

The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*

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Large floral displays allow high fecundity but in addition have been postulated to disproportionately attract pollinator visitation, resulting in increased pollination rates to flowers on large plants. Balancing this advantage, however, is the presumed cost of increased self-pollination through transfer of pollen within plants (geitonogamy). *Prothystricia huttoni* (Tachinidae) responded to larger floral displays in *Myosotis colensoi* in its native habitat in New Zealand by making more plant-visits per hour, visiting more flowers at each visit, but visiting a declining proportion of the flowers available. As a result, flowers were visited at approximately the same rate (~ 1 visit per flower per hour) on all display sizes. Pollen deposition, pollen receipt and seed set all varied independently of flower number confirming the even pollinator service to flowers across all plant sizes. *Bombus terrestris* and *Apis mellifera* both responded in a very similar way to variation in flower number in naturalised *Mimulus guttatus* in Britain and, similarly, the proportion of flowers successfully pollinated was independent of flower number. The data presented offer little support for the hypothesis of facilitation of visitation to individual flowers on large displays. Instead, pollinators appear to adopt an “ideal free distribution” and utilise floral resources evenly across all plant sizes.

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The reaction of pollinators to variations in flower number on the plants they are visiting is an important but little studied aspect of the dynamics of plant-pollinator systems. Total fecundity is often closely tied to flower number (Wyatt 1980, 1982, Andersson 1988), and a close fit between flower number and fitness is often assumed in other studies. However, there are at least two reasons why we might expect fitness to be uncoupled at least partially from flower number.

Firstly, reproductive success may depend on the relative attractiveness of a display to pollinators. It has been argued that in some cases, visitation rates may co-vary with flower number in a non-linear way. In particular, where the cost of moving between plants is significant, pollinators may ignore small displays as the cost of exploiting the patch is not worth the relatively small gain in

nectar reward (Heinrich 1979). This effect is expected to be particularly pronounced as the degree of isolation of plants increases (Sih and Baltus 1987, Krannitz and Maun 1991). Even where the cost of moving is relatively slight, the increased attractiveness of large displays may lead to a disproportionate increase in visitation rates on a per-flower basis as small displays are overlooked. Balancing this expectation, however, an optimally foraging pollinator is expected to utilise resources whenever a patch offers a sufficient reward to pay the cost of exploiting it and pollinators may be expected to adopt an ‘ideal free distribution’ (Fretwell and Lucas 1970). Under this assumption, pollinators would be expected to visit flowers on all sizes of inflorescence at an equal rate.

Secondly, even if visitation rates appear to increase monotonically with flower number, fitness may decline

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with increased flower number. If pollinators spend longer on larger inflorescences, pollen may be moved between flowers on the same plant rather than between plants. This may result in high levels of pollinator-mediated self-pollination – 'geitonogamy', and may lead to the production of less fit offspring through inbreeding depression in the case of self-compatible species, or to pollen wastage (Hessing 1988, de Jong et al 1993) and stigma clogging with self-pollen (Waser and Price 1991) in the case of self-incompatible species. Geitonogamy may thus depress both seed fitness through the loss of seed viability and pollen fitness through the inability to father seeds on other plants.

Both or either effect may determine the relative benefits and costs of several aspects of floral biology. The age of first flowering may influence the numbers of flowers that are displayed in each season through strategies ranging from producing a small number of flowers each year from year one to a strategy of saving resources by not flowering for several years and flowering later in a 'big bang' (Schaffer and Gadgil 1975, Samson and Werk 1986). Depending on pollinator response to such large displays, the latter strategy may incur a penalty of increasing geitonogamous selfing while the former may risk insufficient pollination on young plants if pollinators ignore small displays. Schaffer and Schaffer (1979) emphasise the importance of non-linear gains in pollinator service to large inflorescences in the evolution of mono-carpic plants (flower only once before dying). Similarly, the relative merits and disadvantages of many small flowers compared with fewer large flowers may depend on the way pollinators handle smaller or larger displays (Cohen and Shmida 1993).

In this study, the effects of flower number on pollinator response and subsequent reproductive success is tested for two self-compatible species – *Mimulus guttatus* visited by pollen-collecting bumblebees, and *Myosotis colensoi* visited by nectar-gathering flies. Both species were studied in relatively dense populations, so the cost of intra-plant movements may have been relatively low. This study attempts to evaluate the effect of floral display size on flower visitation rates and to test the pollination-attraction hypothesis on the evolution of large floral displays.

Materials and methods

The *Myosotis* study system

The study population of *Myosotis colensoi* at Castle Hill, Broken River, Canterbury, New Zealand, (43°15'S, 171°44'E), occupies an open habitat of crumbling limestone largely devoid of other ground-covering vegetation. *M. colensoi* is an herbaceous perennial that has indeterminate growth and spreads through lateral branches. The flowering stems are also prostrate and in November and

December produce a single flower at each node. Vegetative proliferation thus forms 'cushions' that may bear a combined display of many flowers from adjacent ramets. Large plants may be up to 0.3 m across and may bear up to 100 flowers at once. The flowers are visited primarily by a tachinid fly, *Protohystricia huttoni* (Malloch) which probes the flowers for nectar. The flowers are open for several days, although approximately half of that time is spent in a 'post-pollination' condition which is signalled by a colour change at the mouth of the corolla tube. These flowers are largely ignored by the flies and have effectively ended their role as pollen donors or receivers (for more details, see Robertson and Lloyd 1991).

