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Author(s): Steven D. Johnson, Craig I. Peter, L. Anders Nilsson and Jon Ågren

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## POLLINATION SUCCESS IN A DECEPTIVE ORCHID IS ENHANCED BY CO-OCCURRING REWARDING MAGNET PLANTS

STEVEN D. JOHNSON,<sup>1,3</sup> CRAIG I. PETER,<sup>1</sup> L. ANDERS NILSSON,<sup>2</sup> AND JON ÅGREN<sup>2</sup>

<sup>1</sup>*School of Botany and Zoology, University of Natal, P. Bag X01, Scottsville, Pietermaritzburg 3209, South Africa*

<sup>2</sup>*Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villav. 14, SE-752 36 Uppsala, Sweden*

**Abstract.** It has been debated whether pollination success in nonrewarding plants that flower in association with nectar-producing plants will be diminished by competition for pollinator visits or, alternatively, enhanced through increased local abundance of pollinators (the magnet species effect). We experimentally evaluated these effects using the nonrewarding bumblebee-pollinated orchid *Anacamptis morio* and associated nectar-producing plants at a site in Sweden. Pollination success (estimated as pollen receipt and pollen removal) in *A. morio* was significantly greater for individuals translocated to patches of nectar-producing plants (*Geum rivale* and *Allium schoenoprasum*) than for individuals placed outside (~20 m away) such patches. These results provide support for the existence of a facilitative magnet species effect in the interaction between certain nectar plants and *A. morio*. To determine the spatial scale of these interactions, we correlated the visitation rate to flowers of *A. morio* with the density of sympatric nectar plants in 1-m<sup>2</sup> and 100-m<sup>2</sup> plots centered around groups of translocated plants, and at the level of whole meadows (~0.5–2 ha). Visitation rate to flowers of *A. morio* was not correlated with the 1-m<sup>2</sup> patch density of *G. rivale* and *A. schoenoprasum*, but showed a significant positive relationship with density of these nectar plants in 100-m<sup>2</sup> plots. In addition, visitation to flowers of *A. morio* was strongly and positively related to the density of *A. schoenoprasum* at the level of the meadow. Choice experiments showed that bees foraging on the purple flowers of *A. schoenoprasum* (a particularly effective magnet species) visit the purple flowers of *A. morio* more readily (47.6% of choices) than bees foraging on the yellow flowers of *Lotus corniculatus* (17% of choices). Overall similarity in flower color and shape may increase the probability that a pollinator will temporarily shift from a nectar-producing “magnet” plant to a nonrewarding plant. We discuss the possibility of a mimicry continuum between those orchids that exploit instinctive food-seeking behavior of pollinators and those that show an adaptive resemblance to nectar-producing plants.

**Key words:** *Anacamptis morio*; *Bombus*; competition; magnet species; mimicry; nectar; Orchidaceae; pollen limitation; population density; population size; transplant experiment.

### INTRODUCTION

Interactions between plants and animals may be strongly influenced by the local physical and biotic environment (Thomson 1978, Campbell 1987, Johnson and Bond 1992, O’Connell and Johnston 1998). Proximity to other plant species, in particular, has been shown to affect the intensity of pollination or herbivory experienced by a focal species (Thomson 1978, Root 1973, Holt and Lawton 1994, Callaway 1995, Hambäck et al. 2000). Pollination success may be diminished by competition, either when neighboring plants with superior rewards draw pollinators away, or when sharing of pollinators results in reproductive interference through the receipt of heterospecific pollen, or wasted export of pollen to heterospecific stigmas (Free 1968, Waser 1983). Many plant traits, including flowering time, floral specialization for specific pollinators, and

even habitat requirements, have been interpreted as evolutionary outcomes of competition among plants for pollinators (Heinrich 1975).

Although interactions between coflowering plants have tended to be viewed within the paradigm of competition, there is increasing recognition that some plants may actually facilitate the pollination of others in the same community (Feinsinger et al. 1986, Feinsinger 1987). One mechanism for facilitation is the “magnet species effect” (Thomson 1978) whereby a rewarding species increases the pollination success of neighboring plants with inferior rewards. The magnet species, as its name implies, may function by increasing the local abundance of pollinators. Neighboring plants may gain a net benefit from the greater abundance of pollinators around the magnet, even though pollinators may show more or less constancy to the magnet species and cause reproductive interference. Nonrewarding plant species may benefit most from close proximity to magnet species, although the phenomenon may extend to plants with floral rewards (Pellmyr 1986, Laverly 1992).

