RESEARCH PAPER

Effects of distance from models on the fitness of floral mimics

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ABSTRACT

- Rewardless plants can attract pollinators by mimicking floral traits of rewarding heterospecific plants. This should result in the pollination success of floral mimics being dependent on the relative abundance of their models, as pollinator abundance and conditioning on model signals should be higher in the vicinity of the models. However, the attraction of pollinators to signals of the models may be partially innate, such that spatial isolation of mimics from model species may not strongly affect pollination success of mimics.
- We tested whether pollination rates and fruit set of the rewardless orchid *Disa pulchra* were influenced by proximity and abundance of its rewarding model species, *Watsonia lepida.*
- Pollination success of the orchid increased with proximity to the model species, while fruit set of the orchid increased with local abundance of the model species. Orchids that were experimentally translocated outside the model population experienced reduced pollinaria removal and increased pollinator-mediated self-pollination.
- These results confirm predictions that the pollination success of floral mimics should be dependent on the proximity and abundance of model taxa, and thus highlight the importance of ecological facilitation among species involved in mimicry systems.

INTRODUCTION

Batesian mimicry in plants involves a rewardless plant that mimics floral signals of a co-occurring heterospecific rewarding plant in order to dupe a signal receiver (pollinator) into pollinating its flowers (Johnson 2000; Anderson & Johnson 2006; Johnson & Schiestl 2016). This is in contrast to animal systems, where such mimicry involves harmless and palatable animals adopting the signals of harmful and/or unpalatable animals in order to gain protection from predators (Joron & Mallet 1998). A basic, but not absolute, requirement of Batesian mimicry is that the mimic should occur at a lower frequency than that of its model (Joron & Mallet 1998; Wong & Schiestl 2002; Anderson & Johnson 2006; de Jager *et al.* 2016). This should maximise encounters of operators with models and thus enhance operator behaviour that is favourable to the mimic (Jiggins *et al.* 2001). However, the effects, and even existence, of such negative frequency dependence on the fitness of mimetic plants remain unclear (Johnson 1994; Peter & Johnson 2008; Johnson & Schiestl 2016).

The behaviour of pollinators in communities with floral mimics and models is expected to be influenced not only by the ratio of mimics to models, but also by the absolute abundance of both mimics and models in terms of density and population size. As the fecundity of plants is often pollen-limited due to pollinator and/or mate limitation (Burd 1994), pollinator-dependent plants often suffer reduced fecundity with decreasing aggregation. This is normally because pollinators optimise their reward gain and visit larger populations more frequently and because more mates are available in these larger populations (Alexandersson & Ågren 1996; Duffy *et al.* 2013). Previous studies have shown that pollination success of rewarding species typically increases with aggregation up to some point when pollinators are saturated and interactions among conspecifics start to become competitive (Brys *et al.* 2008; Johnson *et al.* 2012). The pollination success of deceptive plant species, on the other hand, is often maximal in small populations (Fritz & Nilsson 1994; Tremblay *et al.* 2005). The only benefit that deceptive plants gain from aggregation is mate availability. Indeed, the learned avoidance of pollinators when deceptive plants are aggregated means that competition among conspecifics is expected at even lower aggregations than is the case for rewarding plants (Johnson & Schiestl 2016). Another factor that needs to be taken into account when considering the effect of plant aggregation and spatial isolation on pollination success is that limited mate availability on the fringes of populations may increase the rate of pollinator-mediated self-pollination (Johnson *et al.* 2009). Therefore, the effects of spatial aggregation on pollination success need to be measured not only in terms of the quantity of pollination, but also in terms of its quality.

Approximately 40% of all orchid species are rewardless (Jersáková *et al.* 2006). Most of these rewardless species exploit food-seeking pollinators, either by a generalised resemblance to their floral food plants or specific mimicry to one or a few particular food plants Jersáková *et al.* (2012). Previous experimental work has shown that rewardless orchids tend to have higher fecundity in the presence of nectar rewarding plants (Johnson *et al.* 2003; Anderson & Johnson 2006; Juillet *et al.* 2007; Peter & Johnson 2008). These facilitative effects probably involve a

combination of magnet effects (higher abundance of pollinators in the vicinity of food plants) and, in cases where deceptive orchid share signals with food plants, a role for associative conditioning of pollinators. In some studies, presence of food plants did not have detectable effects on pollination success of deceptive orchids (*e.g.*, Johnson & Morita 2006). This may be due to innate attraction of pollinators to the signals of deceptive species or pollinators retaining conditioned behaviour even when they have moved several hundred metres or even a few kilometres from patches of their rewarding food plants (Newman *et al.* 2012). Hence, increased proximity of a food plant model should result in increased fecundity of a floral Batesian mimic, but this needs to be tested directly, as the extent to which it does may depend on the foraging behaviour of the pollinator, and whether it has learned the relevant floral cues.

