AMERICAN JOURNAL OF

BOTANY

FEBRUARY 1998 VOLUME 85 NUMBER 2

Official Publication of the Botanical Society of America, Inc.

American Journal of Botany 85(2): 219–224. 1998.

EFFECTS OF VARIATION IN FLOWER NUMBER ON POLLINATOR VISITS IN *CIRSIUM PURPURATUM* (ASTERACEAE)[1]

KAZUHARU OHASHI[2,3] AND TETSUKAZU YAHARA[3]

Department of Biology, College of Arts and Sciences, University of Tokyo,
Komaba 3-8-1, Meguro-Ku, Tokyo 153, Japan

We examined the functional relationships between floral display and two types of bumble bee response, the visitation rate per plant and the number of flowers visited on a plant, in an artificially arranged field population of *Cirsium purpuratum*. To reduce the variance in data, we collected data for each day separately and adopted a Latin square design in selecting the focal plants within a day. We then tested several types of regressions to each set of data to find the best-fitting line accounting for the observed relationship between pollinator response and display size. We found that the visitation rate of bumble bees per plant was a decelerating function of floral display, and that the number of flowering heads visited on a plant increased linearly with display size. Predicted from the above two functions, the visitation rate per head was independent of floral display and nearly constant within each day. Our results suggest that conventional methods in collecting and analyzing data on pollinator visitation may yield large variance in data derived from temporal and spatial heterogeneity and that improved methods employed here are effective in reducing the variance and estimating patterns of pollinator response to floral display more accurately.

Key words: Asteraceae; *Cirsium purpuratum*; floral display; Latin square design; pollinator visitation.

The number of flowers open at any one time on a plant is a major element of floral display in animal-pollinated angiosperms, and its variation may affect plant fitness through pollinator visitation in at least two ways. First, plants with large displays may receive more visits of pollinators (Schmid-Hempel and Spieser, 1988; Thomson, 1988; Klinkhamer, de Jong, and de Bruyn, 1989; Klinkhamer and de Jong, 1990; Rodríguez-Robles, Meléndez, and Ackerman, 1992; Ohara and Higashi, 1994; Robertson and Macnair, 1995). This will lead to an improvement of plant fitness through both male and female function. Second, the number of flowers visited on a plant may also increase with floral display. This may impose some mating costs associated with large floral displays through geitonogamous selfing or pollen clogging (Klinkhamer, de Jong, and Metz, 1994; Harder and Barrett, 1995). Thus, to quantify the above two types of pollinator response to variation in flower number open at once is essential to understand the evolution of floral display.

The response of pollinators to variation in flower number open at once on a plant is, however, a little-studied aspect of the dynamics of plant-pollinator systems (Robertson and Macnair, 1995). Quantitative relationships have been studied only in a limited number of plant-pollinator systems and available data show largely inconsistent patterns. Based on visitation rates, pollen deposition or removal rates, or realized fitness, the success of plants increased with flower number following accelerating (Wilson and Price, 1977; Schemske, 1980), linear (Campbell, 1989; Devlin, 1989; Ohara and Higashi, 1995) or decelerating (Klinkhamer, de Jong, and Bruyn, 1989; Klinkhamer and de Jong, 1990; Devlin, Clegg, and Ellstrand, 1992) functions. Similarly, increase in the number of flowers visited on a plant was a linear (Dreisig, 1995) or decelerating (Klinkhamer and de Jong, 1990) function of flower number. This lack of consistency may reflect real diversity in pollinator response. However, most of the previous findings were based on pooled data collected within several days (Klinkhamer, de Jong, and de Bruyn, 1989; Klinkhamer and de Jong, 1990) or within a week (Ohara and Higashi, 1994; Robertson and Macnair, 1995) and thus associated with large variance derived from temporal heterogeneity of the environment. Also, we do not know of any study that made an effort to reduce the bias due to the observation time and to the location of observed plants. Therefore, to accurately estimate the functional relationship between flower number and the two types of pollinator response, we must contrive to reduce the variance in data using more adequate experimental design in collecting data. In addition, we need to test several types of regression lines to obtain the best mathematical fit to a set of data because we cannot have any structural mathematical model. Most previous workers have fitted a single function to the data often using log-log plots, but this may preclude equally plausible functional relationships. This is particularly a problem when data show large variance, as is the case in most previous studies.

