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Effects of plant size, plant density and sex differential nectar reward on pollinator visitation in the protandrous Echium vulgare (Boraginaceae)

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The number of bumblebee approaches to viper's bugloss (*Echium vulgare* L.) plants increased with the number of flowers per plant. The proportion of the number of flowers visited after an approach was smaller in plants with many flowers. Individual flowers on large plants received significantly fewer visits than flowers on small plants. Compared with plants in dense parts of a population, isolated plants received fewer approaches that lasted longer. The result of this was that the number of visits to individual flowers did not differ between plants in dense parts of a population and isolated plants. The protandrous flowers lasted for two to three days. During the male phase the flowers presented a higher nectar reward and were more frequently visisted than during the female phase.

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Introduction

Schaffer and Schaffer (1979) suggested that increased pollinator visitation to larger inflorescences may lead to a disproportionate increase in fitness with size, which in turn may select for a semelparous life history (Bell 1980). Large floral displays may lead to more pollinator approaches to plants and/or longer visiting times (Silander and Primack 1978, Schaffer and Schaffer 1979, Augspurger 1980, Davis 1981, Udovic 1981, Schmitt 1983, Waser 1983, Geber 1985, Bell 1985, Schmid-Hempel and Speiser 1988). The effects of plant size on the number of visits to individual flowers is less clear. Large plants may receive more approaches but the proportion of flowers visited after an approach can at the same time be smaller (Schmitt 1983, Geber 1985, Andersson 1988, Schmid-Hempel and Speiser 1988, Klinkhamer et al. 1989). Geber (1985) found that flowers on all plants with different numbers of flowers received about equal amounts of foreign pollen. In some species individual flowers on plants with many flowers received more pollinator visits (e.g. Schemske 1980, Klinkhamer et al. 1989).

The number of pollinator visits will also depend on the density of flowers within the population or within the direct vicinity of the plant. In dense floral patches, bumblebees tend to turn more and to visit more plants than in sparse patches (Rathcke 1983, Real 1983 and references therein). In dense patches individual plants may be able to attract more pollinators than each could independently, but in such patches individuals also compete and the number of flowers visited after arrival of the pollinator on the plant may be less.

Fitness in hermaphrodites is the result of male and female function. It is assumed that female fitness is often limited by resources and that male fitness is limited by access to females (Bateman's (1948) principle, see also Willson and Burley 1983). Consequently, in plants selection may favour traits that increase the access to females: i.e. increase the transfer of pollen to

399

conspecific stigmas. In insect pollinated plants flower longevity, nectar volume and nectar quality are such traits. Plants with dichogamous flowers (male and female phases are separated in time within the same flower) provide the opportunity to gain insight in the effort of the plant to attract pollinators during the male and female function of the flower. We would expect that the nectar reward is higher during the male phase of the flower and that the pollinators react to this by an increased number of visits compared with the female phase of the flower (e.g. Devlin and Stephenson 1985).

In this paper we study the monocarpic, protandrous species *Echium vulgare* L. We will ask if individuals with a large floral display attract more pollinators and if individual flowers on such plants are visited more frequently. We will also study the impact of plant density on the number of pollinator visits to individual plants and flowers. In addition, the relation between flower age, nectar volume and flower visitation during the male and female phase of the flower is studied.

We will use the word approach for a bee arrival on a plant if this arrival is followed by the visit of at least one flower. We will use the word visit for a bee visit to an individual flower.

The plant

Echium vulgare is a monocarpic perennial. Under favourable conditions it flowers from June to September of its second year. However, in most natural habitats flowering is delayed to a later year (Klinkhamer and de Jong 1983). Even though some populations of *Echium vulgare* are gynodioecious (Knuth 1899, Thijsse 1903), all plants we studied were hermaphrodites. Each plant may produce 1–20 inflorescences, on each inflorescence are a number of cymes and each cyme carries a number of flowers (of which usually one or a few are open at the same time). In total each plant may produce hundreds of flowers. Flowers may carry four seeds but usually mean seed set per flower is between one and two (A. van Breemen, pers. comm.). On each moment only a proportion of the flowers is open. Individual flowers are about 20 mm long, the petals are fused at their bases to form a tube. Before and a few hours after opening, flowers are pink, turning into pink-blue during the first day. On the second day flowers are blue, turning into dark-blue when they begin to wilt on the third day. Flower morphology in relation to pollination by insects has been described by Jordan (1892), Knuth (1899), Thijsse (1903) and Jaeger (1949). Flower opening is spread over the day (Corbet 1978). Flowers are protandrous. After opening the stamens exceed the style, the anthers dehisce revealing dark blue pollen. Then the style grows longer and when it equals the longest stamen the stigmatic lobes have begun to diverge and their surfaces become rough and sticky. Eventually the style grows to exceed the stamens (Corbet 1978). Nectar volume varies between 50 to 400 nl per flower, being