Here we investigate the effect of proximity of the nectar-rewarding iris *Watsonia lepida* on pollination success of the rewardless orchid *Disa pulchra*, with the aim of testing the extent to which pollination and fruiting success of *D. pulchra* depends on *W. lepida*. Johnson (2000) showed that *D. pulchra* is a Batesian mimic of *W. lepida*. Pollination success was measured in terms of pollen deposition and removal and also in terms of the rate of pollinator-mediated self-pollination (an indicator of pollination quality).

MATERIAL AND METHODS

Study species

Disa pulchra Sond. (Orchidaceae) is a perennial, montane orchid that grows on rocky basalt substrates in KwaZulu–Natal, South Africa. It produces an average of 23 pink, scentless, non-rewarding flowers. Flowering starts in early December each year and finishes in early to mid-January, with fruits maturing over a 6–8-week period. Individual flowers wilt within 24 h of pollen deposition on the stigma. *D. pulchra* shows a remarkable morphological similarity to flowers of the iris *Watsonia lepida* (Fig. 1a), and previous studies have shown that both species are pollinated by the long-proboscid fly *Philoliche aethiopica* Thunberg (Tabanidae). This fly does not discriminate between inflorescences of the two species in the field in terms of approaches, but probes many more flowers on the inflorescence of the rewarding iris. Previous experimental work has shown that self-pollination in *D. pulchra* results in reduced seed production due to inbreeding depression (Jersáková & Johnson 2006).

Study design

This study was conducted between December 2013 and February 2014 on Mount Gilboa (1,780 m a.s.l.), near Pietermaritzburg, KwaZulu-Natal. We geo-referenced a total of 2,742 flowering *W. lepida* individuals and a total of 109 *D. pulchra* plants at the site using a handheld GPS (Garmin eTrex 10®; Garmin International, Inc., Olathe, KS, USA). Previous observations revealed that the nearest distance to individual *W. lepida* plants has no detectable effect on the pollination of *D. pulchra* (K.J. Duffy, personal observations). This is because *W. lepida* occurs in varying aggregations, from single plants to very high-density patches, that are patchily distributed throughout the summit of Mt. Gilboa, and *P. aethiopica* likely
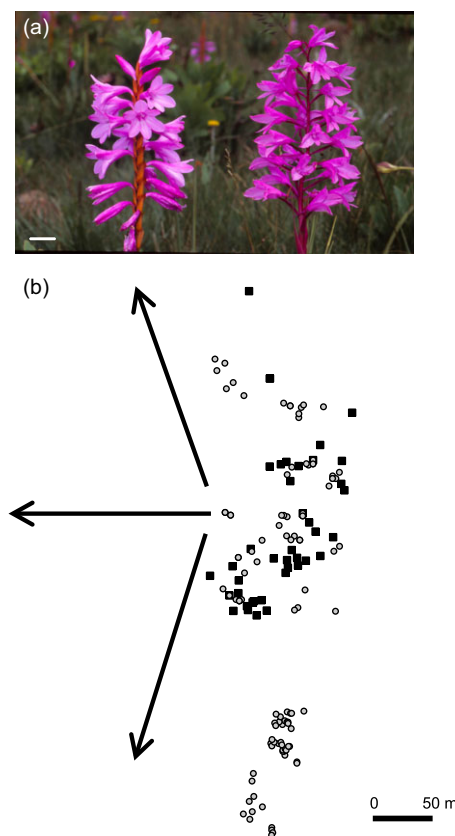

Fig. 1. a: Habit of *W. lepida* (left) and *D. pulchra* (right) co-flowering on Mount Gilboa, KwaZulu–Natal. Scale bar = 5 cm. b: Location of *D. pulchra* individuals (grey circles) and *W. lepida* patches (black squares) in the study population. Arrows reflect the directions in which experimental plants were placed from the centre of the study population.

forages on many food plants during a bout. Therefore, in order to calculate local abundance, we measured the distance of each *D. pulchra* plant to the nearest patch of *W. lepida* – operationally defined as areas with more than five *W. lepida* plants m⁻²; hence a total of 55 patches were mapped. These distances were measured in Quantum GIS (Quantum GIS Development Team 2015) using the GPS data collected from the population. We then counted the total number of individual *W. lepida* plants within and between each patch and each *D. pulchra* plant, and used: (i) the number of neighbouring *W. lepida* plants (abundance) and (ii) the distance of *D. pulchra* to each *W. lepida* patch (isolation) (Fig. 1b) as explanatory variables in our analyses. There was no significant interaction between the two explanatory variables, so we did not include this in our models.

