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The potential for floral mimicry in rewardless orchids: an experimental study

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More than one-third of orchid species do not provide their pollinators with either pollen or nectar rewards. Floral mimicry could explain the maintenance of these rewardless orchid species, but most rewardless orchids do not appear to have a rewarding plant that they mimic specifically. We tested the hypothesis that floral mimicry can occur through similarity based on corolla colour alone, using naive bumble-bees foraging on arrays of plants with one rewarding model species, and one rewardless putative mimic species (*Dactylorhiza sambucina*) which had two colour morphs. We found that when bees were inexperienced, they visited both rewardless morphs randomly. However, after bees had gained experience with the rewarding model, and it was removed from the experiment, bees resampled preferentially the rewardless morph most similar to it in corolla colour. This is the first clear evidence, to our knowledge, that pollinators could select for floral mimicry. We suggest that floral mimicry can be a selective force acting on rewardless orchids, but only under some ecological conditions. In particular, we argue that selection on early-flowering rewardless orchids that receive visits from a large pool of naive pollinators will be weakly influenced by mimicry.

Keywords: pollinator; bumble-bee; *Dactylorhiza sambucina*; visitation rate

1. INTRODUCTION

Mimicry in animals has long excited naturalists and evolutionary biologists (Bates 1862). Observations of close resemblance in the appearance of some animals to other animals or inanimate objects, which have frequently been suggested to be predator avoidance strategies, have led to a range of experimental and comparative approaches to elucidate the evolutionary and ecological pressures behind this phenomenon. Mimicry has also been suggested to occur in the plant kingdom, but mimicry in plants has remained enigmatic and poorly studied (reviewed by Roy & Widmer 1999).

Mimicry in plants has been most frequently suggested in the context of plant–pollinator interactions (Wiens 1978; Dafni 1984). Some species of flowering plants, particularly amongst the Orchidaceae, produce no nectar, pollen or other forms of rewards for their pollinators (Ackerman 1986; Dafni 1987). The evolution of such a rewardless strategy is difficult to explain, because many rewardless species appear to have lowered reproductive success compared with their rewarding relatives (Neiland & Wilcock 1998). Theoretical models have suggested, however, that rewardlessness could only spread in a species under a Batesian mimicry system (Bell 1986), where pollinators confuse a rewardless species (the mimic) with a coflowering plant species that produces abundant reward (the model). Mimicry theory would predict that visitation rates to rewardless forms would decrease with their increasing abundance relative to rewarding forms (Ferdy *et al.* 1998), but also that selection would favour the mimics most similar in form to those of the model. In contrast to these predictions, very little evidence for floral mimicry in nature has been produced (Dafni & Ivri 1981; Johnson 1994, 2000)—in particular, there are very few convincing cases where the floral form of a rewardless mimic has evolved to closely resemble that of a rewarding model, nor experimental evidence that the fitness of a rewardless species increases in the presence of its putative model (Roy & Widmer 1999; Johnson 2000). Orchids have also been suggested to have evolved mimicry of other stimuli; in particular, in pseudocopulatory systems the orchid apparently resembles a female insect and is pollinated by a mating male (Dafni 1984, 1987; Ackerman 1986), although such systems also appear to be comparatively rare. How, then, can the continued successful pollination of the large number of rewardless orchid species be explained? It has been suggested that mimicry based purely on corolla colour, without further resemblance in floral form, is sufficient to cause pollinators to confuse model and mimic (Nilsson 1980, 1983; Gumbert & Kunze 2001). By contrast, it has also been suggested that no specific mimicry is involved in pollinator attraction, and that rewardless orchids rely on mistaken or sampling visits from naive pollinators attracted to a potential source of food (non-model deception; Ackerman 1986; Dafni 1987). Pollinators are expected to sample all available species randomly, in proportion to their abundances, at the start of their foraging careers, but learning processes are subsequently expected to lead to discrimination and avoidance of rewardless species (Smithson & Macnair 1997; Ferdy *et al.* 1998). Many rewardless species have been suggested to attract pollinators through non-model deception (Ackerman 1986; Dafni 1987). However, the

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relative importance of the similarity of signals between rewarding co-flowering and rewardless species in terms of pollinator attraction have never been investigated in detail. Is resemblance in corolla colour sufficient for pollinators to confuse rewarding and rewardless species, or is strong resemblance in terms of both colour and morphology essential for floral mimicry?

