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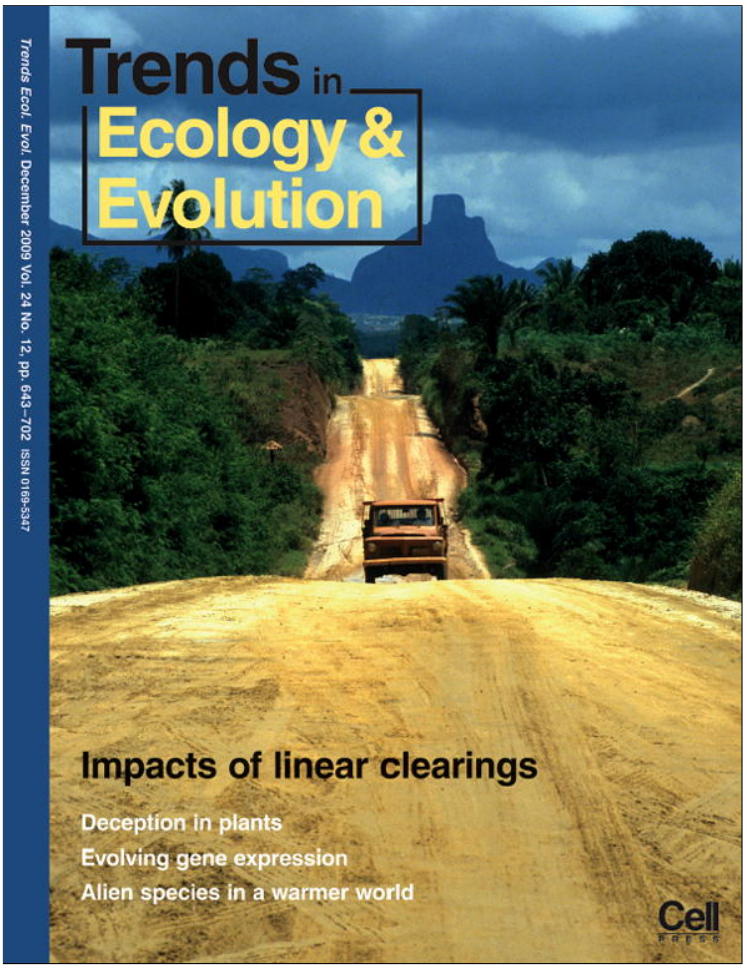

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Review

Deception in plants: mimicry or perceptual exploitation?

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Mimicry involves adaptive resemblance between a mimic and a model. However, despite much recent research, it remains contentious in plants. Here, we review recent progress on studying deception by flowers, distinguishing between plants relying on mimicry to achieve pollination and those relying on the exploitation of the perceptual biases of animals. We disclose fundamental differences between both mechanisms and explain why the evolution of exploitation is less constrained than that of mimicry. Exploitation of perceptual biases might thus be a precursor for the gradual evolution of mimicry. Increasing knowledge on the sensory and cognitive filters in animals, and on the selective pressures that maintain them, should aid researchers in tracing the evolutionary dynamics of deception in plants.

The evolution of deception

Species resemble each other owing to a shared phylogenetic history or adaptation to a similar abiotic or biotic environment. Among the various adaptations that plants show, deception of other organisms is arguably one of the most intriguing. Traditionally, mimicry has been the primary concept put forward to explain deception. The mimicry hypothesis rests upon the principal assumptions that the model (species that is imitated) and the mimic (species imitating the model) interact with the same receiver individuals, that the receiver mistakes one for the other, and that this mistake has important fitness consequences for the mimic and, often, also for the model [1–5]. Mimicry is a theoretically and empirically well established phenomenon in the animal kingdom [1], but mimicry involving plants is contentious. This is partly due to the fact that deception, and to a lesser extent resemblance, might also arise through a different, albeit related, mechanism: exploitation of perceptual biases (EPB; see Glossary).

The EPB model posits that receivers have pre-existing sensory and/or cognitive biases (Box 1) for particular traits and that selection therefore favours any sender that evolves a trait matching these biases. The EPB model is broader than two related models of signal evolution: sensory exploitation and sensory traps [6–8]. These models differ in their relative emphasis on sensory and cognitive biases; with sensory biases being more important in sensory exploitation and cognitive biases in sensory traps [9]. The EPB model is also different from the pre-existing biases model that emphasises that biases of animals occurred before the evolution of a trait [10]. All of these models have been developed in the context of mate choice, and only sensory exploitation has recently been explicitly applied to the evolution of plant traits [11,12]. We use the EPB model because the selective pressures on plants are a product of the sensory and cognitive abilities of animals, and it will often be difficult to identify unambiguously a specific proximate mechanism. Moreover, biases might arise at the interface of sensory and higher cognitive processes (e.g. during the initial coding of colour information). Lastly, plant–animal interactions are often the result of diffuse coevolution [13]. This complicates

Glossary

Advergent evolution: one-sided evolution of a mimic to resemble a model species.
Batesian mimicry: model and mimic resemble each other but have different qualities. In protective mimicry, the mimic is a potential prey species (e.g. plant) that avoids predators (e.g. herbivores) by mimicking a better defended plant. In reproductive mimicry, a model flower offers a reward, whereas the mimic is rewardless and benefits from pollinators that mistake it for the model.
Diffuse coevolution: occurs in the interactions between multiple species. In such interactions, selection is not pairwise, between one plant species and one animal species, but depends on the composition of the plant and animal community interacting with the focal species.
Exploitation of perceptual biases: this model predicts that traits evolve that exploit perceptual biases of the animals that the sender communicates with. In contrast to other models, this model explicitly encompasses sensory, neuronal and higher cognitive processes within the term 'perceptual bias'.
Generalisation: the treatment of stimuli that can be discriminated as equivalent. Generalisation is an important component of categorisation.
Generalised food deception: rewardless flowers that do not mimic a particular model species. Orchids that rely on generalised food deception often bloom gregariously, exhibit large, flamboyant floral displays, and are often polymorphic in floral colour. They exploit the tendency of pollinators to react to large or conspicuously coloured displays.
Peak shift: the development of a new preference that results from discrimination learning. Learning to discriminate between differently rewarding stimuli results in a stronger response towards new stimuli that are more differentiated from the unrewarding stimulus that the animal learned to avoid.
Pre-existing biases: this model predicts that sensory or cognitive biases are ancestral, pre-dating the evolution of novel traits matching those biases.
Sensory exploitation: sensory systems have innate properties that affect the perception of, and the preference for, stimuli. Traits that are most successful in stimulating the sensory system of the receivers are favoured.
Sensory trap: an out-of-context response to signals that are similar to those that the signal receiver responds to in a different context.
Sexual deception: sexually deceptive flowers use visual and olfactory mimicry of female pollinators to sexually entice males. In all known cases, chemical mimicry of the sex pheromone is the basis of the initial and long-distance attraction of pollinators to the orchid flowers, whereas visual mimicry probably operates on a shorter range. Pollination occurs during a pre-mating routine or attempted mating with the flower.
Syndrome: a set of plant traits that evolves under the selective pressure of animal mutualists.

