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FLORAL DISPLAY, REPRODUCTIVE SUCCESS, AND CONSERVATION OF TERRESTRIAL ORCHIDS

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ABSTRACT. Almost a third of all species in the family Orchidaceae offer no reward to insect pollinators. In the absence of a reward, the number of flowers may be the most important component of insect attraction; however, the importance of the number of flowers in the inflorescence for fruit production has not yet been satisfactorily explored. We have examined reproductive success in the European orchid species *Orchis morio* in different years and at various locations. We have tested the following hypotheses: (i) For a species under given conditions, there exists an optimal number of flowers in the inflorescence, and plants with this optimal number of flowers are the most common ones in the population; (ii) Increase of the number of pollinators results in an increase in fruit set of the orchid. Neither of the hypotheses was supported by our data; however, our data suggest that fruit set may be positively correlated with the amount of rewarding co-flowering plants. Based on these findings, we propose that promotion of rewarding co-flowering plants, rather than augmentation of the presence of pollinators, seems to be a promising conservation strategy for nectarless orchid species.

Key words: deceptiveness, fruit set, number of flowers, *Orchis morio*, terrestrial orchids

INTRODUCTION

Fruit set (percentage of flowers that develop fruits), an important component of reproductive success in non-autogamous orchids, is usually associated with pollinator reward, which is mainly nectar. Nectar production, however, entails a cost to a plant in terms of growth and/or reproduction. Ackerman (1986) and Proctor and Harder (1996) therefore hypothesized that, from the evolutionary point of view, it should be more advantageous for orchids to deceive pollinators by not producing nectar and only imitating rewarding species, than to offer them a reward. Nilsson (1992) also argues that deception is advantageous in terms of present and future fitness. This may explain why almost a third of orchid species (8000–10,000 out of ca. 25,000 existing orchid species; Dressler 1990) are nectarless.

Nectarless orchids have a lower fruit set than rewarding orchids (Zimmerman & Aide 1989, Alexandersson & Agren 1996). For example, Neiland and Wilcock (1998) found that among European orchid species, 27.7% of flowers in deceptive species developed fruit, as opposed to 63.1% in rewarding species. Johnson and Nilsson (1999) proposed that it is more advantageous for pollinator-limited orchids to invest resources in increasing the number of flowers in the inflorescence ("floral display") to attract pollinators, rather than into nectar production. The effect, however, of the number of flowers in the inflorescence on plant fitness may be dubious: large inflorescences may attract more pollinators, which results in a larger fruit set, but may also cause successive probes by a pollinator within an inflorescence, which may result in an increase in geitonogamous pollination, as more pollen is transferred between different flowers within the same plant (Geber 1985, Harder & Barrett 1995, Klinkhamer et al. 1989, Robertson 1992, Snow et al. 1996, Rademaker & De Jong 1998). In empirical data, the relationship between the number of flowers in the inflorescence and fruit set in orchids does not show a common trend (Montalvo & Ackerman 1987, Schemske 1980, Zimmerman & Aide 1989, Calvo 1990, Willems & Lahtinen 1997). Fruit set is often independent of the number of flowers in the inflorescence (Firmage & Cole 1988, Zimmerman & Aide 1989, Mattila & Kuitunen 2000, Vallius 2000, Jacquemyn et al. 2002).

Here we pursue the following two hypotheses: (i) One might expect that 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, some optimal number of flowers should exist in the inflorescence, and plants with this optimal number of flowers should be the most common ones in the population. (ii) If the number of pollinators and not rewardlessness by itself is a limiting factor for fruit set, then an increase of the number of pollinators should result in an increase in fruit set of the orchid.

