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14

Behavioral responses of pollinators to variation in floral display size and their influences on the evolution of floral traits

The number of flowers open at any one time on a plant, i.e., floral display size, varies greatly among plant species. For example, some species flower during a brief period and have many open flowers, while others have extended flowering with only a few open flowers at one time (Gentry 1974; Bawa 1983). Also, floral display size often varies among individuals of the same plant species (e.g., Willson & Price 1977; Pleasants & Zimmerman 1990). The causes of such variations in floral display size are enduring interest to plant ecologists (reviewed by de Jong *et al.* 1992).

Numerous studies have reported that variation in floral display size produces marked alterations in pollinator behavior. Especially, two types of pollinator response to increased floral display size have been recognized from the perspective of their influences on pollen dispersal. First, larger floral displays attract more pollinators per unit of time (Fig 14.1A; reviewed by Ohashi & Yahara 1998). This will promote cross-pollination in terms of increased pollen receipt, removal, or potential mate diversity (Harder & Barrett 1996). Second, the number of flowers that individual pollinators probe per plant also increases with floral display size (Fig. 14.1B; also reviewed by Ohashi & Yahara 1998). This will increase self-pollination among flowers on the same plant ("geitonogamy"; Richards 1986; de Jong *et al.* 1993). Thus, variation in floral display size may lead to a substantial difference in pollen dispersal and, in turn, plant fitness.

To understand how plant fitness can be related to floral display size, we have to know the shapes of the functional relationships between floral display size and the two types of pollinator response, i.e., visitation rate per plant and the number of flowers probed per plant visit. One possible approach is to examine the actual pollinator behaviors empirically (e.g., Ohashi & Yahara 1998). Another is to consider how pollinators should

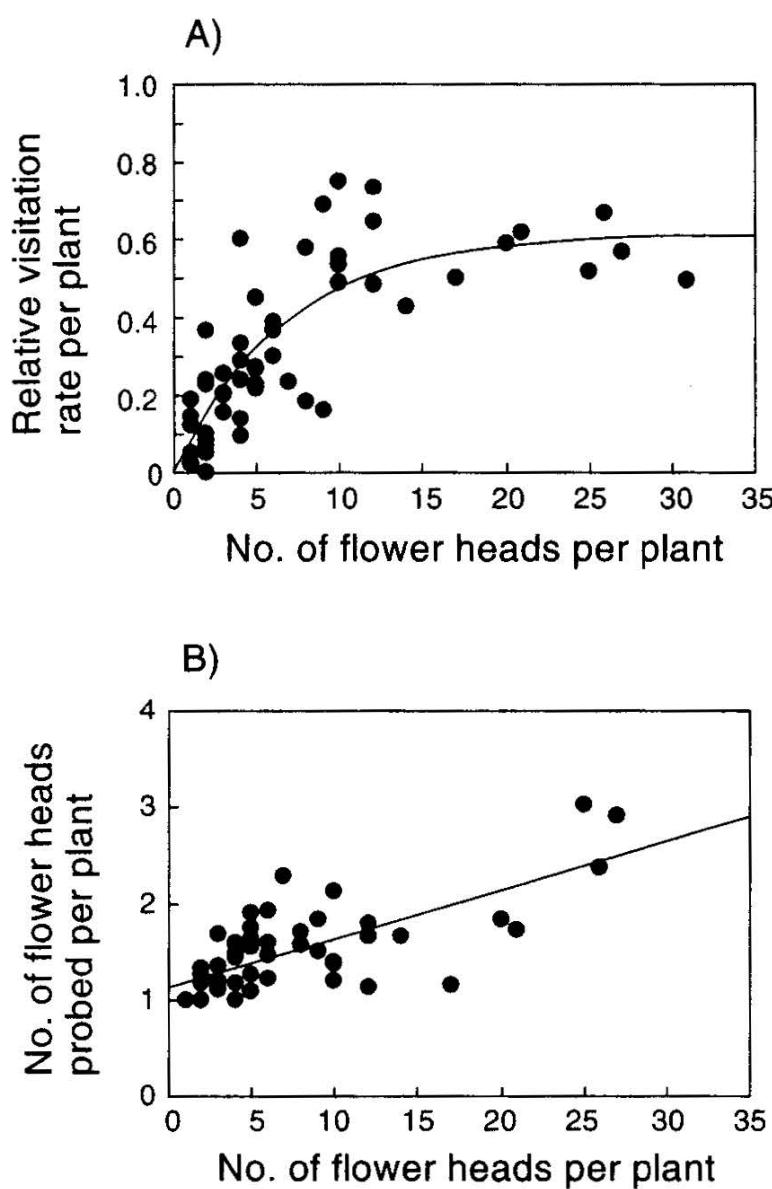


Fig. 14.1. The relationships between the number of flower heads on a *Cirsium purpuratum* plant and (A) the relative bumble bee visitation rate per plant ($y = 0.612[1 - \exp(-0.148x)]$, $n = 57$, $R^2 = 0.637$, $p < 0.0001$), and (B) the number of flower heads probed by a bee per plant ($y = 1.117 + 0.051x$, $n = 57$, $R^2 = 0.533$, $p < 0.0001$), obtained from six 1-day observations for 9–13 plants. Relative visitation rate per plant (y axis of 1A) is calculated as [(number of bee visits to the focal plant)/(total number of bee visits to the observed plants)] for each of six 1-day observations. (Adapted from Ohashi & Yahara 1998.)

behave on plants to maximize their rates of energy gain. Pollinators have been often used as model animals for studying “optimal foraging.” In particular, behavioral ecologists have regarded a plant or an inflorescence as a “patch” and have made intensive efforts to test the prediction of the optimal patch-use model, originally formulated by Charnov (1976), the so-called marginal-value theorem. Despite numerous relevant studies on pollinator behavior, however (reviewed by Orth & Waddington 1997), the

functional response of pollinators to floral display remains to be solved theoretically. Bearing this in mind, here we provide a theoretical analysis of the optimal pattern of pollinator responses to variation in floral display size and its influences on pollen transfer within and between plants. Based on the results, we consider how pollinators could affect the evolution of floral display size and other floral traits.

