

Double floral mimicry and the magnet species effect in dimorphic co-flowering species, the deceptive orchid *Dactylorhiza sambucina* and rewarding *Viola aethnensis*

Dvojitá květní miméze a sdílení opylovačů mezi dimorfní šálivou orchidejí *Dactylorhiza sambucina* a nektar nesoucí violkou *Viola aethnensis*

Giuseppe Pellegrino, Francesca Bellusci & Aldo Musacchio

Dipartimento di Ecologia, Università della Calabria, Arcavacata di Rende, I-87036 Cosenza, Italy, e-mail: giuseppe.pellegrino@unical.it

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Reproductive success of food-deceptive orchids may be affected by interactions with co-flowering rewarding species, either negatively through competition for pollinators, or positively by means of a magnet species effect and floral mimicry. In this study, potential interactions between a dimorphic (yellow or purple flowers) non-rewarding orchid *Dactylorhiza sambucina* and a dimorphic (yellow and blue flowers) rewarding, co-flowering species, *Viola aethnensis*, were explored in a natural stand in southern Italy. To evaluate the interactions between these two species, plots of all possible arrays of presence/absence of the four colour morphs were arranged in the field and fruit production of the orchid morphs assessed. Natural aggregations of both colour morphs of the orchid had the highest reproductive fitness for each colour morph. Patterns in fitness variation detected in treated plots provided direct and indirect evidence that *D. sambucina* may benefit from the co-occurrence of *V. aethnensis* through floral mimicry and/or magnet species effect. Since the fitness of each orchid morph was strongly increased by the presence of a viola morph of similar colour, a double mimetic effect occurs between the two species, which to our knowledge has not been previously reported. Moreover, the co-occurrence of an orchid morph with a non-matching viola resulted in competition for pollinators, whereas in the absence of the rewarding plant the fitness was balanced due to positive interactions between the two orchid colour morphs. These findings suggest that *D. sambucina*, like many other European deceptive orchids, possesses a set of display traits suitable for exploiting potential facilitative interactions with a number of rewarding species. In addition, the unequal morph frequencies occurring in natural populations could result from unbalanced events in floral mimicry.

Key words: colour morphs, plant interactions, reproductive success, remote habitat hypothesis, rewardless orchid

Introduction

While most flowering plants reward their pollinators with pollen or nectar, many do not offer food rewards and lure insects in different ways. This reproductive strategy is called “food-deceptive pollination”, was originally described by Sprengel (1793), and is particularly frequent in the *Orchidaceae*. Indeed, one third of the orchid species is able to manipulate the food-foraging, sexual or oviposition behaviour of potential pollinators by means of an amazing variety of flower signals, involving colour, shape, size and fragrance (van der Cingel 1995, Jersáková et al. 2006a).

Reproductive success of deceptive orchids is reported to be lower than that of rewarding species (Neiland & Wilcock 1998, Tremblay et al. 2005) because experienced pollinators avoid non-rewarding plants (Ackerman 1986, Ayasse et al. 2000). To avoid the risk of very low reproductive fitness, deceptive orchids have evolved a remarkable intraspecific floral polymorphism. Since flower colour is the most important signal for pollinators (Menzel & Shmida 1993, Gumbert 2000), deceptive species that possess a floral colour polymorphism may increase their chances of reproduction by prompting more visits on differently coloured co-specific individuals (Internicola et al. 2007). In addition, there is increasing evidence that reproductive fitness of deceptive orchids may also be affected by different types of interactions with co-flowering rewarding species, which elicit positive or negative reactions by pollinators (Gumbert & Kunze 2001, Johnson et al. 2003). If rewarding and deceptive plants compete for pollinators, the rewardless species are at advantage in habitats with few rewarding plants, as predicted by the “remote habitat hypothesis” (Lammi & Kuitunen 1995). Conversely, co-flowering rewarding species may facilitate pollination of adjacent or intermingled deceptive plants, which may benefit from the greater abundance of insects attracted by the rewarding “magnet species” (Thompson 1978).

Classical cases of close morphological resemblance between mimic and model species occur in the food deceptive genus *Disa* (Johnson 2000), in which many species show a close morphological similarity with a given co-flowering rewarding species. In addition, many studies have shown that some rewardless orchids also have a higher reproductive fitness when their flower colour resembles that of a co-blooming rewarding plant, a phenomenon called “non-model mimicry” (Dafni 1984). Recently, studies have shown that the distances flown by pollinators and their choice of polymorphic rewardless plants depends on the presence and abundance of polymorphic rewarding plants. Indeed, insects visit the colour morphs of rewardless plants that closely resemble the most recent rewarding flower visited (Gumbert & Kunze 2001, Gigord et al. 2002, Johnson et al. 2003, Internicola et al. 2007).