Pollination and fruiting success

On 2 days during flowering of the *D. pulchra* population (13–14 December 2013) we surveyed all (N = 65) flowering *D. pulchra* plants and measured the proportion of flowers with pollinaria removed and proportion of flowers that had pollen massulae deposited. This time period was chosen as it was approximately 10 days after the first *D. pulchra* plants started flowering in the population, and represented when many plants

had their flowers open (K. J. Duffy personal observation). We related the proportion of flowers effectively visited (those that had pollinaria removed and/or massulae deposited) to both neighbouring *W. lepida* abundance and isolation from the nearest *W. lepida* patch (Fig. 1b). These data were analysed using GLM (McCullough & Nelder 1989) in R (R Core Team 2015), with a binomial error distribution. These models had an event/trial structure and were corrected for overdispersion.

We used Mantel tests with 9,999 randomisations of the original matrix in the 'ade4' package for R (Dray & Dufour 2007) to test whether pollinaria removal and massulae deposition were related to geographic location of *D. pulchra* individuals in the population. There was no spatial autocorrelation for the proportion of pollinaria removed (correlation coefficient = 0.004, $P = 0.416$) or the proportion of pollinaria deposited (correlation coefficient = -0.04, $P = 0.828$). At the end of the flowering period, we counted the proportion of flowers that set fruit for 70 georeferenced *D. pulchra* individuals. We again used Mantel tests to test for potential spatial autocorrelation on fruit and found that there was no effect on spatial location in the population on fruit set (correlation coefficient = -0.019, $P = 0.583$). We used a GLM with a binomial error structure, corrected for overdispersion, to analyse the relationship between the proportion of fruit set of *D. pulchra* and used (i) the number of neighbouring *W. lepida* plants and (ii) the distance of *D. pulchra* to each *W. lepida* patch, as explanatory variables in our analyses. As before, there was no significant interaction between the two explanatory variables, so we did not include this in our model.

Pollination of translocated individuals

As an additional, more tightly controlled, test of whether distance from *W. lepida* population affects pollination success, we artificially translocated a total of 15 pairs of *D. pulchra* inflorescences (to control for potential mate limitation) to the centre of the *W. lepida* population and at varying distances from the centre of the population. Previous observations have indicated that *P. aethiopica* can fly hundreds of metres between plants, and flies throughout the entire flowering season of *D. pulchra* and *W. lepida* (K.J. Duffy personal observation; Johnson 2000). We colour-labelled the pollen in these plants (as described below) so that we could distinguish between pollinator-mediated self- and cross-pollination. We placed pairs of *D. pulchra* plants in three different directions from the *W. lepida* population to control for effects of general wind direction and aspect that might affect pollinator foraging. One pair was placed at each of five different distances in three directions from the population: (i) within the centre of the population, (ii) 50 m, (iii) 100 m, (iv) 300 m and (v) 500 m from the edge of the *W. lepida* population. The three directions in which the plants were placed in a linear fashion from the centre of the population were separated by >100 m. To track pollen movement in these experimental plants, we injected the anther sac of all flowers on one individual of each pair with either 2 μl rhodamine (0.2% mass per volume water) histochemical stain and 2 μl gentian violet in a premixed medicinal preparation (Alpha; Johnson *et al.* 2005) on the other plant. Previous work showed that these two stains do not affect the properties of pollen transfer in *D. pulchra* and other orchids (Peakall 1989; Johnson *et al.* 2005; Duffy & Johnson 2014). Each *D. pulchra*

