

EFFECT OF FLORAL DISPLAY ON REPRODUCTIVE SUCCESS IN TERRESTRIAL ORCHIDS

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Abstract: Almost one-third of all species in the family *Orchidaceae* offer no reward to insect pollinators. In the absence of a reward, floral display (number of flowers), may be the most important component of insect attraction but the role of floral display in capsule production of both deceptive (nectarless) and rewarding (nectariferous) orchids has not yet been satisfactorily explored. Based on our theoretical considerations, we propose and test here the following hypotheses: (i) deceptive species flower earlier than rewarding ones, (ii) reproductive success in deceptive species is lower than that in rewarding ones, (iii) reproductive success is independent of the number of flowers in the inflorescence in both deceptive and rewarding orchids. Our data supported hypotheses (i) and (ii). In 9 out of our 12 populations of deceptive species and in 10 out of 12 populations of rewarding species we found support for our hypothesis (iii).

Keywords: Deceptivity, Floral display, Orchid, Reproductive success, Reward

INTRODUCTION

Reproductive success in non-autogamous orchids is usually associated with pollinator reward (nectar, pollen, stigmatic exudates, oily substances or provision of nesting/shelter place). In orchid flowers, the formation and placement of pollinia (small pollen packets) prevents insects from using it as food. Consequently, the most common reward is nectar. Nectar can be a substantial source of energy for pollinators (SCHMID-HEMPEL 1987). Estimates of the cost of nectar production for the plant range from 3.3% of flower costs in the short-lived flowers (HARDER & BARRETT 1992), to ~30% of flower cost in the long-lived flowers (PLEASANTS & CHAPLIN 1983, SOUTHWICK 1984). PYKE (1991) was the first to demonstrate that nectar production entails a cost to a plant also in terms of growth and/or reproduction. Given that many orchid flowers are long lived, ACKERMAN (1986) and PROCTOR & HARDER (1996) hypothesized that from the evolutionary point of view it should be more advantageous to deceive pollinators than to offer them a reward. This hypothesis may explain why almost one third of orchid species (8,000–10,000 out of the approximate 25,000 existing orchid species; DRESSLER 1990) are deceptive.

Deceptive orchids rely on a variety of ploys to attract pollinators (NILSSON 1992); nevertheless, they have a lower reproductive success than rewarding orchids (ZIMMERMAN & AIDE 1989, ALEXANDERSSON & ÅGREN 1996). For example, the overall proportion of flowers that develop fruit for deceptive and rewarding orchids in Europe were 27.7% versus 63.1%, respectively (NEILAND & WILCOCK 1998). However, some authors argue that

deception provides a reproductive advantage in terms of present and future fitness (NILSSON 1992). JOHNSON & NILSSON (1999) proposed that it is more advantageous in pollinator-limited orchids to invest resources in advertising display, rather than into nectar production.

One would expect that a larger floral display should attract more pollinators from a greater distance for both rewarding and deceptive orchids. However, one would also expect that arriving pollinators would probe many/most flowers on a rewarding orchid, assuming that the plant has abundant nectar and has not been visited recently by another pollinator. Conversely, visitors to deceptive orchids are expected to sample just a few flowers before leaving the inflorescence since flowers are empty of nectar (NILSSON 1980, 1984). Thus for deceptive orchids the number of flowers in the inflorescence that develop fruit may be positively associated with the numbers of pollinators attracted and thus the proportion of flowers that develop fruit is expected to be more or less independent of the number of flowers in the inflorescence. For rewarding orchids, a constant relationship between the proportion of flowers that develop fruit and the number of flowers in the inflorescence is also expected, as the former in temperate orchids is often close to 100% (JERSÁKOVÁ 1998, NEILAND & WILCOCK 1998).

Empirical evidence for these considerations is scarce and sometimes contradictory, and therefore additional observations are needed. Larger displays often attract more pollinators (KLINKHAMER et al. 1989, KLINKHAMER & DE JONG 1990, OHARA & HIGASHI 1994, OHASHI & YAHARA 1998, ROBERTSON & MACNAIR 1995, THOMSON 1988), but sometimes do and sometimes do not affect the proportion of flowers that develop fruit (MONTALVO & ACKERMAN 1987, SCHEMSKE 1980, ZIMMERMAN & AIDE 1989, CALVO 1990, WILLEMS & LAHTINEN 1997). For example, the proportion of flowers that develop fruit in the deceptive species *Calopogon tuberosus* (FIRMAGE & COLE 1988), *Aspasia principissa* (ZIMMERMAN & AIDE 1989), *Dactylorhiza incarnata* (MATTILA & KUITUNEN 2000), *Dactylorhiza maculata* (VALLIUS 2000) and *Orchis purpurea* (JACQUEMYN et al. 2002) is independent of the number of flowers in the inflorescence. In addition, reproductive success in deceptive species also often depends on the presence of naive pollinators, which emerge early in spring after hibernation (NILSSON 1984).