The primary purpose of this study was to overcome these drawbacks of previous works and clarify functional

---

[1] Manuscript received 20 March 1996; revision accepted 16 June 1997.

The authors thank Drs. N. G. Dengler, H. E. M. Dobson, Y. Iwasa, S. Sakai, and I. Washitani for critical reading of the manuscript, Drs. I. Terashima, A. Takenaka, and the members of Terashima's laboratory for their valuable suggestions and continuous encouragement; Dr. E. Kasuya, T. Kubo, and K. Ooi for their assistance in data analysis; Dr. K. Suzuki for identification of bumble bee species; and S. Funayama, Y. Inui, C. Kikuchi, A. Konuma, A. Kuwata, F. Nagaishi, T. Miyake, H. Sato, W. Taniguchi, D. Tobata, and H. Yashiroda for their patient assistance in our field work.

[2] Author for correspondence.

[3] Current address: Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812-81, Japan; FAX: (+81)-(0)92-642-2645.

relationships between flower number and the two types of pollinator response using an artificially arranged field population of *Cirsium purpuratum* (Maxim.) Matsum. that is visited by bumble bees. The following questions are addressed. (1) Is the increase of the visitation rate per plant and the number of flowers visited on a plant accelerating, linear, or decelerating? (2) How do the functional relationships between the two variables and flower number vary between days? We collected data on pollinator visitation for 6 d separately. To reduce the bias in data due to the observation time and to the location of the observed plants, we adopted a Latin square design within each daily observation. We tested five types of regression equations to find the best-fitting lines accounting for the observed relationships.

The second purpose of this study was to derive a functional relationship between flower number and the visitation rate of pollinators per flower. Recently, Dreisig (1995) has shown that nectar-foraging bumble bees distribute themselves on plants according to an ideal free distribution so that they can gain equal amounts of nectar rewards per flower. He provided effective evidence for ideal free distributions that the observed visitation rate per flower was independent of flower number per plant. We aimed to demonstrate whether the visitation rate per flower is independent of flower number in a changing environment. Since the visitation rate per flower is a function of the two independent variables stated above, namely the visitation rate per plant and the number of flowers visited on a plant, we derived the functional relationship between flower number and the visitation rate of pollinators per flower using regression equations for the two independent variables.

MATERIALS AND METHODS

Organisms—*Cirsium purpuratum* is a perennial herb that occurs on floodplains or volcanic barrens in the Kanto and the Central districts of mainland Japan. Large radical leaves form a rosette that sometimes reaches 200 cm in diameter. In late August, several flowering stalks with a few tiny leaves and one or two large nodding flower heads (the maximum diameter of 10 cm) elongate. Flower heads initiate blooming at the beginning of September. A flower head is composed of 400–700 florets surrounded by many stiff phyllaries. All florets are monomorphic, hermaphroditic, and protandrous. Each head lasts 6–8 d (male phase, 4–5 d; female phase, 2–3 d).

Study site—We conducted the study with a population located on a floodplain along the Kinu River (~800 m altitude) in northern Tochigi Prefecture, Japan. This population grows in an open and dry habitat. At this site, individuals of *C. purpuratum* originally occurred in native stands, but most of them were transplanted along the road (Route 152), roughly arranged in two lines. Therefore, any difference in the degree of isolation between plants would be minimal in this population (interplant distance: mean ± 1 SD = 1.43 ± 0.55 m, N = 92).

Pollination system—At our site, the primary pollinators of *C. purpuratum* are workers of the bumble bee, *Bombus diversus* Smith. Workers of *B. honshuensis* Tkalcu and *B. hypocrita* Pérez also visit *C. purpuratum*, but only rarely. The other minor visitors of *C. purpuratum* are several species of butterfly (*Papilio machaon hippocrates* C. et R. Feder, *Vanessa indica* Herbst, *V. cardui* L., etc.), honey bee (*Apis mellifera* L., introduced for apiculture), and some syrphid species. However, these insects hardly touch the anthers and stigmas during their visits, and are poor pollinators for *C. purpuratum* (Ohashi and Yahara, personal observation). Therefore, at this site, *C. purpuratum* is pollinated mostly by *B. diversus*. There are no other plant species that share the same visitors in our population. *C. purpuratum* is not autogamous and pollination by bumble bees is essential to its seed success, although it is self-compatible (Ohashi, unpublished data).