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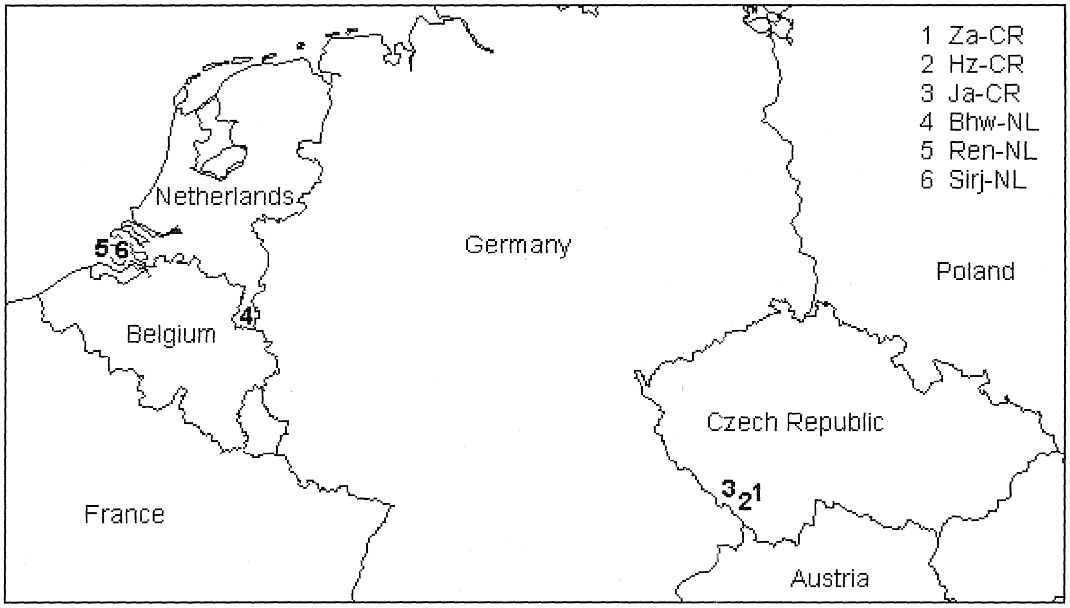

FIGURE 1. Study sites in The Netherlands and Czech Republic.

Previously we examined the effect of the number of flowers on fruit set in 12 European orchid species, but—consistently with previous authors—we did not find a common trend (J. Jersáková & P. Kindlmann unpubl. data). The relationship was sometimes linear, sometimes parabolic, but in many cases it was constant. In theory, this may be because the trends described in hypothesis (i) may occur only in particular years and/or sites. Therefore, here we are repeating the observations for only one species, *Orchis morio,* but in several different years and at various locations. In addition, we investigate not only the effect of the number of flowers in the inflorescence but also of the site and year on the fruit set. To test hypothesis (ii), we added bumblebee hives to some sites to see whether a strong increase in the number of pollinators will positively affect reproductive success of the plants.

MATERIAL AND METHODS

Orchis morio has disappeared from some sites in many countries in Europe (Schmid 1980, Böhnert 1991, Šmiták & Jatiová 1996, Kreutz & Dekker 2000). A perennial herb with tuber roots, *O. morio* prefers neutral to slightly basic oligotrophic soils. It occurs in semi-wet meadows, pastures, and shrubby slopes from lowland up to 1000 m elevation (Delforge 1995). Phenologically, *O. morio* has a rosette persisting during wintertime. The inflorescence, produced in early May, is composed of 2–25 purple to whitish flowers. All flowers on a spike open usually within 3 days and wilt within 4 days after pollination. Non-fertilized flowers can last up to 21 days. *Orchis morio* can also reproduce vegetatively, and clumps of genets of the same petal color and number of flowers often can be found. This non-autogamous species is nectarless and acts by deceit. The orchid benefits from unconditioned behavior of naïve or newly emerged insects ensuring pollination (Nilsson 1984). Flower visitors recorded from other parts of Europe include *Bombus* spp. queens, honeybees (*Apis mellifera*), and several solitary bees (*Osmia* spp. and *Andrena* spp.). In the Czech Republic, we observed *Bombus terrestris* and *B. lapidarius* as the most common pollinators.

Study Sites

The research was carried out at six sites situated in the Czech Republic (region South Bohemia) and the Netherlands (regions South Limburg and Schouwen en Duiveland (FIGURE 1, TABLE 1). The sites Ren-NL and Sirj-NL (wet grasslands) and Bhw-NL (dry grassland) are representatives of biotopes with oceanic climate. The Czech sites represent dry grasslands with continental climate including strong winters with snow cover. Observations were carried out during the 1997–2000 period (TABLE 1).

TABLE 1. Study site description.

