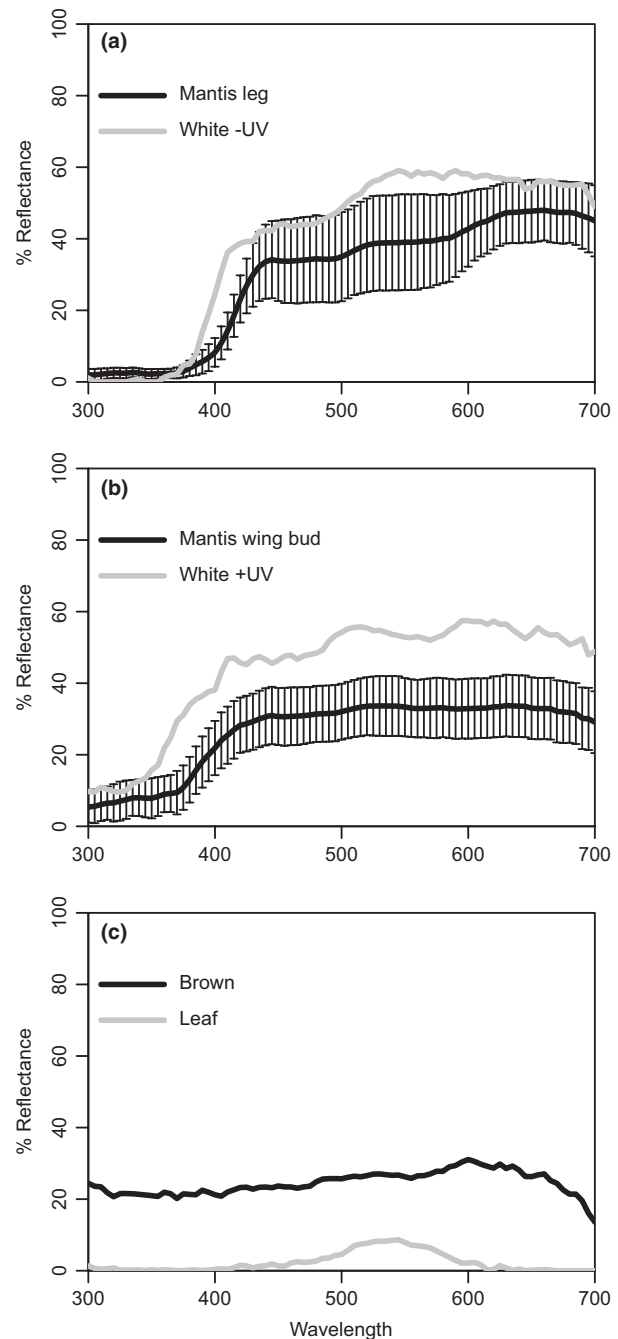
Simulated replicas of organisms are commonly used to study many aspects of interspecific signalling including plant–pollinator interactions (e.g. Jersákova et al. 2012), crypsis (e.g. Cuthill et al. 2005), predator recognition (e.g. Smolka et al. 2011), mate choice (e.g. Callander et al. 2011), aposematism (e.g. Veselý et al. 2013) and warning colouration (e.g. McLean et al. 2010). To identify the salient signal characteristics in deceptive predation, artificial models simulating predators are often presented to live prey (e.g. Fan et al. 2009; Cheney 2010; Nelson et al. 2010). By controlling and manipulating the characteristics of models resembling orchid mantises, the response of pollinators to varying stimulus parameters can be observed.

## Methods

### Model Construction

To identify signal components in the orchid mantis' predatory strategy, models were constructed to match as closely as possible the size and shape of a subadult female *H. coronatus* (Fig. 1). The main body of each model was constructed using oven-baked clay (Fimo – Staedtler, Nürnberg) glued to an armature of aluminium wire that also formed the mid-leg and hind leg. Femoral lobes were cut from sheets of firm plastic and glued to the armature.

