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Deceptive pollination of *Dactylorhiza incarnata*: an experimental test of the magnet species hypothesis

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Abstract Floral deception, which mainly appears in highly evolved families such as Orchidaceae, was studied in Central Finland. In nectarless *Dactylorhiza incarnata*, the deceptive pollination system has been considered to function best in remote habitats such as marshes, where flowering plants attractive to pollinators are rare (remote habitats hypothesis). In contrast, the magnet-species theory predicts that a nectarless plant benefits from growing in the vicinity of nectar-containing species. We tested these hypotheses by adding attractive, nectar-containing violets (*Viola* × *wittrockiana*) to orchid populations. The percentage of fruit set in *D. incarnata* was adversely affected by the violets, probably because interspecific exploitation competition for pollinators took place in favour of the violas at the expense of the orchids. This result gave no support for the magnet-species theory and supported the remote habitats hypothesis.

Key words Reproductive success · Magnet-species theory · Deceptive pollination system · Nectarless orchids

Introduction

Most insect-pollinated plant species attract their pollinators with rewards, usually nectar or pollen or both. Nevertheless, some species do not offer rewards and yet they are pollinated by insects. These species have deceptive pollination systems that are supposedly derived from reward pollination systems (Ackerman 1986). Deception is especially common in highly evolved plant families such as Orchidaceae and Asclepiadaceae. In the former family, perhaps 10 000 species deceive their pollinators (Little 1983; Dafni 1984; Ackerman 1986; Nilsson 1992). The means by which orchids deceive their pollinators may be categorised into several types of manipulation of pollinator behaviours: territorial defence, brood-site selection, sexual response and, most commonly, food-foraging behaviour of the pollinators (Ackerman 1986; Nilsson 1992).

Many deceptive orchids exploit pollinator foraging behaviour by attracting insects with a variety of dummy signals and nectarless or pollenless structures. Food frauds either mimic certain co-blooming rewarding flowers or function without models. These two strategies result in different evolutionary outcomes. In mimicry systems, fitness in the mimic orchids should be sensitive to variation in relative frequency, density and display of models. Associative learning by pollinators of the model controls selection on the mimic (Dafni 1983; Nilsson 1983, 1992). Food-fraud orchids without a model, however, often bloom gregariously and exhibit display polymorphisms that impede subsequent associative learning of the pollinators. Generalist foragers, such as bumblebees, have evidently constrained flowering phenology in these species to periods when emergent, naive bees begin to search for food and can be deceived (Nilsson 1980, 1984, 1992).

In *Dactylorhiza* there is no evidence of mimetic resemblance to food flowers. All species are nectarless and deceive their pollinators (Nilsson 1981), although some populations of *D. fuchsii* produce glucose-rich stigmatic fluid that could be exploited by bumblebees (Dafni and Woodell 1986). Marsh dactylorchids, such as *D. incarnata*, are apparently adapted to exploit short visits by inexperienced or unconditioned bumblebee workers (Daumann 1941; Nilsson 1981) which find their first food flowers solely by optical cues (Kugler 1935). Deception continues throughout anthesis because fresh workers emerge from nests continuously (Nilsson 1980). *D. incarnata* is self-compatible, but spontaneous autogamy does not occur in nature (A. Lammi, unpublished data). Each plant produces

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an average of 15 bright pink nectarless and scentless (Nilsson 1980) flowers, borne in a spike.

According to Nilsson (1981), certain conditions should occur for deception to function in *Dactylorhiza*: (1) concurrently flowering plants attractive to the bumblebees are rare or infrequent in the habitat, (2) floral display is exceptionally attractive in the habitat, (3) food flowers for bumblebees are abundant in adjacent habitats, (4) suitable nest sites for bumblebees are present in adjacent habitats. These conditions indicate that the deception system of marsh dactylorchids will function best in remote habitats such as marshes, where there are no concurrently flowering plants attractive to the pollinators and even a nectarless species may gain enough pollinations.

An alternative theory predicts that nectarless species take advantage of nectar-containing, co-blooming species. According to this "magnet-species theory" nectarless plants benefit from growing in the vicinity of a nectar-containing species because they receive more pollinators at the expense of the nectar-containing species (Thomson 1978; Rathcke 1983; Laverty and Plowright 1988; Laverty 1992). We tested how nectar-containing and attractive plants would affect the fruit set of *D. incarnata* by adding violets (*Viola* × *wittrockiana*) to the mire community.

