

The effects of floral mimics and models on each others' fitness

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Plants that lack floral rewards may nevertheless attract pollinators by mimicking the flowers of rewarding plants. It has been suggested that both mimics and models should suffer reduced fitness when mimics are abundant relative to their models. By manipulating the relative densities of an orchid mimic *Disa nivea* and its rewarding model *Zaluzianskya microsiphon* in small experimental patches within a larger population we demonstrated that the mimic does indeed suffer reduced pollination success when locally common relative to its model. Behavioural experiments suggest that this phenomenon results from the tendency of the long-proboscid fly pollinator to avoid visits to neighbouring plants when encountering the mimic. No negative effect of the mimic on the pollination success of the model was detected. We propose that changes in pollinator flight behaviour, rather than pollinator conditioning, are likely to account for negative frequency-dependent reproductive success in deceptive orchids.

Keywords: Batesian mimicry; density dependence; fitness; foraging behaviour; orchids

1. INTRODUCTION

Mimicry is one of the classic examples of adaptation through natural selection (Joron & Mallet 1998). The evolution of mimicry may even have been a major driving force behind the speciation of some groups such as butterflies and orchids (e.g. Smith *et al.* 1993; Mallet *et al.* 1998; Jiggins *et al.* 2001; Soliva *et al.* 2001). Protective Batesian mimicry involves palatable animals that gain protection from predation by adopting the signals of unpalatable animals. Batesian mimicry is a good example of 'advergent evolution' where selective pressures cause phenotypic convergence of one species on another, but not vice versa (Brower & Brower 1972; Johnson *et al.* 2003). In floral Batesian mimicry, non-rewarding plants adopt the floral signals of sympatric rewarding plants in order to attract pollinators (Bierzychudek 1981; Dafni & Ivri 1981; Johnson 1994, 2000). Both represent a form of dishonest signalling that exploits the conditioned behaviour of animal 'operators'. Since conditioning plays a central role, there is an expectation of frequency dependence. In theory, the fitness of mimics should decline as they become more numerous relative to their models, because operators would show weaker conditioned responses or learn to distinguish between mimics and models (Bierzychudek 1981; Dafni & Ivri 1981; Joron & Mallet 1998).

Few natural studies have examined whether increased frequencies of mimics relative to their models has the detrimental effect on fitness that is predicted by theory (cf. Bierzychudek 1981; Dafni & Ivri 1981; Johnson 1994). In animal systems, this may be due to the formidable methodological difficulty of manipulating relative frequencies of models and mimics in the wild. In plants, the major problem is how to control for the effects of random differences in pollinator abundance among sites.

It is important to control for pollinator abundance as this variable may be even more important than pollinator conditioning for determining the reproductive success of plants. High densities of rewarding plants can increase local abundance of pollinators (cf. Kunin 1993), which, in turn, could benefit associated non-rewarding plants through the 'magnet' effect (Laverty 1992; Johnson *et al.* 2003). Because of these methodological difficulties, no studies of floral mimicry that we are aware of have examined the question of frequency dependence in the wild while also controlling for the magnet effect.

The relative density of floral mimics and their models may also have direct effects on pollinator flight behaviour. Pollinators are known to depart rapidly or increase their flight distances from non-rewarding patches (Pleasants 1981; Waddington 1981; Dukas & Real 1993; Wong & Schiestl 2002). We hypothesize that a tendency for pollinators to depart from patches dense in mimics relative to models would lead to diminished reproductive success in both mimics and their models.

While the effects of relative density on the fitness of mimics has received the most theoretical and empirical attention, it is also conceivable that Batesian mimics may be deleterious to the fitness of their models, particularly when the mimics are relatively abundant. This has spawned the controversial idea of a coevolutionary chase between mimics and models similar to the classic host-parasite arms race. In mimicry systems, models would evolve to look different from mimics, and by so doing uncover the disguise (Turner 1984a). Mimics on the other hand would track the morphologies of their hosts as much as possible in order to blend in. Such a coevolutionary chase could give rise to speciation and possibly cospeciation events. Recently, the idea behind the coevolutionary chase has come under attack (see Turner 1984b, 1995 and references therein); however, we are not aware of any natural studies that test whether

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Batesian mimics have density effects on their models (see Wong & Schiestl 2002). The only other study known to us on the effect of Batesian mimics on models is that of artificial prey items offered to bird 'operators' (Lea & Turner 1972). 'Models' (simulated by pieces of coloured pastry dipped in quinine) suffered higher predation rates when they were rare relative to 'mimics' (coloured pastries with no bitter taste).