There are two main components of orchid mantis colouration: UV absorbent white, which covers most of the body of the orchid mantis, and UV-reflecting white, which is present on the orchid mantis' wing buds. The models were painted to match as closely as possible the colour of orchid mantises (see Fig. 2). To match the orchid mantis' UV absorbent colouration, a



**Fig. 2:** Reflectance spectra of (a) orchid mantis femoral lobes ( $\bar{x} \pm \text{SD}$ ), UV-absorbing white model paint, (b) orchid mantis wing buds, UV-reflecting model paint, (c) brown model paint and green plastic leaves.

wide range of commercially available paints were measured using a spectrophotometer (Jaz EL-200 with PX2 light source and 200  $\mu\text{m}$  reflectance probe, Ocean Optics, FL), and the closest resembling paint was selected (Taubmans<sup>®</sup>, Sydney, Australia – 'Faint

Gold'; Fig. 2). To make UV-reflecting white, a mixture of unbaked Fimo clay (Staedtler, Nürnberg) was used. A thin layer was applied to either the wing bud area of the model or the entire model surface (see Fig. 3). The brightness of the reflectance spectra of both UV-absorbing and UV-reflecting materials could not be perfectly matched to orchid mantises; however, the overall shape of reflectance curves was similar (Fig. 2).

With the exception of experiment one (see below), models were placed on artificial green leaves so that the immediate background of the models could be kept constant. The reflectance spectra of the artificial leaves showed a curve similar to real leaves with a peak approx. 540 nm (Fig. 2c).

Other aspects of orchid mantis colouration were replicated in the models including a green band on the prothorax and stripes on the ventral abdomen surface (Fig. 1). I was unable to measure reflectance spectra of these small colour patches with the available spectrophotometry equipment. As such, these colour patches were matched by sight as closely as possible. UV photography shows that there is no UV reflectance in these colour patches, suggesting that they are only reflecting in human visible wavelengths (O'Hanlon et al. 2013).

#### Colour Similarity between Orchid Mantises and Artificial Models

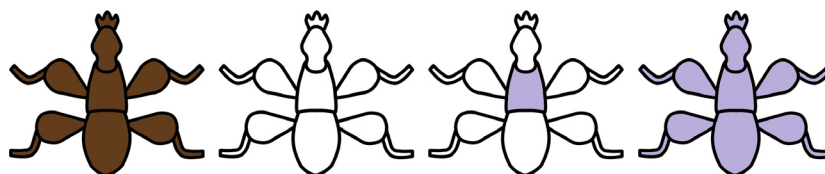
The reflectance spectra of models were compared to those of live mantises from the perspective of pollinators using two physiological models of hymenopteran vision: the colour hexagon (Chittka 1992) and noise receptor threshold models (Vorobyev & Osorio 1998). These models estimate the response of an animal's visual system to reflectance spectra when the receptor sensitivities for that animal are known. Colours can then be plotted in multidimensional colour space for a given set of receptors. The ability of the animal to distinguish between two colours can then be inferred from the distance between the coordinates of points in colour space. These models have been widely used

to make predictions about the abilities of animals to distinguish between colours and algorithms can be found in Chittka (1992) and Vorobyev & Osorio (1998). These methods have previously been used to describe the colouration of orchid mantises (O'Hanlon et al. 2013) and demonstrate that their colouration is often indistinguishable to that of flowers (O'Hanlon et al. 2014a,b). Here, I compared the reflectance spectra of live orchid mantis femoral lobes and wing buds (as published by O'Hanlon et al. 2013) to the model materials used in this study.

Bees commonly inspect live orchid mantises and were the most likely organism to interact with the models in this study (J. C. O'Hanlon, pers. obs.). Thus, to estimate pollinator visual capacity, I used physiological models incorporating the receptor sensitivities of the honeybee *Apis mellifera* (Menzel & Backhaus 1991). Orchid mantis spectra used for comparison in this study are described elsewhere (see O'Hanlon et al. 2013). Daylight illumination standard D65 was used as the ambient light spectrum and the green of the artificial leaves used during field observations as the background reflectance spectrum. Chromatic contrast between the UV-absorbing white paint and the live orchid mantises (femoral lobe) was very low measured as colour contrast (CC) in the colour hexagon ( $\bar{x}$  CC = 0.024) and just noticeable differences (JND) for the noise receptor threshold models ( $\bar{x}$  JND = 0.299). The UV-reflecting white material also had very low chromatic contrast when compared to the wing buds of live orchid mantises ( $\bar{x}$  CC = 0.026;  $\bar{x}$  JND = 0.350).