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<sup>3</sup> E-mail: Johnsonsd@nu.ac.za

Plants that do not produce floral rewards are surprisingly common, and include approximately one-third of all orchids, by some estimates the largest angiosperm family (Dafni 1984, Ackerman 1986). Some of these deceptive plants are spectacular mimics of co-occurring food plants or even female insects, but the large majority simply exploit the instinctive food-seeking behavior of pollinators, a phenomenon termed generalized food deception (Nilsson 1992). It seems reasonable that deceptive plants would compete poorly with nectar plants for pollinator visits. The common occurrence of deceptive orchids in habitats lacking many rewarding plants, such as marshes, has been considered as consistent with the competition hypothesis (Heinrich 1975, Nilsson 1980, Firmage and Cole 1988). The competition hypothesis has received empirical support from decreased pollination success in patches of the deceptive marsh orchid *Dactylorhiza incarnata* following experimental addition of nectar-producing *Viola* flowers (Lammi and Kuitunen 1995). Lammi and Kuitunen (1995) referred to increased success of their orchids in the absence of rewarding plants as the "remote habitat" effect. On the other hand, Lavery's (1992) study, showing that pollination success in non-rewarding mayapples *Podophyllum peltatum* L. is positively related to the proximity of a cluster of nectar-producing lousewort *Pedicularis canadensis* L. colonies, supports the alternative facilitation hypothesis and, more specifically, the magnet species effect proposed by Thomson (1978). In another test of the magnet species effect, Alexandersson and Ågren (1996) found that pollen export from flowers of the deceptive orchid *Calypso bulbosa* L. was positively related to the density of the nectar-producing plant *Salix caprea* L. in one of three years of study.

In light of the equivocal evidence for these two contrasting hypotheses (competition vs. facilitation), it has not been possible to generalize about the importance of rewarding plants for the pollination success of sympatric nonrewarding plants. Furthermore, we know little about the spatial scale and density dependence of such interactions. Do food-deceptive species depend on rewarding species in the larger habitat (on the scale of hectares), yet benefit from growing in smaller habitat units, such as marshes, that have few rewarding species, or do food-deceptive species gain benefit from intermingling with rewarding species at all spatial scales and densities? Finally, we know even less about the role of floral traits in determining the outcomes of these interactions. For example, does similarity in color and shape between a deceptive and rewarding species increase the likelihood that the rewarding species will act as a magnet species?

The aims of this study were (1) to test whether the pollination success of a nonrewarding orchid is enhanced or diminished by the presence of nectar producing plants, (2) to determine the influence of both spatial scale and plant density on these interactions,

and (3) to gain some insights into whether floral traits (and their influence on pollinator behavior) could explain why some plants might act as magnet species while others do not.

## METHODS

### *The study species*

Fieldwork took place during May through June 2001 on the island of Öland off the east coast of Sweden. The study species, *Anacamptis morio* (L.) Bateman, Pridgeon & M. W. Chase (syn. *Orchis morio* L.), occurs in large populations in virtually all of the open grazed meadows in the vicinity of the Ecological Field Station of Uppsala University at Ölands Skogsby. This orchid is nonrewarding and pollinated almost exclusively by queen bumblebees at this site (Nilsson 1984). As the purple-pink flowers of *A. morio* do not closely resemble the color or shape of flowers of any sympatric rewarding species, its pollination system has been characterized as generalized food deception (Nilsson 1984). Queen bumblebees in the meadows around the Ecological Research Station feed mainly on nectar in the flowers of *Geum rivale* L. (Rosaceae), *Anthyllis vulneraria* L. (Fabaceae), *Lotus corniculatus* L. (Fabaceae), and *Allium schoenosprasum* L. (Alliaceae) during the time that *A. morio* is in flower (Fig. 1, Nilsson 1984). *Anacamptis morio* grows intermingled to a greater or lesser degree with all of these species, except *G. rivale*, which tends to occupy deeper soils than the orchid.

Previous studies have shown that *A. morio* is self-compatible, but relies on pollinator visits for fruit set (Nilsson 1984). Like many deceptive orchids, fruit set in *A. morio* is strongly pollen limited, and ~50% of the plants fail to produce fruits in a given year (Nilsson 1984, Johnson and Nilsson 1999).

### *Translocation experiments*

We carried out two separate translocation experiments to determine the consequences for pollination success of individual plants of *A. morio* when they flower in patches of bumblebee-pollinated nectar plants vs. when they flower outside such patches.

In the first experiment, involving *G. rivale* as the nectar plant, 168 orchids were excavated in sods of original turf and potted individually at the beginning of the flowering season. All flowers on the experimental plants were checked, and those with pollen on the stigma or pollinia removed were excised. The plants were then randomly assigned to one of two treatments in a paired design with each replicate consisting of four plants, placed 50 cm apart in a square configuration, in a flowering patch of *G. rivale* and another four plants placed in the same configuration ~20 m away from the patch. This "remote" location matched the patch location in terms of physical and vegetation attributes, but lacked flowers attractive to bumblebees. Pots were