Study site (code)	Vegetation description	Altitude m	Mean annual temperature °C	Mean annual precipitation mm	Years of observation
Zábrdí (Za-CR)	Dry flowering meadow	620	6–7	600–700	1997–2000
Horní Záblatí (Hz-CR)	Dry flowering meadow	680	6–7	600–700	1997–1999
Javorník (Ja-CR)	Dry flowering meadow	900	4–5	850–1000	1998–2000
Berghofweide (Bhw-NL)	Dry flowering meadow	170	9–9.5	850–900	2000
Renesse (Ren-NL)	Wet sedge grassland	0	9.5–10	750–800	2000
Sirjansland (Sirj-NL)	Wet sedge grassland	0	9.5–10	750–800	2000

Effect of Floral Display on Fruit Set

The effect of the number of flowers per spike on fruit set (proportion of flowers that developed into fruits) was investigated on data sets from all studied populations (TABLE 1). We used regressions to determine relationships between fruit set as dependent variable and number of flowers as its predictor. Prior to the analyses, we averaged data for plants with the same number of flowers in each population. Data were fitted by linear and quadratic regressions, as we supposed fruit set to depend linearly or parabolically on floral display. As the relation between fruit set and number of flowers in the inflorescence was not always linear, we fitted data first by a quadratic regression. If the quadratic term was significantly different from zero, we used quadratic regression; if not, we used linear regression. If the slope of this regression was not significantly different from zero, we fitted the data by a constant. Histograms with relative frequencies of plants with a particular number of flowers were inset in the figures showing the regression analyses. Possible evolutionary trends suggested by the regressions (selection for a particular number of flowers or selection for maximum/minimum number of flowers per inflorescence) then were compared with the actual frequency distributions of the number of flowers. Skewness of the frequency distributions of the numbers of flowers was calculated.

Variation in Fruit Set between Years and Sites

We expected that fruit set at the oceanic sites (The Netherlands) would differ from that at the continental sites (Czech Republic), because of different climatic conditions for both plants and pollinators and because of different co-flowering plant species. Fruit set was monitored in all six populations, at the Czech sites during the 1997–2000 years, at the Dutch sites only in 2000 (TABLE 1). At each site, we recorded co-flowering plant species visited by bees and bumblebees as food sources. The effect of site on fruit set was tested on five populations in 2000 (Za-CR, Ja-CR, Bhw-NL, Sirj-NL, Ren-NL). To obtain further information, we counted the proportion of individuals with 0% and with 100% fruit set in each population to show how many plants achieve maximal fruit set under natural conditions and how frequent are totally unsuccessful plants. Our expectation that fruit set may vary between years was tested on the set of Czech sites studied during 1997–2000 (Za-CR, Hz-CR, Ja-CR). Differences between sites and years were tested by one-way ANOVAs with subsequent post hoc comparisons (Tukey HSD test). Results obtained were compared with climatic data (TABLE 4, FIGURE 2).

Pollination Augmentation Experiment

We used commercially available hives with *Bombus terrestris* (distributed by Biola Chelčice, CZ), each containing ca. 40 individuals. At two sites, Zábrdí (1999) and Horní Záblatí (1998), we placed two hives per site in the year indicated at the edge of the site and left it there during the whole flowering period of *Orchis morio.* We used one-way ANOVA with subsequent post hoc comparisons (Tukey HSD test) to test for differences between fruit set in different years to see whether fruit set was higher in years when bumblebee presence was augmented.

As the distance from bumblebee hives could have influenced fruit set, each experimental site was divided into three parts, 0–25, 25–50, and more than 50 m apart from the hive. We used

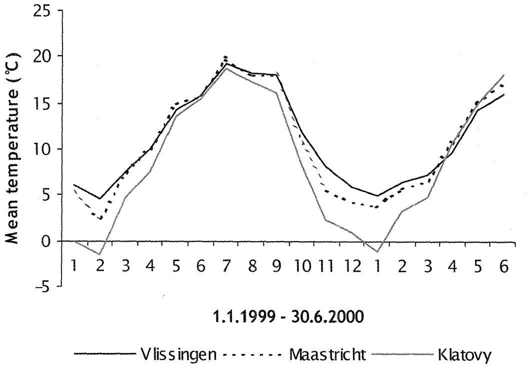

FIGURE 2. Mean air temperature from January 1, 1999–June 30, 2000, illustrates climate differences between oceanic (Dutch) and continental (Czech) sites. The data were obtained from three meteorological stations close to the study sites. Station Vlissingen (in the region of Ren-NL and Sirj-NL) and station Maastricht (close to Bhw-NL) are both in The Netherlands; station Klatovy (in the region of Za-CR, Hz-CR, and Ja-CR) is in the Czech Republic.