The purpose of this study was to test, experimentally, the possibility for mimicry on corolla colour alone by quantifying the behaviour of pollinators in response to arrays of plants of three types: one rewarding and thus a putative model, and two rewardless and thus potential mimics. Each rewardless morph was presented at equal frequencies, with one morph being of similar colour to the putative model, and the other of dissimilar colour. Rewarding and rewardless types had dissimilar flower morphologies. We suggested that, if pollinator behaviour was not influenced by colour resemblance alone, pollinators would visit the two rewardless morphs equally throughout the experiment as they were sampling, but learn to avoid both morphs with increasing experience. However, if there was mimicry by corolla colour similarity, we expected that the rewardless morph most similar in colour to the rewarding model would be significantly preferred. Further, visitation to this rewardless morph is not expected to decline with experience, although pollinators would be expected to learn to avoid the alternative rewardless morph. In addition to higher visitation rates, the number of flowers visited per inflorescence, and the time spent per flower by pollinators, are also expected to be greater for rewarding plants than rewardless ones (e.g. Mitchell & Waser 1992). This can lead to changes that may be related to the plants' reproductive fitness, for example an increased number of flowers visited per inflorescence can increase the amount of geitonogamously selfed pollen deposited on those flowers' stigmas (de Jong *et al.* 1993). If a pollinators' response to the model also leads to a greater expectation for finding a reward in the putative mimic, the number of flowers visited per inflorescence and the time spent per flower might also be greater on the rewardless morph similar in colour to the rewarding model. This could result in additional fitness differences between rewardless morphs. One constraint of our experimental design was that if pollinators learned to avoid rewardless morphs they would visit very few rewardless plants at the end of the experiment, and thus it would be difficult to obtain sufficient visits to test for the influence of mimicry as experience increased. Thus, we incorporated a second experimental phase, where the rewarding model was removed after the pollinators had gained experience with all three morphs. Pollinators would therefore resample the rewardless morphs, and the effects of experience on morph preference could therefore be quantified.

2. MATERIAL AND METHODS

(a) *Plant species*

We used two plant species, one rewarding and one rewardless, each with two corolla colour morphs. The rewardless species, *Dactylorhiza sambucina* Soó, is a widespread European orchid with a boreal–alpine distribution (Tutin *et al.* 1980). *Dactylorhiza sambucina* has red and yellow corolla colour morphs that are present in all populations throughout the range of the species (Nilsson 1980; Tutin *et al.* 1980). Because both morphs are identical in all floral traits (plant height, number of leaves and flower number and size (Gigord *et al.* 2001); floral scent (Nilsson 1980)) other than colour, this species is ideal for testing hypotheses relating to mimicry. Individuals of *D. sambucina* used in experiments originated from a natural population in France (Massif des Cévennes: 44°06′998″ N, 3°29′209″ E). In natural populations, *D. sambucina* flowers in early spring and is pollinated by newly emerged bumble-bee queens (Nilsson 1980). Because the main aim of the experiments was to study pollinator visitation patterns, we removed all the pollinia from *D. sambucina* individuals used in this experiment to prevent flower pollination and therefore early flower wilting. We also ensured that the plants from each of the morphs used in this experiment had similar numbers of flowers (there was no significant difference between morphs in terms of number of open flowers: $F_{1,39} = 0.05$, $p > 0.05$).

We used a cultivar of the common garden plant *Mimulus guttatus* (var. Magic) as the rewarding model. We used this species because, although it does not naturally occur with *D. sambucina*, both red and yellow colour morphs were easily available to act as putative models in an experimental model–mimic system. Flowers of this cultivar are zygomorphic but different in shape from, and considerably larger than, *D. sambucina*, and thus potentially distinguishable by pollinators on floral traits other than colour. *Mimulus guttatus* produces insignificant amounts of nectar (Grant 1924), rewarding its pollinators principally with pollen (Robertson *et al.* 1999). This enabled us to control, by supplementation with sucrose solution, the precise volume of reward contained in individual flowers throughout experiments, without having to consider changes caused by natural nectar production. In common with *D. sambucina*, *M. guttatus* is pollinated in the wild primarily by bumble-bees (Robertson *et al.* 1999).