Optimal number of flowers probed per plant in relation to floral display size

Possible factors causing patch depression during foraging on a plant

How many flowers does a pollinator probe after landing on a plant or inflorescence? As shown in Fig. 14.1B and Table 14.1, previous authors have found that pollinators tend to probe only a few flowers on a plant or inflorescence before leaving even when far more flowers are present. Furthermore, the proportion of flowers probed generally declines considerably with increasing display size. Reasons suggested by plant biologists for short visitation sequences include: (1) satiation of pollinators; (2) draining all floral rewards on a plant; (3) the need to avoid predator or (aggressive) competitors; and (4) the need to find mates or other types of food (Stephenson 1982; Snow *et al.* 1996). However, none of these ideas seems applicable to most plant–pollinator systems studied so far, especially to bumble bees and their flowers.

Instead, here we address this problem from the standpoint of optimal foraging. We use “plant” as a general term that may indicate either an individual plant or an inflorescence, which would in practice be regarded by pollinators as one flower patch. Because plants are distributed as discrete patches, moving between plants is more costly for a pollinator than moving within a plant in terms of time and energy expended (Heinrich 1975). Therefore, the pollinator should probe all available flowers on a plant unless the rate of energy gain declines as it stays longer on it. Thus, a pollinator’s decision largely depends on the presence or absence of a gradual decrease in the rate of energy gain within a plant, i.e., “patch depression” (originally termed “depression” in Charnov *et al.* 1976).

Two major mechanisms could cause patch depression on a plant. One possibility is variation in nectar productivity coupled with pollinators’ non-random flower choice. For example, plants that have flowers on simple vertical inflorescences often have a pattern of decreasing rate of

Table 14.1. A tabulation of reports concerning how parameters of pollinator visitation (visitation rate per plant V_p , number of flowers probed on a plant t_c , proportion of flowers probed per plant t_c/F , and visitation rate per flower V_f) correlate with floral display size (F); the notations +, -, and ± indicate positive, negative, and statistically non-significant relationships found between these parameters and floral display size

Plant density and plant species	V_p	t_c	t_c/F	V_f	Pollinator	References
High (≥ 0.1 plants m^{-2})						
<i>Aconitum columbianum</i>	?	+	-	?	bumble bee	Pyke (1982)
<i>Aconitum columbianum</i>	+	+	-	+	bumble bee	Pleasants & Zimmerman (1990)
<i>Asclepias exaltata</i>	+	?	?	?	bumble bee, butterfly, honeybee	Broyles & Wyatt (1997)
<i>Asclepias syriaca</i>	+	+	-	±	bumble bee, honeybee, etc.	Morse (1986)
<i>Cirsium purpuratum</i>	+	+	-	±	bumble bee	Ohashi & Yahara (1998)
<i>Cynoglossum officinale</i>	+	+	-	±	bumble bee	Vrieling <i>et al.</i> (1999)
<i>Delphinium nelsonii</i>	+	+	-	+	bumble bee	Pleasants & Zimmerman (1990)
<i>Eichhornia paniculata</i>	+	+	-	±	bumble bee	Harder & Barrett (1995)
<i>Epilobium angustifolium</i>	+	+	-	±	bumble bee	Schmid-Hempel & Speiser (1988)
<i>Glycine max</i>	+	?	?	?	honeybee	Robacker & Erickson (1984)
<i>Mertensia ciliata</i>	+	+	-	±	bumble bee	Geber (1985)
<i>Mimulus guttatus</i>	+	+	-	±	bumble bee, honeybee	Robertson & Macnair (1995)
<i>Myosotis colensoi</i>	+	+	-	±	tachnid fly	Robertson & Macnair (1995)
<i>Myosotis colensoi</i>	?	+	-	?	tachnid fly	Robertson (1992)
<i>Pulmonaria collina</i>	+	+	-	?	bumble bee, beefly	Oberrath & Böning-Gaese (1999)
<i>Viscaria vulgaris</i>	+	+	-	±	bumble bee	Dreisig (1995)
Low (< 0.1 plants m^{-2})						
<i>Anchusa officinalis</i>	±	+	±	±	bumble bee	Dreisig (1995)

Table 14.1 (cont.).