ANOVA with subsequent post hoc comparisons (Tukey HSD test) to test for differences between the three parts in the number of fruits and reproductive success.

RESULTS

Effect of Floral Display on Fruit Set

The number of flowers per inflorescence was found to have a highly variable (positive, negative, none) effect on fruit set (TABLE 5). In most cases (8 samples), fruit set was independent of number of flowers per inflorescence. In two cases, fruit set monotonously increased with the number of flowers per inflorescence; in one case, it decreased; and in two cases, dependence was a curved-down parabola, expected by hypothesis (i). The trends were variable within and between populations in various years (FIGURES 3, 4, 5). None of the frequency distributions of numbers of flowers was significantly skewed.

Variation in Fruit Set between Years and Sites

Site significantly affected fruit set in five *Orchis morio* populations ($F_{(4,\ 926)} = 67.01$; $P > 0.001$). In the Netherlands, two oceanic populations at wet meadows (Ren-NL, Sirj-NL) had the lowest capsule production, 22.5% and 12.1% compared to other sites (TABLE 2). The number of individuals that did not develop any capsules was relatively high at Ren-NL and Sirj-NL, and

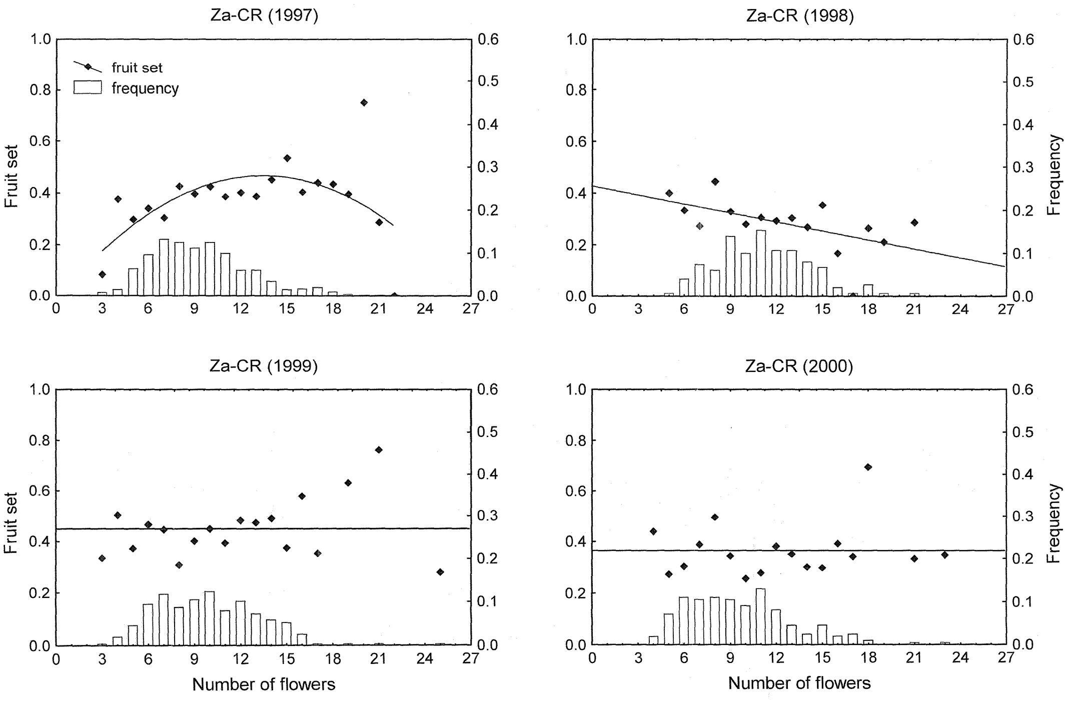

FIGURE 3. Effect of floral display on fruit set and frequency distribution of individuals in relation to the number of flowers in the inflorescence at the site Za-CR.