Dactylorhiza sambucina is a non-rewarding orchid, which shows flower colour polymorphism. Natural populations are composed of different proportions of yellow- and purple-flowered individuals (Kropf & Renner 2005) (rarely pink, Pellegrino et al. 2005), which grow in mixed grasslands with different nectariferous species. While it has long been assumed that colour polymorphism is maintained by negative frequency-dependent selection produced by pollinators that over-visit the rare colour morph (Gigord et al. 2001), there is no field evidence to support this hypothesis (Pellegrino et al. 2005, Jersáková et al. 2006b), which indicates that other factors may influence the variable and often unbalanced morph ratio observed in natural populations (Pellegrino et al. 2005, Jersáková et al. 2006b).

For example, interactions with rewarding co-flowering plants may influence reproductive success of *D. sambucina*, nonetheless, they have not previously been thoroughly investigated. Moreover, while potential flower mimicry by *D. sambucina* morphs of a putative model species (*Mimulus guttatus*) has been identified (Gigord et al. 2002), there is no evidence of a magnet species effect occurring in natural populations growing in variable grassland communities (Jersáková et al. 2006b).

The aim of the present study is to explore the potential interactions occurring in a natural community between *D. sambucina* (characterized by an even morph ratio) and the abundant

rewarding co-flowering species, *Viola aethnensis* (which in turn possesses two colour morphs, yellow and blue). All the possible arrays of presence/absence of the four phenotypes were arranged within the population. Our goals were to answer to the following questions: (i) Does aggregation between a dimorphic rewardless orchid and a dimorphic rewarding species increase the reproductive success of the deceptive orchid? (ii) Is reproductive success of each orchid morph differently affected by the presence of a nectariferous colour morph? (iii) Is it possible to distinguish between potential facilitative and/or competitive interactions? And finally, (iv) Are these interactions linked with the presence/absence of colour morphs within natural populations of the deceptive orchid?

Material and methods

Study species

Dactylorhiza sambucina (L.) Soó is a widespread rewardless orchid, occurring throughout the Mediterranean, Central Europe and S Scandinavia (Tutin et al. 1980), which shows flower colour polymorphism, with variable morph-ratios of both yellow- and purple-flowered individuals co-occurring within natural populations. The flowers' lip (labellum) provides a landing place for bees and has a basal long empty spur. The labellum and the entrance to the spur have pigmented spots, which form a false nectar guide; the flowers emit a scent containing terpene hydrocarbons (Nilsson 1980). Pollination occurs mainly by deceiving naïve bees. The main pollinators of *D. sambucina* are bumblebees (*Bombus* spp.), mainly queens of *B. lapidarius*, *B. terrestris*, *B. lucorum* and *B. pascuorum*, cuckoo bumblebees (*Psithyrus* spp.) and bees of other genera, like *Apis* spp. and *Osmia* spp. (Nilsson 1980, Gigord et al. 2001). Each flower has a pollinarium with pollen packed into two pollinia (as in all the *Orchidoideae*; Dressler 1981), which can be removed by a single successful visit of a pollinator.

Viola aethnensis Parl. (*Violaceae*) is an endemic species of S Italy (Sicily and Calabria; Pignatti 1982) with 3–4 cm long flowers, bearing a spur. Its flowers vary in colour, with both yellow- and blue-flowered individuals present in the same natural populations. Information on the pollination strategy of this species is scarce, but field studies on other *Viola* species report that bumblebees (*Bombus* spp.) are the main pollinators (Beattie 1969, 1971, Freitas & Sazima 2003). In common with *D. sambucina*, *V. aethnensis* is pollinated primarily by bumble-bees since our personal field observations confirm that foraging bumblebees move between *Viola* and orchids.

Study site

The experiment was conducted during spring 2006 (15 May–26 June), at a site in the National Park of Calabria (Sila, S Italy). The population of *D. sambucina* (with approximately 40,000 individuals) is large with a long standing (since 2001; G. Pellegrino, personal observation) density of 4.00 ± 0.34 per m^2 and morph ratio of yellow and purple colour plants of 1:1. *Viola aethnensis* is the only abundantly co-occurring nectariferous species (7.0 ± 0.4 plants per m^2) with a typical colour polymorphism of 1:1 of yellow and blue-violet phenotypes. Few other co-flowering rewarding species grow in the area (*Bellis sylvestris* and *Ranunculus* sp.) and are present at low densities (approximately 0.1 per m^2).