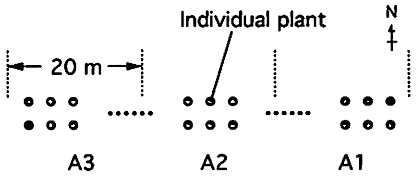

Fig. 1. Diagram of the plot established for observations of pollinator visits. Circles represent individual plants of *C. purpuratum*, which are roughly arranged in two lines. This plot is 16 × 60 m long, divided into three subareas of 16 × 20 m defined as A1, A2, and A3 from east to west. Black dots are a simplification of the two lines of plants and dotted lines represent border lines between the subareas.

Visitation rates of bumble bees in relation to the number of flowering heads of C. purpuratum—In mid-August 1994, we established a 16 × 60 m quadrat at our population. We numbered consecutively all of the adult plants within the plot with plastic tape and recorded their locations on a map. This numbering procedure allowed us to identify individual plants at a distance of ≥2 m.

We measured the visitation rate of bumble bees per plant and the number of heads visited on a plant. In these observations, visitation rates were quantified by a direct observation and/or an indirect observation with 8-mm video cameras. We recorded one visit only when a bumble bee probed for nectar. Since each individual bumble bee restricted its foraging to a limited area of the population (Ohashi and Yahara, personal observation; see also Thomson, Maddison, and Plowright, 1982) and often changed its foraging area depending on the time of day (Yahara, personal observation), we selected the focal plants in the following way to minimize bias in the data derived from observations of individual bumble bees. First, we divided our population into three equal-sized subareas, defined as A1, A2, and A3 from east to west, respectively (Fig. 1). Second, we divided the observation time within each day into three parts, separated by 1-h intervals (T1 0700–0900; T2 1000–1200; T3 1300–1500). Third, we distinguished three categories of floral display size based on the number of flowering heads per plant (large >7, middle 7–3, and small <3 flowering heads). Since the florets within a head were highly synchronized in their anthesis, the difference in total number of open florets among heads appeared to be too small to affect the behavior of the bees. For data collection, we selected three plants that differ from each other in display size category and in population area, and monitored their insect visits for 2 h. The same procedure was repeated for each time period within a day (T1–3). As shown in Fig. 2, the three levels of display sizes are assigned to each row (time of day) and column (subarea) at random, except that each level is represented exactly once in each column and each row within a day. This type of configuration is referred to as the 3 × 3 Latin square design (Sokal and Rohlf, 1995).

We collected data at two separate times during the flowering season in 1994 (16–21 September, 6–8 October). In each time, we conducted the observations over 3 d, taking care not to select the same individual plant more than once. We adopted three different designs of Latin squares for the 3-d observations (Fig. 2).

Trailing of individual pollinators—In the middle of the flowering season in 1994, we randomly selected bumble bees visiting the plot and trailed them, recording the sequence of individual plants they visited until they left the plot or we lost track of it. We trailed one bee after another for 6 h during the peak of pollinator activity within each day

	1st day T1	1st day T2	1st day T3	2nd day T1	2nd day T2	2nd day T3	3rd day T1	3rd day T2	3rd day T3
A1	L	S	M	M	L	S	S	M	L
A2	M	L	S	S	M	L	L	S	M
A3	S	M	L	L	S	M	M	L	S

Fig. 2. Experimental designs used for observations of pollinator visits in relation to floral display. Three categories of floral display (L > 7, M 3–7, and S < 3 flowering heads per plant, respectively) laid out according to a Latin square design within each observation day to control for time (T1 0700–9000, T2 1000–1200, and T3 1300–1500) and location (A1–A3, see Fig. 1). Each level of floral display is replicated only once in a given row or column. Three different designs of Latin squares were adopted for the 3-d observations.