To study the response of flies to variation in flower number, an area of several square metres was marked out and all the plants within this area labelled. For several hours on three consecutive days in November 1988, all the plants in the area were observed and the number of times each plant was visited by *P. huttoni* was recorded. In addition the number of flowers on each plant was also counted and averaged over the three-d period. The plants were observed for a total of more than five h. In November 1987, individual flies were followed and the number of flowers that were probed and the number available on the plants visited were measured. To estimate the rate of visitation to individual flowers per unit time on plants of different sizes, the relationship between the number of flowers visited as a proportion of the total presented observed in 1987 and the rate of visitation to plants of different sizes observed in 1988 were multiplied. It was not possible to observe both parameters simultaneously in this population as there was frequently many flies simultaneously visiting the plot.

To test for an effect of the size of floral display on reproductive success, three measures were made. In December 1988, plants of differing size were chosen haphazardly within an area of ca 20 m² and a flower, chosen at random with the proviso that it was just entering the 'post-pollination' phase – a point which flowers pass through relatively quickly, was removed and pickled in alcohol, formalin and acetic acid. Subsequently, the amount of pollen deposited on the stigma was counted and the amount of pollen remaining in the flower was measured. Whole mounts of stigmas were made and stained with calberla's stain. All the pollen adhering was counted. Investigations revealed that pollen adherence following hand-pollinations was very rapid (less than 30 min) and that very little pollen washed off into the pickling solution (unpubl.). The remainder of the flower was softened with NaOH, squashed through a sieve and rinsed with water and the preservative from the vial in which it was collected. The wash was centrifuged at 3000 rpm and decanted. The pollen pellet was re-suspended in 0.1 ml of acetic acid and glycerol and counted with a haemocytometer slide. For further details see Robertson and Lloyd (1991). In January 1989, fruits were collected from a further set of plants that had been observed when flowering six weeks previously. The number of seeds per fruit