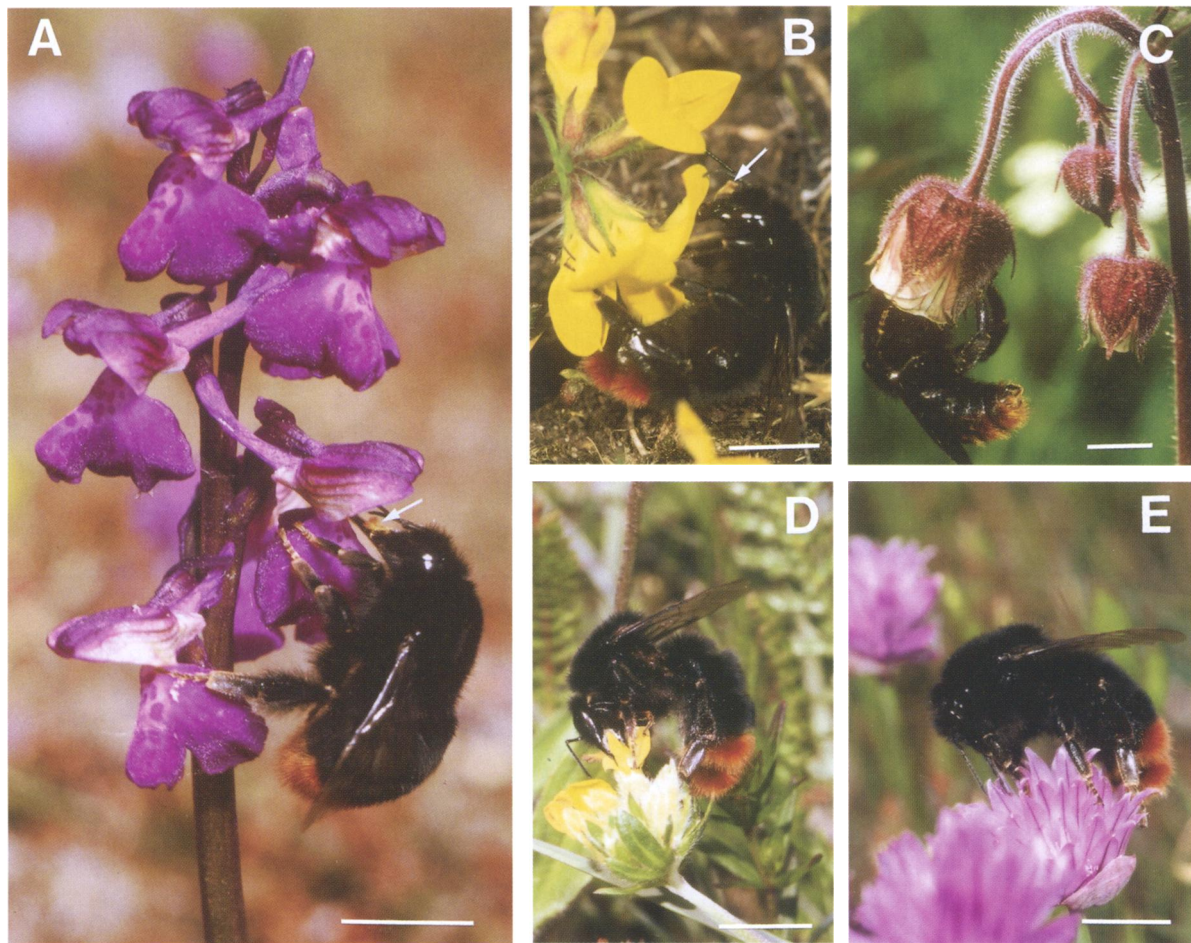


FIG. 1. *Bombus lapidarius* queens visiting flowers of the plant species used in this study: (A) *Anacamptis morio*; (B) *Lotus corniculatus*; (C) *Geum rivale*; (D) *Anthyllis vulneraria*; (E) *Allium schoenoprasum*. Scale bars are each 10 mm.

buried in the soil and the orchids did not require watering throughout the 10-day duration of the experiment, which was characterized by intermittent rainfall. Twenty-one pairs were placed in the meadows around the field station, each using a separate patch of *G. rivale*. The mean number of flowers per plant did not differ significantly between the treatments (9.4 inside vs. 8.8 outside patches of *G. rivale*; paired *t* test,  $t = 1.1$ ,  $df = 19$ ,  $P = 0.27$ ). The orchids were replanted in their original habitat once flowering was completed.

In the second experiment, involving *A. schoenoprasum* as the nectar plant, 112 orchid inflorescences were cut at ground level and placed in film canisters filled with florist's foam and water. Flowers with pollen on the stigma or pollinia removed were excised. Each inflorescence was then randomly assigned to one of two treatments in a paired design consisting of two inflorescences placed 50 cm apart in a flowering patch of *A. schoenoprasum*, and two inflorescences placed in the same configuration, but ~20 m away in a location that was matched in terms of physical and vegetation attributes, but lacked any flowering plants attractive to

bumblebees. The film canisters were buried at ground level and topped up with water daily. Twenty-eight pairs, each utilizing a separate patch of *A. schoenoprasum*, were placed in the meadows around the field station. Flower number per inflorescence did not differ significantly between the two treatments (7.6 inside vs. 7.5 outside patches of *A. schoenoprasum*; paired *t* test,  $t = 0.23$ ,  $df = 26$ ,  $P = 0.82$ ). The inflorescences were harvested after three days when they started to show signs of wilting.