#### Experiment 1 – Attractiveness of Model Orchid Mantises

To further establish that the models were suitable surrogates for orchid mantis-like stimuli to pollinators, I conducted a field experiment to examine their attractiveness to pollinators and compare this to the attractiveness of live orchid mantises. Three stimuli were presented to wild, naturally occurring pollinators: a live subadult female orchid mantis, a model



**Fig. 3:** Diagram of models with (l-r) brown, white, white+UV and UV colouration used to investigate the effect of colour on pollinator attraction. Shading indicates where UV reflectance was present on models.

orchid mantis and a control stimulus. Orchid mantises were perched on the end of a 1-m high, upright, wooden stick. The artificial model mantises tethered to the end of a 1-m wooden stick, and the control stimulus consisted of an empty 1-m wooden stick. The models used for this trial included UV-reflecting wing buds, abdominal stripes and a green prothorax band. Live orchid mantises were perched on a stick as has been used in previous observational research (O'Hanlon et al. 2014a) as they would not remain in place if placed upon a flat leaf surface (J. C. O'Hanlon, pers. obs.). As such, the model orchid mantises in this experiment were similarly presented tethered to the end of a stick rather than placed upon artificial flowers (see experiments 2 and 3). When perched upon the stick, mantises were free to move, as such the orientation and position of orchid mantises could vary. Orchid mantises are still able to catch and attract prey when in varying postures and positions (J. C. O'Hanlon, pers. obs.). Thus, the orientation of the model mantises was chosen arbitrarily as facing upwards at a roughly 45° angle from the ground, and this was kept consistent throughout all experiments.

These three stimuli (mantis, model and control) were placed amongst shrubby vegetation at least 1 m apart within view of a human observer and were observed for 1 h. During the observation period, all inspections by flying insects were noted. Attractiveness of models was measured as the per hour rate at which naturally occurring flying insects inspected the stimuli. Inspections were identified by pollinators deviating from their flight path and hovering within approx. 10 cm of the stimulus whilst orienting towards the stimulus. This included inspections that resulted in insects landing upon the models or being captured as prey by the mantis. This was repeated ten times with each replicate occurring at a different site within the field station and the relative positioning of the different stimuli within randomly allocated. Observations took place during the day between 9:00 am and 3:00 pm in September 2011 at the Ulu Gombak Field Studies Center in the Selangor region of Peninsular Malaysia. This field station is within the known distribution of the orchid mantis, and orchid mantises occur naturally at the field site (H. S. Yong, pers. comm.). Live mantises for this experiment were obtained from captive populations of private insect keepers in Peninsular Malaysia.

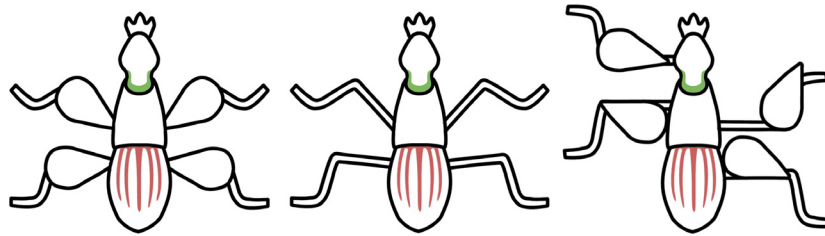
#### Experiment 2 – Effects of Colour on Attractiveness

To investigate the influence of orchid mantis colour on pollinator attraction, I observed the behaviour of

wild pollinators towards model orchid mantises differing in colour. Four differently coloured models were used: (1) all brown, (2) all UV-absorbing white, (3) UV-absorbing white with UV-reflecting wing buds and (4) UV-reflecting white covering the whole model (see Fig. 3). These four stimuli are herein referred to as brown, white, white + UV and UV, respectively. A brown paint (Chroma Australia, Sydney) was chosen so that it contrasted against the artificial green leaf background but was not a typical flower colour. These combinations were chosen specifically to investigate the contribution of the mantis' overall UV-absorbing white colouration and the UV-reflecting patch on mantis wingbuds. For simplicity, the models used in this experiment did not include the features of abdominal stripes or green prothorax bands. These four different models were placed on artificial green leaves and tethered to the end of 1-m high sticks. These were placed amongst shrubby vegetation at the Ulu Gombak field studies centre as described above and observed simultaneously for 1 h during which time all pollinator inspections were noted. This was replicated 22 times, each time at a different site within the field station. Ten sets of models were constructed for this experiment, each trial used a different combination of models, and are treated here as independent samples.

#### Experiment 3 – Effects of Shape on Attractiveness

A separate experiment investigated the effect of the presence and arrangement of femoral lobes on pollinator attractiveness. All models used in this study included UV-reflecting wing buds, abdominal stripes and prothorax bands. Only the presence and orientation of femoral lobes were altered. Three different model types were constructed: (1) a full model, (2) a model without femoral lobes and (3) a model with femoral lobes arranged into an asymmetric pattern (Fig. 4). The models were placed upon artificial leaves and tethered to the end of 1-m high, wooden sticks as described above. These were placed amongst shrubby vegetation at the Ulu Gombak field studies centre and observed simultaneously for 1 h during which all pollinator inspections were noted. Twenty replicate observation sessions were conducted at different sites within the field station. The models used in this experiment included green prothorax bands, abdominal stripes and UV-reflecting wing buds (see Fig. 4). Five sets of models were constructed for this experiment, each trial used a different combination of models, and are treated here as independent samples.