Materials and methods

The study was undertaken at the Katajaneva-mire, situated in Toivakka, Central Finland (62° 3′N, 26° 12′E). The mire types found in Katajaneva are complex, but *Dactylorhiza incarnata* grows only at mesotrophic sedge fens or *Sphagnum papillosum* fens. The vegetation was covered mainly by *Menyanthes trifoliata* (L.), *Scheuchzeria palustris* (L.), *Drosera rotundifolia* (L.), *D. anglica* (Huds.), *Vaccinium oxycoccos* (Hill.), *Andromeda polifolia* (L.), *Carex lasiocarpa* (L.), *Rhynchospora alba* (L.) and *Eriophorum angustifolium* (Honck.). Other species occurring at the same site included *Molinia caerulea* (L.), *Equisetum fluviatile* (L.), *Trichophorum alpinum* (L.) and *Rhynchospora fusca* (L.). There were also some very small stands of *Drosera intermedia* (Hayne), *Trientalis europea* (L.) and *Utricularia intermedia* (Hayne).

Menyanthes trifoliata, *Vaccinium oxycoccos* and *Andromeda polifolia* are nectar-containing, insect-pollinated species, but in the study area they bloom before *Dactylorhiza incarnata* starts to bloom. Therefore there are usually no other attractive and nectar-containing species in the mire community blooming at the same time as *D. incarnata* (A. Lammi and M. Kuitunen, unpublished data). Pollinator populations are sustained by flowering species in the adjacent habitats.

Inside the main population of *D. incarnata* three separate study areas were formed, each having the same natural density of orchids (0.4 plants/m^2). These areas were about 80 m apart in a triangular pattern. Purple-red garden violets (*Viola* × *wittrockiana*) were added to the first area (these were approximately the same colour as *D. incarnata*), light blue violets (*Viola* × *wittrockiana*) were added to the second area and the third area served as a control area without any addition. Violets of different colours were used to test whether pollinators use colours as a cue to choose their food flowers. During this 3-year experiment (1990–1992) the study areas received a different treatment each year. The densities of violets were similar in both areas (0.5 plants/m^2) each year. The violets, each having approximately five open flowers, were placed in plastic boxes near each orchid in the experiment just before mid-June, when the blossoming of *D. incarnata* began. Altogether, each study area contained about 25 violets each year and most of the orchids in the study areas were included in the experiment. The violets were watered when necessary during the 3-week flowering period of *D. incarnata*. We used microcapillary tubes (2 μl) to verify that *D. incarnata* in the study population had no nectar in the spurs. The violets (usually pollinated by species of Hymenoptera (Apoidea), as for the *Dactylorhiza* species) produced substantial quantities of nectar in the spur, as tested by microcapillary tubes and sensitive glucose-paper (Clinistix, Ames Co.), and therefore markedly increased food supply for the pollinators in the mire community. Behaviour of the pollinators was not observed because pollinator visitation rates are so low in *Dactylorhiza* (Nilsson 1980). Instead, the percentage of fruit set was used as a measure of pollination success. For *D. incarnata* plants, the heights of inflorescence (from the base of the lowest flower to the top of the inflorescence), height of individual orchids, and the number of flowers per orchid were measured to ensure that differences in fruit set were not caused by the different size and floral display of individuals (Nilsson 1980, 1983; Fritz 1990).

Results

On average, the proportion fruit set (after arcsin transformation) of *D. incarnata* did not differ between years of the study ($F = 0.59$, $df = 2$, $P = 0.58$). However, there were differences in fruit set between the areas where *D. incarnata* was growing together with *Viola* × *wittrockiana* or alone [ANOVA, years were a block and violets (none, red-purple or blue) the within-block treatment (treatment: $F = 16.36$, $df = 2$, $P = 0.01$; block: $F = 3.64$, $df = 2$, $P = 0.13$)]. The fruit set of *D. incarnata* was greater if growing alone than the fruit set of *D. incarnata* growing with *Viola* × *wittrockiana*. The fruit set of *D. incarnata* was especially low when growing with purple-red *Viola* × *wittrockiana* which was approximately the same colour as the orchids [Tukey's test between *D. incarnata* and purple red *Viola* × *wittrockiana* ($P = 0.011$), between *D. incarnata* and blue

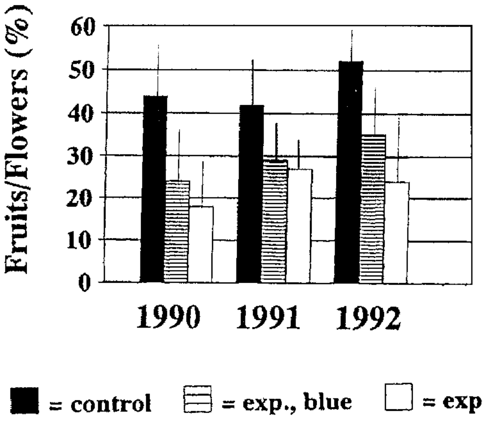

Fig. 1 Percentage fruit set of *Dactylorhiza incarnata* (mean and SD) in different treatments from 1990 to 1992 [control *D. incarnata* without violets (*Viola* × *wittrockiana*), *exp. blue D. incarnata* with blue violets, *exp. red D. incarnata* with red violets]

Table 1 Number of flowers per plant of *Dactylorhiza incarnata* in different treatments during 1990–1992 (ANOVA)