We use a plant Batesian mimicry system to examine the frequency dependence of reproductive success in a mimic and its model. *Disa nivea* is a non-rewarding South African orchid that is an apparent mimic of *Zaluzianskya microsiphon*, a rewarding species with which it grows in close association (Anderson *et al.* 2005). Both are specialized for pollination by the long-proboscid fly *Prosoeca ganglbaueri* (Nemestrinidae). We manipulated the density of the two species in small patches (0.4 m²) that were unlikely to have any effect on either local pollinator abundance or levels of pollinator conditioning. Our aims were to test the hypothesis that the fitness of a mimic would decrease with increasing density as a simple result of altered pollinator behaviour, namely the tendency to depart from rewarding patches. We simultaneously tested whether the fitness of the model would decline with increasing mimic density.

2. METHODS

(a) Study species

Z. microsiphon (Kuntze) K. Schum. (Scrophulariaceae), the model in this system, is a very widespread and abundant species in the Drakensberg mountains of South Africa. Each plant usually produces a single inflorescence at the terminal portion of a seasonal growth shoot. Flowering takes place between January and March. The species is self-incompatible and thus reliant on pollinator visits for seed set (Johnson *et al.* 2002). It is pollinated almost exclusively by the long-proboscid nemestrinid fly *P. ganglbaueri* (Johnson *et al.* 2002; Anderson *et al.* 2005).

D. nivea H. P. Linder is a non-rewarding terrestrial orchid that is endemic to the Drakensberg region, having been recorded from just five sites. It flowers between January and March, bears a strong overall resemblance to *Z. microsiphon*, and is also pollinated by the long-proboscid fly *P. ganglbaueri* (Anderson *et al.* 2005). Breeding system data indicate that this species is partially self-compatible: 93% of seeds are viable in hand cross experiments versus 32% in selfed capsules, but fully dependent on pollinators for seed set, since bagged flowers set zero fruit (J. Jersakova and S. D. Johnson, University of KwaZulu-Natal 2004, unpublished data).

P. ganglbaueri Lichtwardt (Nemestrinidae) is widespread throughout the Drakensberg region where it has a flight period from January to March. *Z. microsiphon* is its most important source of nectar (Anderson *et al.* 2005), but the fly is also known to pollinate at least seven other species in the Drakensberg region, and these form a guild characterized by cream or pink flowers with dilute nectar and often long corolla tubes (Johnson & Steiner 1995; Goldblatt & Manning 2000). The length of the proboscis of this fly varies from 19 to 42 mm between populations (Goldblatt & Manning 2000; B. Anderson and S. D. Johnson 2005, unpublished data). Anderson *et al.* (2005) showed that the proboscis length of

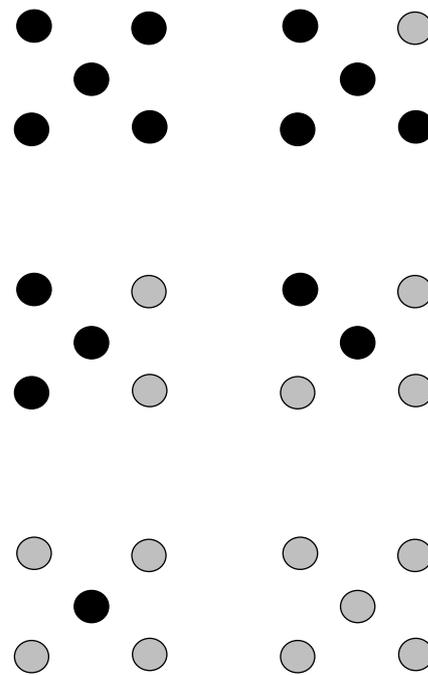


Figure 1. Experimental design (replicated five times) where black dots represent *Z. microsiphon* cuttings and grey dots represent *D. nivea* cuttings. Each replicate had a focal cutting of *Disa* and a rooted focal *Zaluzianskya* plant, from which reproductive success was measured.

the flies closely matches the corolla tubes of *Z. microsiphon* and the spurs of *D. nivea* in each population.