(~0700–1300). Daily observations were repeated three times during the season (18 September, 5 October, and 9 October).

Data analysis—To test for an effect of display size on pollinator visits, we compared the average visitation rates per plant among the three categories of floral display size with one-way analysis of variance (ANOVA). In addition, we investigated the functional relationships between visitation rate of bumble bees per plant (N_p) and display size (F_i) by fitting some linear and nonlinear regression lines to the plots using a BASIC program that estimates parameters with the polytope (simplex) method (Nash and Walker-Smith, 1987). Each function is expressed as: $N_p = A + BF_i$ (linear function), $N_p = A\exp(-B/F_i)$ (S-shaped function), $N_p = A[1 - \exp(-BF_i)]$ (saturating function 1), $N_p = AF_i/(1 + BF_i)$ (saturating function 2), $N_p = AF_i^B$ ($B < 1$) (nonsaturating function); A and B are constants.

We examined the functional relationships between the mean number of heads visited per plant (N_f) and display size (F_i), fitting some regression lines for each observation day separately. Further, we derived the functional relationship between the visitation rate per head (N_pN_f/F_i) and display size for each day using regression equations for the above two types of pollinator response to display size.

Finally, we calculated the distances between flowering plants that bumble bees visited consecutively in their foraging and classified the flight distances as short (<2 m), middle (2–2.99 m), and long (>3 m). To examine the effect of flight distance on the bees' choice of plants, we determined the mean number of flowering heads on plants chosen by bees after flying each distance category. We then compared the number of flowering heads per plant among the three distance categories using the Kruskal-Wallis test.

RESULTS

Bumble bees preferred to visit plants with a large display size (F_i). Differences in the visitation rate per plant (N_p) among the three categories of floral display were statistically significant for both observation periods (Table 1).

The functional relationships between the visitation rate per plant and the number of flowering heads per plant was described better by fitting the four decelerating functions than by applying a linear function to the whole (Table 2). The best-fitting function was $N_p = A[1 - \exp(-BF_i)]$. Figure 3 shows actual plots of the data and regression lines. The estimated values of regression parameters varied remarkably among observation days. In particular, the regression lines for the second observation period decelerated more rapidly and their maximum levels were much higher than those of the first observation period.

In all 6 d of observation, the mean number of flowering heads visited per plant (N_f) was best described by a linear function of display size (F_i). We compared regression lines among the 6 d and found that the heterogeneity of slopes was not significant (df = 5, 41, $F = 0.50$, $P = 0.78$), while the intercepts differed significantly (df = 5, 46, $F = 2.42$, $P = 0.05$, range = 0.006–0.32). Figure 4 shows that the mean number of heads visited per plant (N_f) increased with the display size (F_i), although the increase was less than proportional. This means that the proportion of heads visited at a single bout (N_f/F_i) follows an exponential decline with increasing number of flowering heads on the plant (F_i).

The net effect of an increased visitation rate per plant (N_p) and a decreased proportion of heads visited during a single visit to a plant (N_f/F_i) in relation to floral display size (F_i) leads to the prediction that the visitation rate per head (N_pN_f/F_i) varies independently of floral display (Fig. 5). Individual flowering heads were predicted to receive approximately equal number of visits except on small displays (1–5 heads per plant), despite the fact that the level of visitation rate per head varied substantially among observation days.

Effects of flight distance—Bumble bees tended to visit larger displays when they had flown longer distances (Table 3). This tendency was most remarkable in the first observation day. Differences in the mean number of flowering heads on the visited plants were significant among the three flight distance categories on all three observation days.

DISCUSSION

We found that the visitation rate of bumble bees per plant was better described by decelerating functions over the number of flowering heads on the plant than by a linear function. While this tendency did not change throughout the 6-d observations, the estimated values of

TABLE 1. Comparisons of bumble bee visits to *Cirsium purpuratum* plant having different floral display sizes. Values are mean number of bumble bee visits ± 1 SE per plant per 2 h, pooled over 3 d, for each category of floral display size (L: >7, M: 3–7, S: <3 heads per plant). N is the number of plants.