high in the early morning and evening (Boetius 1948, Corbet 1978). The rate of nectar secretion depends on flower age (Boetius 1948). In our study area, flowers of *Echium vulgare* are predominantly visited by bumblebees (e.g. *Bombus pascuorum, B. terrestris* and *B. hortorum*) but other visitors may contribute to the pollination (Knuth 1899). In the absence of pollinators plants do not set seed (C. Smith, pers. comm.). Most seeds result from geitonogamous pollination (Nicholls 1987).

Study area and methods

The study was carried out at Meijendel, a sand dune area near The Hague, The Netherlands. In this area *Echium vulgare* is a common species, growing in open unfertile habitats. *Echium* shows a clumped distribution. High-density areas with one to occasionally up to 20 flowering individuals per m^2 are separated by areas in which *Echium* is almost absent. To study the relation between plant size, plant density, and pollinator visitation we selected 90 plants in high-density areas (hereafter referred to as "population plants") and 40 plants with no flowering neighbours within 5 m (hereafter referred to as "isolated plants"). Each of the 130 plants was monitored once for 15 min between 1200 and 1500 hours on one of four successive overcast but dry days in June 1988. For each plant we recorded the number of inflorescences, the number of open flowers, the number of neighbouring inflorescences within 1 m, the number of bumblebee approaches to each plant and the number of flowers visited after each approach. Plants were randomly assigned to one of the observation days.

In the statistical analyses all data were log-transformed to obtain normally distributed variables and to make variances homoscedastic. We tested for proportionality between (a) the number of approaches, (b) the mean number of flowers visited after an approach, or (c) the total number of flowers visited during the observation period (Y_i) and the number of open flowers (X_i). (c) was calculated as the product of (a) and (b). Testing for proportionality was done by performing an F-test on the ratio of variances under the null hypothesis $b = 1$ and the alternative hypothesis $b \neq 1$ in the model:

$$Y_i = e^a X_i^b e^{E_i} \text{ or,}$$
$$\log Y_i = a + b \log X_i + E_i,$$

where i indexes plant number and E_i is an error term. The variance under the null hypothesis was calculated from the deviations of the log Y_i's from their predicted values, according to a line with slope = 1 and intercept $\overline{\log Y} - \overline{\log X}$. $\overline{\log Y}$ and $\overline{\log X}$ are the mean values of log Y and log X, respectively. If $b > 1$, then Y_i increases more than proportionally with X_i. If $0 < b < 1$, then Y_i increases less than proportionally with X_i (Klinkhamer et al. 1990). For instance, if in the relation between the total number of flowers visited and the number of open flowers of a plant $b < 1$, this implies that individual

400   OIKOS 57:3 (1990)

Tab. 1. Stepwise multiple regression (forward) for three measures of pollinator visitation to population plants with the log of number of open flowers of the plant (flowers), the log of number of inflorescences per plant and the log of number of neighbouring inflorescences within 1 m from the plant (density) as independent variables. Number of cases 90. F-to-enter > 4.00; F-to-remove < 4.00 (α = 0.05).

a) dependent variable: log number of approaches (R^2 = 0.57)

variables in the model	coefficient	F-remove	variables not in the model	F-enter
1. flowers	0.46	64.70	3. inflorescenses	2.07
2. density	0.18	9.42		

b) dependent variable: log number of flowers visited after an approach (R^2 = 0.57)

variables in the model	coefficient	F-remove	variables not in the model	F-enter
1. flowers	0.41	114.14	3. inflorescenses	1.87
2. density	−0.24	35.97		

c) dependent variable: log total number of flowers visited (R^2 = 0.72)

variables in the model	coefficient	F-remove	variables not in the model	F-enter
1. flowers	0.69	63.59	3. density	0.15
2. inflorescenses	0.27	5.07		

flowers on a large plant receive fewer visits than those on a small plant. Because we found no significant effect of observation days, data for the four days were pooled.