At the end of both translocation experiments, we recorded for each inflorescence the number of flowers with conspecific pollen on the stigma, the number of flowers with pollinia removed, and the total number of flowers with signs of visitation (either pollen deposited, pollinia removed, or both). As groups were treated as replicates, we calculated means of each measure from the individual plants in a group. We used paired *t* tests to examine whether the proportion of stigmas pollinated, proportion of flowers from which pollinia were removed, and mean overall visitation (proportion of flowers showing signs of either pollination or pollinia

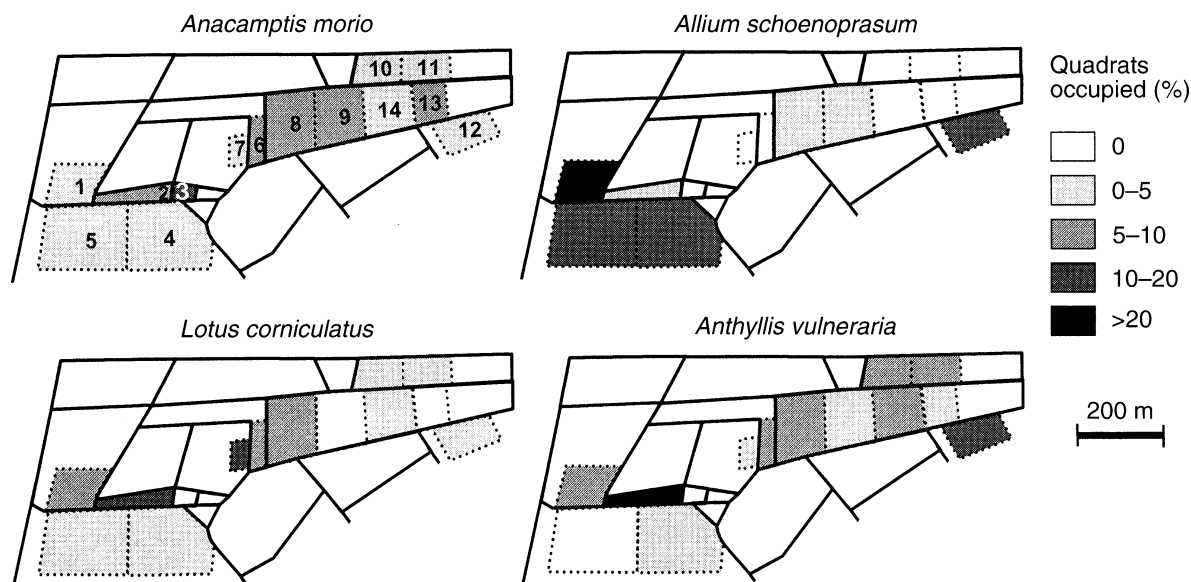


FIG. 2. Distribution and relative density (percentage of occupied 0.4-m<sup>2</sup> quadrats) of the study species in 14 meadows (numbered) at the study site. Thick black lines indicate meadows bounded by stone walls and hedgerows.

removal) differed between groups of translocated orchids placed inside and outside patches of nectar plants. We also recorded the density of nectar plants (flowering stems) in square plots of 1 and 100 m<sup>2</sup> around each group of orchids translocated into patches of nectar plants. The effect of nectar plant density on the proportion of flowers visited, proportion of flowers receiving pollen, and proportion of flowers from which pollen was removed was analyzed using linear regression (analyses based on means for each group of translocated orchids). All proportions were arcsine-square-root transformed prior to analysis.

#### Meadow surveys

To determine whether the pollination success of *A. morio* is influenced by the nectar plant density at a larger habitat scale than examined in the translocation experiments, we carried out a survey of the density of *A. schoenoprasum*, *A. vulneraria*, and *L. corniculatus* in 14 meadows in which *A. morio* occurs close to the Ecological Field Station (Fig. 2). Meadows at this site are surrounded by stone walls overgrown with shrubs and trees and can differ markedly in the abundance of nectar plants as a result of differing management practices. Three exceptionally large or narrow meadows were divided a priori into several smaller meadows that shared a common boundary without a stone wall (Fig. 2). We laid out parallel transects across each meadow at 10-m intervals and recorded the occurrence of the three nectar plants as well as *A. morio* in 0.4-m<sup>2</sup> quadrats spaced at 1-m intervals along each transect. Orchids encountered along these transects were scored for pollination success in the same manner as those in the translocation experiments. If few orchids were en-

countered along these transects, additional transects were laid out until the total number of orchids scored per meadow reached at least 20.

We used multiple regression to examine how measures of pollination success (proportion of flowers visited, proportion of flowers receiving pollen, and proportion of flowers from which pollen was removed) were related to five meadow variables (densities of the three nectar plants, density of orchids, and meadow size). Univariate regression was used to explore the relationship between overall nectar plant density and the proportion of orchid flowers visited. All proportions were arcsine-square-root transformed prior to analysis.