**Fig. 4:** Diagram showing how models were used to manipulate the presence and orientation of femoral lobes. This diagram shows (l-r) a full model, a model with femoral lobes removed and a model with femoral lobes arranged in a non-radiating, asymmetrical pattern.

**Statistical Analyses**

For all experiments, I tested for differences between pollinator inspection rates of differing stimuli using pairwise Friedman’s rank-sum tests with *post hoc* pairwise Wilcoxon signed-rank tests. All statistical analyses were conducted using R version 2.14.1 (R Development Core Team 2011).

**Results**

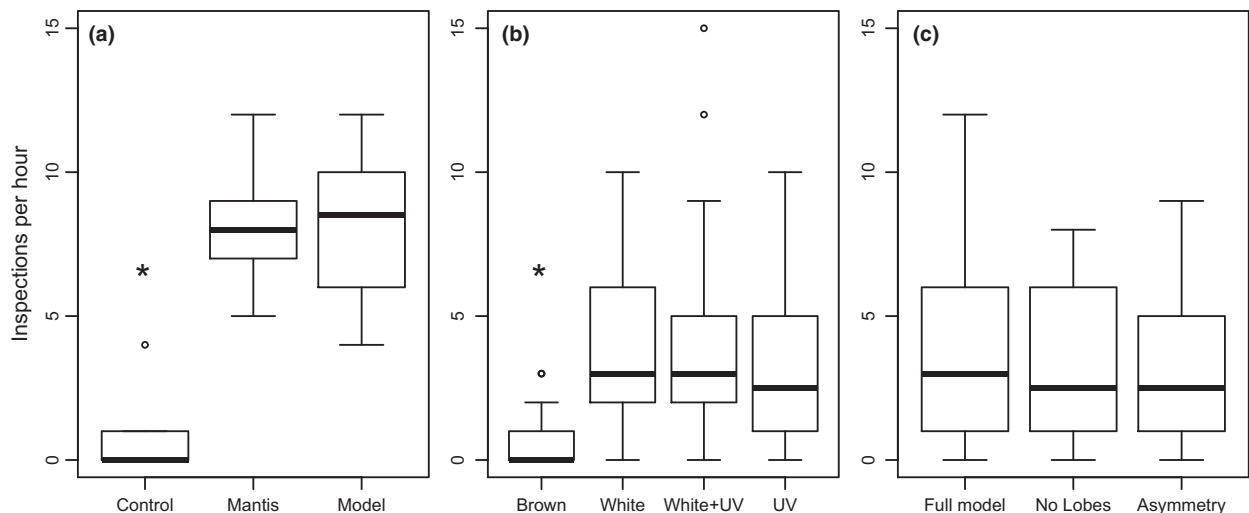
Both live orchid mantises and artificial orchid mantises were inspected frequently by flying insects. The most common insects included several types of bees with butterflies and flies also observed making inspection flights. Pollinator visitation rates were lower overall for experiments 3 and 4. The reasons for this can only be speculated upon at this stage yet may involve the presentation of models on artificial leaves or the particular environmental conditions on the days these experiments were conducted.

**Experiment 1 – Attractiveness of Model Orchid Mantises**

I found significant differences between pollinator inspection rates of control sticks, mantises and models (Friedman’s rank-sum test;  $\chi^2 = 15.436$ ,  $df = 2$ ,  $p < 0.001$ , Fig. 5). There was no evidence for significant differences in the attractiveness of artificial mantises compared with live mantises, both attracted pollinators at similar rates (Wilcoxon signed-rank test;  $W = 26$ ,  $p = 0.719$ ). Not surprisingly, control sticks were visited at significantly lower rates compared with the model ( $W = 0$ ,  $p < 0.006$ ) and live mantises ( $W = 0$ ,  $p < 0.006$ ).