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0169-5347/$ – see front matter © 2009 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2009.06.006 Available online 14 August 2009

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Box 1. Perceptual biases.

Biases driving signal evolution might originate in the sensory system or they might be cognitive and induced by learning. Cognitive biases appear to be a general property of discrimination learning [18]. If a signal receiver is faced with two or more stimuli that differ consistently in their returns, animals learn to distinguish among them. Learning is enhanced if the time lag between encountering the stimuli and experiencing the returns is short [66]. Learning should thus be rapid if nutritional rewards can be assessed by gustatory rather than post-ingestive feedbacks, as is likely for the sugary rewards of many pollinators. This view is compatible with the pronounced learning abilities that well-studied generalised pollinators, such as bees, exhibit [67], but which are also found in other pollinators [41]. Cognitive biases can also arise from the retrieval functions of memory. Colour preferences in honeybees shift during the day according to the circadian rhythm of the retrieval of colour memories. This circadian rhythm apparently tracks the circadian rhythm of nectar and pollen production in differently coloured flowers [68].

Learning to associate olfactory or visual stimuli and their respective rewards leads to generalisation, which occurs if an animal treats similar stimuli as equivalents. Generalisation is thus a cognitive bias that depends upon chemical properties in olfaction [69], and upon perceived colour similarity in vision [70–72]. Learning abilities might lead ultimately not only to the evolution of innate sensory colour biases [17], but also preferences for stimuli that have not been experienced before [73]. Learning to distinguish among differently rewarding stimuli results in a new preference for stimuli that is more extreme on the dimension separating the original stimuli [74]. The shift thus occurs on an axis away from the non-rewarding stimulus. This mechanism is termed 'peak shift' because the peak of the preference shifts during the learning process. Peak shift is a common phenomenon, being taxonomically widespread in animals (including pollinators [73]). Currently, it is unknown if peak shift phenomena are sufficiently consistent to influence plant colour evolution. Spatial and temporal variability in species composition as well as weak penalties associated with misidentification might argue against a strong influence of learning upon trait evolution in plants. Yet, investigation of perceptual errors, attention limited by the rate of information processing [75] and the retrieval and devaluation rate of memory properties will be crucial for understanding pollinator behaviour as an adaptation and driver of diffuse coevolution between animals and plants.

assumptions on the sequence of events, most specifically whether biases usually pre-date the evolution of a trait that exploits them or *vice versa*.

To understand the evolutionary significance of perceptual biases, it is important to remember that, in general, perception is a subjective filter through which objective reality is processed. Natural selection upon the perceptual system of animals might lead to sensory and cognitive biases. Sensory biases occur because the sensory system of the signal receiver is stimulated more effectively by certain properties of stimuli [9]. Widespread sensory biases include the generalised preferences for larger sizes in mates that species from many animal classes exhibit [14]. Interestingly, size preferences are also apparent when animals forage on the rewards provided by plants [12,15,16]. Cognitive biases arise from generalisation and peak shift phenomena that occur during associative learning of signal and reward [17,18]. Sensory and cognitive biases can be a consequence of natural selection on other behaviours or traits and form sensory traps. For example, the crab spider *Thomisus spectabilis* contrasts strongly with the flower background on which it ambushes pollinators. Yet, flowers with contrasting spiders on them are more attractive to foraging honeybees than those without spiders [19]. Hence, the strong visual contrasts of *T. spectabilis* form a sensory trap that exploits the innate sensory biases of bees to forage on contrasting flowers. Inherent biases of the perceptual system are widespread occurring across different taxa [14,20]. They might, thus, be an important driver of the evolution of deception.

Here, we review recent progress on understanding deception in flowers to illustrate the conditions that studies of plant mimicry need to meet. We compare mimicry with the EPB model to elucidate the distinct proximate mechanisms underlying each model. Specifically, we show why exploitation of the sensory or cognitive biases of animals is a simpler, neglected mechanism compared with mimicry, and one that could explain the imperfect resemblance seen in some (and perhaps many) putative plant mimicry systems. We also show why exploitation of perceptual biases and mimicry are best envisioned as a continuum, and that the EPB model can be a pre-adaptation for the gradual evolution of more specific mimicry. Although deception occurs in distinct plant communication systems, we focus predominantly on pollination, simply because most research has been done in this field.

Floral mimicry and perceptual exploitation

The mimicry hypothesis rests upon more restricted assumptions than does EPB. Only mimicry requires: (i) a specific model; (ii) that mimic and model rely on the same individual animals; and (iii) that individuals mistake one species for a particular other species because mimic and model converge in the perceptual world of the dupe [3,21,22]. Owing to the difficulty of verifying these assumptions, it was concluded ten years ago that the evidence for mimicry in plants was poor, even in flowers, the most intensively studied communication system where, until recently, 'no case of floral mimicry has ever been fully verified' [3].

All the conditions that mimicry relies upon have recently been verified in two studies on adaptive floral colouration [23,24]. These studies capitalised on an increasing wealth of understanding on the sensory abilities of animals. They used visual models that are based on the spectral sensitivities of bees to show that mimic and model are indistinguishable according to the visual perception of bees. Key to establishing mimicry has been the demonstration that resemblance is adaptive. Both studies confirmed that the mimic achieves higher pollination success in the presence of the model than in its absence. Specifically, the pollination success of the rewardless orchid *Eulophia zeyheriana* decreased with increasing distance from the model species [24], probably because the mean rewards that pollinators experience in response to the floral stimuli declines with distance from the model. This result is consistent with the notion that the evolutionary dynamics of mimicry systems depends on the relative abundance of mimic and model [25]. Although these examples show that research on floral mimicry

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Box 2. Mimicry in other plant communication systems.

Fruit mimicry has been suggested in colourful seeds and less rewarding fleshy fruits that might mimic more attractive fleshy fruits (Figure Ia, b [62,63,76,77]). The hypothesis of fruit mimicry is controversial because colourful seeds might benefit from mutualism with birds that use them to aid digestion and defecate them unharmed [78]. As yet, model species for putatively mimetic seeds have rarely been identified, let alone the overlap in consumers between mimic and putative model addressed and fitness benefits quantified. Given that seed dispersers prefer conspicuous fruit displays [43], perceptual exploitation is a plausible alternative mechanism to ensure dispersal of highly contrasting seeds.

The hypothesis of protective mimicry in vegetative tissue predicts that plants mimic infestation by herbivores (e.g. aphids) or the presence of predators (e.g. ants; Figure Ic) to reduce the rate of herbivory [64]. As yet, neither the anti-herbivore benefits of these markings, nor the benefits that arise through mimicry, have been demonstrated. Perceptual exploitation is an unlikely alternative because it is currently unknown which biases could be exploited by the plants.