Plant density and plant species	V_p	t_c	t_c/F	V_f	Pollinator	References
High and low						
<i>Cynoglossum officinale</i>						
high (in population)	+	(strong)	+ (weak)	-	+	bumble bee
low (isolated)	+	(weak)	+ (strong)	±	±	
<i>Echium vulgare</i>						
high (in population)	+		+ (weak)	- (strong)	-	bumble bee
low (isolated)	±		+ (strong)	- (weak)	-	
Unknown						
<i>Anchusa officinalis</i>	+	+	-	-	bumble bee	Andersson (1988)
<i>Aralia hispida</i>	+	+	-	-	bumble bee	Thomson (1988)
<i>Ipomopsis aggregata</i>	?	+	-	?	hummingbird	Pyke (1978b)
<i>Ipomopsis aggregata</i>	±	+	-	±	hummingbird	Brody & Mitchell (1997)
<i>Nepeta cataria</i>	+	+	-	+	honeybee	Sih & Baltus (1987)
	+	+	+	+	bumble bee	
	+	-	-	-	solitary bee	
<i>Sagittaria australis</i>	?	?	?	±	bumble bee, solitary bee	Muenchow & Delesalle (1994)
<i>Sagittaria latifolia</i>	?	?	?	±	bumble bee, solitary bee, etc.	Muenchow & Delesalle (1994)
<i>Symphytum officinale</i>	+	+	-	±	bumble bee	Goulson <i>et al.</i> (1998b)

Source: Adapted from Ohashi & Yahara (1999).

nectar production per flower from bottom to top (Pyke 1978a; Best & Bierzychudek 1982; but see Corbet *et al.* 1981). Pollinators moving vertically up each inflorescence, therefore, may experience a gradual decrease in gain per flower. Even without a spatial gradient of nectar productivity, pollinators that preferentially probe fresh flowers with higher nectar productivity (Gori 1989; Kevan *et al.* 1990; Oberrath & Böhning-Gaese 1999) may also experience patch depression, because they are increasingly likely to encounter an old, less-rewarding flower as they stay longer on a plant.

Another possibility is revisititation of flowers that it has previously probed, receiving little or no nectar. If the risk of revisiting flowers increases with the number of flowers probed, patch depression will result, even in the absence of variation in nectar productivity among flowers. In the few published studies, flower revisititation rates, defined as the fraction of flower visits that are to a flower previously probed while the pollinator was on the same plant, are low (2.9% in Pyke 1979; 3.5% in Pyke 1982; 0.2% and 3.0% in Galen & Plowright 1985). However, if pollinators avoid revisititation by curtailing their visit duration on plants, low frequency of total revisititation does not necessarily mean that it cannot cause patch depression. To evaluate flower revisititation, we must investigate whether the revisititation rate increases with the number of flowers probed on a plant. To our knowledge, only three field studies quantified this relationship (Pyke 1978b, 1981a, 1982), where revisititation rate increased with the number of flowers probed (up to approximately 10%–50% before all available flowers were probed). In an experimental study, Redmond & Plowright (1996) have also reported that revisititation rate increased with the number of flowers probed within a patch (up to approximately 25%).

To what degree can a pollinator remember flowers that it has previously probed on a plant? Pollinators often possess large long-term memory capacity for spatial information, such as the location of the home, the nest, and of flower patches, as well as their positions relative to surrounding landmarks (Heinrich 1976; Gould 1986; Menzel *et al.* 1996). However, the spatial scale on which they can use spatial long-term memory may be limited because a pollinator may probe hundreds of flowers during each foraging trip (Brown & Demas 1994). Even if a pollinator could use long-term memory, the need to browse its “library” at every flower may cause a time delay (Chittka *et al.* 1999). In fact, honeybees and vertebrates use short-term memory (“spatial working memory”) for avoiding revisititation of food sources (Brown & Demas 1994; Brown *et al.*

1997). If short-term memory capacity is limited, the risk of flower revisitation would increase with the number of flowers probed. This scenario is rather speculative and clearly needs further exploration.

A pollinator's directionality in its foraging movement within a patch may help pollinators to avoid revisitation, irrespective of their spatial memory ability. For example, pollinators usually move in the same direction on plants with simple vertical inflorescences (Darwin 1876; Benham 1969), so that they seldom revisit flowers (Heinrich 1975; Pyke 1978a; Best & Bierzychudek 1982). In addition, the presence of landmarks may also promote movement directionality (Pyke & Cartar 1992; Redmond & Plowright 1996). Interestingly, Pyke & Cartar (1992) suggested that such a directional movement itself is partially constrained by pollinators' spatial memory ability for patch arrival direction. At present, we know very little about the perceptual and memory mechanisms underlying such effects.

Other potential mechanisms for avoiding flower revisitation are perceptual discrimination of nectar (Heinrich 1979a) or footprints (scent marks: Goulson *et al.* 1998a; electrostatic change: Erickson & Buchmann 1983). The availability of such mechanisms is likely to depend on pollinators' abilities to discriminate the cues and on pollinator visitation frequency (Dreisig 1995). Therefore, it will require careful investigation to determine how these mechanisms are effective for avoiding revisitation in the context of natural foraging.

The effect of flower number

Recently we have developed a theoretical model to predict the relationship between the optimal number of flowers probed per plant and floral display size (Ohashi & Yahara 1999). We considered the increasing risk of revisitation to be the major cause of depression for a pollinator foraging on a plant, as it seems to be a very probable mechanism. To incorporate this effect into the model, we assumed that a pollinator remembers probing a maximum of m flowers on the plant and avoids revisiting them. We referred to m as "memory size", although it incorporates effects of both the actual memory capacity and of other factors discussed above. If the memory size (m) is limited, as we have noted, the risk of revisitation would increase with the number of flowers probed. Furthermore, larger displays offer more flowers from which to choose, which would decrease the risk of revisitation (e.g., see Table 14 in Pyke 1982). We also incorporated the cost of interplant movement by defining the mean discounting

rate for visiting another plant as $k = [($ flight time between flowers within a plant $) + ($ handling time per flower $)] / [$ (flight time between plants $) + ($ handling time per flower $)]$ ($0 \leq k \leq 1$). For simplicity, the rate of energy expenditure was assumed to be constant. Then, the following formula approximates the relationship between the optimal number of flowers per plant and the display size:

$$\begin{aligned} t_c &= (1 - k)F + mk && (F > m), \\ t_c &= F && (F \leq m) \end{aligned} \quad (14.1)$$

where t_c is the number of flowers probed per plant and F is the size of floral display.