Experimental design

The experiment was designed to evaluate the reproductive success of the deceptive orchid when growing in all the possible combinations of presence/absence of the four phenotypes of *D. sambucina* and *V. aethnensis*. Thus, we selected twelve 20 m diameter circular plots and placed in each plot ten concentric rings 1 m apart, numbered from 1 (centre) to 10 (outer area) (Fig. 1a). In each plot, the areas enclosed by the five outer rings were not manipulated, while in the areas enclosed by the five inner rings the selected plants were left and the undesired plants removed in order to obtain a given combination of presence/absence of the four colour morphs (Fig. 1b). Lines refer to the presence/absence of *D. sambucina* morphs: line A plots contained both yellow and purple morphs, line B only the purple morph, and line C only the yellow morph. Columns refer to the presence/absence of *V. aethnensis* morphs: column 1 plots contained both viola morphs (A1 was the control plot), column 2 only the blue morph, column 3 only the yellow morph, and column 4 any viola morph. Removed plants were replaced in their original positions at the end of the experiment.

Individuals of the few other co-flowering species (*Ranunculus* sp. and *Bellis sylvestris*) growing in the plots were removed in order to exclude the effect of the presence of other rewarding plants.

For each plot fruit production was assessed and the ratio relative to the number of flowers was determined for each colour morph of *D. sambucina*. The effects of our treatments on the reproductive success of each colour morph of *D. sambucina* were evaluated using an analysis of variance (ANOVA) with treatment (presence/absence of *V. aethnensis*) and colour morph (presence/absence of *D. sambucina*) as fixed factors using SPSS software package (SPSS v. 9.0 for Windows; SPSS Inc.). In particular, we compared the percentage of fruits produced in external vs internal areas of each plot and the values for external or internal areas across plots (i.e., among natural dispositions and treatments). Bivariate analyses with SAS package (SAS Institute, Inc., 1988) were used to evaluate the significance of the correlation between fruit set of *D. sambucina* (total and for each colour morph) and presence of rewarding plants, and between fruit set in the five internal areas and their distance from the untreated area.

Results

The total fruit set of *D. sambucina* in the external areas of the plots ranged on average from 17.8% (plot A1) to 19.4% (plot C4), with no significant differences found by ANOVA across the plots ($F_{11,59} = 0.783$, $P = 0.66$). Conversely, mean values for capsule production on the internal area of the 12 plots varied significantly ($F_{11,59} = 7.057$, $P < 0.01$) from 5.8% (plot C2) to 19.1% (plot A1) (Fig. 2). Likewise, variations in the mean reproductive fitness recorded for the external areas for the yellow (from 17.8% to 19.5%, in plots A1 and C4, respectively) and purple (from 17.7% to 19.3% in plots A1 and C1, respectively) morphs of *D. sambucina* were not significant ($F_{11,59} = 0.698$, $P = 0.73$ for yellow; $F_{11,59} = 8.854$, $P = 0.59$ for purple morphs). On the other hand, fruit production on the internal areas was highly significant between colour morphs ($F_{7,39} = 7.360$, $P < 0.001$ for yellow; $F_{7,39} = 7.718$, $P < 0.001$ for purple morphs) and ranged from 7.8% (plot C2) to 18.9% (plot A1) for yellow and from 8.2% (plot B3) to 19.3% (plot A1) for purple morphs (Fig. 2).