Observation period[a]	Floral display >7 heads/plant	Floral display 3–7 heads/plant	Floral display <3 heads/plant	N	F[b]	P
1	52.1 ± 11.3	22.9 ± 4.8	8.2 ± 4.4	27	15.168	0.0002
2	125.4 ± 20.3	70.0 ± 11.7	47.1 ± 10.3	30	13.783	0.0003

[a] 1 = 18–21 September, 2 = 6–8 October.

[b] One-way analysis of variance.

TABLE 2. Regression analysis of the visitation rate per plant (N_p) against the number of flowering heads per plant (F_i). Each value represents the estimated parameter (A, B) and the coefficient of determination (R^2) calculated from daily regression analysis.

	Regression equation														
	$N_p = A + BF_i$			$N_p = A \exp(-B/F_i)$			$N_p = A[1 - \exp(-BF_i)]$			$N_p = AF_i/(1 + BF_i)$			$N_p = AF_i^B$		
Date	A	B	R^2	A	B	R^2	A	B	R^2	A	B	R^2	A	B	R^2
September															
16	−2.17	4.57	0.56	89.27	6.66	0.57[m]	827.92	0.01	0.55	4.40	0.02	0.55	3.86	1.05	0.55
17	4.68	1.31	0.80	35.05	5.15	0.84	34.56	0.09	0.87[m]	3.25	0.06	0.87[m]	4.33	0.64	0.85
21	13.31	3.36	0.77	119.91	6.40	0.73	129.44	0.05	0.78[m]	7.42	0.04	0.77	10.16	0.70	0.78[m]
October															
6	57.30	4.46	0.38	170.97	3.03	0.54	161.37	0.16	0.58[m]	31.40	0.16	0.56	43.46	0.42	0.50
7	46.41	3.93	0.35	117.45	1.83	0.44	114.36	0.23	0.52[m]	33.96	0.24	0.50	39.84	0.37	0.46
8	56.42	1.63	0.06	107.41	2.04	0.12	97.80	0.26	0.13[m]	35.12	0.31	0.12	43.07	0.27	0.10

[m] Maximum value of R^2 within each day.

regression parameters varied substantially among observation days. The observed variance was probably the result of daily or seasonal changes in ambient atmospheric conditions and variation in the frequency of pollinator visits due to fluctuation of bumble bee colony size and activities.

We found that the number of heads visited per plant was an increasing linear function of display size. The 6-d observations further revealed that this functional relationship was nearly constant among days. This means that temporal changes in environment have little effect on the pattern of pollinator movement within plants of a certain display size. Some researchers have suggested that bumble bees leave a plant immediately after probing a flower that has a relatively small volume of nectar so as to minimize the possibility of visiting empty flowers (Hodges, 1985a, b; Cresswell, 1990; Dreisig, 1995). If this departure rule actually determines the degree of within-plant movement of bumble bees, the results obtained here suggest that the number of flowering heads that contain sufficient nectar for bees at any one time increases linearly with display size.

It is notable that the visitation rate per head was independent of display size, in spite of the fact that both the visitation rate per plant and the number of heads visited per plant increased with display size. Such uniform distributions of bumble bees among heads would result in an equalization of the gain per head on plants differing in display size (Dreisig, 1995). The predicted mean visitation rate of bees per head was almost constant within each day over the range of floral display tested, but varied among observation days, suggesting that bumble bees have an ability to achieve an "ideal free distribution" according to temporal changes in the environment day by day. Since the bees did not vary in the number of heads they visited per plant of a given display size throughout the observation days, they may realize an equalization of gain per flower or head by adjusting the level of the vis-

