The University of Chicago

Pollinator Deception in the Orchid Mantis

James C. O'Hanlon,[1],* Gregory I. Holwell,[2] and Marie E. Herberstein[1]

1. Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia;   2. School of Biological Sciences, University of Auckland, Auckland 1142, New Zealand

ABSTRACT: Mimicry has evolved in contexts such as camouflage, predator deterrence, luring of prey, and pollinator attraction. Mimicry of flowers has until now been demonstrated only in angiosperms, yet it has been hypothesized that the Malaysian orchid mantis *Hymenopus coronatus* mimics a flower to attract pollinators as prey. Despite the popularity of this charismatic insect, this long-discussed hypothesis has never been experimentally investigated. We found that, as predicted for mimicry, the color of *H. coronatus* is indistinguishable from the color of sympatric flowers for hymenopteran pollinators. Field experiments show that isolated mantises attract wild pollinators at a rate even higher than flowers and capture these pollinators as prey items. After more than a century of conjecture, we provide the first experimental evidence of pollinator deception in the orchid mantis and the first description of a unique predatory strategy that has not been documented in any other animal species.

Keywords: Hymenopus coronatus, aggressive mimicry, floral mimicry, deception, lure.

Introduction

Mimicry has been described as one of the most influential and illustrative examples of natural selection since the formulation of evolutionary theory (Vereecken and Schiestl 2008). The dynamics of mimetic interactions have been widely discussed and investigated since Henry Walter Bates's initial description of mimicry in 1861 (Bates 1861). As the manifestations and benefits of adaptive resemblances to unrelated organisms are so varied (Starrett 1993), many examples of mimicry are not fully understood, and mimicry theory continues to be a progressing field in evolutionary and behavioral ecology.

Historically, mimicry has been most commonly interpreted in terms of providing a protective function (Ruxton et al. 2004). If a predator learns to avoid particular prey items that are inedible or distasteful, then predators may also avoid palatable species that in some way resemble the unpalatable organism (Bates 1861). However mimicry often functions in the opposite manner, such as in aggressive mimicry where a mimetic resemblance attracts and lures prey items (also termed Peckhamian mimicry; Peckham 1889). Classic examples of aggressive mimicry are the bolas spiders (*Mastophora* sp.) that attract male moths by mimicking female moth pheromones (Eberhard 1977).

On return from travels in Indonesia in 1879, Australian journalist James Hingsley told tales of a carnivorous red orchid that engulfed butterflies in its petals and devoured them alive (Hingsley 1879). The organism behind this extraordinary tale is not a flower but a praying mantis, *Hymenopus coronatus*, which has become renowned for its elusiveness and remarkable resemblance to a flower blossom (fig. 1).

Floral mimicry most commonly occurs in orchids, where more than one-third of species rely on deception

* Corresponding author; e-mail: james.ohanlon@mq.edu.au.

Figure 1: A subadult female orchid mantis (*Hymenopus coronatus*).

for pollination (Dafni 1984). The successful pollination of many deceptive, nonrewarding flower species relates to their morphological similarities with rewarding flower species (Johnson 2000; Johnson et al. 2003*a*; Galizia et al. 2005). Until now a definitive case of floral mimicry occurring outside of the angiosperms has not been documented. While floral mimicry has been suggested to occur in the fungus *Puccinia monoica* (Roy 1993), these fungi produce distinct scents (Raguso and Roy 1998) and nectar rewards for insect visitors (Roy 1993). Thus, deception and mimicry may not be necessary drivers for this pollinator-fungus interaction.