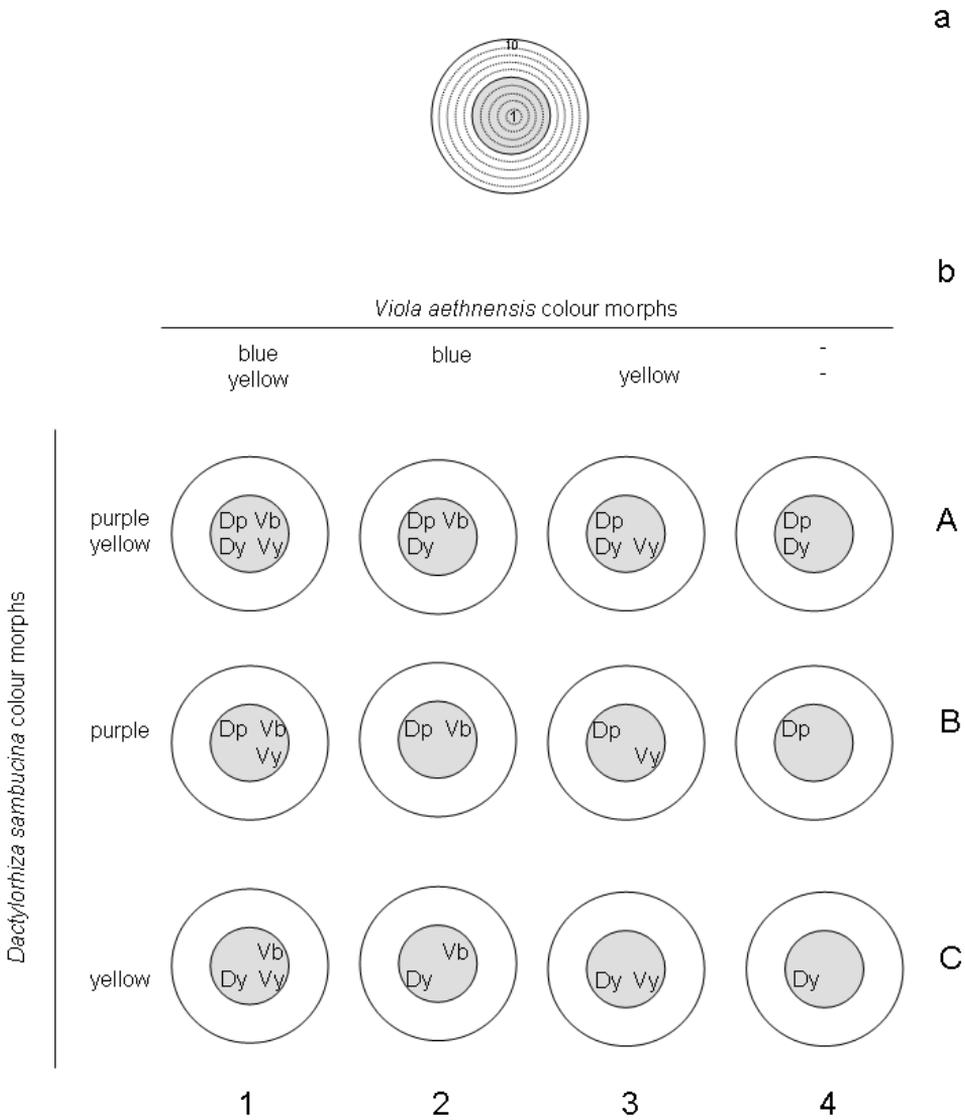


Fig. 1. – Schematic representation of the experimental design. (a) an example of the circular area (20 m in diameter) divided by 10 concentric rings (1m between each) numbered from 1 (central area) to 10 (outer area); (b) in each circular plot, the area enclosed by the five external rings was not manipulated, while that enclosed by the five internal rings was subjected to different treatments, which involved leaving selected plants of *Dactylorhiza sambucina* and/or *Viola aethnensis*. Lines refer to the presence/absence of *D. sambucina* morphs: line A plots contained both yellow and purple morphs, line B only the purple morph, and line C only yellow morph. Columns refer to the presence/absence of *V. aethnensis* morphs: column 1 plots contained both viola morphs, column 2 only the blue morph, column 3 only the yellow morph, and column 4 any viola morph.