(b) Study site

The study was carried out in February, 2005 at Ramatseliso's Gate on the border between South Africa and Lesotho (30°03'09" S, 28°55'50" E, alt: 2200 m). At the time of the study, approximately 300 *Z. microsiphon* plants and 150 *D. nivea* plants were flowering over an area of approximately 100 m by 200 m. Individuals of *P. ganglbaueri* were abundant and were frequently seen visiting both *Z. microsiphon* and *D. nivea*.

(c) Study design

Densities of *D. nivea* and *Z. microsiphon* were manipulated by altering the relative number of plants of each species within patches of a fixed size (21 cm by 21 cm). These patches always contained a total of five plants. Thus, there were six treatment groups, varying from five plants of *D. nivea* through various intermediate proportions to five plants of *Z. microsiphon* (figure 1). Each treatment group was replicated five times, making up a total of 30 patches. Individual patches were separated by between 5 and 6 m and were randomly assigned to a particular treatment. Plants within a patch were equally spaced and separated by a distance of *ca* 15 cm. Each patch, other than those five patches consisting entirely of *D. nivea* inflorescences, contained a single rooted focal *Z. microsiphon* plant. This was to enable the counting of fruits and seeds at a later stage. Each patch, other than those five patches consisting entirely of *Z. microsiphon*, also contained a single focal cut inflorescence of *D. nivea* placed in a water filled test tube buried in the soil. The positions of these focal plants were different in each of the five replicated patches within a treatment group. Other plants in the patches consisted of cut inflorescences of either *D. nivea* or *Z. microsiphon* placed in test tubes filled with water. These

cut inflorescences, but not the focal plants, were regularly changed as the flowers aged and died so that each always had between four and six mature flowers at any time.

The focal plants within each patch were used for estimates of reproductive success. At the commencement of the experiment, four unopened buds on the focal plants were marked with a permanent marker on the bracts. After the four buds on the focal plants (for *Zaluzianskya* and *Disa*) had opened, matured and withered (typically after 7 days), we stopped replacing cuttings in that patch. As each of the four marked *D. nivea* flowers withered, its stigma was examined for deposition of pollen massulae and we also checked for pollinaria removal from the anther. The focal *Z. microsiphon* plants were marked with flagging tape and we returned several weeks later to count the seeds in the four mature capsules of the marked flowers in each treatment. The relationships between reproductive success of the focal plants and relative density were established using linear regression of mean reproductive success measured for each density treatment.

(d) Insect behaviour

To determine whether pollinators discriminate between the two species and to establish whether their behaviour is modified on encountering either the non-rewarding mimic or its rewarding model, we used the 'pollinator interview' technique, developed by Thomson (1988) and modified for two-species choices by Johnson (2000). A long (2.5 m) stick was used with a 30 cm crossbar at one end. On each end of the crossbar we placed either a *Z. microsiphon* or a *D. nivea* inflorescence in a test tube of water, allowing insects to choose between these two plants. Inflorescences were cut to the same height and each had six mature, open flowers. The choice was offered to foraging *P. ganglbaueri* flies on their departure from foraging on an inflorescence of *Z. microsiphon*. We recorded whether flies first visited *Z. microsiphon* or *D. nivea*, how many flowers were probed on each inflorescence, and whether flies moved from *Z. microsiphon* to *D. nivea* and vice versa. After visitation, *Z. microsiphon* inflorescences were replaced with fresh, nectar filled inflorescences and *D. nivea* inflorescences were replaced after every five choices. After five choices the positions of the inflorescences were also swapped.

In a pilot study to determine the ability of pollinators to create mental maps of plant positions, we watched a patch with five mimics versus one 10 m away with five models for most of a day, 3 days after the experiment was set up.