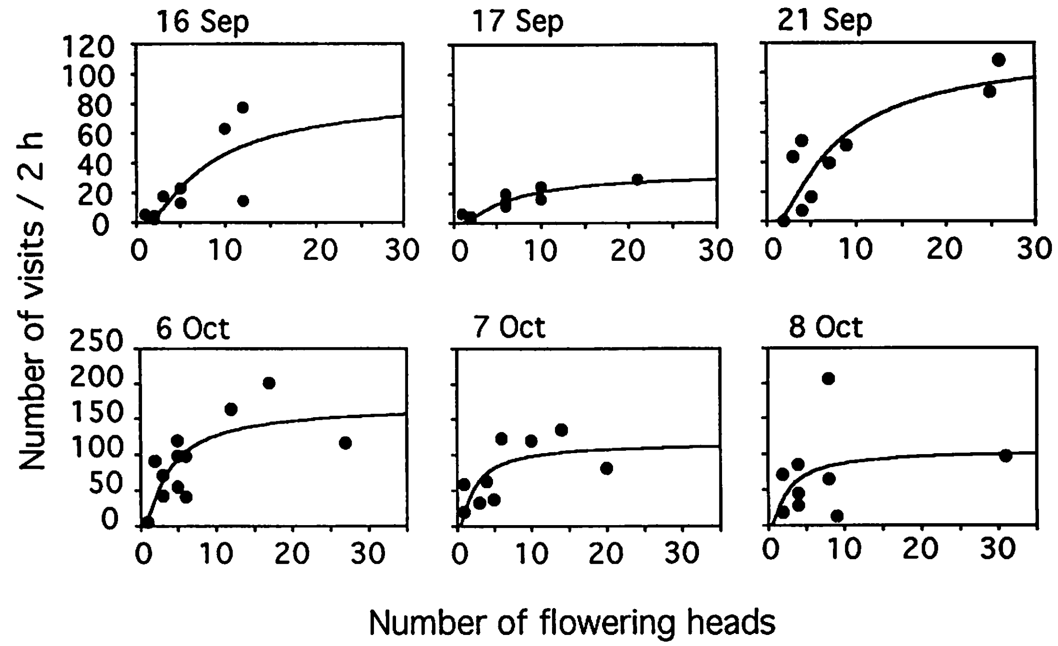

Fig. 3. Patterns of pollinator visitation to *C. purpuratum* plants per 2 h (N_p) as a function of the number of flowering heads at each observation day (F_i). Each point represents a separate plant and the solid lines are the fitted curves from nonlinear regression with a S-shaped function (see text). Dates of observation are shown above each graph.

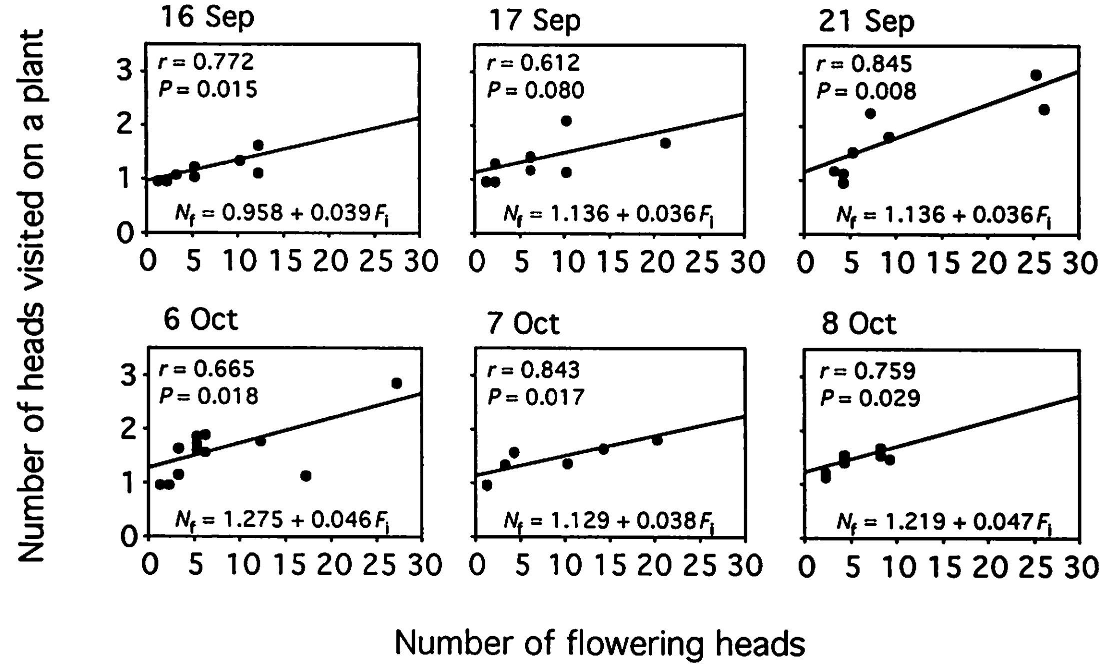

Fig. 4. The relation between the mean number of flowering heads visited by a bumble bee on a plant (N_f) and the number of flowering heads per plant (F_i). Each point represents a separate plant and the solid lines express the results from simple linear regressions. Dates of observation are shown above each graph. Regression equations and simple correlation coefficients are also shown on each graph.