(b) *Experimental design*

Experiments were conducted in a cage 1.83 m × 3.66 m, 1 m high, in glasshouses at Exeter University that were maintained at 20 °C. The cage had a green wooden base onto which a 15×31 square grid system had been drawn, with grid size 11.5 cm × 11.5 cm, giving 465 potential positions for individual plants. During experiments, arrays of plants totalling 70 inflorescences were arranged randomly by grid position. We conducted the experiments as follows:

(i) treatment 1: 20 yellow *D. sambucina*, 20 red *D. sambucina*, 30 red *M. guttatus*;
(ii) treatment 2: 20 yellow *D. sambucina*, 20 red *D. sambucina*, 30 yellow *M. guttatus*.

Each treatment was divided as follows:

(i) phase 1: all plants on array, each pollinator allowed to visit with sufficient bouts to reach a minimum of 50 inflorescence visits (normally three to five bouts);
(ii) phase 2: *M. guttatus* removed and the same pollinators allowed to revisit the arrays containing just *D. sambucina* for one bout only.

Each *M. guttatus* flower was filled with 3 µl of a 30% sucrose solution using a repeat dispensing pipette (Biohit Proline 10 µl Electronic Pipettor; Biohit, Finland). Twenty pollinators (with red *M. guttatus*) and 19 pollinators (with yellow *M. guttatus*) were tested in each experiment. Both the order of runs and the allocation of pollinators to treatments were random to prevent temporal or ordering effects from biasing their foraging preferences. During experiments, pollinators foraged singly on the arrays until satiated and then returned to their nest. After each bout, the positions of all inflorescences were re-randomized and *M. guttatus* inflorescences were emptied of any remaining sucrose solution with a filter paper wick, and refilled. All inflorescences were handled after each bout, and because of this, and the length of time required to reset arrays, scent marking of flowers by bees was unlikely to influence inflorescence choice.

During both phases of each experiment we recorded the number of inflorescences of each morph visited in each bout, the number of flowers visited on each inflorescence, the time spent on each flower, and the time spent moving between flowers and inflorescences.

We used workers from a colony of captive bumble-bees, *Bombus terrestris* L. (Syngenta, Cambridge, UK), as the pollinators for these experiments. Bees were without previous natural or experimental foraging experience. The colony was supplied with pollen to excess, and then supplemented with sucrose solution overnight when necessary to maintain colony energy levels.

To ensure that bees were used to foraging from nectar in the cage provided, we initially trained bees to take 30% sucrose solution in 10 transparent plastic Petri dishes arranged randomly on the grid. Foragers observed actively foraging were marked uniquely on the thorax with solvent-free correction fluid and were subsequently used in the experiments. After a bee had foraged sufficiently to complete phases 1 and 2, it was removed from the colony to stimulate other individuals to forage.

(c) *Data analysis*

(i) *Colour similarity among the four colour morphs*

In order to ensure that, to the eyes of bumble-bees, the yellow and red morphs of *D. sambucina* were most similar in colour to the yellow and red morphs of *M. guttatus* respectively, we quantified the degree of similarity, using the reflectance spectra of the corollas of each species. Spectra were recorded by using a portable reflectance spectrophotometer (High Sensitivity Spectrophotometer S2000, New Electro-Optical Concepts, Beaufays, Belgium) that gave a reflectance spectrum across all of the wavelengths (including UV) to which insect pollinators are sensitive (Peitsch *et al.* 1992). The spectrophotometer was zero adjusted using magnesium oxide, and reflectance was recorded over 300–700 nm.

(ii) *Did bees show a preference for the rewardless morph most similar to the colour of the rewarding model during the experiments?*

We predicted that bees would either visit the two rewardless morphs randomly or show a preference for the rewardless morph most similar in colour to the rewarding model. We therefore compared the number of visits made to the two rewardless *D. sambucina* morphs both during phase 1, where bees were inexperienced, and during phase 2. We used replicated *G*-tests of goodness of fit (Sokal & Rohlf 1981), with expected values calculated assuming equal visitation rates to both rewardless colour morphs.

(iii) *Did bees learn to avoid the rewardless morphs as the experiments progressed?*

We predicted that bumble-bees would progressively learn to avoid either one or both rewardless morphs as the experiment progressed. Analysis of learning behaviour would reveal any influence of mimicry as bees learned, in particular at the end of phase 1, where the total numbers of visits to rewardless morphs may be small, and any influence of mimicry would be difficult to observe through analysis of total numbers of visits. We therefore computed the total number of visits that bees made to the rewardless *D. sambucina* relative to rewarding *M. guttatus*, and compared the proportion of visits made to *D. sambucina* using analysis of variance (ANOVA) with treatment (red or yellow *M. guttatus*), period (comparing visits 1–25 and visits 26–50 in phase 1) and colour morph (red or yellow *D. sambucina*) as fixed factors. The proportion of visits made to *D. sambucina* was arcsine transformed before analysis.