The observed data (Table 14.1; Fig. 14.1B) agree well with the prediction of our model (Fig. 14.2B). First, pollinators probe fewer flowers than available. Second, the number of flowers probed increases with, but less rapidly than, the size of floral display (but see Sih & Baltus 1987). Third, the number of flowers per plant increased more rapidly with floral display size in low-density plant populations than it did in high-density populations (Klinkhamer *et al.* 1989; Klinkhamer & de Jong 1990).

It is worth noting that the aim of our model is not to demonstrate a patch-leaving rule that visitors actually follow, but simply to find the ideal point of plant departure for pollinators. In nature, it is well known that pollinators often leave the plant just after probing one to two flowers with little or no nectar (Fig. 14.3) (Pyke 1978*b*, 1982; Thomson *et al.* 1982; Hedges 1985). Pollinators usually do not have "complete information" on the nectar distribution on the current plant, so that such a simple probabilistic rule may provide a practical method for pollinators to approach the purely mathematical optimum (see also McNamara & Houston 1980; Iwasa *et al.* 1981). In a stochastic environment, probabilistic rules may work better than leaving plants deterministically following Eq. 14.1.

Optimal visitation rate per plant in relation to floral display size

What is "attractiveness" to pollinators in large floral displays? The model described above was based on the implicit assumptions that floral display size is invariable within a population and that pollinators arrive randomly at individual plants. In contrast, natural plant

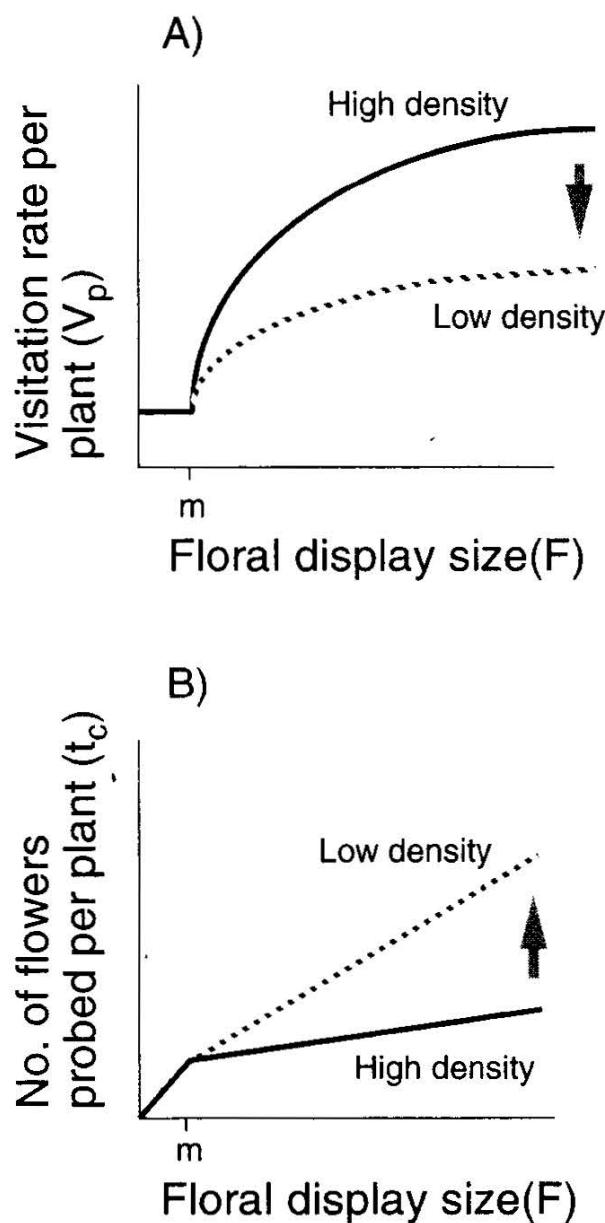


Fig. 14.2. Predicted relationships between floral display size (F) and (A) pollinator visitation rate per plant (V_p), and (B) the number of flowers probed per plant (t_c). (Adapted from Ohashi & Yahara 1999.)

populations usually include plants of various sizes (e.g., Pleasants & Zimmerman 1990). In such populations, pollinators prefer to visit large floral displays over smaller ones (Fig. 14.1A; Table 14.1).

Two major hypotheses have been proposed to account for the observed preference for large floral displays: (1) the detection-advertising hypothesis; (2) the flight-cost hypothesis. The detection-advertising hypothesis states that floral display size limits the distance from which it could be detected because of the insects' limited visual resolution (Dafni *et al.* 1997). For example, Giurfa *et al.* (1996) showed that the minimum display