Here we examine the effect of floral display (expressed as the number of flowers) on reproductive success in 12 European orchid species in different years and at various locations. From the above it seems to follow that the proportion of flowers that develop fruit is independent of the number of flowers in the inflorescence in both deceptive and rewarding orchids and that rewarding orchids should have an overall larger reproductive success compared to deceptive ones. Because of the possible dependence of deceptive species on naive pollinators, it is also reasonable to assume that there will be a stronger selection for early flowering in deceptive species compared with rewarding ones. Therefore, we test the following hypotheses: (i) deceptive species flower earlier than rewarding ones, (ii) the proportion of flowers that develop fruit in deceptive species is lower than that in rewarding ones, (iii) the proportion of flowers that develop fruit is independent of the number of flowers in the inflorescence in both deceptive and rewarding orchids.

Table 1. Presence of reward, type of pollinator and range of plant heights, of numbers of flowers, typical petal colour and month(s) when the species flowers (all according to VAN DER CINGEL (1995), flowering time – our data).

Species	Reward	Pollinators	Plant height (cm)	No. flowers (rank)	Petal colour	Flowering time (month)
<i>Orchis morio</i> L.	-	bees, bumblebees	8–20 (–40)	2–35	purple-whitish	V
<i>Orchis ustulata</i> L. subsp. <i>ustulata</i>	-	flies	10–35	15–65	white-reddish	V
<i>Dactylorhiza sambucina</i> (L.) SOÓ	-	bees, bumblebees	10–20	3–30	red, yellow	IV–V
<i>Dactylorhiza incarnata</i> (L.) SOÓ	-	bees, beetles, flies	25–60 (–90)	14–60	pink	V–VI
<i>Dactylorhiza majalis</i> (RCHB.) HUNT et SUMMERH.	-	bees, beetles, flies	10–50 (–90)	7–36	red-purple	V–VI
<i>Dactylorhiza fuchsii</i> (DRUCE) SOÓ	-	bees, beetles, flies	15–60 (–80)	15–65	pink-whitish	VI–VII
<i>Platanthera bifolia</i> (L.) L.C.M. RICH.	+	hawkmoths, moths	20–55	10–40	white	VI–VII
<i>Platanthera chlorantha</i> (CUST.) RCHB.	+	hawkmoths, moths	20–60	10–40	white-greenish	VI–VII
<i>Gymnadenia conopsea</i> (L.) R. BR.	+	hawkmoths, moths	20–60	20–70	pink	VI–VII
<i>Epipactis atrorubens</i> (HOFEM. ex BERNH.) SCHULT.	+	bees, bumblebees, wasps	20–40	10–30	purple-reddish	VI–VII
<i>Epipactis purpurata</i> SM.	+	wasps	30–60	20–50	violet-greenish	VII–VIII
<i>Coeloglossum viride</i> (L.) C.J. HARTMAN	+	ichneumonid wasps, beetles	6–25	5–25	green-yellowish	V–VI

MATERIAL AND METHODS

We studied the dependence of reproductive success on floral display in 12 European orchid species that were available and abundant enough in sites that we could reach; characteristics of these species known to play an important role in pollinator attraction (plant height, number and colour of flowers, flowering period, presence of reward and kind of pollinators) are summarized in Table 1. During 1994–2001, we counted the number of flowers and the number of capsules of all the plants (50–551) at 24 different sites (see Table 2). Some sites were visited more than once: we have 1–3 years of observations per taxon.

For each species we determined reproductive success as the proportion of flowers that developed into fruits (reproductive success = number of fruits/number of flowers) for each floral display category (group of plants with the same number of flowers) and for all plants in each population. We plotted these proportions and relative frequencies of plants against floral display categories.

The relation between fruit set and floral category was not always linear. Therefore, we first fitted it using a second order polynomial regression – to test whether the relation was significantly non-linear (i.e., whether the quadratic term was significantly different from zero after Bonferroni correction). If it was, we used quadratic regression. If not, we fitted the data by linear regression. If the slope of the linear regression was significantly different from zero after Bonferroni correction, we used linear regression, as it was the best fit. If the slope of the linear regression was not significantly different from zero after Bonferroni correction, we fitted the data by a constant, as linear regression did not have any sense in such case. We used the method of minimizing the residual sums of squares (RSS) in the program Microsoft Excel, the general linear model in the program Statistica v. 5.5, and the significance level 5%; the regressions were weighted by the numbers of plants in each flower number class.

To test hypothesis (i), we used the flowering period of deceptive and rewarding species published in DELFORGE (2001). We assessed the difference in the flowering time between

Table 2. Site descriptions.