#### Choice experiments

Pollinators of deceptive orchids are very seldom observed visiting orchid flowers. For example, Nilsson (1984) recorded sequences of bumblebee visits to flowers of *A. morio* on only eight occasions during 10 years of observations on Öland. To establish the frequency with which queen bumblebees actually accept or reject orchid inflorescences encountered along their foraging routes, we used the "bee interview technique" (Thomson 1988, Johnson and Nilsson 1999). A freshly cut inflorescence with 10 flowers (the average for this population) was tied to the end of a long bamboo rod and placed along the foraging path of individual *Bombus lapidarius* queens (the primary pollinator of *A. morio* at this site, according to Nilsson [1984]). The inflorescence was placed 20 cm away from a bee as it foraged on a flower of a nectar plant, and in such a manner that the bee had a choice to visit the orchid or skip it completely and visit another flower of the nectar plant. We also recorded the number of orchid pollinia on the

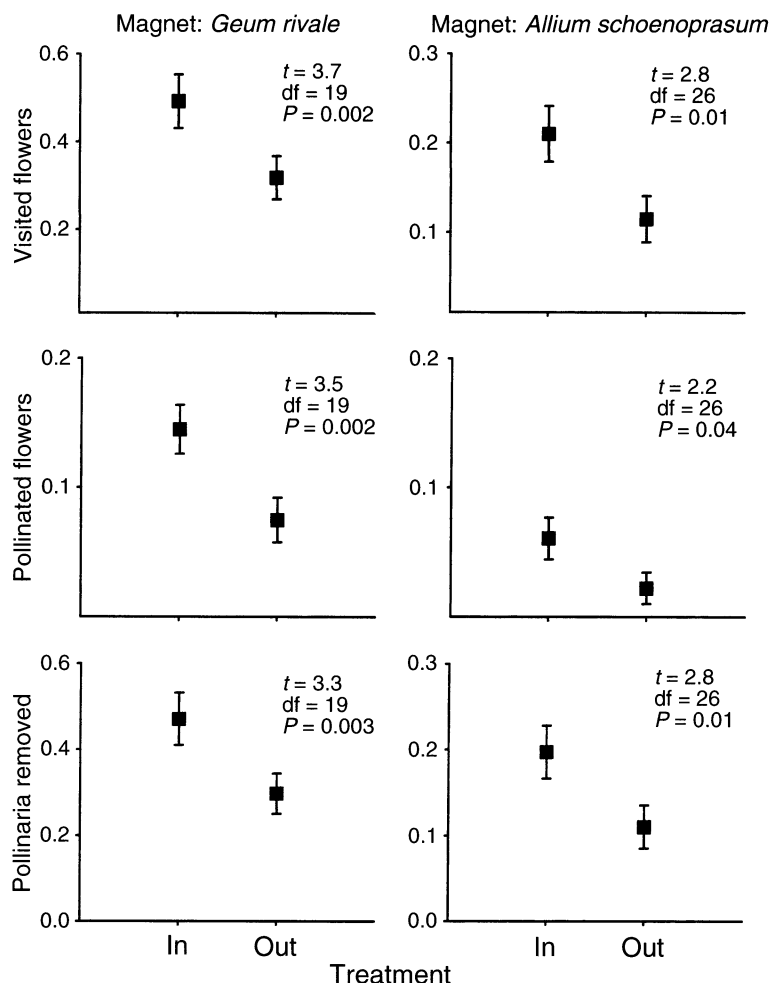


FIG. 3. Mean pollination success (proportion of flowers visited, proportion of flowers pollinated, and proportion of flowers with pollinia removed) of the deceptive orchid *Anacamptis morio* translocated inside (In) or outside (Out) patches of nectar-producing plants. Differences in mean pollination success were examined with paired *t* tests of arcsine-square-root transformed data (*G. rivale*,  $n = 21$  groups of translocated orchids; *A. schoenoprasum*,  $n = 28$  groups).

bees that made these choices. The choice experiments were all conducted over one 48-h period (5 and 6 June) in one meadow to allow comparisons of the behavior of bees feeding on various nectar-producing plants without introducing seasonal changes in bee behavior as a confounding factor. Chi-square tests were used to examine whether the likelihood that a bumblebee would visit *A. morio* was influenced by the nectar plant on which it was feeding (*A. schoenoprasum* or *L. corniculatus*), or by whether it carried pollinia or not.

## RESULTS

### Translocation experiments

Orchids translocated into patches of nectar plants performed significantly better in terms of pollen receipt, pollen removal, and overall visitation than those translocated outside such patches (Fig. 3).

For plants translocated to patches of nectar-producing plants, the proportion of flowers visited was not

related to the density of nectar plants in the 1-m<sup>2</sup> plots for patches of either *Geum rivale* (linear regression,  $R^2 = 0.13$ ,  $P = 0.11$ ) or *Allium schoenoprasum* ( $R^2 = 0.001$ ,  $P = 0.88$ ). However, the visitation rate to orchid flowers was positively related to nectar plant density in the 100-m<sup>2</sup> plots for patches of both *G. rivale* and *A. schoenoprasum* (Fig. 4).