It is conceivable that floral mimicry could function to attract pollinators as prey for predators such as the orchid mantis, yet there is no experimental evidence of this. The orchid mantis, *H. coronatus*, is often described as an aggressive mimic (Starrett 1993), implying that this predatory insect mimics a flower and attracts insect pollinators as prey (Wallace 1877; Annandale 1900). This hypothesis was first discussed more than a century ago by naturalists such as Alfred Russell Wallace (1877) and Lord Nelson Annandale (1900) and was inspired by observations and accounts of single specimens. This hypothesis has never been experimentally investigated yet it continues to permeate scientific and nonscientific literature and is often assumed to be an established fact (e.g., Dawkins 2009). Resemblance of animals to plant parts can function analogously to mimicry in cases of masquerade (Skelhorn et al. 2010*a*, 2010*b*), where animals are misclassified by predators as inedible objects. The possibility that resemblance to plants can act as an aggressive lure rather than for camouflage has not been previously demonstrated. If the orchid mantis is a flower mimic, then pollinators should misclassify the mantis as a flower rather than as a predatory insect. As opposed to masquerade, where being misclassified as a plant part serves a protective function (Skelhorn et al. 2010*b*), floral mimicry should elicit an attractive response from pollinators. We predict that flying insects should be attracted to orchid mantises at similar rates to real flowers. A nonexclusive alternative hypothesis may be that orchid mantis shape and coloration camouflages the insect among flowers for predator avoidance and/or ambush predation of pollinators visiting the flowers. In this case, camouflage among flowers would be necessary for successful prey capture, and a mantis in isolation from flowers would not be attractive to pollinators.

We investigated whether orchid mantises are flower mimics in two ways. First, we applied color modeling to compare orchid mantis and flower coloration from the perspective of a hypothetical pollinator. We utilized two physiological visual models that incorporate the spectral sensitivities of a hymenopteran visual system, generating predictions on whether pollinators such as bees can distinguish between color patterns of *H. coronatus* and sympatric flowers. Second, we experimentally tested the hypothesis that the orchid mantis is a floral mimic by observing the behavioral responses of wild pollinators to live mantises.

Methods

The Orchid Mantis

Orchid mantises are elusive animals that are rarely encountered in the wild. As such it has not been possible to obtain large data sets on their biology, particularly in their native habitat. Captive orchid mantises were obtained from private insect keepers in Peninsular Malaysia for this study. All field observations on live orchid mantis and pollinator behavior (described below) were conducted in forested areas where orchid mantises are known to occur naturally. This study, to our knowledge, is the most extensive data set available on the ecology of the orchid mantis.

Calculation of Chromatic Contrast

The color of orchid mantises and sympatric wild flowers were measured in situ using a portable spectrometer (Jaz EL-200, Ocean Optics, Dunedin, FL). As little is known about the ecology of the orchid mantis, we selected the broadest scope of flowers possible. We included flowers if at least four individual plants could be found and if this species was known to occur in areas were orchid mantises are also known to occur. Orchid mantis spectral reflectance was averaged from three measurements taken from the femoral lobe of the right midleg. Each flower's spectral reflectance was averaged from one measurement on each petal. Spectral reflectances were taken from 14 individual orchid mantises and 13 different species of wildflowers of varying sample sizes (tables A1, A2, available online). The chromatic contrast between each flower and a randomly assigned mantis was calculated using two widely applied models of trichromatic vision, the color hexagon (Chittka 1992) and the receptor-noise-limited model (Vorobyev and Osorio 1998). We used honeybee receptor sensitivities as published by Menzel and Backhaus (1991). Spectral reflectance of background color was measured from a random sample of green leaves found at the Ulu Gombak field studies center, and illumination standard D65 was used as our ambient light spectrum. All reflectance data can be found at the Dryad digital Repository, http://dx.doi.org/10.5061/dryad.g665r (O'Hanlon et al. 2013). The average color contrast values for each flower species were checked for normality using a Kolmogorov-Smirnov test. One-sample *t*-tests were conducted to test whether the average color contrast between mantises and each
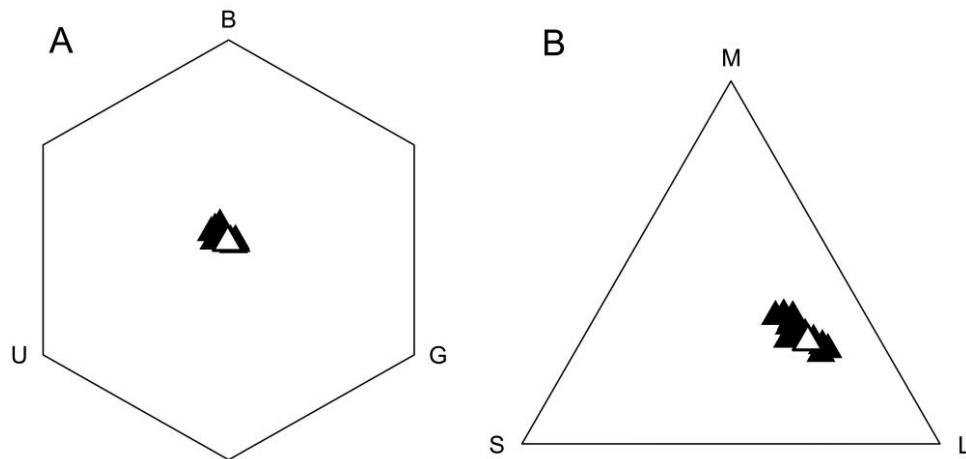
Figure 2: Hexagonal chromaticity diagram (*A*) and Maxwell triangle chromaticity diagram (*B*) showing the average color coordinates of the orchid mantis (filled triangles) and 13 wild flower species (open triangles) as calculated by trichromatic vision models.