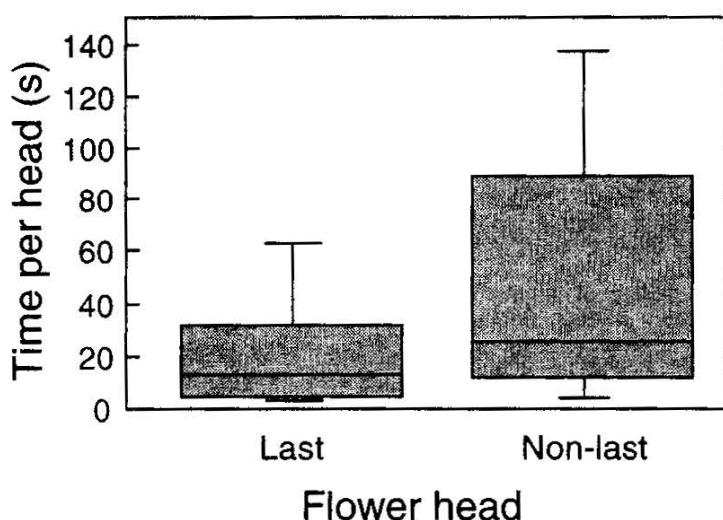


Fig. 14.3 Time spent by bumble bees on the last- and non-last-probed heads in each visit to a *Cirsium purpuratum* plant. The five horizontal lines of the plot indicate the 10th, 25th, 50th, 75th, and 90th percentiles of the data ($U = 824.5$, $p = 0.0056$; Mann-Whitney U-test). (Adapted from Ohashi 1998.)

size that would be detected by honeybees from 45-cm distances is about 5 cm in diameter in the best case. Moreover, color contrast (Lehrer & Bischof 1995; Giurfa *et al.* 1996) and relative motion speed against the background (Lehrer *et al.* 1990; Srinivasan *et al.* 1990) also influence the detectability of objects. Thus, this hypothesis may partially explain preference for large displays, especially when individual flowers are small. If large floral displays are infrequent in the population, however, this hypothesis may not hold; pollinators would more frequently choose small, but closer displays.

On the other hand, the flight-cost hypothesis emerges from an economic viewpoint. Harder & Cruzan (1990) and Harder & Barrett (1996) stated that pollinators visit large inflorescences because the proximity of many flowers reduces pollinator flight costs. Their statements have implied that pollinators prefer to visit larger displays on which they can probe more flowers, so that they can reduce the total movement costs required to probe a fixed number of flowers. That is, total movement costs required to probe N flowers is expressed as:

$$[(T + h) + (t + h)(i - 1)] N/i \quad (14.2)$$

where i is the number of flowers probed per plant, T is the flight time between plants, t is the time between flowers on the same plant, and h is the handling time per flower. As T is usually longer than t , total movement costs would decrease with increasing i . This advantage is greater if pollinators could walk between flowers on plants or inflorescences, which

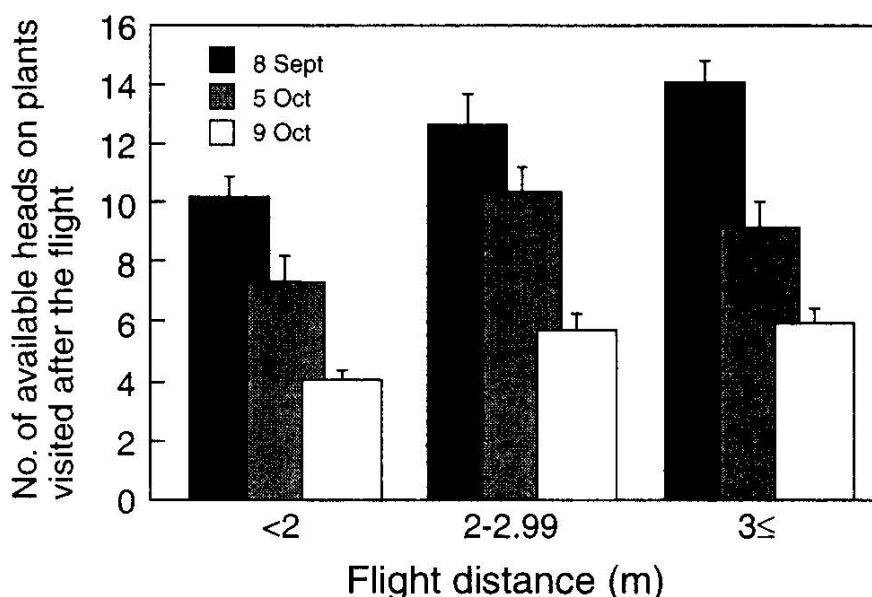


Fig. 14.4. Floral display size of plants visited by bumble bees after flying different distances. Bars indicate the average number of available heads per plant (\pm SE). The size of floral display visited after the flight differed significantly among distance categories (8 Sept $H = 12.04, p = 0.002$; 5 Oct $H = 13.00, p = 0.002$; 9 Oct $H = 12.69, p = 0.002$; Kruskal-Wallis test). (Adapted from Ohashi & Yahara 1998.)

requires about 90% less energy expenditure per time than flight (Heinrich 1975). As above, however, if large floral displays are infrequent in the population, this hypothesis also may not hold because pollinators would choose small but closer displays more frequently. In fact, some authors have found that pollinators often choose small displays when they are close (Fig. 14.4) (Pyke 1981*b*). Moreover, the visitation rate per flower rarely increases with floral display size (Table 14.1), which suggests that the reduced movement costs on large displays are of minor importance in determining pollinators' preferences for large displays. Thus, we have to reconsider our view about "attractiveness" of large floral displays.