To study the relation between flower age and pollinator visitation 15 plants were monitored in June 1987. On these plants we recorded the number of pink or pink-blue flowers (probably all in their first day) and the number of blue flowers (probably all in their second day) and the total number of visits that these flowers received in a 30 min period. Differences in visitation rate were tested with a Wilcoxon matched pairs test. On each of three successive afternoons in June 1988, we marked 36 flowers that were expected to open before 10 a.m. the next morning.

By doing this we obtained a sample of 108 flowers that were in their first, second or third day after opening. Half of the flowers of each of the three age groups were studied between 1030 and 1130 hours; the others were studied between 1530 and 1630 hours. Because not all marked flowers could actually be used, the number of flowers studied per age-group in each of the observation periods varied between 10 and 18. For each flower we recorded the length of the longest stamen, the length of the style, the number of bumblebee visits during 30 min and the nectar volume. The nectar volume was measured with standard glass micropipettes.

Results

Population plants

In all regressions with measures of pollinator visitation, the number of open flowers per plant showed a higher correlation than the number of inflorescences per plant (which varied from 1 to 14) (Tab. 1). In population

plants, the number of approaches (range: 1 to 68) increased with the number of open flowers (Fig. 1 top). This increase was less than proportional to the number of open flowers (F = 77, p < 0.0001). The number of approaches also increased with the number of inflorescences and with plant density. For the number of inflorescenses this appeared, however, not to be significant in a stepwise regression (Tab. 1). Averaged over all plants, after an approach only ca. 10% of the flowers was visited. The number of flowers visited after an approach increased less than proportional to the number of open flowers of the plant (F = 281, P < 0.0001, Fig. 1 middle). This means that the percentage of flowers visited after an approach was smaller on large plants. The number of inflorescences per plant had a positive (but non-significant in a stepwise regression) effect on the number of flowers visited after an approach (Tab. 1). The number of flowers visited after an approach was smaller in dense parts of the populations (Tab. 1). The total number of flowers visited during the observation period (range: 3 to 602) increased less than proportional with the number of open flowers (F = 7.40, P < 0.01, Fig. 1 bottom). This means that individual flowers on plants with many flowers are less frequently visited. In a stepwise regression we also found a positive correlation with the number of inflorescences (Tab. 1). Plant density (which had a positive effect on the number of approaches but a negative effect on the number of flowers visited after an approach) showed no correlation with the total number of flowers visited (Tab. 1).

Isolated plants

In isolated plants too, the number of open flowers per plant showed higher correlations with measures of polli-

flowers

e log (no. of approaches)

e log (no. of flowers visited after approach)

e log (no. of flowers visited per 15 min.)
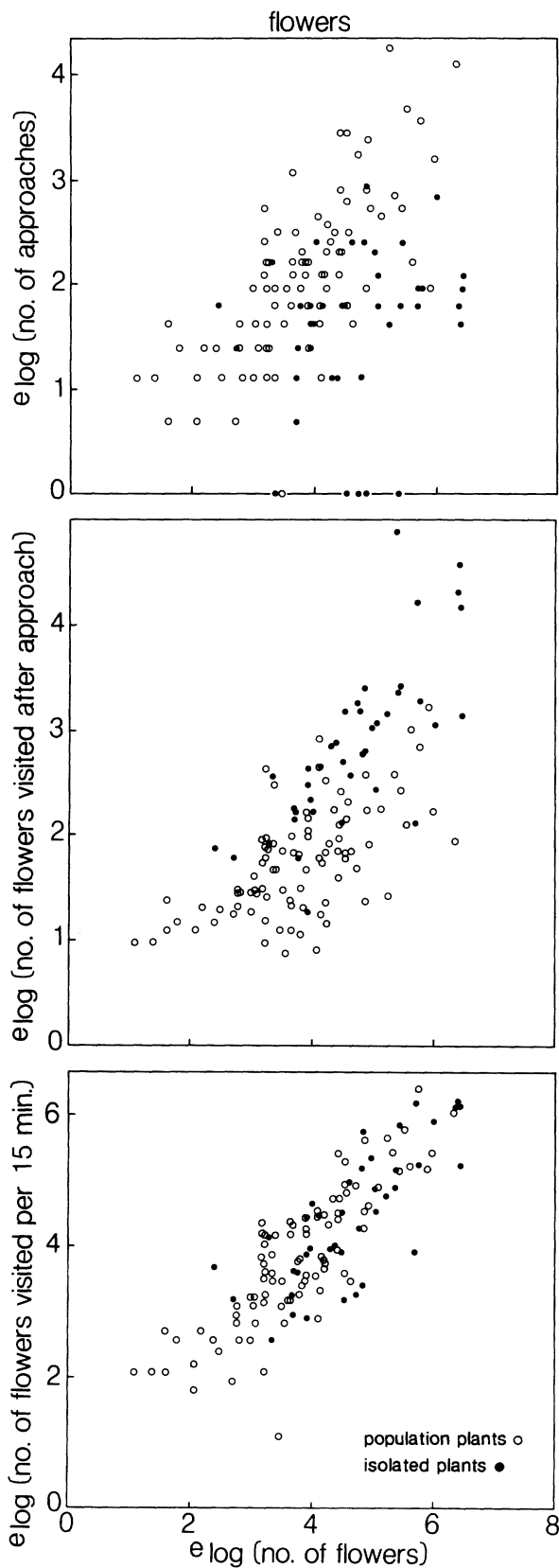
population plants o
isolated plants ●