itation rate per plant within a day. Our results support the prediction of Dreisig (1995) that the visitation rate per plant or patch is more important to achieve an ideal free distribution on plants varying in display size than is the number of flowers visited per plant.

The model of ideal free distributions assumes that foragers are free to forage wherever they choose (Fretwell and Lucas, 1970). However, a plant's attractiveness to bumble bees will depend on the energy expended in foraging for nectar and pollen as well as on the amount of rewards. In all three of our trailing observations, bees preferentially visited plants with many flowering heads after longer flight distances, indicating that flight distance and/or time is a cost to pollinators and that large floral displays give pollinators some advantage that compensates for the cost of movement. Since bees also visited more heads on larger displays, we can expect that a bee counteracts the energy cost of increased movement by visiting larger displays. This might require the bees' ability to learn the location of individual plants and return to the same plants repeatedly, as shown by Thomson (1988). Interplant distance was relatively small in our site, and the cost of movement could be offset by the bees' modification of their trapline according to display sizes included.

In this study, we were able to find consistent patterns of bumble bee responses to display size in *C. purpuratum* by improving on earlier methods in collecting and ana-

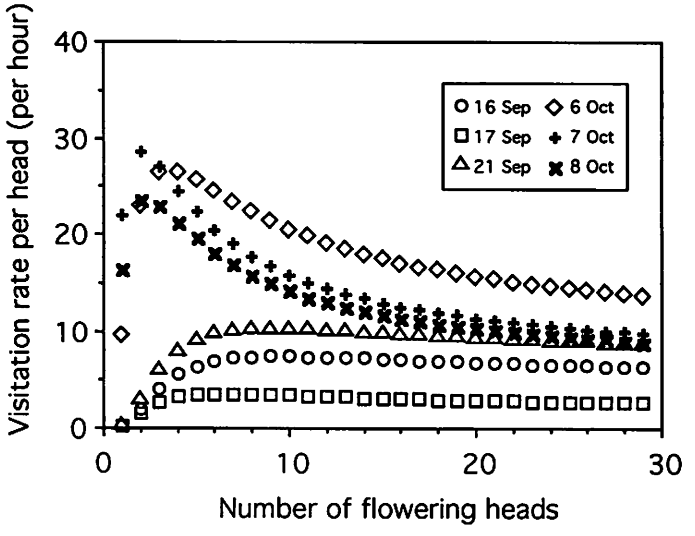

Fig. 5. Predicted pattern of visitation rate per head (N_pN_f/F_i) in relation to floral display size (F_i). Each point indicates the visitation rate per head derived from functions estimated for visitation rate per plant (N_p) and the number of heads visited on a plant (N_f) within each observation day.

TABLE 3. Numbers of flowering heads on plants visited by bumble bees after flying different distances. Values are mean number of flowering heads ± 1 SE. Values in parentheses represent the number of bee flights included.

Observation day	Distance (m)				
	<2	2–2.99	≥3	H^a	P
8 Sep	10.19 ± 0.69 (184)	12.67 ± 1.01 (171)	14.05 ± 0.75 (104)	12.045	0.002
5 Oct	7.33 ± 0.85 (78)	10.33 ± 0.91 (56)	9.14 ± 0.83 (68)	13.004	0.002
9 Oct	4.05 ± 0.30 (104)	5.69 ± 0.57 (83)	5.97 ± 0.43 (158)	12.962	0.002

[a] H = statistic for Kruskal-Wallis test.