3. RESULTS

There was a significant negative relationship between the relative density of *D. nivea* inflorescences in patches and the reproductive success of the orchids in terms of pollinaria removal and deposition, respectively ($R^2 = 0.917$, $p = 0.01$ and $R^2 = 0.975$, $p = 0.002$, respectively, figure 2a,b). In contrast, there was no significant effect of mimic density on the fitness of the model *Z. microsiphon* in terms of either the percentage of flowers developing into fruits (100% in all focal plants) or seed set ($R^2 = 0.018$, $p = 0.830$, figure 2c).

When flies were allowed to choose between model and mimic inflorescences, they showed no tendency to distinguish between the two ($\chi^2 = 0.013$, $p = 0.91$, figure 3a). Flies also probed significantly more flowers per *Z. microsiphon* inflorescence than per *D. nivea*

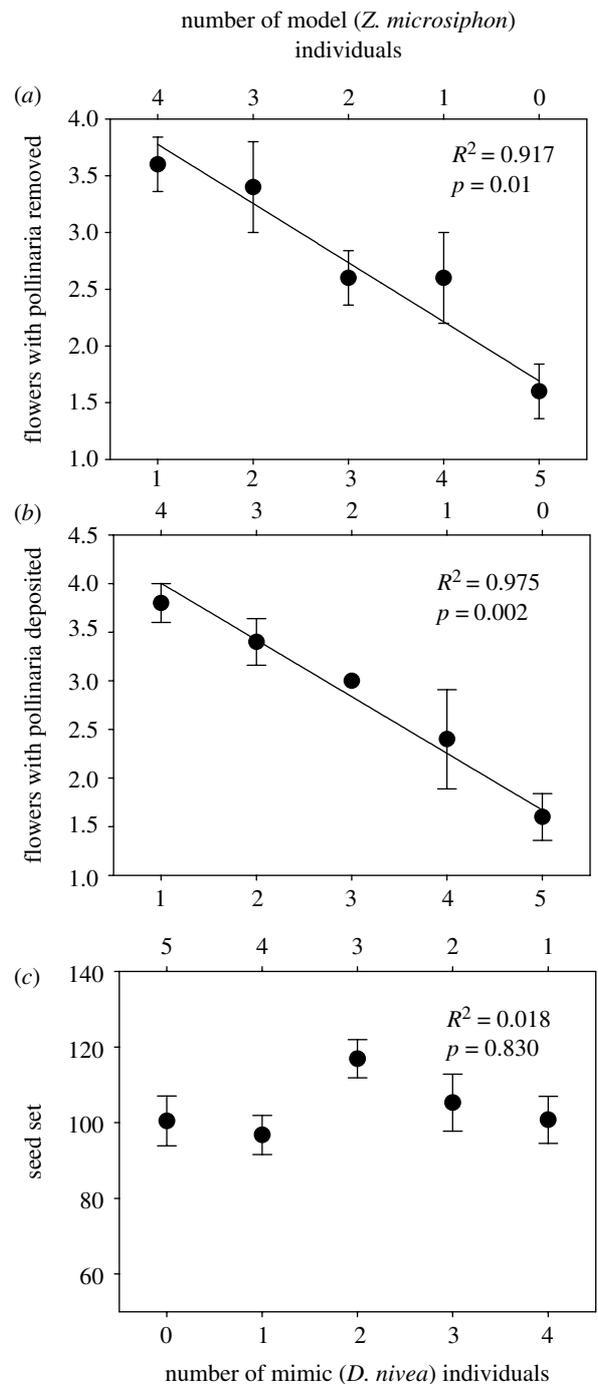


Figure 2. Effects of relative density of *Disa* (mimic) and *Zaluzianskya* (model) on (a) pollinaria removal in flowers of *Disa*, (b) pollen deposition in flowers of *Disa*, and (c) seed set of *Zaluzianskya*. Regression lines are fitted to mean values.

inflorescence ($t = 9.33$, $p < 0.0001$, figure 3b). When flies first chose *Z. microsiphon* (figure 3c), they frequently (72%) visited the *D. nivea* inflorescence directly afterwards, which was the next closest inflorescence by distance. In contrast, flies which first probed *D. nivea* seldom (21%) went on to probe the next nearest inflorescence (the alternative choice of *Z. microsiphon*), instead they flew farther away ($\chi^2 = 11.1$, $p = 0.001$). The mean (\pm s.d.) number of flowers probed per *D. nivea* inflorescence was identical for the 38 flies that chose *D. nivea* first and the 29 flies that chose *D. nivea* second after first visiting the alternative *Z. microsiphon* inflorescence (first choice: 1.39 ± 0.68 ; second choice: 1.39 ± 0.58 , $t = 0.011$, $p = 0.99$).