**Experiment 2 – Effects of Colour on Attractiveness**

During the observation trials, pollinators regularly visited the four models. Colour manipulation significantly affected overall rates of pollinator inspection (Friedman’s rank-sum test;  $\chi^2 = 28.09$ ,  $df = 3$ ,



**Fig. 5:** Hourly rate of wild pollinator inspections towards (a) a control stimulus (stick), a juvenile female *Hymenopus coronatus* and an artificial model of a juvenile *H. coronatus*, (b) model *H. coronatus* with manipulated colour patterns and (c) model *H. coronatus* where the presence and/or orientation of femoral lobes has been manipulated. Box plots display median, interquartile range and 95% confidence intervals.  $\circ$  indicates outliers;  $\star$  indicates significance at 0.05.

$p < 0.001$ ; Fig. 5b). Clearly, brown models were the least attractive as pollinator inspection rates were significantly lower than those of white models (Wilcoxon signed-rank test;  $W = 0$ ,  $p < 0.001$ ), white + UV models ( $W = 3$ ,  $p < 0.001$ ) and UV models ( $W = 10$ ,  $p < 0.001$ ). There was no apparent effect of adding UV reflectance to models; pollinator inspection rates were equivalent between white and white + UV models ( $W = 88.5$ ,  $p = 0.548$ ), white and UV models ( $W = 98.5$ ,  $p = 0.583$ ), and white + UV and UV models ( $W = 122$ ,  $p = 0.113$ ).

### Experiment 3 – Effects of Shape on Attractiveness

Similar to the colour-manipulated models, pollinators regularly inspected the shape-manipulated models. Surprisingly, pollinators inspected models without femoral lobes at similar rates to models with femoral lobes. The arrangement of femoral lobes also did not appear to affect attractiveness of the models. No significant differences were found between inspection rates of the three stimuli (Friedman's rank-sum test;  $\chi^2 = 1.754$ ,  $df = 2$ ,  $p = 0.416$ ; Fig. 5c).

### Discussion

The UV-absorbing white colouration of orchid mantises matches that of a range of flower species within its natural habitat (O'Hanlon et al. 2014a). Mantis models with UV-absorbing white colouration attracted significantly more pollinators than those with an unnatural brown colouration, thus supporting the prediction that the 'flower-like' colouration of orchid mantises is an important component of their deceptive predatory signal. In comparing white to brown models, this study investigates the function of orchid mantis colouration in a broad sense. Further investigations will elucidate whether these effects on pollinator behaviour are influenced by specific components of colouration patterns, such as brightness, chroma and hue.

Models with UV-reflecting white colouration on the wing buds received similar amounts of pollinator visits to those with UV-absorbing white colouration. Pollinators often show preferences for flowers that present contrasting colour patterns, such as a contrasting central spot (Heuschen et al. 2005). In bees, the UV receptor can be 16 times more sensitive to reflected light than other receptor types (von Helversen 1972), and the presence of a contrasting UV-reflecting patch on a flower can be an attractive stimulus to pollinators (e.g. Heiling et al. 2003, 2005). However, adding UV reflectance to orchid mantis

models did not have an effect on their attractiveness. Similarly, models with UV-reflecting white colouration across the entire model did not differ in attractiveness to UV-absorbing models.

One cannot assign salience to the presence of UV alone (Kevan et al. 2001) as UV reflectance is common in natural objects, and the response of pollinators to any wavelength will be context dependent. Despite sensory biases towards UV wavelengths in pollinators, UV-reflecting flowers may actually be less conspicuous to pollinators than UV-absorbing flowers (for discussion see Kevan et al. 1996). The same selective pressures may lead to orchid mantises exhibiting UV absorbance and account for why the addition of UV did not affect the attractiveness of models in this study. It should be noted that the brightness of the UV-reflecting and UV-absorbing materials used was similar. Thus, this study addresses the effect of manipulating the presence of UV reflectance on models, whether brightness differences between the wing buds and femoral lobes of orchid mantises (see Fig. 2a, b) affects their attractiveness is unknown.

Alternatively, colour patterns on the orchid mantis may play a role in fine-scale interactions between orchid mantises and pollinators. When approaching flowers, pollinators use different orientation cues depending on their distance to the flower. Initially pollinators orient towards the edges of flowers (Lehrer et al. 1990; Lunau et al. 2006). Once in close proximity, nectar guides and other contrasting patterns within flowers can direct pollinators towards sites of pollination transfer (Lehrer et al. 1985; Johnson & Dafni 1998; Lunau et al. 2006). In this experiment, pollinator inspection rate was used as an indicator of prey availability; however, whilst a pollinator may be attracted towards an orchid mantis from a distance, it is not available as prey unless it is positioned in front of and within the mantis' striking range. If, as in flowers, the approach behaviour of pollinators is directed by visual features of the orchid mantis, one could predict selection upon characteristics of the orchid mantis that direct pollinator's to within striking range. Closer, fine-scale observations of inspection, orientation and alighting behaviours are necessary to deduce whether this occurs in the orchid mantis.