Incorporating the ideal free distribution into the model

Robertson & Macnair (1995) have suggested that, when plant density is relatively high, optimally foraging pollinators should visit flowers on all sizes of displays at equal rates, following Fretwell & Lucas's (1970) theorem of the "ideal free distribution." The ideal free distribution (IFD) is an equilibrium state that arises as a consequence of repetitive movements of competitors in search of more profitable local areas. In the case of plants and pollinators, the profitability of a plant (mean nectar crop)

may decrease linearly with the average visitation rate per flower, because nectar crop per flower increases linearly with renewal time, at least at the scale of actual inter-visit times (Kadmon 1992). This situation corresponds to the simplest IFD model, i.e., the “continuous input” model (Parker & Sutherland 1986), which expects the average visitation rate per flower to be directly proportional to its nectar productivity. Since nectar production rate per flower often shows no significant correlation with floral display size (Harder & Cruzan 1990 and references therein), this model expects that the average visitation rate per flower would be equal between large and small displays (Dreisig 1995).

Based on this idea, Ohashi & Yahara (1999) have expanded the former model (Eq. 14.1) for the cases where display size is variable. The visitation rate per plant (V_p) is expressed as:

$$\begin{aligned} V_p &= V_f F / [(1 - k)F + mk] && (F > m) \\ V_p &= V_f && (F \leq m) \end{aligned} \quad (14.3)$$

where V_f is the average visitation rate per flower (constant under an IFD). As shown in Fig. 14.2A, pollinator visitation rate per plant (V_p) is a decelerating function of floral display size (F). This prediction agrees well with previous results (Fig 14.1A) (Iwasa *et al.* 1995 and references therein; but see Sih & Baltus 1987; Andersson 1988; Ohara & Higashi 1994). Moreover, visitation rate per plant (V_p) increases more rapidly at higher plant density. This is because a reduction in the proportion of flowers probed per plant reduces the competition among pollinators on large floral displays. This prediction agrees with the observation that bumble bees visited large floral displays less preferentially at lower plant density (Klinkhamer *et al.* 1989; Klinkhamer & de Jong 1990; Dreisig 1995). Note that the prediction of our model is opposite to the intuitive prediction deduced from the previous two hypotheses. If the detectability of floral display is most important, the visitation rate per plant (V_p) would increase less rapidly with display size (F) at higher plant density because pollinators could detect smaller sizes of floral display. The same prediction will result when the flight cost is most important, because both the cost of interplant movement (T in Eq. 14.2) and the proportion of flowers probed per plant (t_c/F) would decrease with increasing plant density. Clearly, observation of pollinator behavior alone is not a sufficient proof for the relative importance of competition among pollinators. We emphasize the value of simultaneously exploring pollinator behavior and nectar availability in future

studies. Moreover, functional responses of pollinators other than bumble bees (birds, honeybees, solitary bees, flies, butterflies, beetles, etc.) need to be explored more intensively.

The strategies that individual pollinators might use to achieve an IFD are still open to question. As Dreisig (1995) suggested, pollinators' preferences for large floral displays may partly explain the IFD. Furthermore, in the real world, nectar distribution among plants may fluctuate over time. If a pollinator could respond to such spatio-temporal variation, it would achieve an IFD more accurately. For example, pollinators are known to fly longer distances after encountering lower rewards ("area-restricted searching"; reviewed by Motro & Shmida 1995). By adopting this rule while foraging along its own "trapline" (Thomson *et al.* 1997 and references therein), pollinators may efficiently reduce the spatio-temporal bias in nectar distribution. Also, a trapline forager may occasionally sample new plants to detect and respond to temporal changes in nectar distribution among plants (Thomson *et al.* 1987). The spatial scale on which pollinators should adopt these strategies will depend on the spatial distribution of flowers, the frequency of revisit, pollinators' energetic requirements, perceptual and memory constraints, and the number of competitors. Clearly too little is known at present to draw any conclusion about these issues.

Evolutionary implications

Effects of plant density on the evolution of floral display

Plants growing at low densities are said to experience some reproductive difficulties through alterations in pollinator behavior for at least three reasons. First, they may have trouble attracting pollinators away from competing resources because they are economically inefficient to exploit (Kunin 1997). Second, pollinators are more likely to behave as generalists on sparsely distributed plants and to lose pollen during interspecific flights or clog stigmas with foreign pollen (Kunin 1993). Third, pollinators may probe more flowers per plant at low density, which may increase geitonogamy (Bosch & Waser 1999 and references therein).

In addition to such population-level effects, lowered plant density may cause changes in pollen dispersal among different-sized displays. Ohashi & Yahara's (1999) model predicts that pollinators probe more flowers per plant with decreasing plant density particularly on larger

floral displays. Moreover, the model predicts that pollinators would show a weaker preference for visiting large floral displays over small ones at lower plant density. Such an effect could aggravate the relative disadvantage of larger displays growing at low densities; it would reduce xenogamy and increase geitonogamy. To clarify these influences, we describe a model by incorporating pollinators' optimal behavior into the model of pollen transfer. We independently developed this model, but very similar theoretical ideas were developed by Iwasa *et al.* (1995), who tried to explain the small number of flowers probed by a pollinator per plant as a plant's strategy to maximize pollen dispersal. We assume that: (1) pollen on a pollinator constitutes a single, homogeneous pool; (2) a pollinator deposits and picks up pollen in equal amounts at each flower ("pollination saturation"; de Jong *et al.* 1993); and (3) this amount is a constant fraction of the amount of pollen held on a pollinator's body. This simple model (the exponential decay model with a constant pollen carryover) is the most commonly used theoretical description of pollen transfer (reviewed by Harder & Barrett 1996). Even when we adopt more realistic models such as the changing carryover model (Morris *et al.* 1994) or models with pollen loss during transports (Rademaker *et al.* 1997; Harder & Wilson 1998), the qualitative conclusion of the present analysis remains unchanged. We further assume that: (4) nectar production rate per flower is constant; (5) pollinators are always competing for floral resources; and (6) the plant is self-incompatible and the total number of pollen grains exported from a plant is a measure of its male fitness.