inflorescence was placed in florists' foam and embedded in the soil 30 cm apart from the other inflorescence. Previous work has shown that *P. aethiopica* moves quickly between *D. pulchra* plants in succession (Johnson 2000); hence we assumed that any stained pollen found on a stigma that is the same colour as the pollinia is self-pollen. We counted an average of 94.7 massulae (SD = 15.3; n = 20) per pollinium. Investigations of 20 pollinia (ten with each stain) from 20 separate flowers showed that we stained an estimated 91.6% of massulae per pollinium for both stains. The number of flowers did not vary between plant pairs (paired *t*-test; $t = 0.773$, df = 25.7, $P = 0.447$). After 72 h, flowers, prior to floral wilting, on each plant were examined with a × 10 hand lens to determine (i) the proportion of pollinaria removed, (ii) the proportion of flowers with cross massulae (pollen stained a different colour or unstained pollen) deposited, and (iii) the proportion of flowers with self massulae deposited. We analysed these three measures separately using a GLM with binomial errors and correction for overdispersion using the quasibinomial distribution. The direction in which the plant pairs were placed from the mountaintop had no effect on pollinaria removal ($t_{28} = 0.613$, $P = 0.545$), flowers with cross-pollen deposited ($t_{28} = 0.193$, $P = 0.849$) or flowers with self-pollen deposited ($t_{28} = 0.913$, $P = 0.369$); therefore we combined the data from the three different directions for our analyses. Differences between distance categories on proportion of flowers with pollinaria removed, cross-pollen deposited and self-pollen deposited were compared using the Tukey HSD test in the 'multcomp' package for R (Hothorn *et al.* 2008).

RESULTS

Pollination and fruiting success in the natural population

Increased distance from neighbouring *W. lepida* patches had a negative effect on the proportion of pollinaria removed from *D. pulchra* flowers ($t_{63} = 2.799$, $\beta = -0.415$, $P = 0.007$; Fig. 2a), however local abundance of *W. lepida* had no effect on pollinaria removal ($t_{63} = 1.540$, $\beta = 0.516$, $P = 0.107$; Fig. 2b). Similarly, increased distance from neighbouring *W. lepida* patches had a negative effect on the proportion of flowers with massulae deposited ($t_{63} = 2.505$, $\beta = -0.352$, $P = 0.015$; Fig. 2c), however local abundance of *W. lepida* had no effect on massulae deposition ($t_{63} = 1.787$, $\beta = -0.534$, $P = 0.079$; Fig. 2d). There was no effect of distance to the neighbouring patch on proportion of fruit set ($t_{67} = 0.442$, $\beta = -0.038$, $P = 0.659$; Fig. 2e), but proportion of fruit set increased with increasing neighbouring *W. lepida* abundance ($t_{67} = 3.049$, $\beta = 1.378$, $P = 0.003$; Fig. 2f).