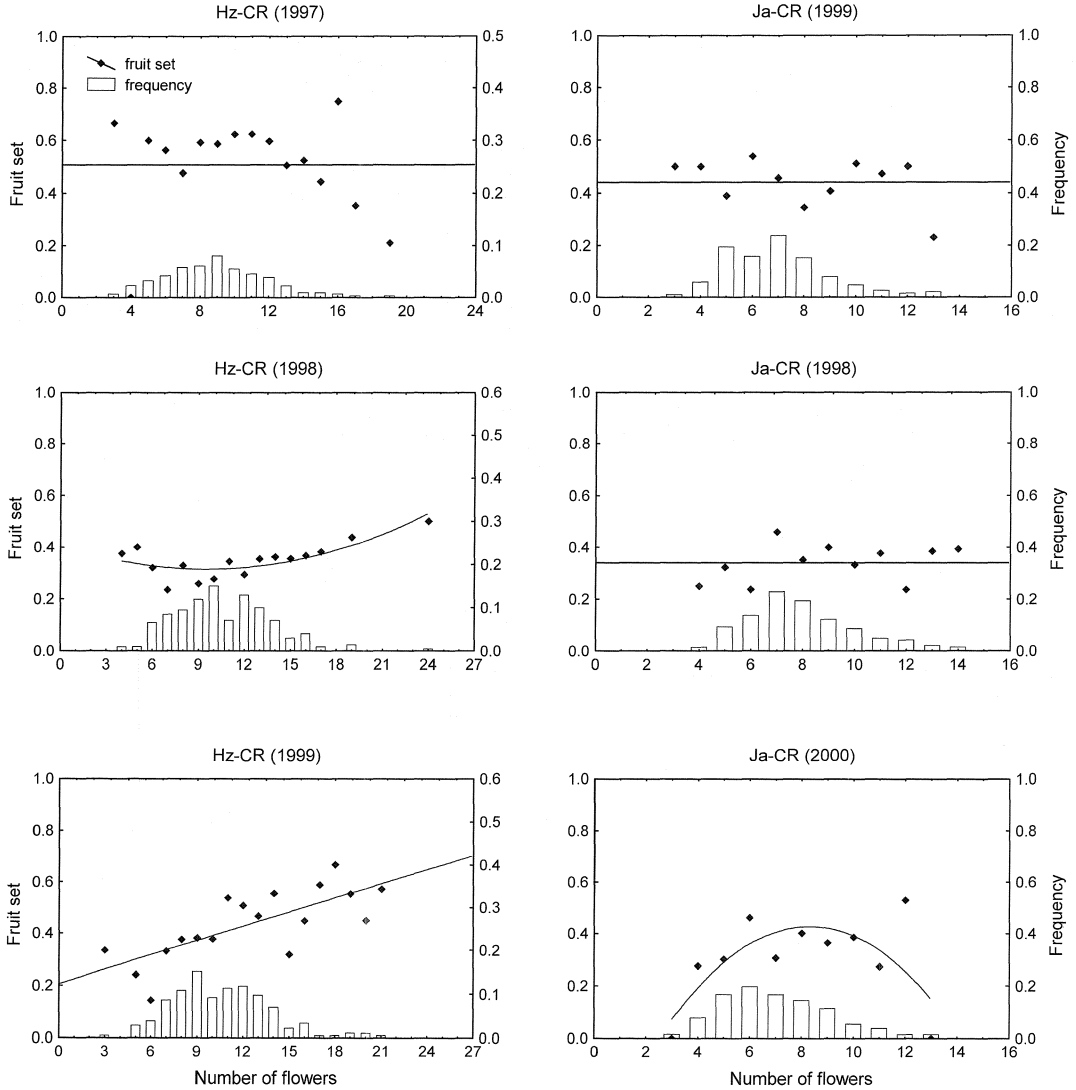

FIGURE 4. Effect of floral display on fruit set and frequency distribution of individuals in relation to the number of flowers in the inflorescence at the sites Hz-CR and Ja-CR.

no individual reached 100% fruit set. On the other hand, the other oceanic site (Bhw-NL) with the lowest number of flowers per spike reached ca. 50% fruit set. The fruit set of Czech continental sites reached ca. 35%, more than the coast sites but less than Bhw-NL. This indicates that fruit set depends more on factors specific for a particular site than on macroclimate variability (FIGURE 2). Also a significant effect of the year on fruit set was found in the Czech populations ($F_{(3, 2199)} = 20.16$; $P > 0.0001$). The fruit set in 1999 was significantly higher than that in any other year (TABLE 3). We found, however, no significant variation in temperatures between years (One-way ANOVA df = 3, F = 0.21, $P > 0.05$; TABLE 4).