The number of pollen grains exported from a plant per pollinator per visit (E) is expressed as:

$$E = A + A(1 - d) + A(1 - d)^2 + \dots + A(1 - d)^{t_c - 1} = A(1 - C^{t_c}) / (1 - C) \quad (14.4)$$

where A is the amount of pollen held on a pollinator's body, d is the fraction of pollen picked up or deposited at each flower, t_c is the number of flowers probed per plant, and C is pollen carryover ($C = 1 - d$). Then, assuming that pollen dispersal is limited by pollinator visits, the total number of pollen grains exported from a plant with F open flowers (male fitness, W) is found by combining Eqs. 14.3 and 14.4:

$$W = V_p E = V_f F A [1 - C^{(1-k)F + mk}] / \{[(1-k)F + mk] (1 - C)\}. \quad (14.5)$$

Figure 14.5 shows that under the assumption of the IFD (i.e., V_f is constant), male fitness (W) increases with floral display size (F), but the average male fitness gain per flower (W/F) decreases with display size.

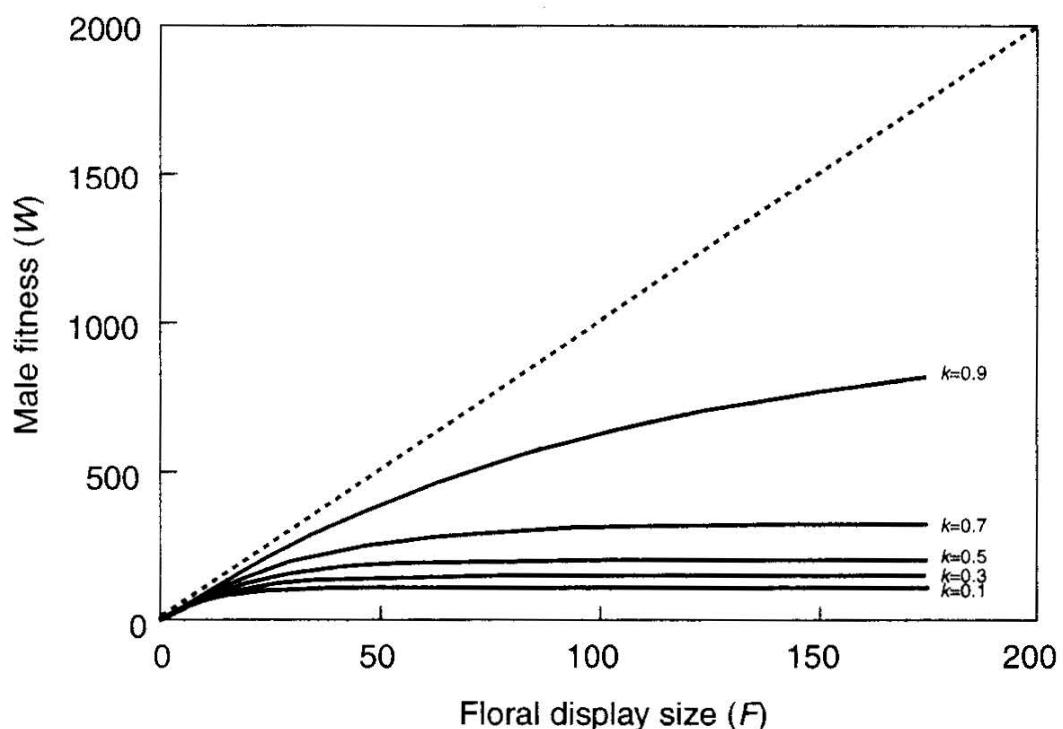


Fig. 14.5. Predicted relationship between floral display size (F) and male fitness (W). W is determined by numerical solution of Eq. 14.5, for $V_f = 1$, $m = 1$, $A = 10$, and $C = 0.9$. The dashed line represents male fitness when $k = 1$.

Furthermore, male fitness gain per flower diminishes as the relative cost of interplant movement ($1 - k$) increases, especially when k is larger than 0.5.

Some authors have suggested that the costs associated with geitonogamy may decrease with increasing display size because the proportion of flowers probed per plant declines on larger plants (Snow *et al.* 1996). However, our model reveals that the benefits of attracting more pollinators do not counteract the cost of increased geitonogamy, even if pollinator availability and pollen carryover is large (see also de Jong *et al.* 1993). In addition to this, we found that a small rise in the relative cost of interplant movement dramatically increases the cost of geitonogamy on larger displays. Based on this result, we can suggest that plants that typically grow at low densities (due to competition, predation, colonization to novel habitats, etc.) will be subject to strong natural selection favoring small displays or extended blooming. Both in warm-temperate and cool-temperate forest on Yaku Island, Yumoto (1987) found a suggestive pattern that climbers, epiphytes, and most of the understory shrubs, which typically grow at low density and are visited by specialist pollinators, exhibited extended blooming. At present, however, there are no

empirical data on such a tendency in any particular plant–pollinator system.