Pollination of translocated individuals

Our artificial translocation experiment involving plants with colour-stained pollen showed that the proportion of pollinaria removed from flowers was highest in plants translocated within the *W. lepida* population compared with all other distance classes ($t_{29} = 4.417$, $P < 0.001$; Fig. 3a). There was no difference between translocated plant pairs at varying distance in the proportion of flowers with cross massulae deposited (Fig. 3b), but there was a higher proportion of flowers with self massulae deposited for plant pairs at the furthest distance (500 m) from the *W. lepida* population (Fig. 3c), particularly between plant placed 50 and 500 m
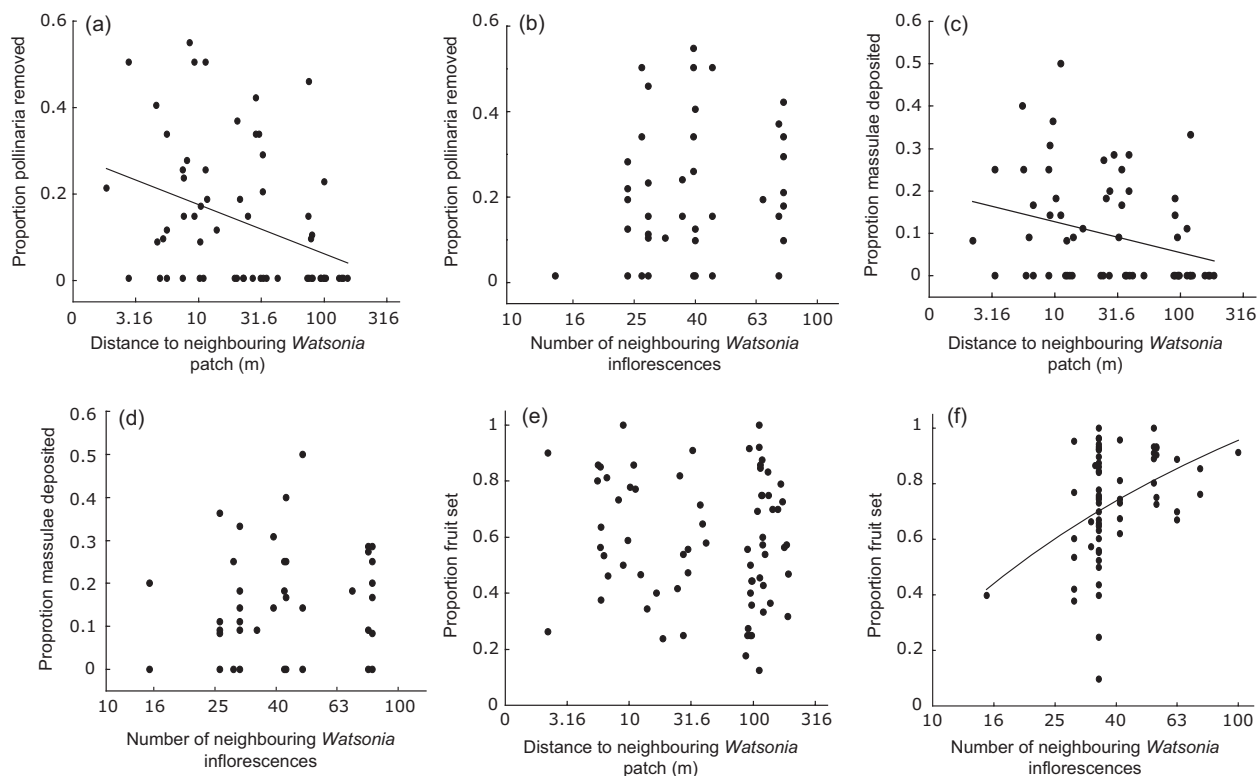
Fig. 2. Proportion of flowers with pollinaria removed according to: a: distance from neighbouring *W. lepida* patch (log) and b: number of neighbouring *W. lepida* plants (log); proportion of flowers with pollinaria deposited according to: c: distance from neighbouring *W. lepida* (log) and d: number of neighbouring *W. lepida* plants (log); and proportion of fruit set of *D. pulchra* according to e: distance from neighbouring *W. lepida* (log) and f: number of neighbouring *W. lepida* plants (log). The x-axes have been scaled logarithmically with the original values presented.
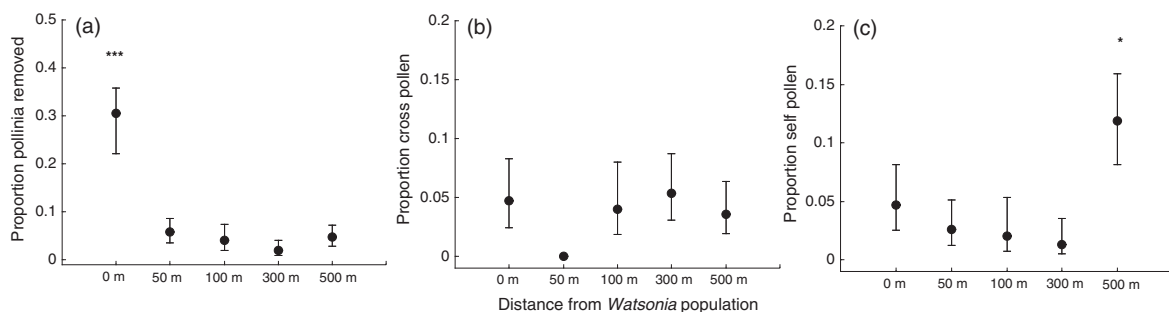

Fig. 3. Effect of experimental translocation of *D. pulchra* inflorescences at varying distances from the *W. lepida* population on a: proportion of flowers with pollinaria removed, b: proportion of flowers with cross-massulae deposited, and c: proportion of flowers with self-massulae deposited. *$P < 0.05$, ***$P < 0.001$. Means ($\pm$ SE) are back-transformed.

away from the *W. lepida* population ($z_{29} = 2.882$, $P = 0.032$) and plants placed 300 m and 500 m away from the *W. lepida* population ($z_{29} = 3.214$, $P = 0.012$).