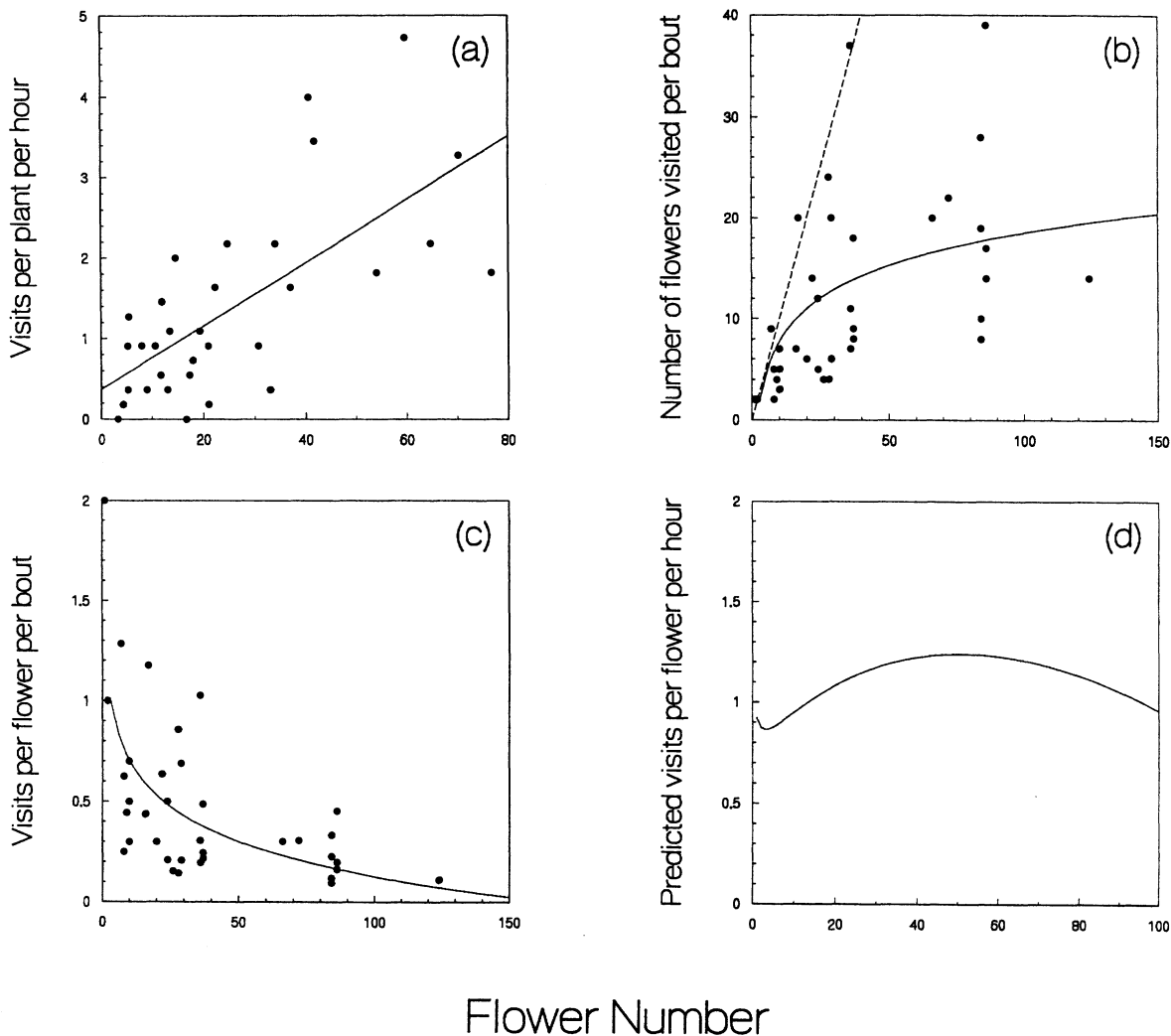


Fig. 1. Visitation patterns of the tachinid fly *Protohystricia huttoni* to *M. colensoi*. The relationships between the number of open flowers on a plant and (a) the number of visits each plant received [bouts] per hour observed [$P < 0.0001$, $R^2 = 0.47$], (b) once on a plant, the number of flowers visited [$P < 0.0005$, $R^2 = 0.33$] (the dotted line represents all flowers visited once), (c) the proportion of flowers visited during bouts [$P < 0.0001$, $R^2 = 0.51$], and (d) the predicted visitation rate per hour of individual flowers. The regression lines from 2(b) and 2(c) were multiplied and a correction made to account for the known habit of *P. huttoni* of making 84.4% of visits to pollination-phase flowers while post-pollination flowers represented, on average, 45.7% of the available flowers (Robertson and Lloyd 1993) to estimate visitation rates per flower per hour.

was counted and compared with the known maximum of four seeds per fruit (Robertson 1989).

The *Mimulus* study system

The plants of *Mimulus guttatus* used in this study were chosen from a group of plants grown in a glasshouse in Exeter, U.K. from seeds collected at Copperopolis mine in Calveras County, CA, USA (37°58'N, 120°38'W). At Copperopolis mine, *M. guttatus* occupies seasonally wet water channels where plants grow to a large size and possibly perennate, and the surrounding areas where

plants are much smaller (mostly less than 10 flowers) and always annual (Martin 1988). The plants form loosely arranged, vertical branching flowering stems and may bear up to 300 flowers simultaneously. *M. guttatus* possesses a sensitive 2-lobed stigma which closes the lobes upon contact. If there is sufficient pollen deposited (above ca 200–300 grains, unpubl.) the lobes remain closed for the duration of the flower. If however, there is less pollen deposited or no pollen at all, the lobes re-open after ca half an hour. The presence of closed stigmas in the morning before visitation begins is thus a reliable indication of successful pollination by bees the previous day.

Table 1. Regression analysis of approaches to plants. The regression coefficient was tested against a slope of 1 by t-test.

Plot	Visitor	Log (visitation rate h ⁻¹) =	R ²	p	p (b < 1?)
<i>Myosotis</i>	<i>Protohystricia</i>	0.992 log (flower number) + 0.01	0.99	<0.001	n.s.
<i>Mimulus</i>					
1990 wk 1	<i>Bombus</i>	0.139 log (flower number) - 0.544	0.07	n.s.	<0.001
	<i>Apis</i>	0.548 log (flower number) - 1.790	0.33	<0.05	<0.05
1990 wk 2	<i>Bombus</i>	0.329 log (flower number) - 1.209	0.13	n.s.	<0.01
	<i>Apis</i>	0.287 log (flower number) - 0.835	0.13	n.s.	<0.01
1991	<i>Bombus</i>	0.371 log (flower number) - 0.558	0.53	<0.001	<0.001
	<i>Apis</i>	0.346 log (flower number) - 1.360	0.21	n.s.	<0.001

Cuttings were made from each plant and were potted into large pots and allowed to flower in a glasshouse in Exeter. When the plants were beginning to flower, they were transferred to a garden plot and arranged ca one metre apart in arrays of approximately 20 plants. Arrays were set out in August 1990 and September 1991. Plants differed quite markedly in the number of flowers present either because of differences in phenology between the plants or because of differences of general plant size. The plants were visited by various species of bumblebees (*Bombus* spp.) and by honeybees (*Apis mellifera*). The two plots differed somewhat in the relative abundance of the different bee species and there were differences in abundance from one week to the next on the 1990 plot. This plot was primarily visited by *B. pascuorum* in the first week and by *A. mellifera* in the second week with occasional passing visits by *B. lucorum* and *B. lapidarius*. The 1991 plot was dominated by *B. pascuorum* with *A. mellifera* less common and there were occasional short visits by *B. pratorum*.

To test the attractiveness of different-sized displays, each plot was monitored for the 8 h that encompassed the majority of the pollinator foraging period on consecutive days over one to three weeks. At the beginning and end of each week, the numbers of flowers present on each plant was counted and the two counts averaged. All visitors to the plants were recorded and identified and the numbers of flowers visited on each plant were recorded. To check on the effectiveness of pollination, each morning before bees began to visit, 30 flowers were chosen haphazardly on each plant and the stigma examined to see if it was closed, indicating whether it had been pollinated.