(iv) *Were there differences in numbers of flowers visited per inflorescence or time spent per flower between rewardless morphs?*

We compared the number of flowers visited and time spent per flower between the two rewardless colour morphs using ANOVA, with treatment (red or yellow *M. guttatus*), *D. sambucina* colour morph (red or yellow) and phase (phase 1 with *M. guttatus* and phase 2 without *M. guttatus*) as fixed effects. Because of the heterogeneity among bees for the number of visited plants, the ANOVA was performed using the mean number of visited flowers per inflorescence, and the mean time spent per flower calculated for each individual bee. To improve normality and homoscedasticity, the number of visited flowers was $\log_{10}$ transformed and time spent per flower was square-root transformed.

Statistical analyses followed Sokal & Rohlf (1981), and data were analysed using SPSS (SPSS v. 9.0 for Windows; SPSS Inc.). Where means are quoted in § 3, standard errors are also given. Where tests were repeatedly analysed over bees, significances were corrected using the sequential Bonferroni method (Rice 1989).

3. RESULTS

(a) *Colour similarity among the four colour morphs*

Reflectance spectra, across the wavelength to which bumble-bee eyes are sensitive, of the four colour morphs show that red corolla colour morphs of each species are more similar to each other than they are to the yellow morphs of the same species, and vice versa (figure 1). None of the corolla colour morphs reflected strongly in the UV range (figure 1).

(b) *Did bees show a preference for the rewardless morph most similar to the colour of the rewarding model during the experiments?*

At the beginning of the experiment, when both the rewarding model and the rewardless mimic were present (phase 1), bumble-bees showed no significant preference for either of the two rewardless morphs ($G_P = 0.16$, d.f. = 1, $p > 0.05$) (figure 2; table 1), thus visiting them at random. However, both treatments showed significant heterogeneity of preference between bees (table 1). Analysis of individual bees showed that for treatment 1, out of 20 bees 1 significantly preferred yellow and 1 significantly preferred red, whereas in treatment 2, out of 19 bees two significantly preferred yellow and one significantly preferred red.

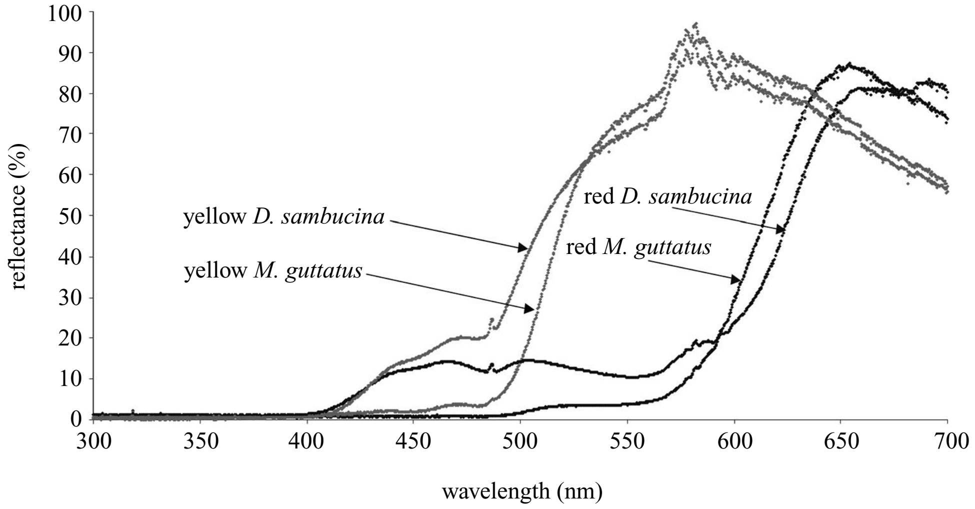

Figure 1. The spectral reflectance of the corolla colours of the species and colour morphs used in the experiments. Relative spectral reflectance is normalized to a white standard (magnesium oxide) and presented over the wavelength range to which bumble-bees' eyes are sensitive.