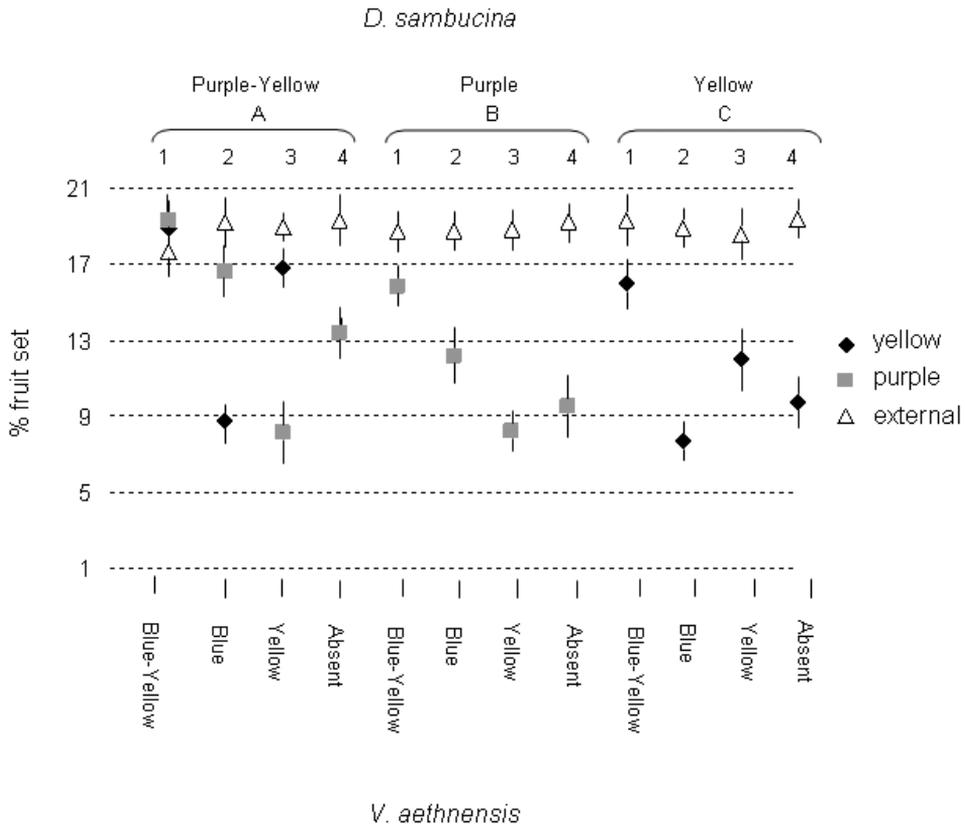


Fig. 2. – Fruit set (%; mean value \pm s.e.) of *Dactylorhiza sambucina* that grew in the area enclosed by the five external rings and for the yellow and purple morphs that grew in the area enclosed by the five internal rings in each plot.

Overall, the manipulated plots may be ordered in three groups with similar levels of total fruit production (Fig. 3). The highest fitness values (19.1%) were recorded for the control plot (A1) and a slightly lower production (15.8–16.0%) was detected in plots B1 and C1 in which there was a single orchid morph with both rewarding viola morphs. An intermediate level of total fitness reduction (12.0–13.4%) was recorded in treated plots of line A (A2, A3 and A4) in which there were two orchid morphs with a single or without a viola morph. Similar levels of fitness were recorded in arrays with a single orchid morph and the rewarding viola morph of matching colour (B2 and C3). The lowest values of total reproductive success (RS) were detected in the plots with a single orchid morph growing in the absence (3.37% and 3.78% for plots B4 and C4, respectively) or presence of a non matching viola morph (2.70% and 2.82% for plots B3 and C2, respectively) (Fig. 3).