Leaf variegation is a phenomenon where white, green, or sometimes red mottling is found on the upper parts of leaves (Figure Id,e). Studies documenting lower damage by herbivores on variegated leaves compared with non-variegated leaves yielded support for a defensive function of leaf variegation [65,79,80]. It might function to mimic damage inflicted by herbivores (the mimicry hypothesis) or to undermine recognition of leaf shape and identity as camouflage (the camouflage hypothesis) [81]. To tease apart these hypotheses, it is necessary to examine whether variegated leaves are detected but not approached or whether they are more difficult to detect than are non-variegated leaves.

Convergence between parasitic mistletoes and their hosts might be explicable by mimicry [82] or as a byproduct of the common environment that both species experience. Mistletoes commonly suffer up to twice as much herbivory as do their better-defended host trees [83]. The obligate association between specialist mistletoes and their hosts, as well as the potential fitness benefits associated with mimicry are conditions that favour the evolution of mimicry. However, the rates of herbivory did not differ between a mistletoe species mimicking the hosts and another that did not [83]. Thus, although the case for adaptive resemblance is striking, the central prediction of a fitness benefit of mimicry in mistletoes has not yet been supported.

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Figure I. Examples of possible mimicry in fruits and vegetative tissue. Colourful seeds, such as those of *Adenanthera pavonina* **(a)** and *Sterculia brevissima* **(b)**, have been suggested to enhance dispersal by mimicking fleshy fruits [62,63]. Dark plant colours have been hypothesised to mimic predator infestation, such as in *Xanthum trumarium* **(c)** [64]. Leaf variegation has been hypothesised to have a protective function by mimicking leaf damage by herbivores, as highlighted by the colouration of an intact leaf of *Caladium steudneriifolium* **(d)** compared with that of a damaged leaf that was attacked by mining moth caterpillars **(e)** [65]. Reproduced with permission from Mauro Galetti (a,b); Simcha Lev-Yadun (c); and Ulf Soltau (d,e).

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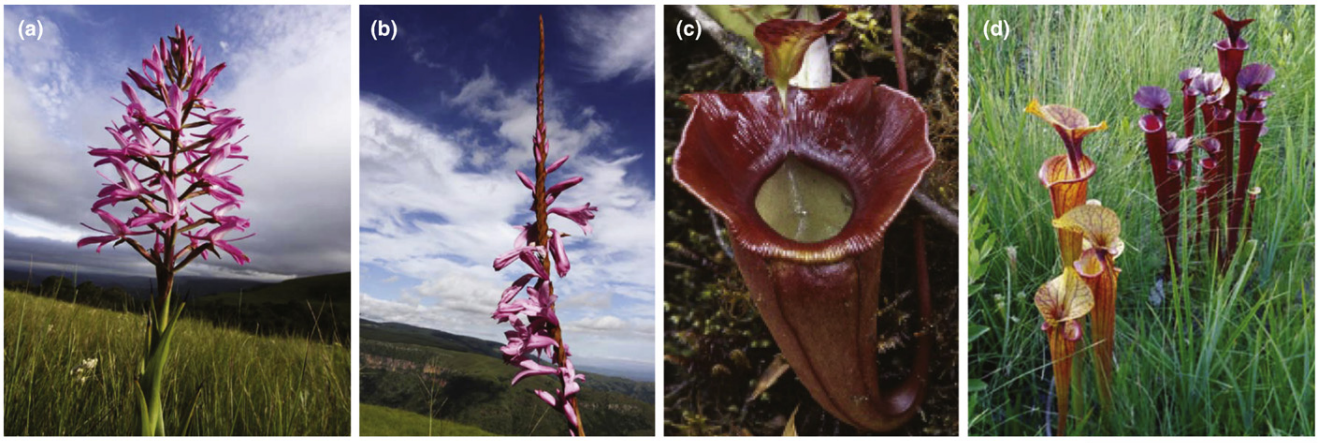

Figure 1. Mimicry and perceptual exploitation in flowers and carnivorous plants. Flowers of the unrewarding orchid *Disa nervosa* **(a)** mimic flowers of the rewarding iris *Watsonia densiflora* **(b)** [61]. Pitcher plants from two families [**(c)** *Nepenthes jacqulinae*; **(d)** *Sarracenia flava*] have been suggested to mimic flowers, although no particular model species has been identified [2,5] and experimental evidence is still lacking. Reproduced with permission from Dennis Hansen (a, b) and Andreas Wistuba (c, d).

has progressed substantially in recent years, a cautious view on mimicry [3] applies to the suggestions of mimicry in other plant communication systems (Box 2).

Permanently unrewarding flowers, such as those of *E. zeyheriana,* have evolved many times across a broad range of flowering plants, occurring in at least 32 families [26]. Orchids are arguably the prime example of deceptive flowers: approximately one-third of all species do not offer rewards to pollinators [27] (Figure 1). Rewardless orchids commonly use food or sexual deception to attract pollinators, although deception can also involve brood site or shelter imitation in orchids and other plant families (e.g. Araceae) [27–29]. All strategies are traditionally described as mimicry. Food-deceptive species mimic rewarding species; whereas sexually deceptive orchids mimic female pollinators and sexually entice males, with pollination occurring during a pre-mating routine or attempted mating with the flower [30]. However, not all rewardless orchids are mimics; many use a strategy of generalised food deception, sporting large, flamboyant and often polymorphic floral displays [27,31]. This strategy lacks a particular model species and relies upon the perceptual exploitation of pollinators. Thus, one key distinction between mimicry and the EPB model is that only mimicry predicts that animals confuse one species (the mimic) with another one (the model). Yet, convergence might also result from the EPB model because rewarding or unrewarding species can form syndromes that are selected for by the perceptual biases of animals (Figure 2).

The colour polymorphisms of orchids with generalised food deception might seem at odds with the exploitation of innate biases. However, different colours could exploit the same perceptual bias for contrasting displays. Given that rare morphs in polymorphic unrewarding flowers can be selectively favoured [32–34], an attractive hypothesis posits that polymorphism is a possible counteradaptation to negative frequency-dependent selection in deceiving plants. This hypothesis needs to be pitted against the alternative hypothesis that flower polymorphisms are selected by differential vegetative fitness rather than by selection imposed by pollinators [35,36].

The mode of deception can have evolutionary consequences on the mechanisms of reproductive isolation. Orchids relying on generalised food deception often show substantial pollinator sharing [37], which reduces premating isolation, possibly leading to the increased arrival of foreign pollen on the stigmata and increased competition for space. As a consequence, orchids show prezygotic, morphological adaptations to direct pollen to distinct parts of the body of pollinators or increasing postzygotic isolation barriers, such as karyotype differentiation [38]. We suggest that morphological adaptations are more likely to have an isolating effect in mimics than in species using perceptual exploitation because mimicry involves fewer plant species. We thus expect postzygotic isolating barriers to be particularly pronounced in species that grow in sympatry and rely on perceptual exploitation.