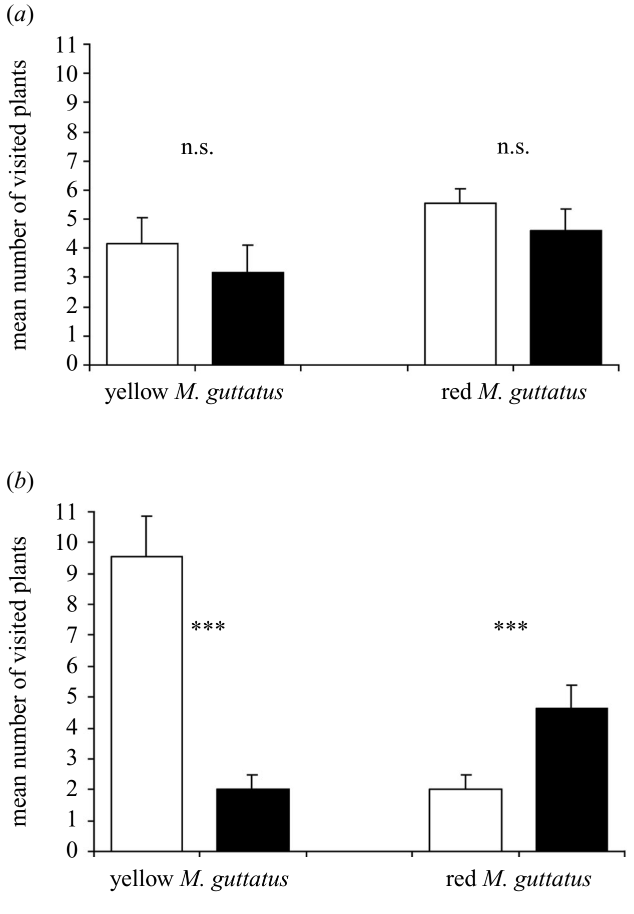

Figure 2. The mean number of visits to yellow (open bars) and red (shaded bars) morphs of *D. sambucina* inflorescences during treatment 1 (red *M. guttatus*) and treatment 2 (yellow *M. guttatus*) (*a*) before (phase 1) and (*b*) after (phase 2) the rewarding *M. guttatus* has been removed. n.s.: $p > 0.05$; $^{***}p < 0.001$.

After bees had gained experience with the rewarding model, and after the models had been removed from the array (phase 2), bees did not visit the two rewardless colour morphs equally ($G_P = 97.88$, d.f. = 1, $p < 0.001$). Instead, they showed a significant preference for one of the morphs in both treatments (figure 2; table 1). The preferred colour morph was, in both cases, the one most similar in corolla colour to the rewarding morph (figure 2). There was no significant heterogeneity of preference between bees (table 1), suggesting that all bees were similarly influenced by the colour of the rewarding morph.

Interestingly, during the first bout in phase 1, inexperienced bumble-bees were significantly more likely to visit *D. sambucina* first rather than *M. guttatus* ($G_P = 16.43$, d.f. = 1, $p < 0.001$).

(c) *Did bees learn to avoid the rewardless morphs as the experiments progressed?*

Bumble-bees significantly avoided both rewardless morphs as the experiments progressed, restricting their visits to the rewarding morph during the second period of phase 1, i.e. visits 26–50 (figure 3; table 2). Neither treatment, colour morph nor interactions were significant (table 2), indicating that the rate of learned avoidance over phase 1 did not differ significantly between the two rewardless colour morphs or experiments.

Interestingly, inexperienced bumble-bees spent less time travelling before visiting the first plant during bout 1 in phase 1 (137 s) than experienced bees did during phase 2 (439 s; $F_{1,71} = 151.88$, $p < 0.001$). We also found a significant positive correlation between the time that a given bumble-bee spent in the cage before visiting a *D. sambucina* inflorescence during phase 2 (after *M. guttatus* was removed), and the number of *D. sambucina* inflorescences that a given bumble-bee visited during phase 1 ($r_s = 0.51$, $p < 0.01$, $n = 39$). However, there was no correlation between the number of *M. guttatus* plants they previously visited and the time before the first visit to *D. sambucina* during phase 2 ($r_s = -0.09$, $p > 0.05$, $n = 39$).