### Meadow surveys

Multiple regression showed that a high percentage of the variation in pollination success of *A. morio* among meadows at the study site can be explained by a model that includes density of the three nectar plants, orchid density, and meadow size (Table 1). Density of *A. schoenoprasum* consistently had a strong positive effect on all measures of pollination success of the orchid (Table 1), while density of *Anthyllis vulneraria* had a significant positive effect on orchid visitation, but no statistically significant effect on the individual



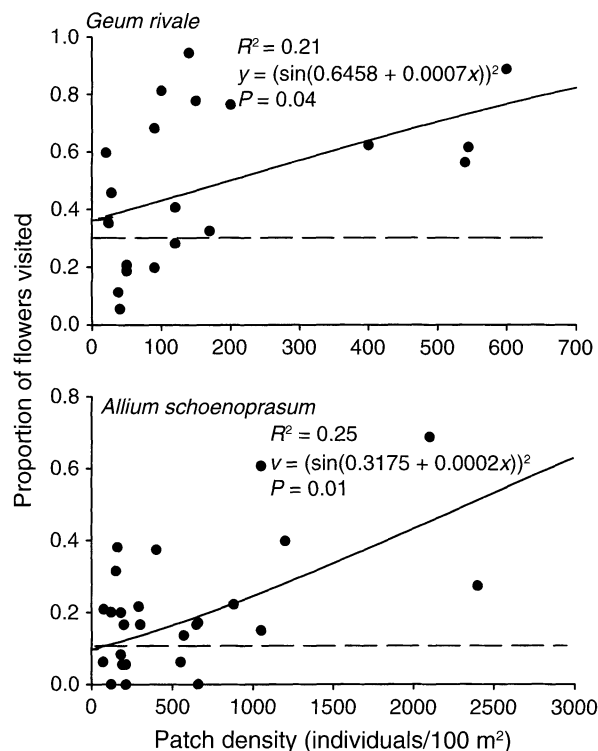


FIG. 4. The relationship between density of nectar plants in 100-m<sup>2</sup> quadrats and the mean proportion of flowers visited on translocated plants of the deceptive orchid *Anacamptis morio*. The dashed line represents the mean proportion of flowers visited on plants translocated into adjacent habitats lacking nectar plants (Fig. 3).

components of pollination success (pollen receipt and removal). Density of *Lotus corniculatus* had a significant negative effect on pollen deposition, but no significant effect on other measures of pollination success. Orchid density and meadow size did not have significant effects on pollination success in the orchids. Overall, much of the variation in the proportion of *A. morio* flowers visited could be explained by a simple univariate linear relationship with bumblebee nectar plant density in the meadows (Fig. 5).

#### Choice experiments

We found that *Bombus lapidarius* queens readily visited inflorescences of *A. morio* that were placed along

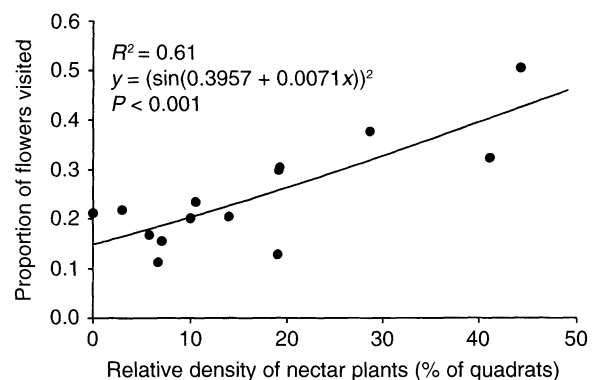


FIG. 5. The relationship between relative density (percentage of occupied 0.4-m<sup>2</sup> quadrats) of nectar-producing plants and mean proportion of flowers visited on inflorescences of *Anacamptis morio* in 14 meadows at the study site (see Fig. 2).

their foraging routes (Fig. 6). In total, we presented bees with 105 choices of which 35.2% resulted in a visit to the orchid. Bees foraging on the flowers of *A. schoenoprasum* were more likely to visit the orchid than bees foraging on *L. corniculatus* (47.6% vs. 17%). Bees carrying pollinia (indicating that they had previously visited *A. morio*) were more likely to visit the orchid than those without pollinia (Fig. 6).

#### DISCUSSION

The results of this study are consistent with the magnet species effect proposed by Thomson (1978). Pollination success in *Anacamptis morio* was significantly enhanced by translocation into patches of nectar plants, and positively correlated with density of nectar plants at both the local habitat (100 m<sup>2</sup>) and the meadow scales. Thus we are able to reject the competition hypothesis and, more specifically, the “remote habitat” effect (Lammi and Kuitunen 1995) as an explanation for spatial patterns of pollination success in this orchid species.

It is of interest to consider why, in light of these results, many, if not the majority, of biologists working on orchid pollination have held the belief that generalized food deceptive orchids face competition from sympatric nectar-producing plants, and thus benefit from growing in “remote” habitats away from such

TABLE 1. Multiple regression models for factors influencing three measures of pollination success (proportion of flowers visited, proportion of flowers pollinated, and proportion of flowers with pollinia removed) in *Anacamptis morio* (analyses based on mean pollination success in 14 meadows).