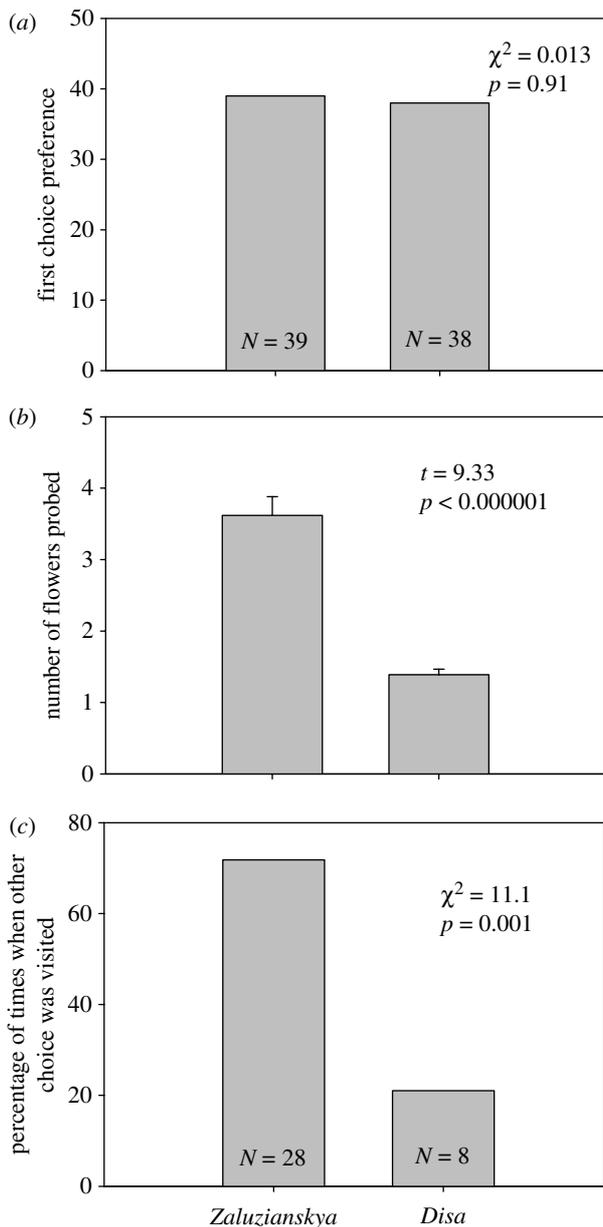


Figure 3. Behaviour of flies on *Disa* (mimic) and *Zaluzianskya* (model). (a) First choices for flies. (b) Mean (+s.e.) number of flowers probed. (c) Frequency of visits to the alternative choice after having first visited *Zaluzianskya* or *Disa*.

Where two patches of plants differing in relative mimic densities were watched for a day, the high model density patch received nine visits and the high mimic density patch received eight ($\chi^2 = 0.06$, $p = 0.81$).

4. DISCUSSION

Our results show that reproductive success in the non-rewarding orchid *D. nivea* declines as these mimics become more frequent relative to their models in small patches. There are several possible explanations for this relationship which we consider below.

The first is the conventional idea (see computer simulations e.g. Turner 1984a) that operators (pollinators) in mimicry systems learn to avoid mimics when they are at higher densities. Although such negative frequency selection has been found in artificial systems and systems where mimicry is generalized (e.g. Smithson & Macnair 1997; Gumbert & Kunze 2001), it seems extremely

unlikely in this instance given the small size of the experimental patches relative to the larger populations and the short period of time (ca 5–60 s) that pollinators spend in the patches. In fact, flies did not seem to be able to discriminate between models and mimics at all (figure 3a), and it is unlikely that they would acquire this ability at the level of a small patch with five plants.