Analyses

Regression models were fitted either linearly against flower number or, where there was an improvement to the fit, against the log₁₀ of flower number. To test the hypothesis that approaches made to plants were in direct proportion to flower number, both variables were log-transformed before fitting an additional linear model. The null hypothesis that the regression coefficient $b = 1$ was tested by t-test against the alternative hypothesis that $b \neq$

1 (Andersson 1991). A coefficient significantly less than 1 would indicate that pollinators fail to increase the plant-visitation rate in direct proportion to flower number.

Results

Myosotis

Individuals of *M. colensoi* varied in the number of flowers presented during the study seasons. Some plants presented up to 100 flowers simultaneously but most plants, however, were relatively small with 49% of plants displaying less than 20 while a further 31% had less than 40 flowers. The fly *Protohystricia huttoni* responded to this variation by visiting the larger plants more often (Fig. 1a) and visited more flowers on larger plants per bout (Fig. 1b). The relationship between visits per plant per hour and flower number was approximately linear (b of double-log transformed data not significantly different from 1, Table 1), while the number of flowers visited per bout was best predicted by a decreasing function of flower number. However, once on a plant, the proportion of flowers visited gradually declined with flower number (Fig. 1c). The net effect of increasing the number of bouts made to large plants but decreasing the proportion of the flowers visited, leads to the prediction that visitation rates per flower per hour varies independently of flower number (Fig. 1d). Individuals flowers were predicted to receive approximately one visit per hour during favourable weather conditions, irrespective of the size of the plant the flower was borne on.

The lifetime success of flowers as measured by pollen donation and receipt and by seed set, also appeared to be independent of flower number (Fig. 2). Of an estimated average pollen production per flower of 35 000 grains (Robertson and Lloyd 1993), most was removed by the end of the male phase (93% on average). The amount remaining varied independently of flower number (Fig. 2a). Similarly, the amount of pollen deposited was also independent of flower number (Fig. 2b) and the average of 55.5 grains per stigma exceeded widely the fixed ovule number of four, indicating that seed set is unlikely to be limited by pollen receipt even on small

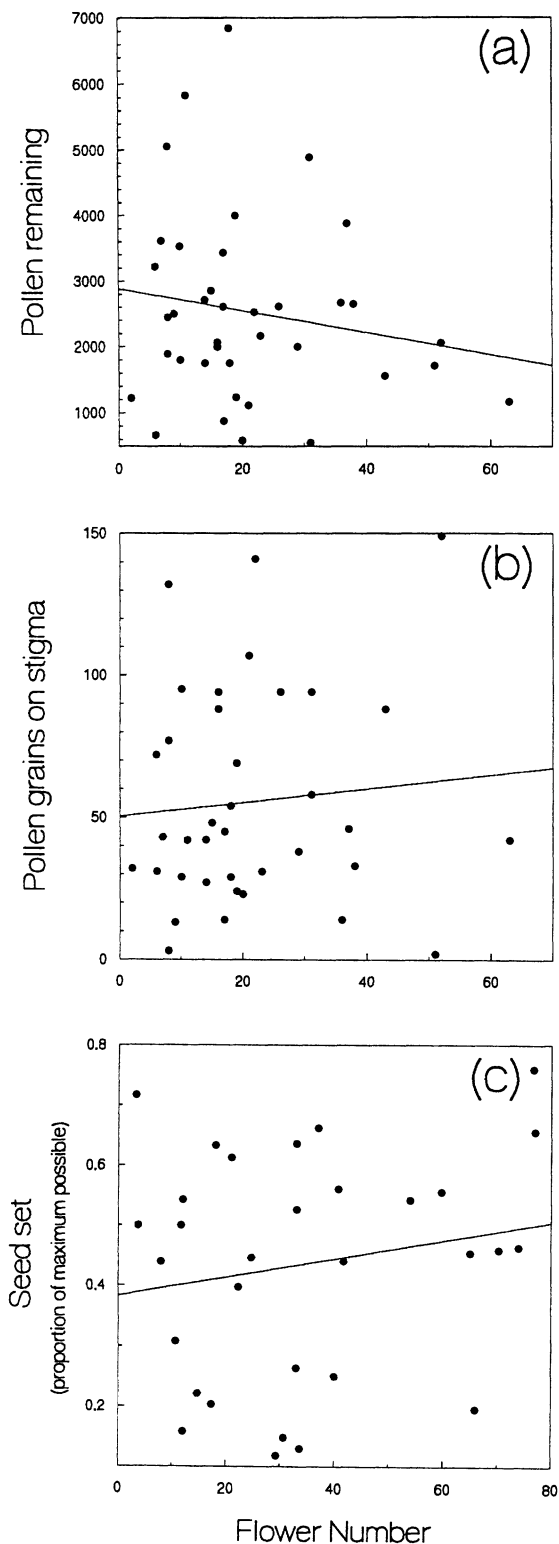


Fig. 2. Flower number and 3 correlates of reproductive success per flower of *Myosotis colensoi*. (a) Pollen remaining [$P = 0.319$, $R^2 = 0.03$]; (b) pollen deposition, [$P = 0.581$, $R^2 = 0.01$]; and (c) seed set [$P = 0.320$, $R^2 = 0.03$].

plants. Seed set per flower varied considerably between plants, but again, this was apparently unrelated to flower number (Fig. 2c).