Dependent variable	Partial regression coefficients					Model		
	ALL	ANT	LOT	ANA	SIZ	F	P	R <sup>2</sup>
Visitation	1.18***	0.70*	-0.31	0.68	-0.90 × 10 <sup>-5</sup>	11.80	0.002	0.81
Pollination	1.00***	0.36	-0.92*	0.42	-0.30 × 10 <sup>-4</sup>	9.19	0.004	0.76
Pollinia removal	1.08***	0.63	-0.18	0.66	-0.83 × 10 <sup>-5</sup>	7.86	0.006	0.73

Notes: Degrees of freedom for all three F values are 5 and 8. Abbreviations are: ALL, density of *Allium schoenoprasum*; ANT, density of *Anthriscus vulgaris*; LOT, density of *Lotus corniculatus*; ANA, density of *A. morio*; SIZ, meadow size.

\* P < 0.05; \*\*\* P < 0.001.

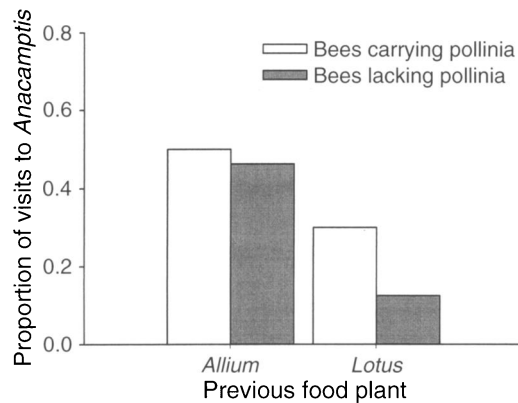


FIG. 6. Results of choice experiments with *Bombus lapidarius* queens using the bee interview technique. Bees foraging on flowers of *Allium schoenoprasum* were more likely to visit *Anacamptis morio* than bees foraging on *Lotus corniculatus* ( $\chi^2 = 12.5$ ,  $df = 1$ ,  $P = 0.008$ ). Overall, bees carrying pollinia were more likely than bees without pollinia to visit *A. morio* ( $\chi^2 = 7.33$ ,  $df = 1$ ,  $P = 0.006$ ).

nectar plants (Heinrich 1975, Boyden 1980, Nilsson 1980, Dafni 1984, Firmage and Cole 1988, Lammi and Kuitunen 1995). The origins of the remote habitats hypothesis can be traced to Delpino (1874) who argued that the common pattern in deceptive orchids for fruits to be set only on the lowermost flowers of inflorescences reflects visitation happening only early in the season when insects are inexperienced and not yet drawn away by nectar-producing plants. During the late 1970s and early 1980s, many plant reproductive ecologists were engaged in studying whether staggered flowering patterns are a response to competition for pollinators (Heinrich 1975, Rathke 1988). Flowering of food-deceptive orchids in early spring was interpreted as an adaptation that reduced competition with nectar-producing plants for pollinator visits and maximized the exposure of these plants to visits by inexperienced newly emerged insects (cf. Nilsson 1980). However, more recent studies have recognized that flowering patterns may reflect factors such as phylogenetic constraints and optimal timing for seed dispersal, as much as competition for pollinators (cf. Johnson 1993). Furthermore, the notion that pollinators of generalized food-deceptive orchids are inexperienced is not supported by the present study. The *Bombus lapidarius* queens that visited *A. morio* in early June had probably emerged for several weeks, and yet investigated and probed flowers of *A. morio* when foraging in dense stands of nectar-producing plants (Fig. 6). Most striking was the fact that queens carrying pollinia (and thus those that had clearly visited the orchid previously) were more likely to visit the orchids than those that did not carry pollinia (Fig. 6). While queen bumblebees may learn to avoid orchid flowers in dense monospecific populations (Smithson and Macnair 1997, Ferdy et al. 1998), it seems that orchids inter-

mingled at low densities with nectar-producing plants may continue to benefit from exploratory visits by bumblebees.

In contrast to the results of the present study, Lammi and Kuitunen (1995) found that the pollination success of the deceptive orchid *Dactylorhiza incarnata* was depressed by addition of potted *Viola* flowers. In the latter study, the densities of orchids and nectar plants were low and roughly equal (0.4–0.5 plants/m<sup>2</sup>). By contrast, the density of nectar plants far exceeded that of the orchids in the present study, which perhaps better approximates the natural situation for most orchids. It is doubtful whether the potted violas in the study by Lammi and Kuitunen (1995) represented a magnet resource capable of creating a local abundance of bumblebees. Rather, the violas may have acted as a distraction from the orchids for bumblebees that were in transit across the habitat. We found that the intercept for the curve for the relationship between nectar plant density and pollination success of translocated orchids closely matched the basal level of pollination success attained for groups of translocated plants in remote habitats (Fig. 4). This suggests that substantial numbers of nectar plants need to be added to orchid patches if a magnet species effect is to be detected.