The second is that pollinators develop a mental map of the population and learn to avoid areas of high localized mimic density, and conversely to concentrate their foraging in areas with more rewarding plants. This type of idea was proposed by Wong & Schiestl (2002) to explain how wasps avoided patches of sexually deceptive orchids which were apparently indistinguishable from female wasps. Again, this seems unlikely at the level of a small patch with five plants nested within the larger populations. Direct observation of pollinator visits to all of the experimental patches during the course of the experiment was not feasible, but our casual observations were consistent with the expectation that the arrival of flies at patches is essentially random. The lack of a significant difference in the arrival rate of flies to a patch with five mimics versus one with five models (see §3) suggests that these insects did not create obvious mental maps of the location of the patches.

The third is that flies probe fewer flowers per visit to a *D. nivea* inflorescence when the orchids are common relative to their models. This seems highly unlikely given that the mean number of flowers probed per *D. nivea* inflorescence did not vary according to whether flies visited the orchids as their first or second choice in the presentation experiments (see §3).

The fourth, and most likely explanation, is that encountering a mimic alters the pollinator's flight patterns and behaviour. We show this in two ways, firstly pollinators visit models and mimics indiscriminately because they cannot distinguish between the two. Secondly, we show that pollinators behave differently when they encounter mimics compared to when they encounter models (figure 3b,c). When a mimic is encountered, pollinators probe fewer flowers and are less likely to visit neighbouring plants than when they encounter models (figure 3b,c). Thus, mimics that are surrounded by other mimics should receive fewer visits than those that are surrounded by models. Although the alteration of flight behaviour may be a result of conditioning, in this third explanation pollinators are forced to sample mimics because they cannot distinguish them from models. Thus, conditioning plays no role in the initial choice of inflorescence.

Changes in pollinator behaviour such as longer flight distances on encountering high densities of mimics should also lead to lower rates of visitation to nearby models. However, we did not find the expected negative relationship between mimic density and reproductive success of models. Levels of fruit and seed set were high for models in all treatments. We suspect that this is due to the tendency for flies to visit (and thus likely pollinate) many flowers on inflorescences of *Z. microsiphon* during a single visit (figure 3b). This is in contrast to inflorescences of *D. nivea* which typically have just one flower probed during a pollinator visit (figure 3b) and would thus need to be visited several times to achieve high levels of fruit set. It is

possible that at lower pollinator densities one may be able to observe some kind of density effect on the female fitness of models. It is also possible that male fitness (pollen export) in *Z. microsiphon* is influenced negatively by mimic density since it may take several more visits to remove all the pollen from one flower. Further exploration of this question would require quantification of pollen removal or the development of paternity markers.

An important consideration is whether the results of this study are applicable only to small patches or whether the same patterns and mechanisms would apply at larger spatial scales, and thus be more relevant to population genetic processes. Non-rewarding orchids with flower colour polymorphisms that are not specific mimics have been shown to exhibit negative frequency-dependent reproductive success at larger spatial scales (Gigord *et al.* 2001) and this has been attributed mainly to learned aversion behaviour in denser patches (cf. Smithson & Macnair 1997). Johnson *et al.* (2003) expressed doubt about the notion of learned avoidance of non-rewarding flowers by pollinators after discovering that experienced bumble bee queens (those already carrying pollinaria) readily visit the non-rewarding flowers of *Anacamptis morio* in dense populations late in the flowering season. It seems quite possible, therefore, that the general tendency for orchids such as *A. morio* to show lower reproductive success in large dense populations (Fritz & Nilsson 1994) arises from the same behavioural modifications (longer flight distances away from neighbouring plants) that we observed by flies in the interview experiments. It is also possible that learned avoidance may never develop in specialized mimicry systems if operators are unable to distinguish between models and mimics and do not suffer strong fitness consequences for making the wrong choice.

In conclusion, pollinator conditioning or discrimination ability may explain why generalized mimics generally suffer lower reproductive success in large dense patches (e.g. Fritz & Nilsson 1994; Smithson & Macnair 1997; Gigord *et al.* 2001). However, our finding that a specialized mimic performs poorly when common relative to its model in small patches is more likely to be explained by the tendency of pollinators to depart from patches after encountering non-rewarding flowers.

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