Assessing the relative frequency of mimicry and perceptual exploitation in rewardless flowers illustrates the relative biological significance of each concept. Despite the repeated evolution of rewardless flowers, data on the mechanism of deception are available only for orchids. In food-deceptive orchids, exploitation of the perceptual biases of pollinators without a specific model is postulated in six times as many genera (38) as mimicry (9) [27]. Similarly, sexually deceptive orchids use mimicry and sensory exploitation (Box 3) [39]. These facts alone should alert scientists against prematurely accepting mimicry of particular species as the primary mechanism of deception in flowers.

Maintenance of perceptual biases

How are perceptual biases maintained in the animals that interact with plants? In the simplest form, perceptual biases such as the preferences of bumblebees for violet, the most rewarding floral colour, are adaptive because they enable pollinators to harvest more nectar per unit time [40]. Although innate preferences can be modulated by experience [41], correlated selection upon the perceptual system of animals can maintain biases even if they are not adaptive in one particular context.

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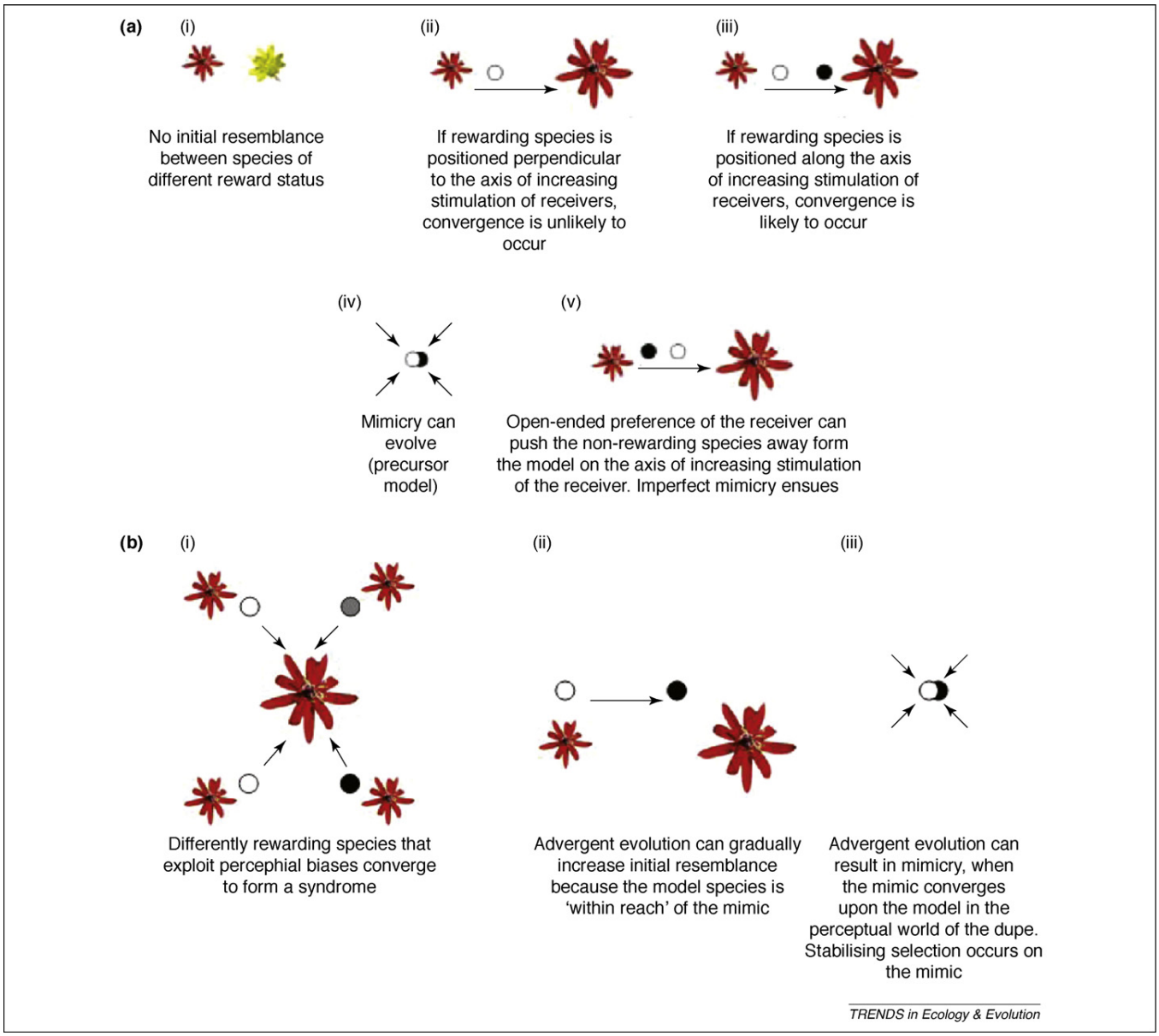

Figure 2. Scenarios of the evolution of deception. The gradual evolution of deception can occur through distinct evolutionary trajectories: the exploitation model **(a)** and the precursor model **(b)**. The figure illustrates the evolution of mimicry and perceptual exploitation in the perceptual world of a signal receiver. To illustrate a perceptual bias, we used differently sized flowers, with larger flowers indicating greater stimulation of the receiver. The bias could, however, concern traits other than size, such as contrasts or particular scents. Arrows document the direction of selection; that is, they depict the predicted trajectory of a given trait. In each model, numbers represent different steps in the gradual evolution of deception. Dot colour indicates variation in rewards: black dots indicate highly rewarding plants; white dots unrewarding plants; and grey dots species offering intermediate rewards. Although both models differ in their initial phase, they can both lead to mimicry as a possible, but not necessary, outcome.

The design of the perceptual systems of most animals is unknown, but there is good evidence that the visual system of frugivorous and folivorous primates is optimised for detecting anything that is not a mature leaf [42]. Thus, the background against which targets are seen, rather than the targets themselves, select for the design of primate vision because variance in the background determines the noise against which signals need to stand out. If background noise selects more generally for the design of visual systems in animals, animals sharing a common environment are likely to have developed similar mechanisms for detecting targets.

Perceptual biases are important in foraging because most insect-pollinated flowers and fleshy fruits differ from their predominantly leafy green background in colour, scent and shape. The colour contrasts of flowers and fruits to their background present one proximate mechanism for their rapid identification. Sensory biases for strong visual contrasts in honeybees and four frugivorous bird species [12,43] are thus probably maintained because they represent a fundamental mechanism used to identify and locate food resources and mates. Interestingly, these species prefer conspicuous plant displays even at close range [12,43], apparently independent of their relative detectability. Hence, animals select for enhanced contrasts of visual traits because they increase the ease of detection from a long range but also because they are more effective in stimulating their sensory systems at close range.

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Box 3. Mimicry versus perceptual exploitation.