Species	Site (region, country)	Site description	Plant community	Geographical coordinates
<i>O. morio</i>	Zábrdí (South Bohemia, CZ) Sirjansland (Schouwen-Duiveland, NL)	dry unfertilized hay-meadow wet "polder" meadow	al. <i>Arrhenatherion</i> al. <i>Junco-Molinion</i>	49°01' N, 13°56' E 51°40' N, 4°00' E
<i>O. ustulata</i>	Albrechtice (South Bohemia, CZ) Vědlice (North Bohemia, CZ)	dry unfertilized hay-meadow dry unfertilized hay-meadow	al. <i>Arrhenatherion</i> al. <i>Geranium sanguinei</i>	49°12' N, 13°34' E 50°31' N, 14°20' E
<i>D. sambucina</i>	Javorník (South Bohemia, CZ) Řetenice (South Bohemia, CZ)	dry unfertilized hay-meadow dry pasture	al. <i>Viola caninae</i> al. <i>Cynosurion</i>	49°07' N, 13°39' E 49°07' N, 13°36' E
<i>D. incarnata</i>	Kyselov (South Bohemia, CZ)	ruderal wet biotope		48°41' N, 14°03' E
<i>D. majalis</i>	Javorník (South Bohemia, CZ)	wet unfertilized meadow	al. <i>Caricion davallianae</i>	49°07' N, 13°39' E
<i>D. fuchsii</i>	Ohrazení (South Bohemia, CZ) Sv. Tomáš (South Bohemia, CZ) Gerendal (South Limburg, NL)	wet unfertilized tall-grass meadow wet unfertilized tall-grass meadow dry unfertilized hay-meadow	al. <i>Molinion</i> al. <i>Molinion</i> al. <i>Bromion erecti</i>	48°56' N, 14°35' E 48°38' N, 14°06' E 50°57' N, 5°51' E
<i>P. bifolia</i>	Javorník (South Bohemia, CZ)	dry unfertilized meadow	al. <i>Viola caninae</i>	49°07' N, 13°39' E
<i>P. chlorantha</i>	Nebe (South Bohemia, CZ) Lipno (South Bohemia, CZ)	dry unfertilized hay-meadow light spruce forest with grass understorey	al. <i>Arrhenatherion</i>	49°08' N, 13°34' E 48°41' N, 14°01' E
<i>G. conopsea</i>	Javorník (South Bohemia, CZ)	dry unfertilized hay-meadow	al. <i>Viola caninae</i>	49°07' N, 13°39' E
<i>E. atrorubens</i>	Majdalena (South Bohemia, CZ) Sudslavice (South Bohemia, CZ)	ruderal dry place, stony railway dike dry grassy railway dike		48°57' N, 14°51' E 49°05' N, 13°47' E
<i>E. purpurata</i>	Eifel (Nordrhein-Westfalen, D)	closed beech forest without herb understorey		50°39' N, 6°21' E
<i>C. viride</i>	Javorník (South Bohemia, CZ) Žhůří (South Bohemia, CZ)	dry unfertilized hay-meadow dry unfertilized montane meadow	al. <i>Viola caninae</i> al. <i>Nardion</i>	49°07' N, 13°39' E 49°05' N, 13°33' E

Table 3. Reproductive success in deceptive and rewarding species. NFL – number of flowers, NFR – number of fruits, RS – reproductive success (number of fruits/number of flowers), s.d. – standard deviation of RS, n – number of individuals.

Species	Site + year	NFL	NFR	RS	s.d.	n
Deceptive species						
<i>O. morio</i>	Zábrdí 1997	9.4	3.7	0.38	0.25	551
	Sirjansland 2000	10.7	1.3	0.12	0.15	202
<i>D. sambucina</i>	Javorník 2000	10.7	2.2	0.19	0.19	246
	Řetenice 2000	11.4	3.5	0.30	0.20	399
<i>O. ustulata</i>	Albrechtice 2001	27.3	1.8	0.06	0.07	84
	Vědlice 2001	38.3	4.5	0.12	0.10	137
<i>D. majalis</i>	Javorník 1998	17.5	4.9	0.27	0.18	100
	Javorník 2000	16.2	5.2	0.31	0.21	164
<i>D. incarnata</i>	Kyselov 2000	31.3	17.0	0.52	0.18	152
<i>D. fuchsii</i>	Ohrazení 1994	23.7	11.7	0.46	0.34	52
	Sv. Tomáš 1998	24.0	11.8	0.47	0.22	106
	Gerendal 2000	28.0	14.0	0.49	0.17	121
Mean reproductive success in deceptive species			0.31			
Rewarding species						
<i>P. bifolia</i>	Javorník 1998	20.8	19.4	0.93	0.09	148
	Javorník 2000	16.1	10.4	0.65	0.20	147
<i>P. chlorantha</i>	Nebe 2000	18.2	15.4	0.83	0.20	252
	Lipno 2000	12.8	8.2	0.64	0.24	150
<i>G. conopsea</i>	Javorník 1998	36.5	32.9	0.89	0.12	100
	Javorník 2000	40.9	33.3	0.81	0.13	130
<i>E. atrorubens</i>	Majdalena 1998	15.0	9.1	0.59	0.29	66
	Sudslavice 2000	16.5	15.5	0.94	0.11	56
<i>E. purpurata</i>	Eifel 2000	29.5	28.3	0.96	0.07	50
<i>C. viride</i>	Javorník 1999	11.4	3.3	0.26	0.24	80
	Javorník 2000	14.3	1.2	0.07	0.12	81
	Zhůří 2000	13.7	5.1	0.35	0.27	64
Mean reproductive success in rewarding species			0.66			