e log (no. of flowers)

Fig. 1. The relation between three measures of pollinator visitation and ln number of flowers (x) for plants in populations (○) and for isolated plants (●) Top: y = ln number of bumble-bee approaches to plants per 15 min. Middle: y = ln number of flowers visited after an approach. Bottom: y = ln total number of flowers visited per 15 min. Regression equations: Top (○): y = 0.05 + 0.52 x, $r^2 = 0.52$, $p < 0.0001$; (●): y = 0.76 + 0.18 x, $r^2 = 0.05$, n.s. Middle (○): y = 0.57 + 0.31 x, $r^2 = 0.40$, $p < 0.0001$; (●): y = 0.04 + 0.60 x, $r^2 = 0.58$, $p < 00001$. Bottom (○): y = 0.62 + 0.84 x, $r^2 = 0.70$, $p < 0.0001$; (●): y = 0.80 + 0.78 x, $r^2 = 0.59$, $p < 0.0001$.

nator visitation than the number of inforescences (which varied from 1 to 12). In stepwise regressions no significant effects of the number of inflorescenses were found (in all cases F-enter < 1). The number of approaches (range: 1 to 19) was not significantly correlated with the number of open flowers (Fig. 1 top). The mean number of flowers visited after an approach var-
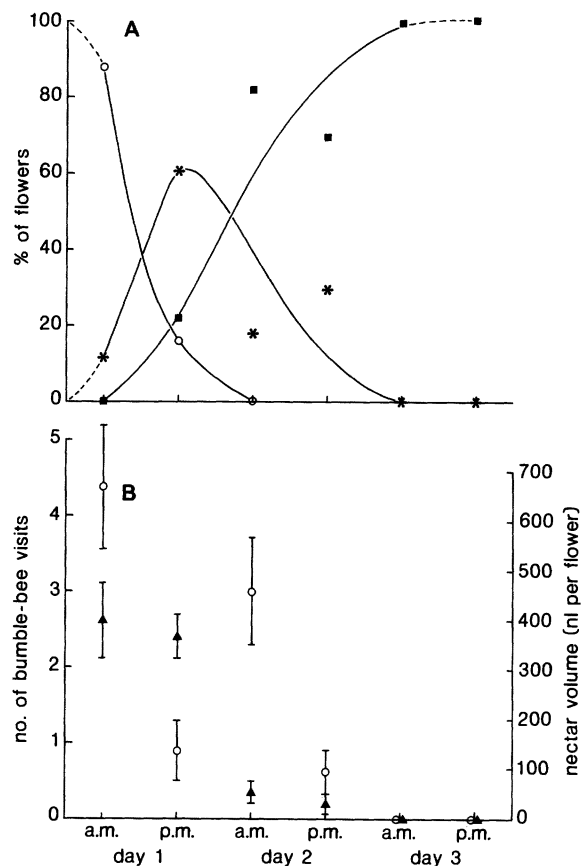

Fig. 2. The flowering stage (A), the nectar volume (B) and the number of pollinator visits (B) of flowers that are in their first, second or third day after flower opening, measured between 1000 and 1200 hours (a.m.) and between 1600 and 1700 hours (p.m.). A: ○ = style is at least 2 mm smaller than longest stamen, ★ = style length equals length of longest stamen (± 2 mm), ■ = style is at least 2 mm longer than the longest stamen. B: ○ = nectar volume. ▲ = number of pollinator visits. Bars indicate S.E. Curves are fitted by eye.