species of flower differed significantly from a detection threshold value for bees. A separate *t*-test was conducted for each flower species. We used a conservative contrast threshold value (Dyer and Chittka 2004) of 0.062 in hexagonal color space (Chittka 1992) and a ΔS threshold value of 1 for the receptor-noise-limited model (Vorobyev and Osorio 1998).

Pollinator Visitation Behavior

Observations of pollinator behavior were performed at the University of Malaya Ulu Gombak field studies center in January 2011. For each experimental replicate, three wooden sticks each 1 m in length were placed vertically among natural vegetation and spaced at least 1 m apart from each other. A live mantis was placed on top of one stick and a live *Asystasia intrusa* flower was tethered to another. *Asystasia intrusa* flowers were chosen for comparison as they were the most common flower in the area and thus likely to be a known rewarding stimulus for pollinators. The third stick was left bare as a control stimulus. Observations of these three stimuli occurred simultaneously for 1 h. This was repeated at different sites within the field station. Inspections by flying insects coming within 10 cm of each stimulus were tallied. A total of 30 h of observations were made; each replicate used one of five mantises available at the time of the study. As the site of observation differed for each replicate and flowers were never reused, each hourly observation was treated here as an independent replicate. To assess the effect of stimuli on the hourly rate of pollinator visitation we conducted a log-likelihood ratio test on a Poisson-lognormal linear mixed effects model, as in Elston et al. (2001). Site was included as a random effect. Post hoc

paired Wilcoxon signed-rank tests were used to assess whether pollinator visitation rates differed between stimuli. All analyses were conducted using the lmer4 package in R v2.14.1 (R Development Core Team 2011). Raw data can be found at the Dryad Digital Repository, http://dx.doi.org /10.5061/dryad.g665r (O'Hanlon et al. 2013).

Results

Chromaticity of Orchid Mantises and Wild Flowers

Two separate models of trichromatic hymenopteran vision—the color hexagon (Chittka 1992) and the receptor noise limited model (Vorobyev and Osorio 1998)—showed that the color of orchid mantises falls within the range of flower petal colors of a number of local flowers (fig. 2). Average chromatic contrast values between orchid mantises and 13 flower species were overall either significantly below or not significantly different from honeybee discrimination threshold values (tables A1, A2). Results were similar for both the color hexagon and receptor-noise-limited models with only a single flower species found to be significantly above threshold values for the receptor-noise-limited model.

Pollinator Visitation Rates

In field experiments we found that the per-hour visitation rates of flying insects differed significantly between the flower, the mantis, and the bare stick control ($\chi^2 =$ 115.35, df = 2, $P =< .001$; log-likelihood ratio test; fig. 3). Wild pollinating insects inspected live juvenile female orchid mantises significantly more frequently than they did the bare stick ($V = 528$, $P =< .001$; Wilcoxon signed
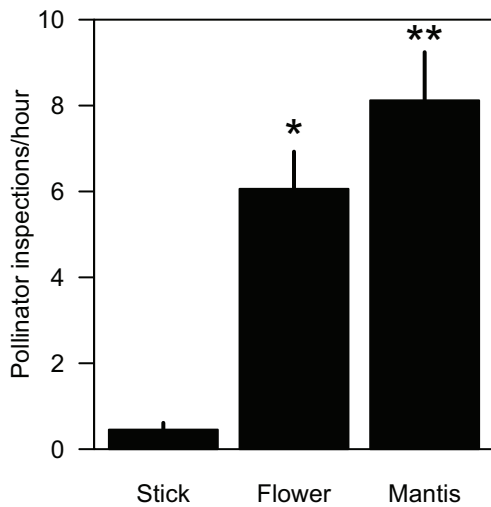
Figure 3: Average (+SE) visitation rates of wild pollinators to stimuli in the field. Asterisks indicate significant differences between treatments.