395 deceptive and 91 rewarding species and in the mean flowering time between 14 deceptive and 20 rewarding genera respectively, using the Mann-Whitney U -test. To test the hypothesis (ii), we compared the mean value of reproductive success for 6 deceptive species with that of 6 rewarding species by means of a t -test. To test the hypothesis (iii), we determined the proportion of cases, when the constant term was the best fit in deceptive and rewarding species using the Bonferroni correction.

RESULTS

Comparison of the timing of peak flowering for the deceptive and rewarding species/genera has shown that the deceptive species/genera flower significantly earlier, compared with the rewarding ones (Mann-Whitney U -test for species, $U = 81$, $P = 0.039$; for genera $U = 4398$, $P = 0.001$), which supports our hypothesis (i).

Table 4. Parameters of fitted curves $y=ax^2+bx+c$, $y=bx+c$, $y=c$ (see text for explanation, which curves were used in individual cases). For fitting by a constant, we present standard deviation (s.d.) of mean reproductive success in all floral categories instead of coefficient of determination (R^2).

Species	Site + year	<i>a</i>	<i>b</i>	<i>c</i>	R^2	s.d.
Deceptive species						
<i>O. morio</i>	Zábrdí 1997	-0.003	0.072	-0.016	0.33	-
	Sirjasland 2000	-	-	0.121	-	0.04
<i>D. sambucina</i>	Javorník 2000	-0.002	0.045	-0.046	0.54	-
	Řetenice 2000	-	0.009	0.203	0.36	-
<i>O. ustulata</i>	Albrechtice 2001	-	-	0.061	-	0.04
	Vědlice 2001	-	-	0.129	-	0.07
<i>D. majalis</i>	Javorník 1998	-	-	0.277	-	0.11
	Javorník 2000	-	-	0.342	-	0.12
<i>D. incarnata</i>	Kyselov 2000	-	0.006	0.339	0.40	-
<i>D. fuchsii</i>	Ohrazení 1994	0.001	-0.028	0.559	0.39	-
	Sv. Tomáš 1998	0.0004	-0.012	0.543	0.30	-
	Gerendal 2000	0.0003	-0.015	0.666	0.33	-
Rewarding species						
<i>P. bifolia</i>	Javorník 1998	-	-	0.921	-	0.12
	Javorník 2000	-	-	0.659	-	0.13
<i>P. chlorantha</i>	Nebe 2000	-0.0003	0.019	0.590	0.67	-
	Lipno 2000	-	-	0.624	-	0.15
<i>G. conopsea</i>	Javorník 1998	-	0.001	0.846	0.11	-
	Javorník 2000	-	-	0.807	-	0.07
<i>E. atrorubens</i>	Majdalena 1998	-	-	0.634	-	0.19
	Sudslavice 2000	-	-	0.943	-	0.05
<i>E. purpurata</i>	Eifel 2000	-	-	0.961	-	0.05
<i>C. viride</i>	Javorník 1999	-	0.022	-0.002	0.67	-
	Javorník 2000	-	-	0.069	-	0.07
	Zhůří 2000	-	0.011	0.181	0.26	-

The mean reproductive success of rewarding orchids, 66%, was significantly higher than that of deceptive species, 31% (two-sample, two-tailed *t*-test assuming unequal variances, $t = -3.64$, d.f. = 17, $P = 0.002$, Table 3). These numbers are conspicuously similar to those obtained by NEILAND & WILCOCK (1998) for a set of European orchid species (63 % in rewarding species and 28 % in deceptive ones). All this supports our hypothesis (ii).

Figs. 1–4 and Table 4 show the results of the regression analyses. In *Orchis morio* and *Dactylorhiza sambucina*, we found a negative (curved down) quadratic relationship between reproductive success and the number of flowers, in one of two sites (Fig. 1, Table 4). We found no relationship between floral display and reproductive success in *Orchis ustulata* and *D. majalis* (Figs. 1, 2, Table 4). In *D. incarnata*, there was a conspicuous positive linear trend in the reproductive success relative to floral display (Fig. 2, Table 4). At all three *D. fuchsii* sites, we found a positive (curved up) quadratic relationship (Fig. 2, Table 4). In the rewarding species, the reproductive success was consistently very high and mostly constant (Figs. 3, 4, Table 4), with the exception of *Coeloglossum viride* and *Gymnadenia conopsea*, in which it was positively associated with the floral display in one year, but not in the other.