Mimulus

In almost every respect the results that were found for the *Myosotis* system are echoed in the results of the *Mimulus* field plots. The response of honey bees (Fig. 3) and bumblebees (Fig. 4) to variation in flower number were similar to each other and to the response of the tachinid fly visiting *Myosotis*. The response to increasing flower number was to a) increase the number of bouts (though not always significantly so and not in direct proportion with flower number, $b < 1$, Table 1); b) visit significantly more flowers per plant; c) decrease significantly the proportion of flowers visited in a bout – with the overall net result of d) no significant effect of flower number on visits per individual flower per hour. The trend in the last parameter, though never significant, was always downwards for all bee species independently and when all species were combined (Fig. 5a). Indeed, as measured by the proportion of pollinated stigmas, the reproductive success of individual flowers was decreased by being part of a large display for both plots, significantly so during the 1991 plot (Fig. 5b).

Discussion

This study examined the response of insect pollinators to variation in flower number of two plant species (*Myosotis colensoi*, visited in its natural habitat by a tachinid fly; and *Mimulus guttatus* visited by honeybees and bumblebees in a garden setting). In both systems studied, the effect of plant size on visitation patterns was consistent and may demonstrate common features of many plant-pollinator interactions that may bear on the evolution of flower number in a diversity of systems. The consistent response demonstrated here occurred despite the involvement of different plant species, different pollinators and different rewards sought (pollen from *Mimulus* and nectar from *Myosotis*).

The aggregation of flowers into displays is often interpreted as a means of increasing the relative attractiveness of a plant to pollinators and is expected to enhance the likelihood of successful pollination. The critical parameter to determine an inherent advantage of this strategy over alternatives such as increasing the size of flowers or lengthening the time over which they are produced, is a measure of the rate at which individual flowers are successfully visited. The postulated advantage of large displays in increased attractiveness to pollinators receives little support from the data presented here. Rather, pollinators appear to exploit flowers equally, regardless of the size of the display on which they are borne. This appears