rank test) and also significantly more than live *Asystasia intrusa* flowers ($V = 349$, $P = .017$).

The majority of insects visiting the stimuli were bees (Apoidea: Hymenoptera); however, flies (Diptera) and butterflies (Lepidoptera) also inspected the flowers and orchid mantises. During the trials, inspecting insects came so close to the orchid mantis that two successful prey captures occurred among a number of prey capture attempts. Additionally, outside of the experimental period of this study, we observed more than 10 instances of successful prey capture following pollinator visitation in the field (see video 1, available online).

Discussion

As predicted for a flower mimic, the difference between the color of the orchid mantis and the sampled flowers falls below detection thresholds suggesting that hymenopteran pollinators are unlikely to be able to distinguish orchid mantises from flowers based on color. Likewise, in food-deceptive pollination systems color similarity to rewarding species can increase the success of a deceptive flower in attracting pollinators (Gumbert and Kunze 2001; Gigord et al. 2002; Johnson et al. 2003*b*; Internicola et al. 2007; Peter and Johnson 2008; Newman et al. 2012). As little is known about the habitat of the orchid mantis, we sampled a broad range of flower species found within the orchid mantis' range in Peninsular Malaysia. Despite what their name may imply, we have no evidence to suggest that the orchid mantis specifically resembles any individual orchid species. Only two orchid species were sampled in this study—*Arundina gram-*

nifolia and *Spathoglottis plicata*. When compared to orchid mantises, both orchid and nonorchid species had similarly low color contrast values (tables A1, A2).

Utilization of flower colors to attract prey has been attributed to a number of predators. Crab spiders (Heiling et al. 2003), assassin bugs (Elliot and Elliot 1991), and other flower mantises (Edmunds and Brunner 1999) use flowers as a habitat for ambush predation on pollinators. A predator with flower-like coloration may camouflage among flowers and attack pollinating insects once they are in close range. Some crab spiders even manipulate flower signals, making them more attractive to pollinators (Heiling et al. 2003). The Australian crab spider *Thomisus spectabilis* reflects brightly in the UV spectrum and creates a strong contrasting stimulus against the UV-dull flower background. The UV signal attracts more pollinators than an empty flower or a spider where the UV has been experimentally removed (Heiling et al. 2003). In these cases, it seems that the combination of spider and flower are important in pollinator attraction with little evidence to suggest that the predator in isolation is attractive to pollinators.

The shape and coloration of *H. coronatus* may allow them to camouflage among flowers and ambush prey. However the hypothesis that *H. coronatus* is an aggressive flower mimic implies that their predatory strategy works quite differently. Pollinators should be deceived by and attracted toward the actual predator rather than the flowers in its vicinity. In our experiment the orchid mantises were presented in isolation from flowers against a natural background of green vegetation. The mantises attracted wild pollinators at a rate significantly higher than either flowers or the control stimulus. As we used live mantises there may have been chemical or movement cues that could have alerted pollinators to the true identity of the predator. We show that, even with these potential cues, the body of an orchid mantis can provide an isolated attractive stimulus to pollinators. In contrast to other flower associated

Video 1: Behavior of pollinators toward live orchid mantises (video 1, available online).

predators (e.g., crab spiders) mantises are often inhabiting foliage rather than flowers and may not have an obligate reliance on flowers for prey attraction. This unique predatory strategy has not been demonstrated for any other animal species.