(d) *Were there differences in numbers of flowers visited per inflorescence or time spent per flower between rewardless morphs?*

The number of flowers visited and the time spent per flower did not differ significantly, either between the two

Table 1. The number of visits to *D. sambucina* colour morphs during phase 1 and 2 for treatment 1 (red *M. guttatus*) and treatment 2 (yellow *M. guttatus*), analysed using replicated *G*-tests of goodness of fit (Sokal & Rolf 1981).

(Results quote pooled (G_P), heterogeneity (G_H) and total (G_T) components of *G*. Expected values were calculated assuming random visitation to both rewardless morphs, which were present in equal proportions. Individual *G*-tests were performed for each bee when it was possible and significances are indicated after Bonferroni correction (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). d.f.: degree of freedom.)

(*a*) treatment 1, red *M. guttatus*

	phase 1				phase 2			
	number of visits to *D. sambucina*				number of visits to *D. sambucina*			
bee number	yellow morph	red morph	*G*	d.f.	yellow morph	red morph	*G*	d.f.
total	111	92			40	93		
			$G_H = 33.16$***	11			$G_H = 9.92$	4
			$G_P = 1.78$	1			$G_P = 21.72$***	1
			$G_T = 34.94$***	12			$G_T = 31.64$***	5
(*b*) treatment 2, yellow *M. guttatus*								
total	79	60			181	38		
			$G_H = 27.66$***	6			$G_H = 14.04$	11
			$G_P = 2.61$	1			$G_P = 101.50$***	1
			$G_T = 30.27$***	9			$G_T = 115.50$***	12

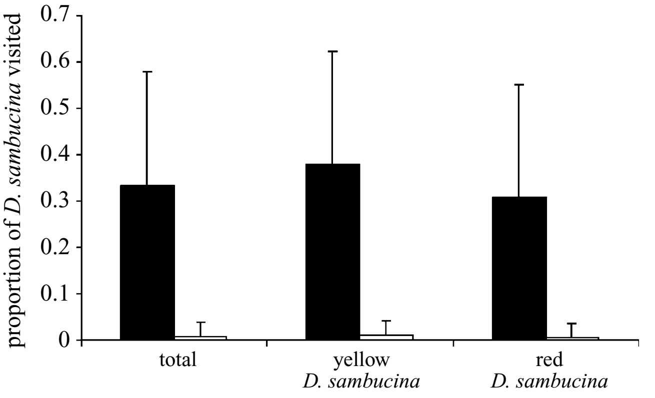

Figure 3. The relative visitation rate to *D. sambucina* during the first (shaded bars) and second (open bars) sets of 25 visits during phase 1.

Table 2. ANOVA on the number of visits to the rewardless *D. sambucina*.

(Fixed effects tested are treatment (red and yellow *M. guttatus*), period (first and second 25 visits during phase 1), colour morph (red or yellow *D. sambucina*) and the interactions among these factors. MS: mean square III. Significances indicated as in table 1.)

source of variation	d.f.	MS	*F*
treatment	1	19.71	2.50
period	1	642.40	81.50***
morph	1	8.24	1.05
treatment × period	1	17.24	2.19
treatment × morph	1	0.17	0.02
period × morph	1	6.51	0.83
treatment × period × morph	1	0.17	0.02
error	148	7.88	

rewardless colour morphs (number of flowers visited, $F_{1,90} = 0.79$, $p > 0.05$; time spent per flower, $F_{1,90} = 0.17$, $p > 0.05$) or between the two treatments (number of flowers visited, $F_{1,90} = 0.03$, $p > 0.05$; time spent per flower, $F_{1,90} = 0.41$, $p > 0.05$). Bumble-bees visited significantly more flowers per rewardless morph during phase 1 than phase 2 ($F_{1,90} = 11.33$, $p < 0.01$; mean number of flowers visited in phase 1, 3.40 ± 0.30; in phase 2, 2.35 ± 0.19 flowers). However, they spent a similar time on each flower during both phase 1 and phase 2 ($F_{1,90} = 1.44$, $p > 0.05$; mean time spent per flower phase 1, 3.06 ± 0.26 s; phase 2, 2.75 ± 0.30 s).