Treatment	1990			1991			1992		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Control	15.2	3.7	7	14.4	4.6	20	10.7	2.8	16
With blue violets	15.9	5.7	24	13.8	5.8	19	10.9	4.1	28
With red violets	14.1	3.9	29	12.6	5.5	20	12.0	4.9	12
F	0.98			0.66			0.62		
P	0.38			0.52			0.54		

Table 2 Height of individual plants (mm) of *Dactylorhiza incarnata* in different treatments during 1990–1992 (ANOVA)

Treatment	1990			1991			1992		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Control	195.0	33.5	7	251.5	41.2	20	206.3	30.7	16
With blue violets	216.7	36.8	24	250.8	33.2	19	186.4	32.6	28
With red violets	227.4	34.2	29	271.0	48.1	20	203.3	39.9	12
F	2.51			1.52			2.15		
P	0.09			0.23			0.12		

Table 3 Height of inflorescence (mm) of *Dactylorhiza incarnata* in different treatments during 1990–1992 (ANOVA)

Treatment	1990			1991			1992		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Control	43.7	11.8	7	47.5	9.9	20	40.3	4.3	16
With blue violets	47.7	12.7	24	45.3	8.4	19	42.7	7.0	28
With red violets	46.9	7.8	29	45.8	8.5	20	38.8	7.4	12
F	0.51			0.34			1.75		
P	0.60			0.71			0.18		

Viola × *wittrockiana* ($P = 0.06$) and between purple-red and blue *Viola* × *wittrockiana* ($P > 10$); Fig. 1].

There were no differences in the number of flowers per orchid, height of individual orchids or height of the inflorescence between individual orchids of different areas that might have affected our results (Tables 1–3).

Discussion

The percentage of fruit set in *D. incarnata* was adversely affected by the addition of nectar-containing species to orchid populations. Therefore our results support the hypothesis of Nilsson (1981), who stated that the deceptive pollination system of marsh dactylorchids functions best in remote habitats like marshes where there are no concurrently flowering plants attractive to the pollinators. Because there were no differences in attractiveness (size) of the orchids between study areas, certain behavioural patterns of pollinators, caused by addition of the violets, could explain the observed differences in reproductive success.

In nectar-containing species (Pleasants and Zimmerman 1979; Zimmerman 1981a, b, 1982a, b) pollinators have been shown to create so-called "hot" and "cold spots". Hot spots are unvisited plants with high nectar content and cold spots are created by pollinators intensively removing nectar from a restricted area. Pollinator visits to a hot spot are usually followed by short flights to the nearest individual, because the probability of finding a new hot spot is high. After a visit to a cold spot, flight distances are longer. As a consequence, the pollinators tend to rapidly move through an unrewarding patch (Heinrich 1983). In this study, the orchids might be considered as cold spots and the addition of hot spots (violets) may have led to shorter flight distances of the pollinators. However, pollinators remaining in areas where nectar-containing species were added did not benefit the orchids. In these areas bumblebees probably visited violets at the expense of the orchids' pollination success. Because the violets differ a lot from the orchids in morphology, the pollinators could have been able to distinguish these two plant species, promoting individual bee forager fidelity (Heinrich 1975, 1979).

In the case of *D. incarnata* the colour of the violets had some effect to the fruit set of *D. incarnata*. The violets that were more similar in colour to the orchids i.e. (purple-red ones) caused a more significant decrease in the fruit set of *D. incarnata*. This result seems to be unexpected, because it should have been more difficult for the pollinators to distinguish between the orchids and the more similar purple-red violets. Therefore the fruit set of orchids should have been higher in areas with purple-red violets. Nevertheless, these results could be explained by increased pollen wastage between orchids and more similar purple-red violets. In experimental areas some pollinarias were probably "wasted" to the violets, at least before the pollinators learned to avoid the orchids. Thus, the orchids with red violets probably had more pollinator visits, but the fruit set was lower because of pollen wastage. After all, most orchids in the populations were matched with the violet, which increases the probability of pollen wastage. At the moment, the importance of pollen wastage to pollination and reproductive success is not fully understood, although pollen wastage is considered to be diminished in species with pollinarias (Harder and Thomson 1989).

In this experiment it appears that interspecific exploitation competition, where one species draws pollinators away from another species (Free 1968; Pleasants 1980; Zimmerman 1980), took place in favour of the violets at the expense of the orchids. As a consequence, the addition of the violets produced no evidence for the magnet-species theory (Thomson 1978) where a nectarless plant achieves greater fruit set in the presence of nectar-containing species, as has been observed by Laverty (1992) in nectarless *Podophyllum peltatum* and nectar-containing *Pedicularis canadiensis* and by Pellmyr (1986) in nectarless *Cimicifuga rubifolia*. Our results support the suggestion by Firmage and

Cole (1988) that the nectarless orchid *Calopogon tuberosa* succeeds best in pollination when growing alone in North American sphagnum bogs.

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