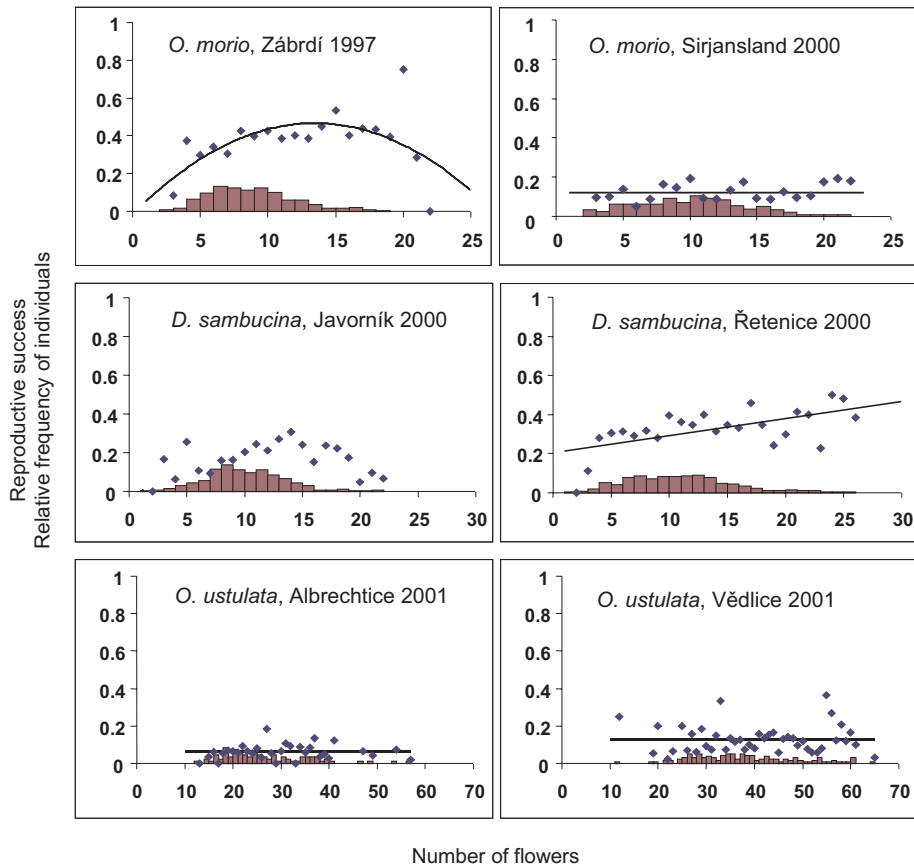


Fig. 1. Proportion of flowers that develop into fruit in relation to floral display (number of flowers) in the deceptive species *Orchis morio*, *Dactylorhiza sambucina* and *O. ustulata*. Histograms represent the relative frequencies of individuals in floral categories. Parameters of fitted curves are listed in Table 4.

In deceptive species, the best fit was a constant in most cases (5 out of 12 cases), followed by a curved-up parabola (3 out of 12 cases), curved-down parabola (2 out of 12 cases) and positive linear dependence (2 out of 12 cases). In rewarding species, the best fit was a constant in most cases (8 out of 12 cases), followed by a negative linear dependence (3 out of 12 cases), and a curved-down parabola (2 out of 12 cases). When Bonferroni correction was used, the number of cases that support our hypothesis (iii) was even larger (9 out of 12 cases in deceptive species and 10 out of 12 cases in rewarding species).

DISCUSSION

We found support for our hypothesis (iii) in 9 out of 12 cases in deceptive species and in 10 out of 12 cases in rewarding species: there is no relation between reproductive success and floral display (the best fit is a constant).