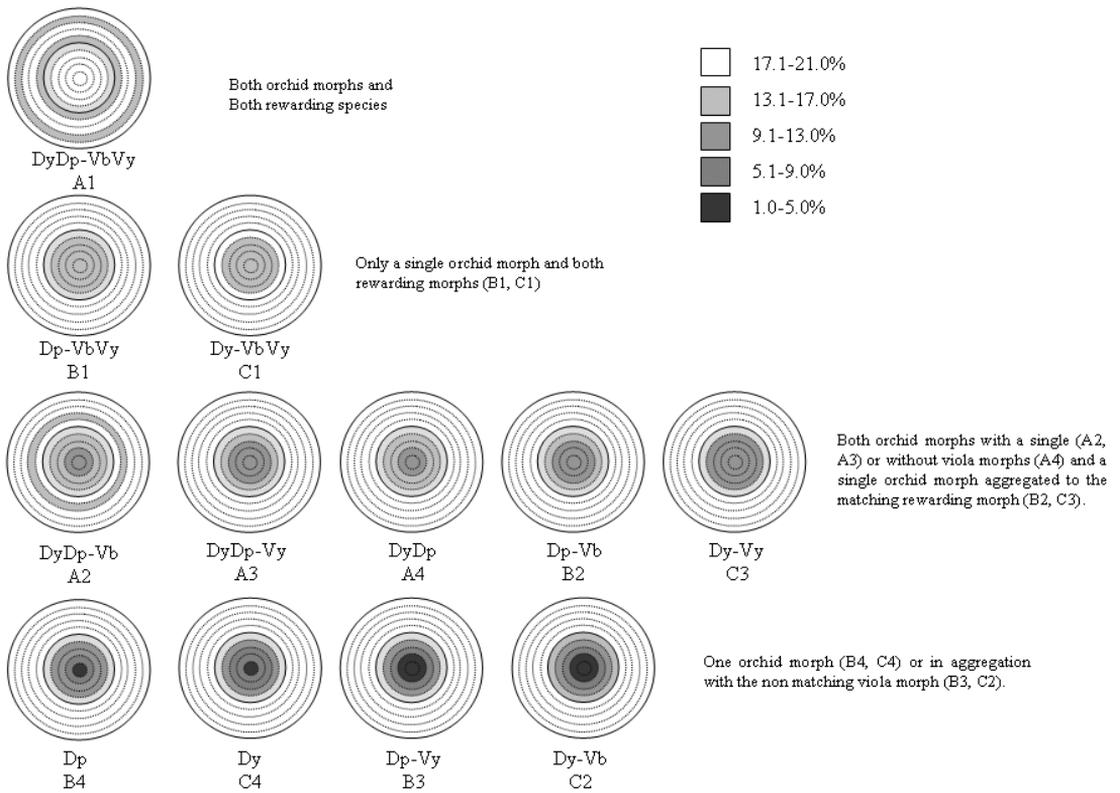


Fig. 3. – Fruit set of *Dactylorhiza sambucina* in the areas enclosed by each ring in the 12 experimental plots.

However, it is evident that the total RS of each *D. sambucina* colour morph depended on the presence of rewarding viola colour morphs. This is particularly evident in plots A2 and A3, where intermediate levels of total fruit set were recorded with the main contribution from the orchid morph that matched the single occurring colour morph of rewarding *V. aethnensis* (Fig. 2). Fruit production of each orchid colour morph was markedly less in the absence of both rewarding viola morphs or presence of non matching viola morphs (Figs. 2 and 3). On the other hand, there was a positive correlation between the fitness of a given colour morph of *D. sambucina* and the presence of rewarding plants with a similar corolla colour ($r_s = 0.79$, $P < 0.001$). In all treated plots, fruit production was variable in the five internal areas, with the strongest negative effects recorded in the central area. Patterns in RS variation were significantly correlated, to different extents, with the distance from the neighbouring external area (Fig. 3), suggesting that interactions between these two dimorphic plants depended on their spatial distribution.

Discussion

Interactions among species and morphotypes

This study indicates that aggregation of dimorphic rewardless *D. sambucina* with dimorphic rewarding *V. aethnensis* is advantageous for fruit production of the rewardless species because of the magnet species effect and floral colour mimicry. In this respect, our findings accord with the view that positive interactions among co-occurring species are more frequent than previously assumed (Johnson et al. 2003 and reference therein). In addition to facilitation among similar co-flowering morphs, our results reveal facilitation between orchid colour morphs and competition between an orchid and viola with non-matching morphs.

The highest reproductive success of the two colour morphs of *D. sambucina* was recorded in natural (control) combinations with the two viola colour morphs (plot A1 and external areas in all other plots), whereas any alteration of the natural conditions resulted in lower levels of fitness. Note however, that the reductions in fitness did not occur in the peripheral area of each plot, and that fitness declines progressively toward the center of the plots, except in areas where there were both viola morphs, suggesting that pollinators entering a zone fly for a few meters (1–2 m) before perceiving differences in plant aggregations. The lowest level of fitness of the orchid morphs were recorded in the presence of the non-matching colour morph of viola (B3, C2), and their fitness was slightly higher when there are no rewarding plants present (B4, C4). This indicates the greater attractiveness of rewarding plants makes them better “competitors” for local pollinators (Lammi & Kuitunen 1995).