Pollination Augmentation Experiment

Multiple comparisons (Tukey-HSD test) for each of the sites where pollinators were added in one of the years of observations revealed that differences in reproductive success could be attributed to a particular year, rather than to the inundative release of bumblebees (TABLE 3). In 1999, fruit set was significantly highest at both sites—even at the site Horni Zablati, where bumblebees were inundatively released that

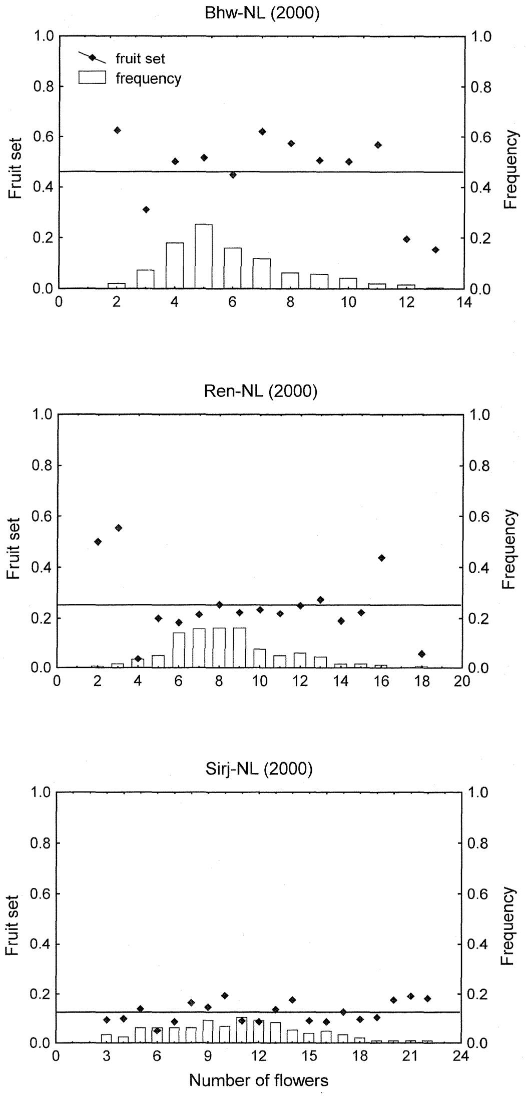

FIGURE 5. Effect of floral display on fruit set and frequency distribution of individuals in relation to the number of flowers in the inflorescence at the sites Bhw-NL, Ren-NL, and Sirj-NL.

year. Fruit set consistently declined with distance from the hive in both experimental sites (TABLE 6) and was well correlated with the distance ($r = -.99$ in both cases).

DISCUSSION

Number of Flowers in the Inflorescence

In most populations and years (8 cases out of 13), fruit set was independent of the number of flowers in the inflorescence (FIGURES 3, 4, 5). A similar trend was observed by Firmage and Cole (1988) in *Calopogon tuberosus,* by Zimmerman and Aide (1989) in *Aspasia principissa,* and by Vallius (2000) in *Dactylorhiza maculata.*

Only in two cases was the dependence a curved-down parabola, as expected by hypothesis (i), which would indicate that plants with the smallest number of flowers are too inconspicuous to be found by pollinators. In plants with the largest number of flowers, low visitation rate combined with low number of flowers pollinated per visit negatively affects fruit set. A similar trend was observed in *Dendrobium monophyllum* (Bartareau 1995), and the maximum was associated with the most abundant plants in the population. In our study, the most abundant plants had slightly less flowers per inflorescence than suggested by the maximum of the parabola.