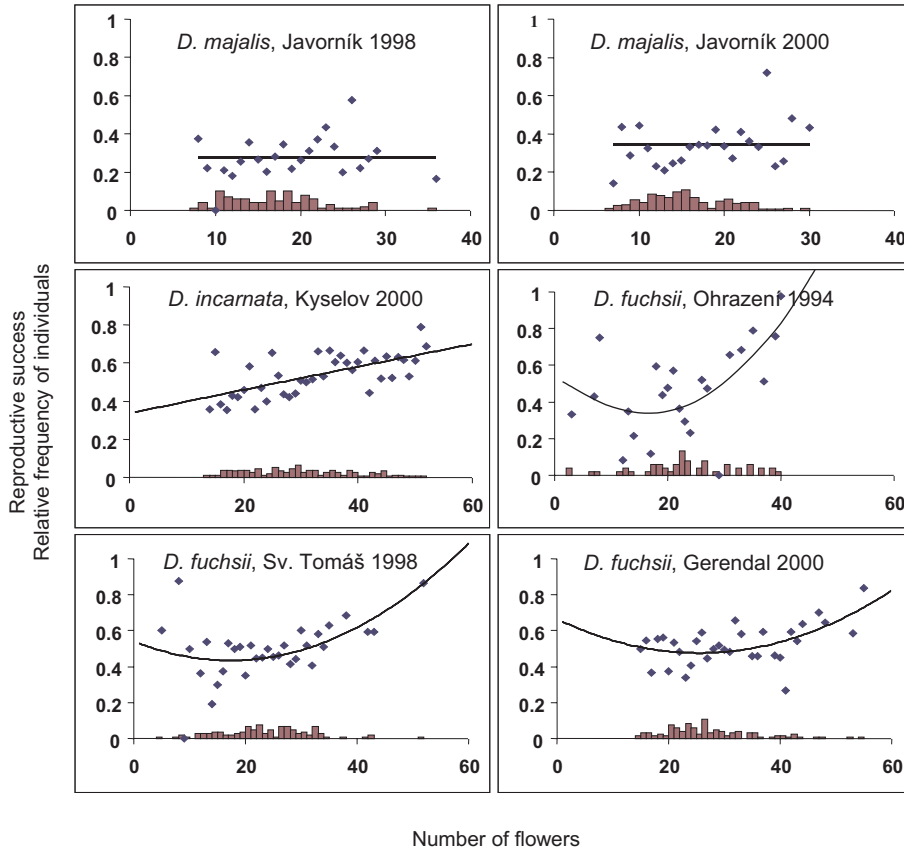


Fig. 2. Proportion of flowers that develop into fruit in relation to floral display (number of flowers) of deceptive species *Dactylorhiza majalis*, *D. incarnata* and *D. fuchsii*. Histograms represent relative frequencies of individuals in floral categories. Parameters of fitted curves are listed in Table 4.

Species-specific trends

We sometimes observed a negative parabolic relationship between reproductive success and the number of flowers in *Orchis morio* and *Dactylorhiza sambucina*, which means that plants with small or large inflorescences were less successful than those with medium-sized inflorescences. NILSSON (1984) observed a similar pattern in a Swedish *O. morio* population with a clear decrease in the number of fruits after reaching a maximum fruit set at about 9-flowered inflorescences. Thus he concluded that multi-flowered spikes are not advantageous in this species. As this did not consistently appear in our data for these species in other years and/or sites, we cannot further support NILSSON's (1984) hypothesis.

The deceptive species *Orchis ustulata* is the only species of the genus *Orchis* pollinated by flies (HARAŠTOVÁ-SOBOTKOVÁ et al. 2005) but this specialization does not seem to be advantageous because the observed fruit set was very low. We found no relationship between

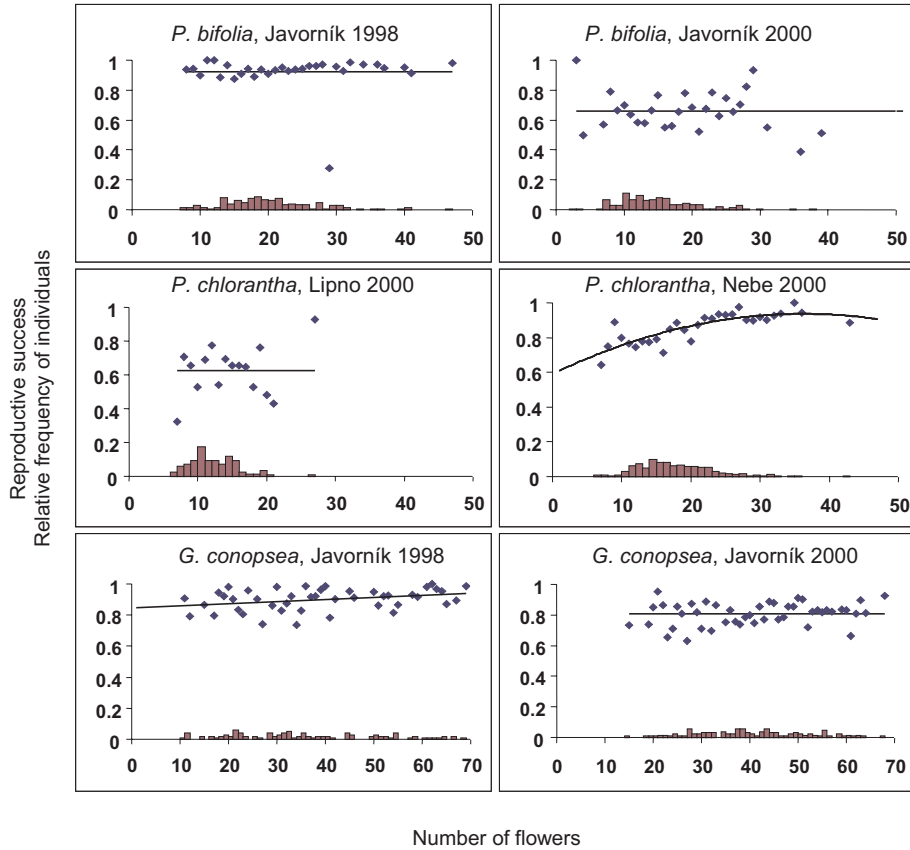


Fig. 3. Proportion of flowers that develop into fruit in relation to floral display (number of flowers) of rewarding species *Platanthera bifolia*, *P. chlorantha* and *Gymnadenia conopsea*. Histograms represent relative frequencies of individuals in floral categories. Parameters of fitted curves are listed in Table 4.

floral display and fruit set, with many plants producing no capsules and few successful plants distributed across all floral display categories.