402

ied from 3.6 to 132 and increased less than proportional with the number of open flowers ($F = 22$, $P < 0.0001$, Fig. 1 middle). As a result, the total number of flowers visited during the observation period increased less than proportional with the number of open flowers ($F = 4.4$, $P < 0.05$, Fig. 1 bottom). This means that individual flowers on larger plants received fewer visits. Compared with population plants, isolated plants had more flowers ($F = 20.4$, $p < 0.0001$) and received fewer approaches ($F = 9.9$, $p < 0.005$) (Fig. 1 top) that lasted longer ($F = 88.2$, $p < 0.0001$) (Fig. 1 middle). The total number of flowers visited is higher in isolated plants ($F = 10.5$, $p < 0.005$) because isolated plants had more flowers (Fig. 1 bottom). When corrected for the impact of the number of flowers, there was no difference between isolated plants and population plants in the total number of flowers visited ($F = 0.5$, $p = 0.5$). The latter means that flowers on population plants and on isolated plants received equal numbers of visits.

Flower age, nectar reward and flower visitation

In the 15 plants that were studied in 1987, the mean number of visits ($\pm$ s.e.) to pink-blue flowers was 2.75 ($\pm$ 0.49), while blue flowers received 1.93 ($\pm$ 0.25) visits. Two plants were not visited during the observation period; in 10 out of 13 of the plants that were visited the pink-blue flowers received more visits (Wilcoxon matched pairs test, $Z = 1.96$, $p = 0.05$). In 1988, the flowers on the first day after opening had a higher nectar volume (Kolmogorov-Smirnov test, $DN = 0.4$, $p < 0.05$) and received more visits (Kolmogorov-Smirnov test, $DN = 0.7$, $p < 0.0001$) than the flowers that were in their second day (Fig. 2B). Flowers in their first day were predominantly male, whereas flowers in their second day were predominantly female (Fig. 2A). Flowers in their third day started to wilt, turned dark-blue, contained no measurable amounts of nectar and were not visited.

Discussion

In *Echium vulgare* there is an advantage in producing many flowers. Plants with many flowers are more often approached and more flowers on these plants are visited. The advantage of producing more flowers, however, clearly diminishes with the number of flowers. The number of approaches is a decelerating function of flower number and the proportion of flowers visited after an approach diminishes with flower number. Individual flowers on large plants thus receive fewer visits than flowers on smaller plants, which is in contrast with the results for *Cynoglossum officinale* in the same area (Klinkhamer et al. 1989). Furthermore, because pollinators visit more flowers on plants with many flowers, they will 1) raise the level of geitonogamous fertilization and therefore the rate of selfing, and 2) will transfer a smaller fraction of the pollen of plants with many flow-

ers to other plants. Because of this relationship, de Jong and Klinkhamer (1989a) suggested that for plants with few resources it is adaptive to emphasize male reproduction (produce relatively many flowers with few seeds per flower) whereas for plants with many resources it is adaptive to emphasize female reproduction (produce relatively few flowers with many seeds per flower). Such a relation is common for many plant species (references in de Jong and Klinkhamer 1989a) and was found for the related *Cynoglossum officinale* studied in the same area (Klinkhamer and de Jong 1987). We do not yet know the relationship between plant size and seed and flower production in *Echium vulgare* but this will be the goal of future research.

The number of inflorescences is less important in attracting bees than the number of flowers. There is an advantage in producing flowers on many inflorescences, because it raises the total number of flowers visited (Tab. 1c). After giving up on one inflorescence bumblebees often visit another inflorescence of the same plant, thereby acting as if it is a new individual.