Sexually deceptive orchids of the genus *Ophrys* are a prime example of mimicry in plants and, surprisingly, also for perceptual exploitation. These orchids are sensory traps that exploit the innate biases of males to respond to the pheromones of females. Batesian mimicry is expected to select for signal convergence between the bouquet of the orchid and that of the sexual pheromone. Indeed, *Ophrys exaltata* emits volatiles that are identical to that of the pheromone, but the relative proportions differ statistically [11]. Imperfect mimicry does not reduce the attractiveness of the flowers. By contrast, males prefer flower bouquets to the sexual pheromone of local females [11]. This is likely to be explained by the perceptual biases of males to prefer unfamiliar pheromones, a tendency that might help them avoid inbreeding or mating several times with the same female. Hence, perceptual biases can select for signal divergence and imperfect mimicry [11].

Imperfect mimicry in the rewarding orchid *Epipactis helleborine* might also be explicable by perceptual exploitation. This orchid emits seven volatiles that attract its wasp pollinators. These volatiles also occur in the emissions of plants when they are attacked by herbivores [84]. Given that wasps often predate on herbivorous insects, the orchid potentially mimics the induced volatiles that many plants use to fight herbivores. However, the absolute amount of emitted volatiles and their relative proportion differ from induced volatiles. Although mimicry does not necessarily lead to perfect mimicry owing to perceptual errors of receivers [58,85], the orchid could also exploit the pre-existing sensory biases of wasps to respond to certain volatiles that are often associated with herbivorous insects. This alternative explanation does not require a match between the bouquet of the orchid and that of attacked plants.

There are two important implications of these studies. First, selection imposed by perceptual exploitation might counter selection imposed by mimicry, and thereby lead to an imperfect match between mimic and model (Figure 2, main text). Second, in some communication systems, perceptual exploitation and mimicry might be complementary [59] rather than mutually exclusive strategies. Understanding the sensory and cognitive biases of pollinators is thus key to explaining the dynamics and evolutionary trajectories of deception, including the initial steps of advergent evolution in signal convergence [40,73].

Rewardless flowers or seeds can thus exploit biases for contrasting displays because animals obtain on average net benefits (in terms of time and energy) by approaching contrasting displays even though some of them turn out to be rewardless.

Perceptual biases arise also from the neuronal coding of colour information [9]. Many herbivorous insects use colour and scent to locate their host plants. Colour vision is based on a comparison of the excitation of receptors that differ in spectral sensitivities. Insects and primates have opponent neural interactions between different sensory receptors to extract colour information. Inhibitory interactions between the green and blue receptors result in a particular strong preference for yellow because it is associated with high excitation of the green receptor and low excitation of the blue receptor [44]. This mechanism explains the widespread preference of herbivorous insects for yellow over green stimuli because yellow targets represent a 'supernormal foliage-type stimulus' [45]. Pollen feeding in hoverflies might have evolved from yellow pollen being a supernormal stimulus for herbivorous insects. This perceptual bias represents the underlying physiological mechanism for why yellow traps are so effective in capturing many herbivorous insects [44].

If an animal responds to a given stimulus in different contexts, such as foraging and mating, correlated selection is likely to restrict the evolutionary potential to respond optimally in both contexts. The preferences of stingless bees for objects with a dark centre accentuated by radial stripes are a possible example for such a correlated response in distinct contexts. Dark centres and radial stripes are visual features that bees quickly discriminate, that facilitate orientation for landing and that are naturally associated with the shaded entrances to their nests [46]. Many flowers and pitchers of carnivorous plants also sport dark centres and contrasting lateral stripes (Figure 1). Whereas pitchers unavoidably also display a dark centre of their opening, as nests do, carnivorous plants might enhance the attractiveness of pitchers by radiating stripes. As such, convergent evolution driven by exploitation of receiver biases has been suggested to explain similarities in the geometrical patterns between unrelated plant organs, such as pitchers in carnivorous plants and flowers [46].

Selection on signal design

The mimicry and the EPB models make different predictions upon the design of an optimal signal. A core tenet of Batesian mimicry is that the signals of the mimic should converge to that of the model in the perceptual world of the animal. In a few flower mimicry systems, convergence in olfactory or visual traits has been documented based upon the perception of the signal receiver [23,24,47,48]. Orchids were the mimics in each case except for one study where both mimic and model offered rewards, but fitness benefits only occurred in one species [23]. Thus, rather than Müllerian mimicry, where species with similar qualities obtain fitness benefits by evolving towards mutual similarity, this relationship between the perennial herbs *Turnera sidoides* (Turneraceae) and *Sphaeralcea cordobensis* (Malvaceae) can be characterised by advergent evolution [21]. Advergent evolution is one sided; it occurs because *T. sidoides*, the mimic, experiences stronger selection converging upon the signal of *S. cordobensis* [21,23].

Whereas the mimicry hypothesis posits convergence upon the phenotype of the model, convergence occurs in the EPB model because optimal signals match the perceptual biases of the signal receiver. This form of convergence is only seemingly more abstract. The cognitive component of decision making entails that even under the mimicry hypothesis convergence needs to occur in the brain of an animal and not in the phenotypes of mimic and model that are commonly measured. Thus, the fitness landscapes of mimics and of species that exploit perceptual biases are both a product of the perception of the beholder.

The form of selection can differ between the mimicry and EPB models. In both models, selection can be directional to converge upon a model or perceptual bias, respectively, and stabilising afterwards. Deleterious effects of the mimic on the model might cause the model to diverge in a mimicry system, resulting in a coevolutionary chase between mimic and model [49]. However, such a coevolutionary chase is unlikely, at least in flowers, because pollinators need to be tolerant towards variable rewards.

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In the EPB model, a coevolutionary chase is even less likely to occur because natural selection upon the perceptual system is expected to stabilise the perceptual bias. One important difference is that exploitation of perceptual biases can result in open-ended preferences, and thus directional selection, for ever-increasing stimulation of the sensory system (Figure 2). For example, the sexually deceptive orchid *Chiloglottis trapeziformis* matches the preference of its pollinator, males of one species of thynnine wasp, for higher amounts of pheromones by producing ten times more 'pheromones' than do the wasp females [50].

Learning

Selection upon convergence depends more strongly upon learning in mimicry compared with the EPB model. In the EPB model, inherent properties of the perceptual system select for the most effective signals that senders should converge on. Under the mimicry hypothesis, however, selection for convergence depends upon the penalties associated with mistaking one species for another [51] and the resultant extent of learning and generalisation (Box 1) of the receiver.

In plants, the penalties associated with mistakes are often minor. Mistaking flowers is a waste of time and energy for the animal, but it does not inflict as strong a fitness cost as mistaking a harmless snake for a poisonous one. Carnivorous plants that feed on animals are an exception from this rule. Pitcher plants have been hypothesised to mimic flowers by duping insects into landing on pitchers in the mistaken belief that they are flowers [2,5]. However, empirical support for floral mimicry is lacking and unlikely to occur [52]. Joel [52] argued that pitchers do not strongly resemble flowers, that the overlap between trap activity and floral activity is poor, and that insects do not visit pitchers by mistake. He argued that insects visit pitchers because these provide them with nectar rewards with only few visitors being caught by the plant.