Three other deceptive species, belonging to the genus *Dactylorhiza*, have showy attractive inflorescences and usually grow in wet places (wet meadows, swamps) lacking other co-flowering species. In *D. majalis*, we found no relationship between floral display and reproductive success. In *D. incarnata*, there was a conspicuous positive linear trend in the reproductive success relative to floral display based on observation in one site in one year. In other sites and/or years this relationship might be different. At all three *D. fuchsii* sites, we found a positive parabolic relationship indicating that both small and large plants are the most successful. This is in contradiction to the observation of fruit set in *D. fuchsii* by WAITE et al. (1991), who found no correlation between number of flowers setting fruit and the total number of flowers per inflorescence.

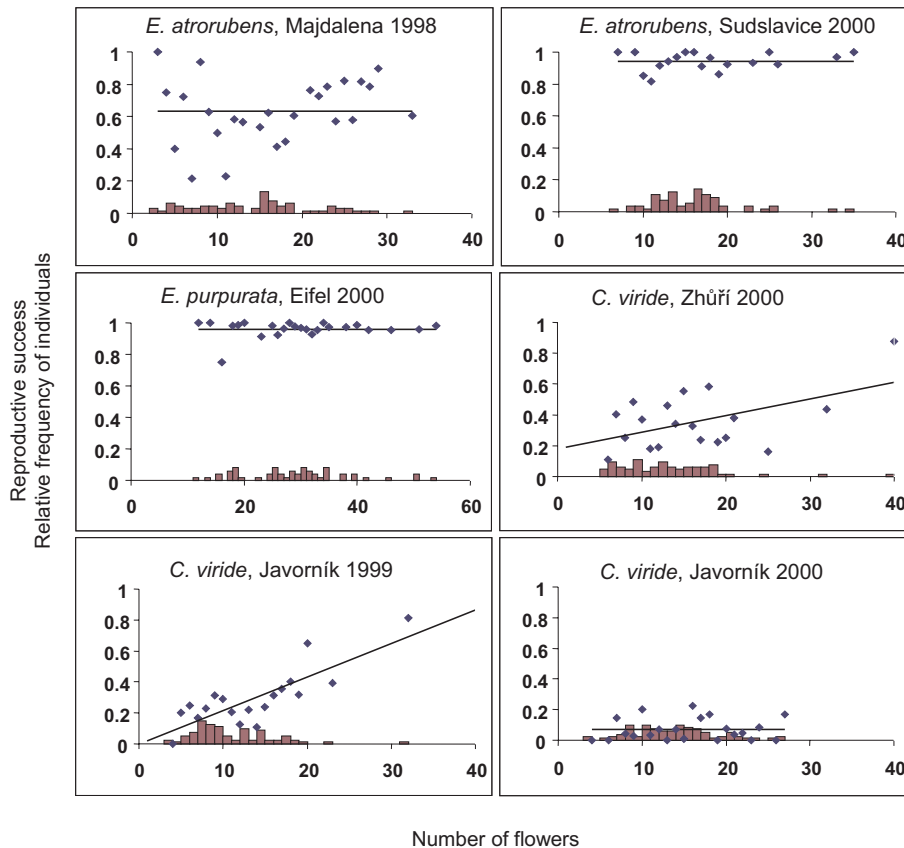


Fig. 4. Proportion of flowers that develop into fruit in relation to floral display (number of flowers) of rewarding species *Epipactis atrorubens*, *E. purpurata* and *Coeloglossum viride*. Histograms represent relative frequencies of individuals in floral categories. Parameters of fitted curves are listed in Table 4.

Data gathered for *Platanthera bifolia* at the Javorník site demonstrate that even for rewarding species there may be differences in reproductive success between years. In *P. chlorantha* at the Nebe site, the plants having large inflorescences had a higher reproductive success than similar-sized plants at the Lipno site. As the former site is an open meadow, and the latter a light spruce forest, the differences between both sites could be an effect of biotope, which has been recorded also in other orchid species (NILSSON 1978, FRITZ 1990, WAITE et al. 1991, O'CONNELL & JOHNSTON 1998, JACQUEMYN et al. 2002).

Another rewarding species, which often grows with *P. bifolia*, is *Gymnadenia conopsea*. We found that the reproductive success of this species was very high and almost constant in both years of observation. In 1998 there was a positive linear trend indicating large plants had a higher reproductive success than small plants. *G. conopsea* is very attractive to insects, especially moths, so its production of nectar and mass flowering may be more important factors in attracting pollinators than floral display of an individual plant. This is in accord with

the observation that the number of adjacent co-flowering plant species (HANSEN & OLESEN 1999) does not influence the reproductive success of *G. conopsea*.