Thomson (1981) first considered the spatial scale at which flower-feeding insects might assess the profitability of rewarding patches. He concluded that bumblebees responded to the density of flowering daisy plants in blocks that were ~500 m<sup>2</sup> in size. Our results show that the pollination success of *A. morio* is positively correlated with magnet plant density at both the local habitat (100 m<sup>2</sup>) and larger habitat (meadows ~1 ha in size) scales, but uncorrelated with magnet plant density at the microhabitat (1 m<sup>2</sup>) scale. A similar lack of correlation between orchid pollination success and food plant density at the 1 m<sup>2</sup> scale was recently reported by Gumbert and Kunze (2001) for the food deceptive orchid *Orchis boryi*, but nectar plant density at larger spatial scales was not recorded in their study. The correlations we observed between nectar plant density and orchid pollination success probably reflect aggregation of queen bumblebees in rewarding patches. The scale of the entire study area, including the 14 meadows, was within the foraging range of individual bumblebees (Osborne et al. 1999), and thus the patterns of pollination success in the orchids were unlikely to be influenced by geographical differences in the abundance of resident bumblebees. The underlying basis of the magnet species effect is almost certainly that some pollinators show greater constancy to individual rewarding sites than they do to individual plant species (cf. Thomson 1981). Recent studies have shown that *Bombus lapidarius* workers show striking constancy to patches containing flowering plants, even when these patches are contiguous (Osborne and Williams 2001).

Our study provides strong indications that not all nectar-producing species will act as magnet species, in



the sense of imparting pollination benefits to neighboring plants with inferior rewards. In the multiple regression of the meadow data, only *A. schoenoprasum* emerged as having consistently strong beneficial effects on the pollination success of *A. morio*. Is it possible to identify traits that make one species more likely to act as a magnet species than another?

*Bombus lapidarius* queens foraging on the pink-purple flowers of *A. schoenoprasum* (which emerged as a strong magnet species in this study) were more than twice as likely to visit flowers of *A. morio* as were queens foraging on the yellow flowers of the legume *L. corniculatus* (Fig. 6). The flowers of *A. schoenoprasum* are much closer in color to the flowers of *A. morio* in the bee visual spectrum than are the flowers of *L. corniculatus* (Nilsson 1984). We can only speculate as to the role of color in these bee choices because of additional differences in plant height, flower shape, and odor between the species. However, the results are consistent with those of Wilson and Stine (1996) and Chittka et al. (1997), who both showed that bumblebees are more likely to shift to flowers that are similar in color to those on which they have recently been foraging (see also Gumbert 2000). Thus food deceptive orchids are probably more likely to benefit from association with a nectar-producing species that is similar in color (Gumbert and Kunze 2001). This raises the intriguing possibility of a continuum between generalized food deception and true adaptive resemblance. Selection may favor increasing similarity of deceptive orchids to the most effective magnet species with which it shares a common habitat. This might provide a pathway along which evolution may proceed to the well-developed examples of species-specific Batesian floral mimicry (cf. Johnson 1994, Roy and Widmer 1999). If, on the other hand, orchids do not coexist with a stable assemblage of species, then selection would favor a generalized set of display traits that allows the orchid to exploit a number of possible magnet species. The latter scenario seems more likely in the European flora, which is characterized by floral assemblages which are unlikely to have remained stable in the face of postglacial and anthropogenic changes.

An explicit prediction of any mimicry hypothesis is that mimics should enjoy greater fitness when occurring with their model than when alone (Dafni 1984). Thus, increased pollination success in deceptive orchids when growing together with certain nectar plants has been used to argue for the existence of specific Batesian mimicry in flowers (cf. Dafni and Ivri 1981, Dafni 1983, Nilsson 1983, Johnson 1994). Our results suggest that this pattern may be a general phenomenon that occurs even when orchids do not closely resemble nectar flowers. This does not mean that true adaptive resemblance does not occur, but rather that additional evidence must be sought before it is concluded that orchids bear an adaptive resemblance to a particular plant species. Such evidence might include very close

matching of spectral reflectance (cf. Nilsson 1983, Johnson 1994), behavioral experiments that establish that pollinators are literally unable to distinguish mimic from model (Johnson 1994, 2000), or a correlation between among-population variation in attractive traits in the putative mimic and variation in the attractive traits of model species (Johnson 1994). Such criteria have seldom been met in any studies of floral mimicry. Indeed, some published studies of floral mimicry may need to be reinterpreted as being a magnet species effect between an orchid and a nectar plant with which it shares a nonspecific overall resemblance.

As was first pointed out by Thomson (1982), we have no reliable way of predicting whether the interaction of any two plant species will be characterized by competition or facilitation for pollination. Orchids with their pollen aggregated into pollinia may be relatively buffered from reproductive interference, as pollen wastage to foreign stigmas generally does not take place (other orchids excepted), and their broad stigmas seldom become clogged with foreign pollen (Harder and Thomson 1989, Johnson and Edwards 2000). In this sense, orchids may benefit more than other plant families from the magnet species effect. However, benefits from magnet species may extend to both nonrewarding (Pellmyr 1986, Lavery 1992) and rewarding (Thomson 1978) plants in other families, and even include fungi with pseudoflowers (Roy 1994). Because of the deeply entrenched notion that plant interactions for visits by pollinators are characterized by competition, ecologists may often have overlooked, or omitted to test for, facilitation in plant assemblages that share common pollinators.

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