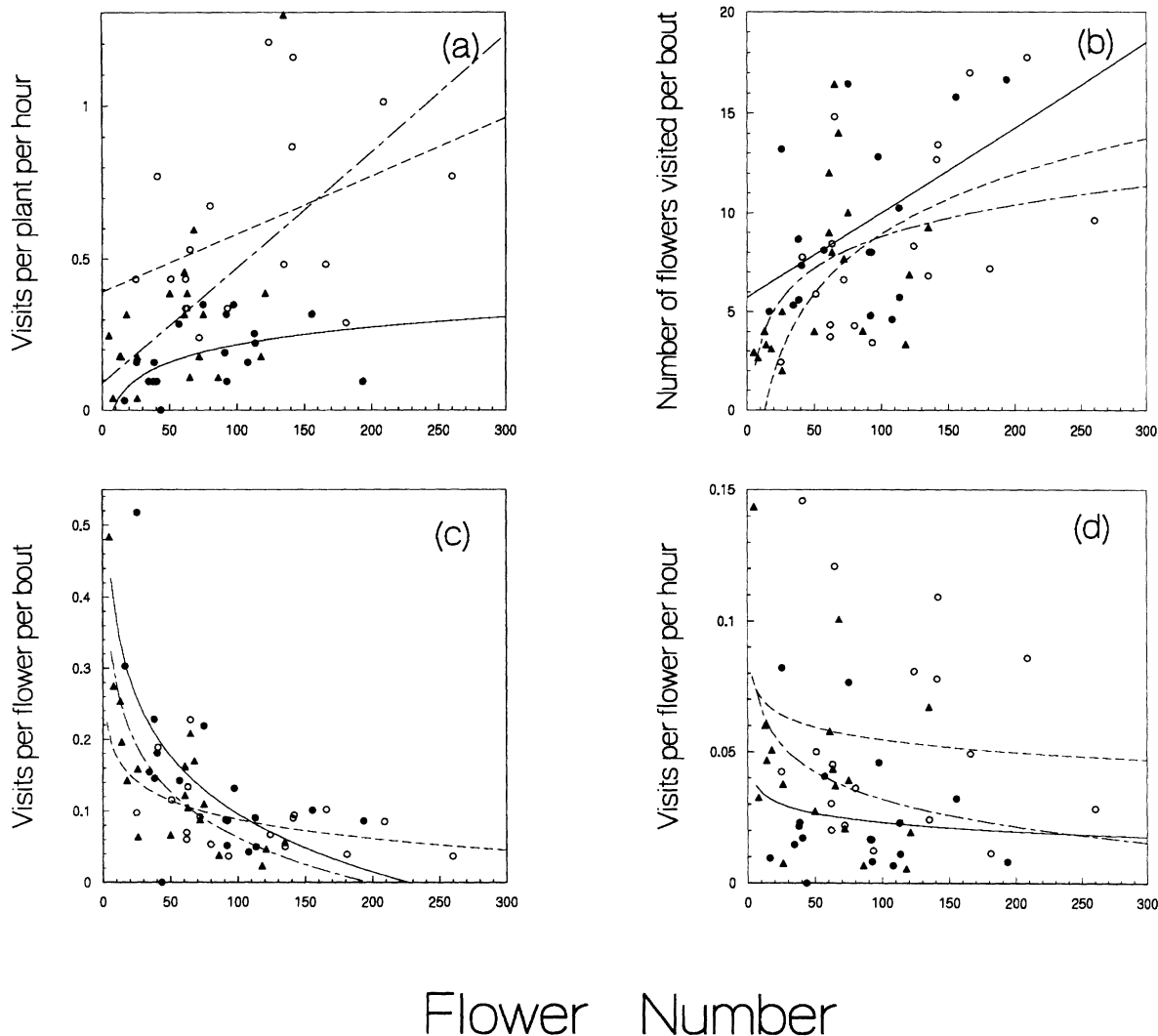


Fig. 3. Visitation patterns of honeybees, *Apis mellifera* to *Mimulus guttatus* during the 1990 plot (—, ●, week 1; ---, ○, week 2) and 1991 plot (· · ·, ▲). The relationships between the number of open flowers on a plant and (a) the number of visits each plant received (bouts) per hour observed, (b) once on a plant, the number of flowers visited, (c) the proportion of flowers visited during bouts, and (d) the estimated visitation rate per hour of individual flowers (the multiplication of values in (a) and (c) for each observation). (a) 1990, week 1, $P < 0.05$, $R^2 = 0.26$; 1990 week 2, $P = 0.09$; 1991, $P < 0.05$, $R^2 = 0.30$; (b) 1990, week 1, $P < 0.05$, $R^2 = 0.23$; 1990, week 2, $P < 0.05$, $R^2 = 0.33$; 1991, $P < 0.05$, $R^2 = 0.28$; (c) 1990, week 1, $P < 0.01$, $R^2 = 0.43$; 1990, week 2, $P = 0.05$, $R^2 = 0.22$; 1991, $P < 0.0001$, $R^2 = 0.66$; (d) 1990, week 1, $P = 0.481$, $R^2 = 0.03$; 1990, week 2, $P = 0.684$, $R^2 = 0.01$; 1991, $P = 0.067$, $R^2 = 0.18$.

to be a result of the pollinating insects visiting a smaller proportion of the flowers on the largest individuals for both study systems and from a tendency for bees to fail to visit plants in proportion to flower number in the *Mimulus* study system. The general independence of flower number and per-flower visitation rates shown here is confirmed by the more direct measures of maternal and paternal reproductive success. Seed set per fruit, the amount of pollen deposited, and the amount removed from a flower over its lifetime, all showed little relationship with plant size in *M. colensoi*. Virtually all flowers

had large numbers of pollen grains on their stigmas by the end of the functional presentation phases. Similarly, all flowers had at least 80% of their pollen removed by this stage. It is unlikely that there is much error associated with measurements of female fitness as there is a fixed number of four ovules per flower. Likewise, the rate of successful pollination per flower was independent of flower number in *Mimulus* in 1990 and actually declined with increasing flower number in 1991.

Other published data is inconsistent in pattern. Based on visitation rates per flower or capitula, or pollen depo-