Conversely, when the yellow or the purple orchid phenotype occurred with either the yellow or blue viola morphs (B2, C3), their fitness was markedly increased, suggesting that yellow/yellow (C3) and purple/blue (B2) coupling of unrewarding and rewarding plants gives rise to a mimetic effect based on floral colour similarity. The same sort of interaction may account for the higher fitness of orchids with the matching viola colour when both orchid morphs were occurred with a single viola morph (A2, A3). These findings accord with the observation that bumblebees tend to visit flowers with similar corolla colour to those they have previously successfully visited (Gumbert 2000, Internicola et al. 2007, Raine & Chittka 2007). Slight colour differences may be irrelevant because although bees can discriminate between colours, flower colours are not optimally discriminated by bees (Chittka & Menzel 1992). In particular, flowers that appear blue or purple to human eyes have the same reflectance spectrum for bees (Chittka et al. 1994) so could act as mimics in spite of their apparent colour differences (Nilsson 1983). Moreover, the purple morph of *D. sambucina* (Gigord et al. 2002, Kropf & Renner 2005) has the same reflectance spectrum as the blue petals of *V. tricolor* (Wertlen 2006). Finally, when rewarding plants are absent (A4), the two orchid morphs had similar fitnesses, which indicate that *D. sambucina* benefits from its flower colour polymorphism. In this case, the positive interaction is assumed to result from the behaviour of inexperienced insects, which shift between yellow and purple flowers when foraging for nectar (Johnson et al. 2003).

Floral mimicry in *Dactylorhiza* was suggested by Neiland and Wilcock (2000) who observed that the removal of pollinia from *D. lapponica* and *D. traunsteineri* is associated with the presence of large quantities of pollen on their stigmas from rewarding co-flowering *Pedicularis sylvatica*. Recently, it was demonstrated that in *D. sambucina* there is flo-

ral mimicry of the rewarding, dimorphic, putative model species *M. guttatus* (Gigord et al. 2002). These authors record that inexperienced insects visit both rewardless morphs, but learned to avoid them after they gained experience of rewarding plants.

In our study the maximum levels of orchid fitness was recorded in treated plots where a single orchid morph co-occurred with both viola morphs (B1 and C1); a benefit that may be explained by invoking the magnet species effect due to the higher density and greater attractiveness of rewarding plants (Internicola et al. 2007). As a consequence, in these two plots, orchid fitness was possibly positively affected by both mimetic (due to a single couple of matching phenotypes) and magnet effects, but it was impossible to determine their respective contributions. Thus, we suggest that the presence of colour-matching rewarding and unrewarding phenotypes strengthens the mimetic effect, which plus the magnet effect exerted by the abundance of rewarding plants, resulted in the increase in fitness of the unmanipulated and control plants. However, it is not possible to state whether the effect counter balance one another or they are in balance.

The magnet species effect has not been recorded for *Dactylorhiza* growing in nature. Previous studies report that *D. incarnata* is negatively affected by the introduction of potted viola (*Viola ×withrockiana*) at a low density, which supports the remote habitat hypothesis, because of the interspecific exploitation competition for pollinators, which prefer nectariferous species (Lammi & Kuitunen 1995). Moreover, Jersáková et al. (2006b) found that the cumulative abundance of yellow and purple co-flowering rewarding species had either a negative (yellow flowers) or no effect on the reproductive fitness of several, naturally dimorphic populations of *D. sambucina*. Similarly, the reproductive fitness of the yellow morph of *D. sambucina* is negatively affected by its own clumped distribution and that of a blue co-flowering rewarding species, *Muscari neglectum* (Internicola et al. 2006). The facilitative magnet effect of co-flowering species is recorded in other orchid species. For example, Johnson et al. (2003) record a facilitative magnet effect between the nectarless *Anacamptis morio* and some co-flowering rewarding species, and suggest that increased density of the rewarding plant with similar flower colour (*Allium schoenoprasum*) strongly enhanced the fitness of the non-rewarding orchid. Nonetheless, these authors do not argue for the occurrence of a mimetic interaction due to the lack of more convincing evidence, in particular the close matching of their spectral reflectances, incapacity of pollinators to distinguish the mimic from the model, which would indicate a true adaptive resemblance. On the contrary, they suggest that European deceptive orchids have not evolved species-specific Batesian floral mimicry, but rather possess a more generalized set of display traits that allow the orchid to exploit a number of possible magnet species.

Floral colour interactions and orchid morph frequencies

It is suggested that variation in the floral traits of rewardless orchids enhances their reproductive fitness, because after visiting non-rewarding flowers pollinators tend to fly elsewhere and visit a differently coloured flower (Dafni 1987, Smithson & Macnair 1997). Additionally, deceptive plants receive more visits when growing among rewarding plants with a similar flower colour than when with plants with dissimilar flower colours (Internicola et al. 2007; and results therein). By using artificial plots of *D. sambucina*, Gigord et al. (2001) showed that this behaviour would generate a negative frequency de-

pendent selection (NFDS), since rare morphs are over-visited compared to a more common colour and pollinator behaviour maintains a stable flower colour polymorphism. However, field observations carried out on mono- and dimorphic natural populations of *D. sambucina*, of different sizes and morph frequencies, have shown that reproductive success of orchid morphs do not conform with the predictions of the NFDS hypothesis (Kropf & Renner 2005, Pellegrino et al. 2005, Jersáková et al. 2006b). In this case other factors may influence morph reproductive success and lead to unequal morph frequencies in many European orchid populations. For example, a yellow bias exists in S France and Germany (Gigord et al. 2001, Kropf & Renner 2005), and a purple bias in Sweden (Nilsson 1980) and the Czech Republic (Jersáková et al. 2006b).