Bumblebees tend to minimize the flight distance when foraging. They are expected to visit plants in high density patches more often because in such patches they can reduce the time spent on flying. Furthermore the marginal value theorem predicts that bees spend less time on a plant when other food sources are nearby (Charnov 1976, Pyke 1978, Hodges 1981). Our results are consistent with these predictions. Plants surrounded by many inflorescences did attract more pollinators (Tab. 1a). At high densities the number of flowers visited after an approach was lower (Tab. 1b). Also, the number of approaches to isolated plants was low and the number of flowers visited after an approach was high. In our study, we found no difference in the number of visits per flower for equally sized population plants and isolated plants. Since isolated plants represent small foraging patches and population plants are in larger patches, our result seems to contradict those of Sowig (1989) who found that the number of visits per flower decreased with patch size.

It is striking that (compared with the other two measures of pollinator visitation) there is so little variation in the relationship between the total number of flowers visited during the observation period and the number of open flowers on the plant. Apparently fewer flowers are visited after an approach to plants that are approached relatively often. To obtain visitation parameters that are independent of plant size we calculated the residuals of the regression between the number of flowers visited after an approach and the number of open flowers and the residuals of the regression between the number of approaches and the number of open flowers. These residuals are negatively correlated (in population plants $r = -0.26$, $p = 0.01$; in isolated plants $r = -0.52$, $p < 0.01$). This indicates that if a plant is often approached the number of flowers visited after each approach is small. Similarly, Sowig (1989) found that in *Echium*

vulgare the percentage of flowers visited in a patch was positively correlated with the time passed since the patch was visited previously.

To estimate the reward for the bumblebees we measured the nectar volume of the flowers. The nectar volume is not the most accurate measure of the reward because the sugar concentration may vary with factors such as air humidity (Corbet 1978, Corbet et al. 1979 a, b). Nevertheless, it seems clear that the nectar reward diminishes with flower age. It is true that the differences in nectar volume are not large between one-day old and two-days old flowers but the depletion rate had been much higher in one-day old flowers. This implies that the nectar secretion rate must have been much higher in one-day old flowers as was also found by Boetius (1948). Flowers in their second day may still produce nectar (Corbet 1978, see also Olesen (1989) for *Echium wildpretii*) but the depletion by bees exceeds the production. The diminishing reward is reflected by a decrease in pollinator visitation. The result is that flowers in their male phase (first day) attract more pollinators than flowers in their female phase (second day). Similar relations were found for flowers of the protandrous *Lobelia cardinalis* (Devlin and Stephenson (1985). By contrast in the protandrous *Digitalis purpurea* the nectar reward was higher during the female phase of the flower (Best and Bierzychudek 1982). In this species male flowers are at the top of the inflorescence. Bumblebees first visit the female flowers with the higher reward and then move upwards to the male flowers. This pattern of nectar reward reduces self-pollination and interference between female and male function. In *Echium vulgare* such a mechanism must be less important because there is no clear vertical pattern in the arrangement of flowers. If male reproduction is limited by pollinator visitation and if female reproduction is resource-limited we would expect increased nectar production to give a higher pay-off during the male phase of the flower. Similarly it has been suggested that staminate flowers on monoecious and dioecious species should secrete more nectar than pistillate flowers as a result of intrasexual selection (Bawa 1980, Bullock and Bawa 1981). A recent review (Willson and Ågren 1989) showed however that this is not always true (see e.g. Kay et al. 1984). At this point we do not know what limits male and female reproduction in *Echium*. For *Cynoglossum officinale* in the same area and for *Echium vulgare* in Switzerland it was found that seed production was not pollen-limited (Nicholls 1987, de Jong and Klinkhamer 1989b). Female fitness may, however, still increase with enhanced levels of pollination when pollen competition and selective embryo abortion improve the quality of the progeny (Stephenson and Bertin 1983, Sutherland 1987). An increase in nectar production during the male phase and the subsequent increase of flower visitation to male flowers will lead to a higher level of self-pollination; on average a bee will have visited more male flowers on a plant before it visits a female flower. This will effect plants with many flowers differently than plants with few flowers because in the former the level of self-pollination is already much higher. It would therefore be of interest to examine whether or not the difference in nectar production between male and female flowers depends on the number of flowers of the plant. A higher level of self-pollination will be of greater disadvantage in self-incompatible species. Therefore, it would also be of interest to compare the difference in nectar production between male and female flowers for plants that are self-compatible and plants that are not.

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