A large number of flowers could be advantageous under favorable conditions, so-called ecological windows, because resources and pollinators occur unpredictably in time or space (bet-hedging hypothesis, Sutherland 1986). This might be the case of the site Hz-CR in years 1998 and 1999, when fruit set monotonously increased with the number of flowers in the inflorescence (FIGURE 4). This is similar to what was observed by Schemske (1980) in *Brassavola nodosa.*

If large inflorescence size had a fitness advantage, one would expect that the frequency distribution of the number of flowers would be

TABLE 2. Effect of site on fruit set in five *Orchis morio* populations observed in 2000. Average number of flowers (NF), percentage fruit set (RS), standard deviation of fruit set (SD), percentage of plants with no capsule production (RS_0), percentage of plants with maximal fruit set (RS_{100}), number of individuals (No.). Superscripts show results of one-way ANOVA with post hoc comparisons (Tukey test, different letters = significant differences, $P < 0.05$). See TABLE 1 for site codes.

Fruit set	NF	RS	SD	RS_0	RS_{100}	No.
Ren-NL	8.4^a	22.5^a	21.0	28.0	0	202
Sirj-NL	10.7^b	12.1^b	15.3	44.6	0	202
Bhw-NL	5.9^c	49.8^c	29.8	11.3	11.3	195
Za-CR	9.7^d	34.5^d	23.5	11.5	1.0	200
Ja-CR	7.0^e	35.2^d	32.2	24.2	6.8	132

TABLE 3. Effect of year and of addition of two bumblebee hives, each containing ca. 40 individuals, on fruit set in three Czech *Orchis morio* populations during 1997–2000. Values in years when sites were augmented with bumblebees are boldfaced. Fruit set ±SD (%) is followed by numbers of individuals in brackets. See TABLE 1 for site codes.

Year	Za-CR	Hz-CR	Ja-CR	RS ± SD mean
1997	38.0 ± 25.0 (551)^{a}	27.3 ± 24.7 (154)^{a}	—	35.7 ± 25.5^{a}
1998	30.5 ± 22.2 (150)^{b}	**31.2 ± 23.2 (201)**^{a}	35.8 ± 29.0 (140)^{a}	32.3 ± 24.7^{a}
1999	**43.3 ± 22.4 (300)**^{c}	42.3 ± 23.5 (185)^{b}	43.8 ± 29.1 (190)^{b}	43.1 ± 24.7^{b}
2000	34.5 ± 23.5 (200)	—	35.2 ± 32.2 (132)^{a}	34.7 ± 27.2^{a}

^{a,b,c} Superscripts show results of one-way ANOVA with post hoc comparisons calculated for each column, i.e., within each site and for the average over all sites (Tukey test, different letters = significant differences, $P < 0.05$).

skewed to the right. The frequency distribution of inflorescence sizes in our data, however, was not skewed. Conspicuously large was the standard deviation, which approached in size the mean—thus the variation coefficient was often close to 100%.

In conclusion, in most cases, fruit set was independent of the number of flowers in the inflorescence, the frequency distribution of the number of flowers was not skewed, and the variability in fruit set for plants with the same number of flowers in the inflorescence was extremely large. All this indicates that the selection pressure for optimizing the number of flowers with respect to maximizing fruit set is not very strong.

Variation in Reproductive Success between Years and Sites

Fruit set of deceptive orchid species reported from various sites and years is often more variable than that of rewarding species (Nilsson 1978, 1979, 1980, 1983; Ackerman 1981; Firmage & Cole 1988) and is therefore more sensitive to factors like air temperature and plant species composition.

The significantly highest fruit set in 1999 at all three Czech sites is unlikely to have been caused by larger activity of pollinators in response to high temperatures during the peak flowering season of *Orchis morio* (April and May), as the average monthly temperatures in 1999 did not differ from other seasons (TABLE 4). Similarly, there were no differences in temperatures during *O. morio* anthesis (April and May 2000) between oceanic (Dutch) and continental (Czech) sites (FIGURE 2). Thus the lower fruit set at Dutch wet meadows Ren-NL and Sirj-NL is unlikely to be caused by climate.

TABLE 4. Average monthly temperatures (°C) during *Orchis morio* anthesis in the region of Czech sites taken at the Klatovy meteorological station.