DISCUSSION

These results suggest that proximity and abundance of *W. lepida* plants have a positive effect on pollination success and fecundity of individuals of the deceptive orchid *D. pulchra*. Because *D. pulchra* naturally grows intermingled with *W. lepida*, it is difficult to isolate the effects of isolation from *W. lepida* on *D. pulchra* from the effects of isolation from

conspecifics. While reduced pollen deposition on stigmas of *D. pulchra* plants isolated from *W. lepida* plants could therefore indicate mate limitation rather than lack of ecological facilitation by *W. lepida*, we found no effect of isolation of *D. pulchra* from conspecifics on any component of pollination or fecundity (K.J. Duffy unpublished data). However, pollen removal (a process largely unrelated to mate availability) was enhanced by proximity to *W. lepida* patches (Fig. 2), indicating that fly visitation to the orchid is enhanced by the presence of *W. lepida*.

We found increased pollen removal and deposition rates in *D. pulchra* when *W. lepida* plants were in close spatial

proximity, while the number of *W. lepida* inflorescences in the neighbouring patch had no effect on pollination success. This indicates that as long as there are *W. lepida* plants available in the neighbouring patch, *D. pulchra* will be successfully pollinated. These results are similar to those found by Peter & Johnson (2008) in the rewardless orchid *Eulophia zeyheriana*, whereby pollen removal and deposition rates decreased with distance from its model, *Wahlenbergia cuspidata*. They found that the decrease in pollination rates occurs within ~50 m from individual *W. cuspidata* plants. We found that the decrease in pollination rate in *D. pulchra* occurs at distances >100 m from *W. lepida* patches, but not necessarily from individual *W. lepida* plants. Pollinator-mediated ecological facilitation among plant species at larger spatial scales (*e.g.*, >100 m) is more likely to result from magnet species effects (spatial aggregation of pollinators; Laverty 1992) than from spatial differences in pollinator conditioning, particularly in cases where pollinators are highly mobile. We think it also unlikely that pollinators use a learned mental map to avoid patches that have a high frequency of mimics, as in the case of sexually deceptive orchids (Wong & Schiestl 2002), because *D. pulchra* and *W. lepida* provide no scent cues, which could make avoidance learning easier.

The decrease in pollination rate with decreasing distance from *W. lepida* patches did not translate into decreased fruit set per plant (Fig. 2e). Instead, we found that fruit set increased positively with numbers of *W. lepida* plants (Fig. 2f). Hence our proxy measure of pollinator visitation (proportion of flowers with pollinaria removed and massulae deposited) did not always equate to increased fecundity. Such discrepancy between pollination success and fruit set may arise when fecundity is not pollen-limited or when additional pollinator visits occur after the initial survey of pollination success (Alexandersson & Ågren 1996). The latter explanation seems more likely in this case. Initial pollination success of *D. pulchra* may be determined by increased proximity to *W. lepida*. Increased abundance of the model in neighbouring patches might be more important in determining fecundity of *D. pulchra*, as *P. aethiopica* is highly mobile and visits patches with a higher aggregation of *W. lepida* more frequently over the course of the flowering season. Monitoring pollinaria removal and deposition rates of *D. pulchra* in relation to abundance of *W. lepida* over the flowering season may

reveal a stronger effect of abundance of neighbouring patches, rather than their distance, on pollination success.

As was the case for naturally occurring orchids, pollinaria removal for translocated orchids decreased rapidly outside of the immediate *W. lepida* population (Fig. 2a), suggesting that visits by flies to the orchids decrease with isolation from the model species. Another effect of isolation of these translocated plants was an increase in the amount of self-pollination (Fig. 2c). Increased rates of pollinator-mediated self-pollination have been reported for isolated plants of rewarding orchid species (Johnson *et al.* 2009), but we are not aware of this phenomenon being recorded previously in deceptive orchids. The most likely explanation is that pollinators probe more flowers per plant, even of deceptive species, when encounter rates with plants are lower. This effect would be expected to be most pronounced when rewarding plants are scarce or absent and pollinators are more motivated to find nectar. Increasing self-pollination rates with increased distance from the *W. lepida* population may ultimately cause increased inbreeding depression and reduced recruitment of *D. pulchra* individuals further away from *W. lepida*. Such optimal foraging by *P. aethiopica* highlights the extreme spatial reliance of *D. pulchra* on *W. lepida* for its fecundity.

In conclusion, pollination success and fecundity of *D. pulchra* plants are influenced by proximity to plants of *W. lepida*. This form of ecological facilitation of the reproduction of one plant species by another is probably widespread in floral mimics and their models and also in more generalised systems of exploitation of food-seeking animals. Although these ecological interactions were studied at the population scale, we expect the effects to be even greater at large spatial scales and to have consequences for the geographic distributions of food-deceptive plant species.

ACKNOWLEDGEMENTS

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