Our study provides evidence of a differential reproductive success of the colour morphs of *D. sambucina* when both colour morphs grew amongst a single colour morph of the rewarding dimorphic *V. aethnensis* (plots A2 and A3). In particular, each morph was separately favoured by a mimetic interaction with rewarding plants of a similar colour, suggesting that variations in time and/or in space in our natural community could profoundly affect orchid morph ratios. The fact that differential floral mimicry may selectively affect the morph frequencies of *D. sambucina* was previously suggested by Gigord et al. (2002) for results they obtained using artificial arrays of an equal proportion of the orchid morphs and a single morph of the dimorphic, rewarding, putative model species *M. guttatus*. They consider this combination to be representative of natural situations, given that *D. sambucina* largely grows in mixed, variable grassland communities alongside rewarding plants. However, since *D. sambucina* blooms early in the season when inexperienced insects prevail, they argue that, unless there are ecological situations where many pollinators resample rewardless species, the orchid is more likely to experience selection for rare morphs than for floral mimicry.

It is of interest that the two orchid morphs growing in the absence of rewarding plants (plot A4) reached similar levels of fruit production, probably because they are predominantly visited by inexperienced pollinators. Conversely, orchid morphs growing with a single rewarding morph (A2, A3) showed very different levels of reproductive fitness, possibly because the pollinators were experienced. These findings, although indirect, favour the selective value of flower mimicry, however, it has not been detected in populations with an unbalanced proportion of orchid morphs.

Further studies on natural populations of *D. sambucina* are needed in order to ascertain the frequency of the facilitative effects of co-flowering rewarding species and their impact on the morph ratio. One hypothesis is that a stable, balanced ratio of orchid morphs, like that in the community studied, evolved because facilitative interactions with rewarding plants were advantageous for both orchid morphs and accounts for the greater fitness of these and other plant species.

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Souhrn

Reprodukční úspěšnost šálivých druhů orchidejí může být ovlivněna vzájemnými vztahy s okolními kvetoucími rostlinami, a to negativně, soupeřením o opylovače, nebo pozitivně, díky podobnosti orchidejí s jinými atraktivnějšími druhy rostlin (květní miméze) a sdílením jejich opylovačů. V předložené studii jsme se zabývali možnou interakcí společně kvetoucích druhů: dimorfní (žlutě a nachově kvetoucí) šálivou orchidejí *Dactylorhiza sambucina* a dimorfní (žlutě a modře kvetoucí), nektar produkující violkou *Viola aethnensis*. Abychom zachytili možné interakce mezi barevnými formami obou druhů, vytvořili jsme na jejich přirozeném stanovišti v jižní Itálii sadu ploch se všemi možnými kombinacemi přítomnosti a absence všech čtyř barevných forem a zaznamenali reprodukční úspěšnost orchideje. Nejvyšší tvorbu semeníků měly obě formy orchideje v plochách s jejich přirozeným společným výskytem. Rozdíly ve tvorbě semeníků v manipulovaných plochách poskytly přímé a nepřímé důkazy o tom, že *D. sambucina* může mít reprodukční výhodu v přítomnosti *V. aethnensis* díky květní mimézi a zvýšenému počtu opylovačů. Protože produkce semeníků orchideje byla mnohem vyšší v přítomnosti stejně barevné violky, jedná se o dvojitou květní mimézi mezi stejně barevnými formami obou druhů, která nebyla dosud vědecky popsána. Zatímco společný výskyt orchideje s violkou opačné barvy vedl ke kompetici o opylovače, negativní vliv absence violky na fitness orchideje byl vyvážen pozitivní interakcí mezi oběma formami orchideje. Naše výsledky ukazují, že *D. sambucina*, podobně jako mnohé další šálivé druhy orchidejí, má soubor květních charakteristik vhodný k potenciálnímu využívání okolních nektar nesoucích druhů rostlin.

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