Thus, if animals experience overall moderate-to-low fitness costs when verifying plant signals, the mimicry hypothesis requires signal convergence and a tight spatial and temporal association between mimic and model [53]. Given the many examples of signal convergence in Batesian mimicry in the animal kingdom, it is necessary to examine why it is apparently rarer in plants, particularly because it has been suggested that most evolution occurs on the side of the plant in some systems, such as orchid–pollinator interactions [31].

Several mechanisms related to the ecology of plant–animal interactions severely restrict the potential for learning-induced selection for signal convergence. First, the typically low frequency of most unrewarding plants reduces selection for learned avoidance because most pollinators do not encounter permanently non-rewarding plants often. Second, pollinators need to be tolerant towards variable returns of nectar or pollen in rewarding plants because they are unable to distinguish from a distance flowers that were recently depleted by another pollinator from those that were not [26,54]. Variance in nectar returns considerably diminishes the learning rate of pollinators even under the reduced complexity of laboratory conditions [55,56]. Thus, it is this unpredictability of nutritional returns that probably explains why negative stimuli are learned more slowly than positive stimuli in honeybees and bumblebees [57].

If one envisions the ecological setting in a vegetation community where flower species differ in their nutritional returns (both in terms of quality and quantity), and individuals of rewarding species differ unpredictably in their returns, one can expect that even the most skilful pollinators need at least a few repeated visits to a given species to learn its average reward status. If learning requires repeated visits to associate the signal and reward of a given flower species, selection for convergence is relaxed. Rewardless flowers might thus achieve efficient pollination without mimicking rewarding models, as evidenced by the many rewardless orchids that lack a model.

Mimicry and perceptual exploitation as a continuum

Thus far, we have focussed on the difference between mimicry and the EPB model. However, it is important to note the interdependence of the distinct functional mechanisms that both models rely upon. If the perceptual biases of animals are consistent across taxa, for example owing to the inherent coding of visual information, they can select for apparent mimicry in plants even though there is no model. Thus, the EPB model could explain the initial phase of convergence as well as the maintenance of the imperfect resemblances that have long intrigued evolutionary biologists [58] (Figure 2).

The EPB model is unaffected by temporal and spatial variability in plant species composition. Variability of species assemblages should strongly select against mimicry because it reduces the consistent association between mimic and model [59]. Given that the exploitation of perceptual biases is, ecologically, a less restrictive strategy than mimicry, it might be a precursor for more specialised mimicry in non-rewarding plants if mimic and model show consistent spatio-temporal association. In this scenario, the EPB model resolves the debate about whether mimicry evolves gradually owing to micromutations or by punctuated leaps of macromutations [60]. This is because if distinct plants exploit similar sensory biases, they can be 'within reach' in animals' perceptual world for mimicry to evolve gradually (Figure 2). Conceivably, mimicry, once it has evolved, could also revert back to perceptual exploitation if, for example, variability in ecological factors reduces the consistency of the association between mimic and model.

There is as yet insufficient knowledge on the mode of deception in plants to establish firmly the sequence of events in the evolution of deception. The available evidence does support the precursor model. Mimicry in rewardless orchids is based upon apomorphic features of relatively recent origin [21]. Likewise, the mimic *Eulophia zeyheriana* is a derived species from an ancestral lineage of orchids that exploit perceptual biases [24].

Conclusions

Mimicry is a flagship example of adaptation to biotic interactions. Recent studies unequivocally established that it occurs in rewarding and unrewarding flowers.

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Box 4. Outstanding questions.

- Community ecology: what is the relative frequency of perceptual exploitation and mimicry in distinct plant–animal communication systems? Can we identify (based on such data) the specific ecological conditions that lead to the maintenance of perceptual biases? Does perceptual exploitation occur more often in flowering plants that are prone to environmental perturbations and, consequently, are characterised by high species turnover [59]? Do geographically variable receiver biases and preferences select for population differentiation in the traits used for communication by plants [86]?
- Learning: the variability in returns that an insect experiences for a given stimulus will determine the impact of learning on the evolution of deception. What is the variability in nutritional returns to a given stimulus (e.g. flower size) at the timescale of the life of an insect and over evolutionary time? Low variability in returns over evolutionary time could favour the evolution of perceptual biases. The variability in returns over both timescales is mostly unknown but is important for understanding how selective pressures on plant traits can be inferred from the results from laboratory experiments.
- Evolution of deception: can mimicry and perceptual exploitation be precursors for each other (Figure 2, main text)? If so, what are the ecological or evolutionary factors that promote a switch from perceptual exploitation to mimicry and *vice versa*? It will be important to understand whether we can generally expect the selective pressures underlying each concept to be opposed [11]. In sexually deceptive flowers, it will be important to quantify the relative contribution of exploitation versus mimicry in the maintenance of this communication system.
- Evolutionary significance of the mode of deception: are the selective pressures of perceptual exploitation upon the visual or chemical appearance of plants more relaxed than those associated with mimicking a particular model? Does mimicry generally involve fewer plant species than the exploitation of perceptual biases? If so, is prezygotic isolation generally more important in floral mimicry than for sensory exploitation?
- Exploitation of biases: how consistent are perceptual biases across generations and across species? How important is learning in the ecological settings of natural vegetation communities in modulating such biases? A better understanding of the cognitive processes that are involved in the recognition of visual and olfactory stimuli will enable signal convergence according to the perceptual world of animals to be tested more rigorously. It might also enable one to differentiate between convergence driven by mimicry and convergence driven by the exploitation of perceptual biases.

However, mimicry is a rare phenomenon in plants. Exploitation of the perceptual biases of animals is a related and possibly more widespread strategy. In contrast to mimicry, it is not reliant upon a consistent spatio-temporal association between species. The mimicry and EPB models rely on different functional mechanisms leading to different degrees of resemblance. Given that the EPB is the less restricted model, it might be the precursor for the evolution of mimicry. This is an exciting perspective because the initial steps of gradual evolution towards mimicry result in only a vague resemblance that is often seen as maladaptive. The precursor hypothesis is easily testable if an explicit phylogenetic approach is combined with models of the visual or olfactory perception of animals. In sum, to understand the evolutionary trajectories of deception in plants and perhaps even in animals, it will be necessary to differentiate between mimicry and the exploitation of perceptual biases on the one hand and address their interdependence on the other (Box 4).

Acknowledgements

We thank Lars Chittka, Florian Schiestl, Steve Johnson, Simcha Lev-Yadun and two anonymous referees for many helpful comments on this manuscript and all photographers for permission to use their images. H.M.S is supported by DFG grants (Scha 1008/4-1, Scha 1008/5-1) and G.D.R is supported by NERC grants NE/F002653/1, NE/E016626/1, NE/D010772/1 and NE/D010500/1.