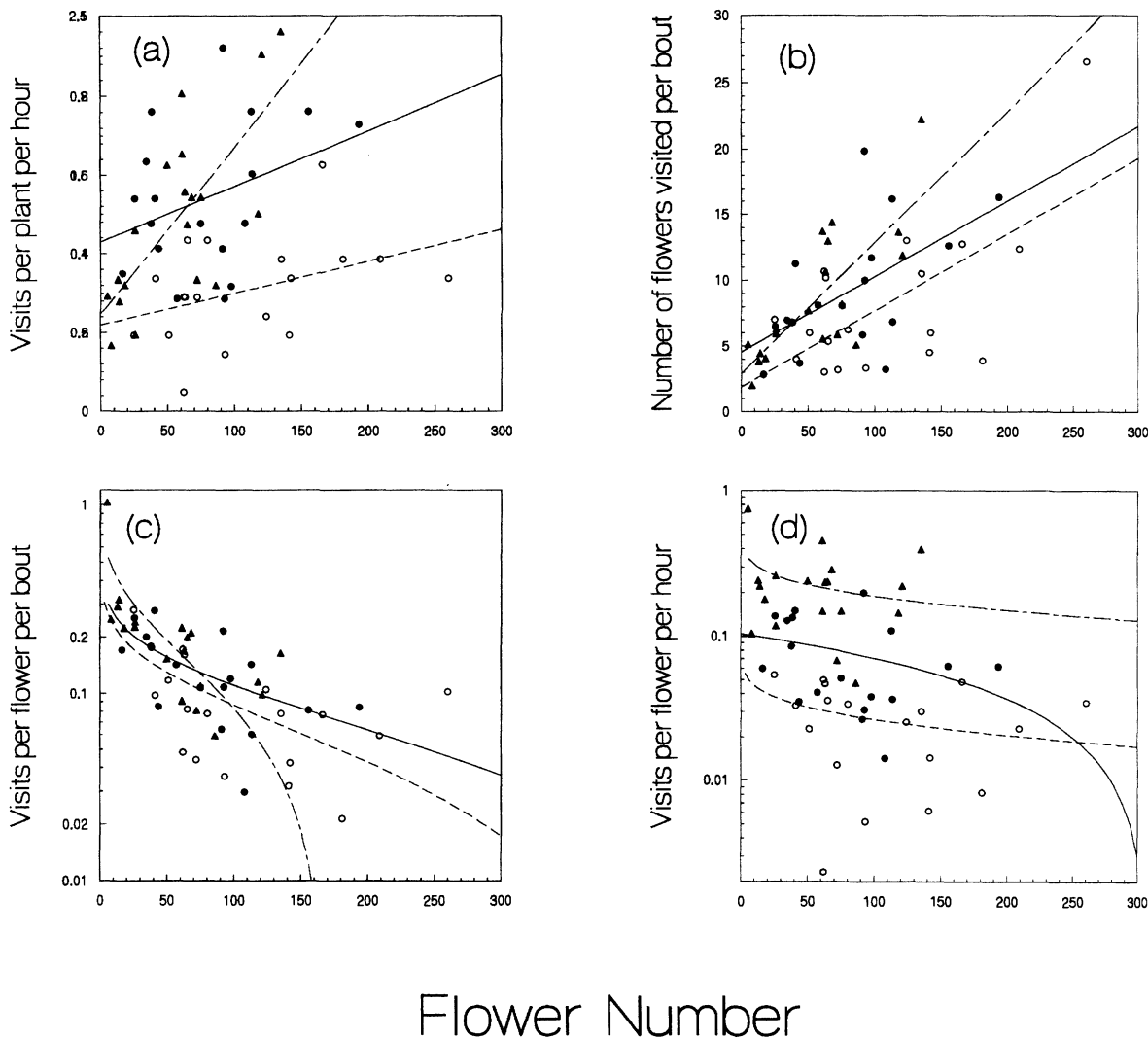


Fig. 4. Visitation patterns of *Bombus pascuorum* to *Mimulus guttatus* during the 1990 plot (—, ●, week 1; ---, ○, week 2) and 1991 plot (—, ▲). The relationships between the number of open flowers on a plant and (a) the number of visits each plant received (bouts) per hour observed, (b) once on a plant, the number of flowers visited, (c) the proportion of flowers visited during bouts, and (d) the estimated visitation rate per hour of individual flowers (the multiplication of values in (a) and (c) for each observation). (a) 1990, week 1, $P = 0.146$, $R^2 = 0.13$; week 2, $P = 0.11$, $R^2 = 0.16$; 1991, $P < 0.001$, $R^2 = 0.54$; (b) 1990, week 1, $P < 0.05$, $R^2 = 0.33$; 1990, week 2, $P < 0.01$, $R^2 = 0.42$; 1991, $P < 0.001$, $R^2 = 0.60$; (c) 1990, week 1, $P < 0.01$, $R^2 = 0.42$; 1990, week 2, $P < 0.01$, $R^2 = 0.38$; 1991, $P < 0.001$, $R^2 = 0.53$; (d) 1990, week 1, $P = 0.220$, $R^2 = 0.09$; 1990, week 2, $P = 0.203$, $R^2 = 0.10$; 1991, $P = 0.173$, $R^2 = 0.11$.

sition or removal rates, the success of flowers increased with display size in a few studies (Schemske 1980a,b, Paton 1982, Cruzan et al. 1988 – pollen removal, Klinkhamer et al. 1989, Andersson 1991, Dudash 1991 – pollen deposition) but in many other cases, no relationship existed between individual flower success and flower number, except perhaps for plants with a very low number of flowers (Chaplin and Walker 1982, Bell 1985, Geber 1985, Wolfe 1987, Cruzan et al. 1988 – pollen deposition, Piper and Waite 1988, Bullock et al. 1989, Campbell 1989, Klinkhamer and de Jong 1990, Dudash

1991 – pollen removal). In *Anchusa* (Andersson 1988), there was actually a decrease in seed set per flower in larger plants apparently as a result of size-dependent visitation patterns of pollinators.

One possible reason for the disparity of these studies may result from the relative costs to pollinators of exploiting small displays. There is an expectation that pollinators should adopt a strategy of foraging that maximises their rate of energy gain (Charnov 1976). It is not clear from these results that the insects studied here are showing rate-maximising behaviour although other experi-