4. DISCUSSION

In these experiments, we aimed to test whether pollinator visitation to colour morphs of rewardless plants could be influenced by floral mimicry, based on corolla colour alone. We found that, when pollinators were inexperienced, they sampled both colour morphs equally, as predicted by the non-model deception hypothesis, and as pollinators gained experience with the rewarding species they learned to avoid both rewardless colour morphs at an equal rate. However, when experienced pollinators were forced to revisit the rewardless morphs after the rewarding plants were removed, we found that mimicry influenced their foraging decisions. In both experiments, bees showed a significant and strong degree of preference for the morph most similar in corolla colour to the rewarding plant on which they had gained experience. To our knowledge, this is the first experimental demonstration that pollinator behaviour could potentially result in selection for floral colour mimicry in plant populations. According to our experiments, strong resemblance in floral morphology or traits other than colour between model and mimic are not necessary for a Batesian floral mimic to be favoured.

Does the foraging situation encountered by bees in our experiments realistically represent those that they would encounter in nature? Although we studied two species, *D. sambucina* and *M. guttatus*, that pollinators would not normally encounter together in the field, we suggest that the experimental system is generally representative of that likely to be encountered by pollinators foraging on rewardless orchids. Indeed, we have found that *D. sambucina* usually flowers in mixed grassland communities alongside rewarding plants, like *Primula veris*, of dissimilar form but similar colour to one or other morph. Further, while we 'forced' pollinator resampling of the rewardless species, we suggest that such pollinator resampling could occur naturally in two situations. First, nectar availability in rewarding plants may vary temporally, either through daily changes in nectar production rates, or seasonally. Thus, pollinators may run out of nectar in the rewardless species on which they are foraging and be forced to resample other plants. Second, availability of rewarding and rewardless species may fluctuate between patches or populations, such that pollinators shifting to a new foraging area may encounter only rewardless species. We suggest, therefore, that our experimental system and protocol are representative of situations that pollinators could encounter naturally when foraging in plant communities containing rewardless orchids.

What selection pressures could the pollinator behaviour that we observed cause in natural populations? We found that factors other than visitation rates that might affect final plant reproductive success, such as time spent per flower or numbers of flowers visited per inflorescence, did not differ significantly between rewardless morphs. Thus, if visitation rates are positively correlated with plant reproductive success either through female (Waser & Price 1981) or male (Stanton *et al.* 1986) function, our results suggest that foraging on rewardless plants by experienced pollinators could strongly selectively favour the morphs most similar in corolla colour to those of the rewarding species on which the pollinator is foraging. However, selection caused by inexperienced pollinators will not result in selection for mimicry by corolla colour, since we found that pollinators foraged randomly when there were equal numbers of both rewardless corolla colour morphs. Our previous results (Smithson & Macnair 1997) show that naive pollinators forage disassortatively on rewardless corolla colour morphs, and significantly over-visit rare colour forms in comparison to their abundances in a population. This could potentially cause a selective advantage for rare rewardless corolla colour morphs. We have argued that such selection pressures could selectively maintain corolla colour variation in non-model deceptive rewardless species (Smithson & Macnair 1997; Gigord *et al.* 2001). When, therefore, would selection on corolla colour in a rewardless species favour rare morphs and when would it favour mimicry? Clearly this will hinge on the cumulative total number of visits that are received by rewardless plants from initial sampling by inexperienced pollinators, compared with those received from resampling by experienced pollinators. This is likely to depend on the ecological conditions that the species is growing in—for example, the total number of available pollinators and co-flowering species, and the patchiness of the community. Indeed, it is possible that a species could be selected partially for mimicry, or that selection pressures could differ between years or populations. Thus, rewardless plants that flower very early in a season, like *D. sambucina* used in these experiments, are likely to receive many more visits in total from inexperienced pollinators, because there will be a large pool of inexperienced queen and worker bees emerging to forage for the first time. These early-flowering rewardless species are, we argue, unlikely to be selected for mimicry. By contrast, there may be the potential for mimicry in rewardless species that flower later in the season, or occur in ecological situations where many pollinators resample rewardless species.

There is clear evidence for Batesian mimicry in some rewardless orchids (Johnson 1994, 2000): *Disa ferruginea*, for example, has two allopatric colour morphs, that each resemble two differently coloured rewarding models (Johnson 1994). Once Batesian mimicry through colour is favoured, will selection subsequently favour phenotypic variants that increase further the resemblance of the colour or morphology of the mimic to the model? This is likely to depend on the sensory capabilities of the pollinators and the strength of selection favouring mimicry. It has been argued that in some Batesian floral mimics, resemblance between model and mimic is so strong that pollinators fail to distinguish between them (Johnson 1994, 2000). Further field investigations and manipulative experiments are required to test these ideas.

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