It is often assumed that the orchid mantis' femoral lobes simulate flower petals and appears intuitively obvious (Annandale 1900; Edmunds & Brunner 1999). I predicted that removing femoral lobes would affect mantis attractiveness by reducing their likeness to a flower. Surprisingly, I found no evidence to suggest that the presence of femoral lobes affects the attractiveness of model orchid mantis.

Bees show an innate preference for symmetrical patterns (Giurfa et al. 1996a; Wignall et al. 2006). Symmetrical patterns in flowers may be an important cue for identifying food resources, and as such, I predicted that symmetry in the orchid mantis would play an important role in being misclassified as a 'flower-like' stimulus. I found no evidence that asymmetry in femoral lobe positioning affected the attractiveness of models to pollinators. There are several potential explanations. First, pollinators may only respond to shape characteristics in the context of other signal components. When viewing flowers, pollinators can assess signal components in a hierarchical manner leading to preferences for particular components predominating over others (Giurfa et al. 1995a; Lehrer et al. 1995). For example, when trained to coloured objects in a particular orientation, bees prefer experimental stimuli based on correct colour rather than correct orientation (Giurfa et al. 1995a). Further, Lehrer et al. (1995) showed in naïve bees that the presence of radiating pattern elements predominated over any preference for symmetrical patterns.

By only manipulating the presence of femoral lobes, this experiment did not address potential interactions between the presence of femoral lobes and other signal components such as size. The models used in this experiment were built to the proportions of subadult female orchid mantises. The models without femoral lobes therefore still presented a relatively large stimulus to pollinators (approx. 5 cm in length). As such, the addition of femoral lobes to an already large stimulus may not have significantly increased attractiveness. Similarly, the presence of a large stimulus may have negated any effects of an asymmetrical femoral lobe arrangement.

An animal's morphology can be the result of selection from a suite of signal receivers (e.g. Pekár et al. 2011). Orchid mantis femoral lobes may be important in interactions other than pollinator deception, such as predator avoidance. The presence of legs can be a conspicuous feature that enables predators to identify insect prey more easily (Robinson 1973). Thus, the orchid mantis' femoral lobes, by concealing the legs, may obscure their insect-like shape and enable them to avoid being detected by predators. A manipulative approach similar to that used here could also be applied to understand adaptations for camouflage in the orchid mantis.

The white colour of orchid mantis models was the only signal component that had a significant impact on pollinator attractiveness. The fact that removing 'flower-like' characteristics, such as contrasting colour patterns, symmetry and false petals, did not affect the

attractiveness of models suggests that pollinator deception in the orchid mantis may result from sensory exploitation using colour, rather than cognitive misclassification. Whether pollinator deception results from sensory exploitation as opposed to mimicry can be a contentious definition even in cases of non-rewarding flowers (Schaefer & Ruxton 2009). Flowers themselves are sensory exploiters that take advantage of the existing sensory biases of pollinators (Chittka 1996). There are many flowers that do not provide rewards for pollinators yet elicit visits by resembling rewarding flowers (Jersákova 2009). This is often described as floral mimicry; however, sensory exploitation could also account for the success of deceptive flowers (Schaefer & Ruxton 2009). Recognition and sensory exploitation are not necessarily mutually exclusive processes and how pollinators process cognitive representations of flowers when foraging is incredibly complex and unclear.

I have shown here that artificial stimuli, matching the colour and shape of orchid mantises, are an effective tool for studying the mechanisms behind pollinator deception. The models provided sufficient detail to elicit the same rates of pollinator inspections as live mantises. Model orchid mantises could also provide ideal subjects to investigate the role of other morphological aspects not considered here, such as orchid mantis abdominal stripes and green prothorax bands (see O'Hanlon et al. 2013). Whether additional behavioural cues from the mantis, such as its resting posture and the orientation of its body axis (e.g. facing upward or downward), affect how they are perceived by prey is also unknown. Whilst this study investigates the efficacy of pollinator attraction from a distance, future studies should investigate pollinator flight paths and fine-scale orientation behaviour of approaching pollinators. Further research manipulating other variables such as size and abdominal colour patterns may provide information on the interplay between different visual cues in deceiving pollinators and the predatory behaviour of orchid mantises at different life stages.

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