lyzing data. Our results may support our initial hypothesis that variance derived from temporal heterogeneity of the environment, the location of plants, and observation time is responsible for the disparity of data reported in the previous studies. In particular, the visitation rate to a given floral display size fluctuated wildly from day to day. This suggests that the conventional approach of pooling results of pollinator observations conducted over different days can lead to misleading conclusions about the true shapes of the regression curve. Also, the number of heads visited on a given floral display size changed little throughout the observation days, which disagrees with most of the previous data containing too large a variance to estimate an accurate shape of the relationship (Klinkhamer, de Jong, and Bruyn, 1989; Klinkhamer and de Jong, 1990; Robertson and Macnair, 1995). This suggests that the Latin square designs we chose may be effective in reducing the variance in data within a day. Further studies using methods employed here are needed to clarify how widespread these patterns are among plant–pollinator systems. It also remains to be determined how observed patterns of pollinator responses to display size arise, and how these responses contribute to the bee's achieving an ideal free distribution. Detailed investigations of movement rules as well as nectar distributions on plants may be necessary to answer these questions in the future.

LITERATURE CITED

CAMPBELL, D. R. 1989. Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. *Evolution* 43: 318–334.

CRESSWELL, J. E. 1990. How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Laminaceae)? *Oecologia* 82: 450–460.

DEVLIN, B. 1989. Components of seed and pollen yield of *Lobelia cardinalis*: variation and correlations. *American Journal of Botany* 76: 204–214.

———, J. CLEGG, AND N. C. ELLSTRAND. 1992. The effect of flower production on male reproductive success in wild radish populations. *Evolution* 46: 1030–1042.

DREISIG, H. 1995. Ideal free distributions of nectar foraging bumblebees. *Oikos* 72: 161–172.

FRETWELL, S. D., AND H. L. LUCAS. 1970. Territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16–36.

HARDER, L. D., AND S. C. H. BARRETT. 1995. Mating cost of large floral displays in hermaphrodite plants. *Nature* 373: 512–515.

HODGES, C. M. 1985a. Bumble bee foraging: the threshold departure rule. *Ecology* 66: 179–187.

———. 1985b. Bumble bee foraging: energetic consequences of using a threshold departure rule. *Ecology* 66: 188–197.

KLINKHAMER, P. G. L., AND T. J. DE JONG. 1990. Effects of plant size, plant density and sex differential nectar reward on pollinator visitation in the protandrous *Echium vulgae* (Boraginaceae). *Oikos* 57: 399–405.

———, ———, AND G-J. DE BRUYN. 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos* 54: 201–204.

———, ———, AND J. A. J. METZ. 1994. Why plants can be too attractive—a discussion of measures to estimate male fitness. *Journal of Ecology* 82: 191–194.

NASH, J. C., AND M. WALKER-SMITH. 1987. Nonlinear parameter estimation: an integrated system in BASIC. Marcel Dekker, New York, NY.

OHARA, M., AND S. HIGASHI. 1994. Effects of inflorescence size on visits from pollinators and seed set of *Corydalis ambigua* (Papaveraceae). *Oecologia* 98: 25–30.

ROBERTSON, A. W., AND M. R. MACNAIR. 1995. The effects of floral display size on pollinator service to individual flowers of *Mysotis* and *Mimulus*. *Oikos* 72: 106–114.

RODRÍGUEZ-ROBLES, J. A., E. J. MELÉNDEZ, AND J. D. ACKERMAN. 1992. Effects of display size, flowering phenology, and nectar availability on effective visitation frequency in *Comparettia facalta* (Orchidaceae). *American Journal of Botany* 79: 1009–1017.

SCHEMSKE, D. 1980. Evolution of floral display in the orchid *Brassavola nodosa*. *Evolution* 34: 489–493.

SCHMID-HEMPEL, P., AND B. SPIESER. 1988. Effects of inflorescence size on pollination in *Epilobium angustifolium*. *Oikos* 53: 98–104.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry, 3rd. ed. W. H. Freeman, New York, NY.

THOMSON, J. D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*. *Evolutionary Ecology* 2: 65–76.

———, W. P. MADDISON, AND R. C. PLOWRIGHT. 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54: 326–336.

WILSON, M. F., AND P. W. PRICE. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495–511.