In both *Epipactis atrorubens* and *E. purpurata* we found no relationship between reproductive success and floral display. Even though the latter species was growing in a dark beech forest, its fruit set was close to 100%. WAITE et al. (1991) studied another allogamous orchid, *E. helleborine*, and did not find any significant relationship between the proportional levels of fruit set and inflorescence size, either.

Coeloglossum viride plants are usually very small (9–30 cm) and hidden by surrounding vegetation. Therefore we speculate that pollinators (e.g. ichneumonid wasps, beetles) could not discover a lot of the flowers and the overall fruit set was low. Nectar and weak odor production in this species probably cannot compensate for its unattractiveness (small plant with green flowers). WILLEMS & MELSER (1998) reported similar low fruit set (10 %) in the Dutch population of *C. viride*, finding no significant correlation between capsule number and number of flowers per plant.

General trends and confounding issues

The results are somewhat puzzling in that some parabolic or positive linear relationships between flower number and percentage of flowers that developed fruit were recorded. The negative (curved down) parabolic dependence sometimes observed in the deceptive species (*O. morio* in Zábřdi 2000 and *D. sambucina* in Javorník 2000) might be explained as follows. One might expect that a low number of flowers in the inflorescence is suboptimal, as then the plant is inconspicuous and not attractive for pollinators. Large number of flowers may also be suboptimal, as their production is costly. If this is true, then for a species under given conditions there should exist some optimal number of flowers in the inflorescence. The negative parabolic dependence observed in the rewarding *P. chlorantha* in Nebe 2000 and the three positive parabolic dependencies for deceptive *D. fuchsii* are hard to explain, but all the quadratic terms here are so small that they do not differ too much from a linear dependence or constant. Sometimes positive linear trends were observed in rewarding species (*G. conopsea* in Javorník 1998, *C. viride* in Javorník 1999 and Zhůří 2000). This may be explained as follows. For rewarding orchids, a constant relationship between flower number and fruit production is only expected a priori if pollinators fully saturate female reproductive success irrespective of the flower number. If female reproductive success is not saturated, then fruit set should depend both on long distance attraction of pollinators, and on numbers of flowers visited by each attracted pollinator, which are both expected to increase as flower number increases.

There are also some alternative explanations for variation in floral display than its influence on reproductive success, however. This is because reproductive success is not the only determinant of plant fitness.

For example, costs of reproduction have been demonstrated to be particularly strong in some deceptive orchids (e.g., PRIMACK & HALL 1990, PRIMACK & STACY 1998), but not in others (JERSÁKOVÁ & KINDLMANN, unpubl.). If costs of reproduction are large, then a large investment in reproduction in one year may negatively affect the amount of reserves the plant creates in the tuber or other storage organ for the subsequent year and consequently result in

lower number of fruits or even sterility in the subsequent year. The overall effect of reproductive success on plant lifetime fitness then becomes dubious, as the effects in individual years counteract each other. This becomes less important in rewarding orchids as in these, the reproductive success is consistently large and therefore its variance is small.

Geitonogamy may reduce fitness of large displays – if inbreeding depression varies among orchids, small displays may be adaptive in certain cases (GEBER 1985, ROBERTSON 1992). Variance in reproductive success is another factor neglected in the literature. It may very well be that the low selection pressure for optimization of the number of flowers in the inflorescence, which we have found, is a consequence of large variability in reproductive success – but this remains to be proved. The formula for reproductive success contains the number of fruits in the inflorescence, but not the number of seeds in each fruit; however, for plant fitness the latter and not the former matters. Fortunately, this effect is not large (JERSÁKOVÁ & KINDLMANN 1998, WILLEMS et al. 2001).

Several studies compare fruit set among orchid species with the aim of determining the relationships between reproductive success and a particular life-history strategy (NEILAND & WILCOCK 1998). However, the pattern of fruit set in one species can vary not only within the distribution area of a species, but also between closely situated sites within the same year. This often reflects effect of the site – particular type of management (JERSÁKOVÁ et al. 2002) and composition of the surrounding vegetation (FRITZ 1990). Climatic changes may explain fluctuations in fruit set at one site in different years (ALEXANDERSSON & ÅGREN 1996, LIGHT & MACCONAILL 2002). Thus fruit set fluctuates between years and sites, which can be a confounding issue, as fruit set determinations are very often based on data from only one site and one year.

Although this discussion clearly demonstrates that there is large variability in the reproductive success and floral display between species, years and sites, some common trends appear: (1) Deceptive species flower earlier than rewarding ones. (2) Reproductive success in deceptive species is lower than in rewarding ones. (3) There is no evidence that reproductive success is generally dependent on the number of flowers in the inflorescence in both deceptive and rewarding orchids.

Acknowledgements: This work was supported by the GA AV ČR grant No. KJB6141302 to J. Jersáková, and by the GA ČR grant No. 206/00/1124 and ESF (program Plant adaptation) travel grant to P. Kindlmann.

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