Note that the optimal floral display size in actual plant–pollinator systems may be often larger than our models would predict because: (1) a plant population consisting of small displays cannot attract sufficient pollinators (Kunin 1997), so that among-population selection for larger displays may be strong enough to oppose individual selection for smaller displays; (2) flowering time can be constrained by biotic and/or abiotic factors such as frost, rainfall, or the availability of seasonal pollinators (Rathcke & Lacey 1985); and (3) the opportunity of geitonogamy can be reduced by spatio-temporal separation of sexes such as dioecy or gynodioecy (Thomson & Brunet 1990), synchronized dichogamy (Cruden 1988), and dichogamy coupled with vertical inflorescences (Pyke 1978a).

Can plants manipulate pollinators to their own advantage? Some possibilities of plant traits that promote movements between plants

If plants can shorten pollinators' visit sequences, they can increase male fitness as a result of decreased geitonogamy. Iwasa *et al.* (1995) modeled this effect and found that pollinator behavior that maximizes pollen export (male fitness) is qualitatively similar to observed pollinator behavior. Is this agreement fortuitous, or a result of pollinator manipulation by plants in an evolutionary sense? Based on considerations of optimal foraging, we now discuss possible strategies by which plants can manipulate their pollinators to their own advantage.

- (1) Low nectar reward. Many authors have reported that lower nectar rewards often cause pollinators to depart earlier from plants and promote interplant movements (e.g., Heinrich 1979b). Lower nectar reward might therefore be advantageous unless pollination is inefficient (Robertson 1992; Iwasa *et al.* 1995). Moreover, decreased investment in nectar production will allow plants to reallocate resources into ovules, which can improve fitness (Pyke 1991; Sakai 1993).
- (2) Gradient of nectar production within a structured inflorescence. On plants with vertical inflorescences, spatial gradient in the nectar productivity (or crop) decreasing from bottom to top may be an important cause of patch depression in place of flower revisitation (see above). In fact, Orth & Waddington (1997) found that carpenter bees foraging on vertical inflorescences with no spatial gradient of nectar

rewards probed a larger proportion of flowers than reported in other studies where there was a nectar gradient.

- (3) Within-plant variation in nectar productivity per flower. Rathcke (1992) stated that if within-plant variation in nectar per flower increases the likelihood of pollinators' encountering low-reward flowers, it might shorten visit sequences. Observed simple departure rules adopted by pollinators (e.g., Fig. 14.3) seem to support this idea. However, pollinators may alter their departure rules in response to changes in spatial distribution of nectar rewards (Iwasa *et al.* 1981). Moreover, different pollinator species may adopt different rules of plant departure (Collevatti *et al.* 1997). Thus, further empirical and theoretical studies are needed before generalizing this argument.
- (4) Retention of old flowers coupled with floral color (or scent) change. After they have landed on plants, pollinators often avoid old, less-rewarding flowers by their color or scent, while they have little or no ability to discriminate between different-aged flowers at a distance (Oberrath & Böhning-Gaese 1999 and references therein). Therefore, some authors have suggested that the retention of old flowers – coupled with floral color or scent changes – may enable plants to increase the pollinator visitation rate per plant while simultaneously decreasing the proportion of flowers probed per plant (Gori 1983; Oberrath & Böhning-Gaese 1999). The adaptive value of this strategy may be greatest in plant species bearing small flowers, where the cost of retaining an old flower will be small, pollinators cannot discriminate different-colored flowers at a distance, and clustering of flowers may greatly improve the plant's long-distance attractiveness.
- (5) Plant traits increasing the risk of flower revisit. Spatial memory or directional movement may be affected by some plant traits. For example, Redmond & Plowright (1996) found that bumble bees revisited artificial "flowers" more often in irregular than in uniform configurations. They showed in addition that the presence of landmarks significantly reduced flower revisits when bees had to fly between flowers, but had no effect when bees could walk between flowers. Also, Brown *et al.* (1997) suggested that spatial working memory capacity of honeybees is limited by their ability to discriminate among locations in close proximity. Therefore, inflorescence architecture (complex or close-packed arrangements of flowers, the absence of bract leaves, etc.) may shorten pollinators' visit sequences, mediated through the increased risk of flower revisit.
- (6) Plant traits reducing the relative cost of interplant movement. If plants can reduce the relative cost of inter-plant movement, they can greatly improve their male fitness (Fig. 14.5). Based on our definition of the

mean discounting rate for visiting another plants (k ; see above), we suggest two possible strategies. One is asynchronous flowering of adjacent flowers, which would increase the average flight distance within a plant. Another strategy is producing deep flowers – or veiling nectaries behind complex floral structures – which would increase handling time per flower (Harder 1983, 1986). This strategy may be efficient only when autogamy does not increase with handling time per flower (Zimmerman 1988). Deep flowers have been discussed in the context of nectar protection (Corbet 1990), evolutionary race with pollinator tongue (Darwin 1862; Nilsson 1988), the exclusion of generalists (Heinrich 1979b; Laverty 1980), and the promotion of flower constancy (Darwin 1876; Laverty 1994). In addition to these, we indicate a novel functional value of deep flowers, i.e., the promotion of pollen dispersal.

We must note that plants or populations adopting any strategies discussed above may sometimes increase the risk of pollinator deficiency because they could be economically inefficient to exploit (Zimmerman 1988). For example, pollinators often learn to avoid patches with low reward levels (Dreisig 1995) or high reward variation (“risk-aversive foraging”; Perez & Waddington 1996). Despite such possibilities, we feel that the available data indicate that plants can improve their pollen dispersal by altering pollinator behavior. The importance of these characteristics in improving pollen dispersal is totally hypothetical at this time, and again, awaits theoretical and empirical exploration.

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