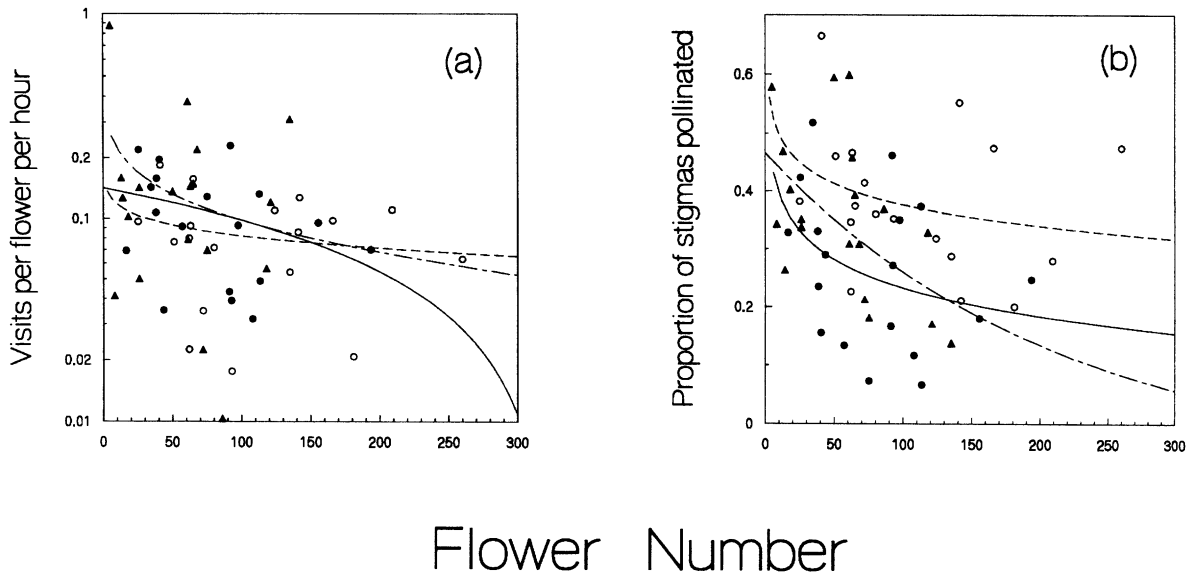


Fig. 5. Flower number and reproductive success per flower of *Mimulus guttatus* in the 1990 (—, ●, week 1; ---, ○, week 2) and 1991 plot (—, ▲). (a) Visitation per flower per hour for all bees combined, 1990, week 1, $P = 0.180$, $R^2 = 0.10$; week 2, $P = 0.400$, $R^2 = 0.04$; 1991, $P = 0.156$, $R^2 = 0.11$; and (b) the proportion of stigmas successfully pollinated 1990, week 1, $P = 0.151$, $R^2 = 0.10$; 1990, week 2, $P = 0.279$, $R^2 = 0.07$; 1991, $P < 0.05$, $R^2 = 0.25$.

mental studies (unpubl.) show that bumblebees discriminate against *Mimulus* plants that produce poor pollen quantity or quality, and hence appear to be concerned with harvesting optimally. In general we might expect an optimally foraging pollinator to visit flowers on all plants at equal rates following Fretwell and Lucas's (1970) theorem of the 'ideal-free distribution'. However, Pyke (1981) predicted that larger plants should be favoured because the costly time spent moving between plants is minimised. Whether small plants are visited may depend on the relative costs of moving between plants. The density of plants will be an important parameter determining the size of the moving cost. Thomson (1981) found a positive correlation between plant density and per flower visitation rate by bumblebees to two alpine herbs suggesting a significant cost of exploiting low density patches. Similarly, Sih and Baltus (1987) found that for catnip, per flower visits by bumblebees and honeybees were higher in large patches relative to small patches but lower by solitary bees. In the studies presented here, plant densities were high and the cost of moving presumably relatively low. Hence, it is perhaps not surprising that flowers on even very small plants receive similar visitation rates to flowers on larger plants.

Flowers on large plants may actually be at a disadvantage relative to those on smaller plants for another reason. As a larger proportion of flower visits on large plants are preceded by visits to flowers on the same plant, the frequency of self-pollination may increase. Inbreeding depression following self-fertilisation, or the interference of the pollen transfer process with self-pollen in self-incompatible species, may be expected to increase

with flower number. Several recent studies have highlighted the effects of increased geitonogamy in large plants. Crawford (1984) has shown that the frequency of self-fertilisation increases with flower number in artificial arrays of *Malva moschata* in which the outcrossing rate was measured using a genetic marker. Similarly, studies by Hessing (1988) on *Geranium caespitosum* and de Jong et al. (1992) on *Ipomopsis aggregata* both showed an increase in the amount of fluorescent dye deposited by geitonogamous transfer in large plants compared with small. Despite this, the realised selfing rate in *I. aggregata* showed little relationship with plant size presumably due to post-pollination phenomena such as selective fruit or seed abortion. Moreover, the observed behaviour of a declining proportion of flowers visited on large plants reduces the potential for geitonogamy. All the insects studied here showed this response and data for other pollination systems confirm that this behaviour may be general (Andersson 1988, Klinkhamer 1989, 1990). Pollen carryover may reduce the potential still further by retaining a portion of outcross pollen on a pollinator's body over several geitonogamous visits. Geber (1985) failed to find a relationship between self-fertilisation (inferred from evidence of inbreeding depression in offspring) and plant size in *Mertensia ciliata* and attributed this to a relatively high pollen carryover and a saturating response of the pollinators to increased flower number. Pollen carryover appears to be also high for *M. colensoi* and this combined with a similar saturating response by its pollinator has been estimated to result in a weak relationship between flower number and self-pollination (Robertson 1992).

In conclusion, it appears that plants that produce many flowers will enjoy a fecundity advantage over smaller plants as more seed is produced and presumably more pollen dispersed. However, there is no advantage in terms of the *efficiency* of pollination in producing a large display as there is no gain in per flower visitation rates. There may be in fact a genetic disadvantage through increased self-pollination, though this may be relatively mild because of the behaviour of pollinators on large plants and the influence of pollen carryover. It is predicted that in both cases studied here, plants should produce as many flowers as resources allow as there is no advantage per se of delaying reproduction to produce a larger display.

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