The *Asystasia intrusa* flowers observed in this study occur commonly in areas where orchid mantises are found. We are not suggesting that the orchid mantis is mimicking *A. intrusa* flowers specifically. Rather our data suggest that pollinators may view the orchid mantis as an alternative "flower-like" rewarding stimulus. Not only did orchid mantises attract more pollinators than the control stimulus, they also attracted more pollinators per hour than the flowers. The orchid mantises used in this study were slightly larger than the *Asystasia* flowers, which may account for this pattern as pollinators often show preferences for larger inflorescences during foraging bouts (Duffield et al. 1993; Martin 2004).

Through a number of adaptations the orchid mantis appears to have converged upon the perceptual space occupied by flowers in the sensory systems of pollinating insects. Our data suggest that this convergence is not specific for a single flower species but may represent an average flower type. This raises further questions as to whether other signal receivers, such as predators of the orchid mantis, may also be duped by this floral resemblance. Mimicry can serve multiple simultaneous functions depending on the signal receiver. Many myrmecomorphic species of jumping spider (Salticidae) have been described as ant mimics (Cushing 1997). Ant mimicry can protect spiders from ant-averse predators (Nelson et al. 2006; Durkee et al. 2011; Huang et al. 2011) and also allow spiders access to ant broods as prey (Allan and Elgar 2001). It is possible that floral mimicry, in addition to attracting prey, could conceal the orchid mantis from predators through masquerade, as has recently been demonstrated in twig-mimicking caterpillars (Skelhorn et al. 2010*b*). Other praying mantis species are known to closely resemble plant parts such as twigs and leaves (Edmunds and Brunner 1999) and have also been hypothesized to benefit from masquerade. Further research examining the response of a wide diversity of signal receivers towards orchid mantises is necessary to fully understand the potential benefits of floral mimicry.

Other signal components may also play a role in the predatory strategy of the orchid mantis. Scent cues are important cues used by pollinators for flower detection and recognition (see Raguso 2008). It could be hypothesized that chemical cues affect the interactions of orchid mantises with pollinators; however, as this study investigated only the visual characteristics of orchid mantises, the role of chemical cues is unknown.

Frequency-dependant selection predicts that mimics should occur in lower densities than their models, thus reducing the opportunities for signal receivers to learn and recognize deceptive signals (e.g., Pfennig et al. 2001). Similarly nonrewarding flowers are predicted to be more successful in attracting pollinators when in lower relative densities to rewarding flowers (e.g., Johnson et al. 2003*b*). Orchid mantises occur in low densities, which may be a critical aspect of their success. Their rarity may ensure that the chances of pollinators encountering successive orchid mantises are low and reduce the likelihood that pollinators will learn to distinguish deceptive orchid mantises from rewarding flowers.

The cognitive processes of signal receivers and how they are exploited by deceptive strategies are often unclear and difficult to elucidate when studying potential mimicry systems (Schaefer and Ruxton 2009). Further investigations may give more specific information as to what behavioral processes of the pollinators facilitate the predatory strategy of the orchid mantis. What is clear from our study is that pollinating insects are attracted to the body of the orchid mantis their resemblance to flowers is the most likely functional explanation for this. The orchid mantis provides to our knowledge the first evidence for potential floral mimicry as a predatory strategy in the animal kingdom.

Acknowledgments

APPENDIX

Color Contrast between Orchid Mantises and Flowers

Table A1: Chromatic contrast (CC) between flowers and orchid mantises calculated as Euclidean distances in hexagonal color space, ordered by increasing degree of contrast

Flower type	N	Mean CC	SD	t	df	P
Melastoma sp. 1	4	.0217	.0131	−6.127	3	.008
Ageratum conyzoides	10	.0256	.0189	−6.079	9	<.001
Tabernaemontana sp. 1	5	.0325	.0356	−1.851	4	.138
Sonerila sp.	9	.0367	.0332	−2.278	8	.052
Arundina gramnifolia	5	.0395	.0293	−1.717	4	.161
Medinilla sp. 1	5	.0446	.0132	−2.947	4	.042
Asystasia intrusa	10	.0502	.0133	−2.805	9	.021
Unknown sp.	4	.0506	.0271	−.840	3	.462
Tabernaemontana sp. 2	8	.0582	.0165	−.650	7	.536
Melastoma sp. 2	4	.0668	.0125	−.765	3	.500
Medinilla sp. 2	4	.0741	.0141	1.721	3	.183
Spathoglottis plicata	4	.1004	.0514	1.494	3	.232
Mimosa pudica	5	.1073	.0412	2.450	3	.070

Note: Significance values are two-tailed.