References

1 Ruxton, G.D. *et al.* (2004) *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry,* Oxford University Press
2 Wickler, W. (1968) *Mimicry,* Kindler Verlag
3 Roy, B.A. and Widmer, A. (1999) Floral mimicry: a fascinating yet poorly understood phenomenon. *Trends Plant Sci.* 4, 325–330
4 Endler, J.A. (1981) An overview of the relationships between mimicry and crypsis. *Biol. J. Linn. Soc.* 16, 25–31
5 Pasteur, G. (1982) A classificatory review of mimicry systems. *Annu. Rev. Ecol. Syst.* 13, 169–199
6 Ryan, M.J. *et al.* (1990) Sexual selection for sensory exploitation in the frog Physalaemus pustulosus. *Nature* 343, 187–195
7 Christy, J.H. (1995) Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* 146, 171–181
8 Proctor, H.C. (1991) Courtship in the water mite *Neumania papillator:* males capitalize on female adaptations for predation. *Anim. Behav.* 42, 589–598
9 Endler, J.A. and Basolo, A.L. (1998) Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* 13, 415–420
10 Basolo, A.L. (1990) Female preference predates the evolution of the sword in swordtail fish. *Science* 250, 808–810
11 Vereecken, N.J. and Schiestl, F.P. (2008) The evolution of imperfect floral mimicry. *Proc. Natl. Acad. Sci. U. S. A.* 105, 7484–7488
12 Naug, D. and Arathi, H.S. (2007) Receiver bias for exaggerated signals in honeybees and its implications for the evolution of floral displays. *Biol. Lett.* 3, 635–637
13 Strauss, S.Y. and Irwin, R.E. (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Syst.* 35, 433–466
14 Ryan, M.J. and Keddy-Hector, A. (1992) Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* 139, S4–S35
15 Kropf, M. and Renner, S.S. (2005) Pollination success in monochromic yellow populations of the rewardless orchid *Dactylorhiza sambucina*. *Plant Syst. Evol.* 254, 185–197
16 Martin, N.H. (2004) Flower size preferences of the honeybee (Apis mellifera) foraging on *Mimulus guttatus* (Scorphulariaceae). *Evol. Ecol. Res.* 6, 777–782
17 Chittka, L. and Raine, N.E. (2006) Recognition of flowers by pollinators. *Curr. Opin. Plant Biol.* 9, 428–435
18 ten Cate, C. and Rowe, C. (2007) Biases in signal evolution: learning makes a difference. *Trends Ecol. Evol.* 22, 380–387
19 Heiling, A.M. *et al.* (2003) Crab-spiders manipulate flower signals. *Nature* 421, 334
20 Vahed, K. (2007) All that glisters is not gold: sensory bias, sexual conflict and nuptial feeding in insects and spiders. *Ethology* 113, 105–127
21 Johnson, S.D. *et al.* (2003) Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. *Biol. J. Linn. Soc.* 80, 289–304
22 Galizia, C.G. *et al.* (2005) Relationship of visual and olfactory signal parameters in a food-deceptive flower mimicry system. *Behav. Ecol.* 16, 159–168
23 Benitez-Vieyra, S. *et al.* (2007) How to look like a mallow: evidence of floral mimicry between Turneraceae and Malvaceae. *Proc. R. Soc. B* 274, 2239–2248
24 Peter, C.I. and Johnson, S.D. (2008) Mimics and magnets: the importance of color and ecological facilitation in floral deception. *Ecology* 89, 1583–1595
25 Ferdy, J.B. *et al.* (1998) Pollinator behavior and deceptive pollination: learning process and floral evolution. *Am. Nat.* 152, 696–705