Month	1997	1998	1999	2000
April	5.5	9.1	7.6	10.6
May	13.6	13.8	13.6	15.0

For food deceptive species like *Orchis morio,* composition of surrounding plant community may play an important role in determining fruit set. Our data indicate, even though we did not test this hypothesis explicitly, that presence of co-flowering species may support fruit set in *O. morio* through pollinator attraction. All the Czech sites and the Dutch site Bhw-NL have abundant populations of co-flowering nectariferous plant species intensively searched by pollinators of *O. morio* (bees and bumblebees) for food, e.g., *Trifolium pratense, Lotus corniculatus, Polygala vulgaris.* We found no co-flowering plants on the wet meadows Ren-NL and Sirj-NL, however. Thus we suspect that the low fruit set there results from the lack of other co-flowering plants, which lowers the attractiveness of the sites for pollinators. This supports the "magnet-species theory" (Rathcke 1983, Laverty 1992), according to which nectarless plants may benefit from growing in the vicinity of nectar-bearing species, because they receive more pollinators. An alternative theory predicts that the deceptive system of some species will function best in remote habitats such as marshes, where there are no co-flowering rewarding species, which would compete with nectarless orchids for pollinators. This "remote habitat hypothesis" seems to work in deceit pollination of *Dactylorhiza incarnata* (Lammi & Kuitunen 1995), but not in *O. morio.*

Pollination Augmentation Experiment

When pollinators were added, no differences in reproductive success attributable to this augmentation were observed. Fruit set, however, consistently declined with distance from the hive in both experimental sites and was well corre-

TABLE 5. Fruit set (RS) as a function of the number of flowers in the inflorescence (NF) modeled by the function RS = $a.\text{NF}^2 + b.\text{NF} + c$. If a was significantly different from zero, we used quadratic regression; if not, we used linear regression. If neither a nor b were significantly different from zero, we fitted the data by a constant. Notations: degrees of freedom (df), significance level (P), coefficient of determination (R^2), and number of individuals (No.).

Site	Year	Regression	*a*	*b*	*c*	F-value	df	*P*	R^2	No.
Za-CR	1997	quadratic	−0.003	0.072	−0.016	7.29	1	0.015	0.33	551
	1998	linear	—	−0.012	0.427	6.59	1	0.022	0.32	150
	1999	constant	—	—	0.449	1.54	1	0.232	0.09	300
	2000	constant	—	—	0.364	0.31	1	0.587	0.02	200
Hz-CR	1997	constant	—	—	0.253	0.10	1	0.751	0.01	154
	1998	quadratic	0.001	−0.019	0.406	10.75	1	0.006	0.66	201
	1999	linear	—	0.018	0.206	19.70	1	0.001	0.55	185
Ja-CR	1998	constant	—	—	0.340	1.01	1	0.341	0.10	140
	1999	constant	—	—	0.441	1.67	1	0.227	0.16	190
	2000	quadratic	−0.013	0.210	−0.445	7.95	1	0.022	0.39	132
Bhw-NL	2000	constant	—	—	0.459	2.61	1	0.137	0.21	195
Ren-NL	2000	constant	—	—	0.252	1.30	1	0.272	0.08	202
Sirj-NL	2000	constant	—	—	0.126	2.99	1	0.101	0.14	202

lated with the distance from the hive. This suggests that pollinators tend to probe some plants in the vicinity of the hive, and when they do not get a reward, they perform a longer flight—probably outside the site. Thus artificial augmentation of presence of pollinators does not seem to affect the overall fruit set of the plants significantly—the pollinators escape from the site anyway.

CONCLUSIONS

We found that fruit set of *Orchis morio* populations varies across years and types of habitat. Low reproductive success was observed at oceanic wet meadows, probably caused by insufficient amount of other nectariferous co-flowering plants limiting attractiveness of the sites for pollinators. The floral display was found to have highly variable (positive, negative, and mostly none) effect on fruit set. Frequency of floral display sizes reflected a trade-off between pollinator limitation favoring larger, more attractive inflorescences and resource limitation lowering future floral display of highly fruitful plants. Artificial augmentation of presence of pollinators did not affect overall fruit set of the plants significantly. Thus the only way to augment fruit set in these orchids seems to be to enhance the number of co-flowering plants.

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TABLE 6. Effect of addition of two bumblebee hives, each containing about 40 individuals, on percentage fruit set (mean) at different sub-sites within the two experimental sites; number of plants (No.).

Subsite	Distance from hive (m)	Hz-CR		Za-CR	
		Mean	No.	Mean	No.
1	0–25	0.33	100	0.46	100
2	25–50	0.30	76	0.43	100
3	>50	0.25	25	0.41	100

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