Table A2: ΔS values of chromatic contrast between flowers and orchid mantises as calculated by the receptor noise threshold model, ordered by increasing degree of contrast

Flower type	N	Mean ΔS	SD	t	df	P
Tabernaemontana sp. 1	5	.3207	.1513	−10.042	4	<.001
Melastoma sp. 1	4	.3667	.1727	−7.335	3	.005
Medinilla sp. 1	5	.3754	.2136	−6.538	4	.002
Ageratum conyzoides	10	.4943	.3017	−5.310	9	<.001
Sonerila sp.	9	.7739	.6180	−1.098	8	.3043
Asystasia intrusa	10	.8700	.2667	−1.541	9	.158
Arundina gramnifolia	5	.8875	.4845	−.519	4	.631
Medinilla sp. 2	4	.9650	.3192	−.219	3	.841
Melastoma sp. 2	4	.9932	.2540	-.053	3	.961
Unknown sp.	4	1.0497	.2047	.486	3	.661
Mimosa pudica	5	1.2442	.4042	1.351	4	.248
Tabernaemontana sp. 2	8	1.3408	.2938	3.280	7	.013
Spathoglottis plicata	4	1.8246	.9216	1.7894	3	.172

Note: Significance values are two-tailed.

Literature Cited

Allan, R. A., and M. A. Elgar. 2001. Exploitation of the green tree ant, *Oecophylla smaragdina*, by the salticid spider *Cosmophasis bitaeniata*. Australian Journal of Zoology 49:129–137.

Annandale, N. 1900. Observations on the habits and natural surroundings of insects made during the "Skeat expedition" to the Malay Peninsula, 1899–1900. Proceedings of the Zoological Society of London 69:837–869.

Bates, H. W. 1861. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society 23:495–566.

Chittka, L. 1992. The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. Journal of Comparative Physiology A 170:533–543.

Cushing, P. E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. Florida Entomologist 80:165–193.

Dafni, A. 1984. Mimicry and deception in pollination. Annual Review of Ecology and Systematics 15:259–278.

Dawkins, R. 2009. The greatest show on Earth: the evidence for evolution. Transworld, London.

Duffield, G. E., R. C. Gibson, P. M. Gilhooly, A. J. Hesse, C. R. Inkley, F. S. Gilbert, and C. J. Barnard. 1993. Choice of flowers by foraging honey bees (*Apis mellifera*): possible morphological cues. Ecological Entomology 18:191–197.

Durkee, C. A., M. R. Weiss, and D. B. Uma. 2011. Ant mimicry lessens predation on a North American jumping spider by larger salticid spiders. Environmental Entomology 40:1223–1231.

Dyer, A. G., and L. Chittka. 2004. Biological significance of distinguishing between similar colours in spectrally variable illumination: bumblebees (*Bombus terrestris*) as a case study. Journal of Comparative Physiology A 190:105–114.

Eberhard, W. G. 1977. Aggressive chemical mimicry by a bolas spider. Science 198:1173–1175.

Edmunds, M., and D. Brunner. 1999. Ethology of defenses against predators. Pages 276–299 in F. R. Prete, H. Wells, P. H. Wells, and L. E. Hurd, eds. The praying mantids. John Hopkins University Press, Baltimore.

Elliot, N. B., and W. M. Elliot. 1991. Effect of an ambush predator, *Phymata americana* Melin, on behaviour of insects visiting *Daucus carota*. American Midland Naturalist 126:198–202.

Elston, D. A., R. Moss, T. Boulinier, C. Arrowsmith, and X. Lambin. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology 122:563–569.

Galizia, C. G., J. Kunze, A. Gumbert, A.-K. Borg-Karlson, S. Sachse, C. Markl, and R. Menzel. 2005. Relationship of visual and olfactory signal parameters in a food-deceptive flower mimicry system. Behavioral Ecology 16:159–168.

Gigord, L. D. B., M. R. Macnair, M. Stritesky, and A. Smiths. 2002. The potential for floral mimicry in rewardless orchids: an experimental study. Proceedings of the Royal Society B: Biological Sciences 269:1389–1395.