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26 Renner, S.S. (2005) Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In *Specialisation and Generalization in Pollination Systems* (Waser, N.M. and Ollerton, J., eds), pp. 123–144, University of Chicago Press
27 Jersáková, J. *et al.* (2006) Mechanisms and evolution of deceptive pollination in orchids. *Biol. Rev.* 81, 219–235
28 Dafni, A. (1984) Mimicry and deception in pollination. *Annu. Rev. Ecol. Syst.* 15, 259–278
29 Faegri, K. and van der Pijil, L. (1979) *The Principles of Pollination,* Pergamon Press
30 Schiestl, F.P. (2005) On the success of a swindle: pollination by deception in orchids. *Naturwissenschaften* 92, 255–264
31 Nilsson, L.A. (1992) Orchid pollination biology. *Trends Ecol. Evol.* 7, 255–259
32 Ayasse, M. *et al.* (2000) Evolution of reproductive strategies in the sexually deceptive orchid *Ophrys sphegodes:* How does flower-specific variation of odor signals influence reproductive success? *Evolution* 54, 1995–2006
33 Vereecken, N.J. *et al.* (2007) Population differentiation in female mating signals and male preferences in a solitary bee. *Behav. Ecol. Sociobiol.* 61, 811–821
34 Gigord, L.D.B. *et al.* (2001) Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soó. *Proc. Natl. Acad. Sci. U. S. A.* 98, 6253–6255
35 Jersáková, J. *et al.* (2006) Is the colour dimorphism in *Dactylorhiza sambucina* maintained by differential seed viability instead of frequency-dependent selection? *Folia Geobot.* 41, 61–76
36 Schemske, D.W. and Bierzychudek, P. (2007) Spatial differentiation for flower color in the desert annual *Linanthus parryae:* was Wright right? *Evolution* 61, 2528–2543
37 Cozzolino, S. *et al.* (2005) Evidence for pollinator sharing in Mediterranean nectar-mimic orchids: absence of premating barriers? Proc. *R. Soc. B* 272, 1271–1278
38 Cozzolino, S. and Scopece, G. (2008) Specificity in pollination and consequences for postmating reproductive isolation in deceptive Mediterranean orchids. *Philos. Trans. R. Soc. B* 363, 3037–3046
39 Raguso, R.A. (2008) Wake up and smell the roses: the ecology and evolution of floral scent. *Annu. Rev. Ecol. Syst.* 39, 549–569
40 Raine, N.E. and Chittka, L. (2007) The adaptive significance of sensory bias in a foraging context: floral colour preferences in the Bumblebee *Bombus terrestris*. *PLos One* 2, e556
41 Riffell, J.A. *et al.* (2008) Behavioral consequences of innate preferences and olfactory learning in hawkmoth–flower interactions. *Proc. Natl. Acad. Sci. U. S. A.* 105, 3404–3409
42 Sumner, P. and Mollon, J.D. (2000) Catarrhine photopigments are optimised for detecting targets against a foliage background. *J. Exp. Biol.* 203, 1963–1986
43 Schmidt, V. *et al.* (2004) Conspicuousness, not colour as foraging cue in plant-animal interactions. *Oikos* 106, 551–557
44 Kelber, A. (2001) Receptor based models for spontaneous colour choices in flies and butterflies. *Entomol. Exp. Appl.* 99, 231–244
45 Prokopy, R.J. and Owens, E.D. (1983) Visual detection of plants by herbivorous insects. *Annu. Rev. Entomol.* 28, 337–364
46 Biesmeijer, J.C. *et al.* (2005) Convergent evolution: floral guides, stingless bee nest entrances, and insectivorous pitchers. *Naturwissenschaften* 92, 444–450
47 Johnson, S.D. (1994) Evidence of Batesian mimicry in a butterfly-pollinated orchid. *Biol. J. Linn. Soc.* 53, 91–104
48 Schiestl, F.P. *et al.* (2003) The chemistry of sexual deception in an orchid–wasp pollination system. *Science* 302, 437–438
49 Mallet, J. and Joron, M. (1999) Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annu. Rev. Ecol. Syst.* 30, 201–233
50 Schiestl, F.P. (2004) Floral evolution and pollinator mate choice in a sexually deceptive orchid. *J. Evol. Biol.* 17, 67–75
51 Joron, M. (2008) Batesian mimicry: Can a leopard change its spots – and get them back? Curr. *Biol.* 18, R476–R479
52 Joel, D.M. (1988) Mimicry and mutualism in carnivorous pitcher plants (Sarraceniaceae, Nepenthaceae, Cephalotaceae, Bromeliaceae). *Biol. J. Linn. Soc.* 35, 185–197
53 Prudic, K.L. and Oliver, J.C. (2008) Once a Batesian mimic, not always a Batesian mimic: mimic reverts back to ancestral phenotype when the model is absent. *Proc. R. Soc. B* 275, 1125–1132
54 Schaefer, H.M. *et al.* (2004) How plant-animal interactions signal new insights in communication. *Trends Ecol. Evol.* 19, 577–584
55 Dukas, R. and Real, L.A. (1993) Effects of nectar variance on learning by bumble bees. *Anim. Behav.* 45, 37–41
56 Shafir, S. *et al.* (2003) Cognition-mediated coevolution -context-dependent evaluations and sensitivity of pollinators to variability in nectar rewards. *Plant Syst. Evol* 238, 195–209
57 Menzel, F. and Greggers, U. (1992) Temporal dynamics and foraging behaviour in honeybees. In *Biology and Evolution of Social Insects* (Billen, J., ed.), pp. 303–318, Leuven University Press
58 Chittka, L. and Osorio, D. (2007) Cognitive dimensions of predator responses to imperfect mimicry? *PLOS Biol.* 5, e339
59 Johnson, S.D. *et al.* (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84, 2919–2927
60 Franks, D.W. and Sheratt, T.N. (2007) The evolution of multi-component mimicry. *J. Theor. Biol.* 244, 631–639
61 Johnson, S.D. and Morita, S. (2006) Lying to Pinocchio: floral deception in an orchid pollinated by long-proboscid flies. *Biol. J. Linn. Soc.* 152, 271–278
62 McKey, D. (1975) The ecology of coevolved seed dispersal systems. In *Coevolution of Animals and Plants* (Gilbert, L.E. and Raven, P.H., eds), pp. 159–191, University of Texas Press
63 Van der Pijil, L. (1972) *Principles of Dispersal in Higher Plants,* Springer-Verlag
64 Lev-Yadun, S. and Inbar, M. (2002) Defensive ant, aphid and caterpillar mimicry in plants? Biol. *J. Linn. Soc.* 77, 393–398
65 Soltau, U. *et al.* (2009) Leaf variegation in Caladium steudneriifolium (Araceae): a case of mimicry? *Evol. Ecol.* 23, 503–512
66 Yearsley, J.M. *et al.* (2006) A theory of associating food types with their postingestive consequences. *Am. Nat.* 167, 705–716
67 Menzel, R. *et al.* (1993) Functional organization of appetitive learning and memory in a generalist pollinator, the honey bee. In *Insect Learning* (Papaj, D.R. and Lewis, A.C., eds), pp. 79–125, Chapman & Hall
68 Prabhu, C. and Cheng, K. (2008) One day is all it takes: circadian modulation of the retrieval of colour memories in honeybees. *Behav. Ecol. Sociobiol.* 63, 11–22
69 Guerrieri, F. *et al.* (2005) Perceptual and neural olfactory similarity in honeybees. *PLOS Biol.* 3, e60
70 Gumbert, A. (2000) Color choices by bumble bees *(Bombus terrestris):* Innate preferences and generalization after learning. *Behav. Ecol. Sociobiol.* 48, 36–43
71 Jones, C.D. *et al.* (2001) Colour categorization by domestic chicks. *Proc. R. Soc. B* 268, 2077–2084
72 Jansson, L. and Enquist, M. (2003) Receiver bias for colourful signals. *Anim. Behav.* 66, 965–971
73 Lynn, S.K. *et al.* (2005) Peak shift discrimination learning as a mechanism of signal evolution. *Evolution* 59, 1300–1305
74 Shettleworth, S.J. (1998) *Cognition, Evolution, and Behaviour,* Oxford University Press
75 Dukas, R. (2002) Behavioural and ecological consequences of limited attention. *Philos. Trans. R. Soc. B* 357, 1539–1547
76 Burns, K.C. (2005) Does mimicry occur between fleshy-fruits? Evol. *Ecol. Res.* 7, 1067–1076
77 Galetti, M. (2002) Seed dispersal of mimetic seeds: parasitism, mutualism, aposematism or exaptation? In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (Levey, D.J. and et, al., eds), pp. 177–191, CABI Publishing
78 Peres, C.A. and van Roosmalen, M.G.M. (1996) Avian dispersal of 'mimetic seeds' of *Ormosia lignivalvis* by terrestrial granivores: deception of mutualism? *Oikos* 75, 249–258
79 Campitelli, B.E. *et al.* (2008) Leaf variegation is associated with reduced herbivore damage in *Hydrophyllum virginianum*. *Botany Botanique* 86, 306–313
80 Smith, A.P. (1986) Ecology of a leaf color polymorphism in a tropical forest species. habitat segregation and herbivory. *Oecologia* 69, 283–287

Author's personal copy

81 Givnish, T.J. (1990) Leaf mottling: relation to growth form and leaf phenology and possible role as camouflage. *Funct. Ecol.* 4, 463–474
82 Barlow, B.A. and Wiens, D. (1977) Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. *Evolution* 31, 69–84
83 Canyon, D.V. and Hill, C.J. (1997) Mistletoe host-resemblance: a study of herbivory, nitrogen and moisture in two Australian mistletoes and their host trees. *Austr. J. Ecol.* 22, 395–403
84 Brodmann, J. *et al.* (2008) Orchids mimic green-leaf volatiles to attract prey-hunting wasps for pollination. *Curr. Biol.* 18, 740–744
85 Chittka, L. *et al.* (2009) Speed–accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* 24, 400–407
86 Mant, J. *et al.* (2005) Does selection on floral odor promote differentiation among populations and species of the sexually deceptive orchid genus *Ophrys*? *Evolution* 59, 1449–1463