Gumbert, A., and J. Kunze. 2001. Colour similarity to rewarding model plants affects pollination in a food deceptive orchid. Biological Journal of the Linnean Society 72:419–433.

Heiling, A. M., M. E. Herberstein, and L. Chittka. 2003. Crab-spiders manipulate flower signals. Nature 421:334.

Hingsley, J. 1879. The Australian abroad: branches from the main routes round the world. Sampson Low, Marston, Searle and Rivington, Melbourne.

Huang, J.-N., R.-C. Cheng, D. Li, and I.-M. Tso. 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. Proceedings of the Royal Society B: Biological Sciences 278:1356–1364.

Internicola, A. I., P. A. Page, G. Bernasconi, and L. D. B. Gigord. 2007. Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: an experimental test of the effects of floral color similarity and spatial mingling. Functional Ecology 21:864–872.

Johnson, S. D. 2000. Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. Biological Journal of the Linnean Society 71:119–132.

Johnson, S. D., R. Alexandersson, and H. P. Linder. 2003a. Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. Biological Journal of the Linnean Society 80: 289–304.

Johnson, S. D., C. I. Peter, L. A. Nilsson, and J. Ågren. 2003b. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology 84:2919–2927.

Martin, N. H. 2004. Flower size preferences of the honeybee (*Apis mellifera*) foraging on *Mimulus guttatus* (Scrophulariaceae). Evolutionary Ecology Research 6:777–782.

Menzel, R., and W. Backhaus. 1991. Colour vision in insects *in* P. Gouras, ed. The perception of colour: vision and visual dysfunction. Macmillan, London.

Nelson, X. J., R. R. Jackson, D. Li, A. T. Barrion, and G. B. Edwards. 2006. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). Biological Journal of the Linnean Society 88:23–32.

Newman, E., B. Anderson, and S. D. Johnson. 2012. Flower colour adaptation in a mimetic orchid. Proceedings of the Royal Society B: Biological Sciences 279:2309–2313.

O'Hanlon, J. C., G. I. Holwell, and M. E. Herberstein. 2013. Data from: Pollinator deception in the orchid mantis. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.g665r.

Peckham, E. G. 1889. Protective resemblances in spiders. Occasional Papers of the Natural History Society of Wisconsin 1:61–113.

Peter, C. I., and S. D. Johnson. 2008. Mimics and magnets: the importance of color and ecological facilitation in floral deception. Ecology 89:1583–1595.

Pfennig, D. W., W. R. Harcombe, and K. S. Pfennig. 2001. Frequency-dependent Batesian mimicry. Nature 410:323.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raguso, R. A. 2008. Wake up and smell the roses: the ecology and evolution of floral scent. Annual Review of Ecology, Evolution and Systematics 39:549–569.

Raguso, R. A., and B. A. Roy. 1998. "Floral" scent production by *Puccinia* rust fungi that mimic flowers. Molecular Ecology 7:1127–1136.

Roy, B. A. 1993. Floral mimicry by a plant pathogen. Nature 362: 56–58.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press, New York.

Schaefer, H. M., and G. D. Ruxton. 2009. Deception in plants: mimicry or perceptual exploitation? Trends in Ecology and Evolution 24:676–685.

Skelhorn, J., H. M. Rowland, and G. D. Ruxton. 2010a. The evolution and ecology of masquerade. Biological Journal of the Linnean Society 99:1–8.

Skelhorn, J., H. M. Rowland, M. P. Speed, and G. D. Ruxton. 2010b. Masquerade: camouflage without crypsis. Science 327:51.

Starrett, A. 1993. Adaptive resemblance: a unifying concept for mimicry and crypsis. Biological Journal of the Linnean Society 48:299–317.

Vereecken, N. J., and F. P. Schiestl. 2008. The evolution of imperfect floral mimicry. Proceedings of the National Academy of Sciences 105:7484–7488.

Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. Proceedings of the Royal Society of London B: Biological Sciences 265:351–358.

Wallace, A. R. 1877. The colours of animals and plants. American Naturalist 11:641–662.

Natural History Editor: Mark A. McPeek