

# The effect of inflorescence size on pollinator visitation of *Delphinium nelsonii* and *Aconitum columbianum*

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## Resum

PLEASANTS, J. M. & M. ZIMMERMAN (1990). L'efecte de la mida de la inflorescència sobre les visites de pol·linitzadors de *Delphinium nelsonii* i *Aconitum columbianum*. Collect. Bot. (Barcelona) 19: 21-39

S'han suggerit dos factors que juguen un paper en la determinació de la mida de la inflorescència a l'interior d'una espècie: la limitació d'energia i la disminució de la recompensa de la pol·linització per a inflorescències llargues. En un esforç per avaluar la significació de la limitació de la pol·linització, hem examinat l'efecte de la mida de la inflorescència sobre els models de visita dels pol·linitzadors per a dues espècies, *Aconitum columbianum* i *Delphinium nelsonii*. Aquestes espècies tenen una biologia de la pol·linització similar i ambdues presenten una inflorescència racemosa, però difereixen notablement en la mida de llurs inflorescències (*A. columbianum* té 1-26 flors obertes, mentre que *D. nelsonii* només en té 1-6). Per a cada espècie, s'han examinat els paràmetres següents, com a funció de la mida de la inflorescència: visites per inflorescència, flors visitades per visita i visites per flor. Per a *D. nelsonii*, tots tres paràmetres augmenten quan augmenta la mida de la inflorescència, tot i que per a inflorescències llargues, la taxa d'increment se suavitza un xic pel que fa a flors per visita i visites per flor. Per a *A. columbianum*, tots tres paràmetres també augmenten generalment quan augmenta la mida de la inflorescència, però, per a les mides més grans, ja no hi ha més increment en visites per inflorescència o flors per visita, i s'observa una disminució en visites per flor. El model d'un menor increment en l'atractivitat amb inflorescències progressivament més grans correspon al que hom esperaria si l'atractivitat de la inflorescència fos basada en el concepte de diferència exactament perceptible. El model observat, d'un menor increment en flors per visita a mesura que augmenta la mida de la inflorescència, pot ser descrit adequadament per mitjà d'un model en el que hi ha, per regla general, una probabilitat fixada d'abandonar una flor per anar a una altra de la mateixa inflorescència. El nombre de visites per flor és simplement la conseqüència dels altres dos paràmetres. L'absència de cap disminució significativa en les visites de pol·linitzadors a mesura que augmenta la mida de la inflorescència de *D. nelsonii* suggereix que l'energia és probablement el factor limitant de la mida de la inflorescència. Per a *A. columbianum*, les inflorescències més llargues tenen un nombre reduït de visites per flor i el nombre total de visites per inflorescència, per a les inflorescències més extremadament llargues, es veu reduït. Això, conjuntament amb la possible reducció de la qualitat de les visites a les inflorescències més llargues, fa més gran la possibilitat que la mida de la inflorescència en *A. columbianum* pugui ser limitada per la pol·linització.

Mots clau: Pol·linització, Inflorescències, *Aconitum*, *Delphinium*, *Ranunculaceae*.

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### Abstract

PLEASANTS, J. M. & M. ZIMMERMAN (1990). The effect of inflorescence size on pollinator visitation of *Delphinium nelsonii* and *Aconitum columbianum*. Collect. Bot. (Barcelona) 19: 21-39

Two factors have been suggested to play a role in determining the limit to inflorescence size within a species: energy limitation and diminishing pollination returns for larger inflorescence sizes. In an effort to assess the significance of pollination limitation we examined the effect of inflorescence size on pollinator visitation patterns for 2 species, *Aconitum columbianum* and *Delphinium nelsonii*. These species are similar in their pollination biology, and both have a racemose inflorescence, but they differ markedly in inflorescence size (*A. columbianum* has from 1-26 open flowers while *D. nelsonii* has 1-6 open flowers). For each species the following parameters were examined as a function of inflorescence size: visits per inflorescence, flowers visited per visit, and visits per flower. For *D. nelsonii* all 3 parameters increased with increasing inflorescence size although for large inflorescences the rate of increase slowed slightly for flowers per visit and visits per flower. For *A. columbianum* all 3 parameters also generally increased with increasing inflorescence size but for the largest sizes there was no further increase in visits per inflorescence or flowers per visit and there was a decrease in visits per flower. The pattern of a smaller increase in attractiveness with progressively larger inflorescences corresponds to what would be expected if inflorescence attractiveness were based on the concept of just noticeable difference. The observed pattern of a smaller increase in flowers per visit with increasing inflorescence size can be described accurately by a model in which there is, on average, a fixed probability of moving from one flower to another on an inflorescence. The number of visits per flower is simply the consequence of the other 2 parameters. The lack of any significant decrease in pollinator visitation with increasing inflorescence size for *D. nelsonii* suggests that energy is probably the factor limiting inflorescence size. For *A. columbianum*, the largest inflorescences have a reduced number of visits per flower and the total number of visits per inflorescence for the very largest inflorescences is reduced. This, in conjunction with a possible reduction in visit quality for large inflorescences, raises the possibility that inflorescence size in *A. columbianum* may be pollination limited.

Keywords: Pollination, Inflorescences, *Aconitum*, *Delphinium*, *Ranunculaceae*.

## INTRODUCTION

Among angiosperm taxa there is a wide variety of inflorescence shapes (raceme, spike, umbel etc.) and sizes. Only recently have attempts been made to understand the adaptive significance of inflorescence architecture (WYATT, 1982). One aspect of inflorescence architecture of particular interest is inflorescence size (number of open flowers on a stem). Within a taxon there may be little variation in the shape of the inflorescence but size may vary greatly. For example, among species in the genus *Delphinium* in California the number of flowers on an inflorescence ranges from 8 to over 100 (EPLING & LEWIS, 1952). To begin to understand the adaptive significance of differences in inflorescence size among species it is necessary to understand the factors that are important in determining inflorescence size within a species. The adaptive significance of inflorescence size has been addressed for a number of plant species, most notably those in the genus *Asclepias* (WILLSON & RATHCKE, 1974; WILLSON & PRICE, 1977; CHAPLIN & WALKER, 1982).

Attempts to answer the question of what limits inflorescence size have been couched in terms of benefits and costs. With regard to benefits, a number of studies have shown that



inflorescences with larger floral displays are more attractive to pollinators (e.g. WILLSON & BERTIN, 1979; MORSE, 1986; CRUZAN, NEAL & WILLSON, 1988; SCHMID-HEMPEL & SPEISER, 1988; KLINKHAMER, DE JONG & DE BRUYN, 1989). In addition, pollinators visit more flowers per visit to large inflorescences (e.g. GEBER, 1985; MORSE, 1986; ANDERSSON, 1988; HESSING, 1988; SCHMID-HEMPEL & SPEISER, 1988). The combination of inflorescence visitation and number of flowers visited per inflorescence determines the number of visits per flower. Visits per flower in turn can affect pollen donation and seed set per flower. Studies that have examined visits per flower as a function of increasing inflorescence size have found several patterns including no change (GEBER, 1985; MORSE, 1986; SCHMID-HEMPEL & SPEISER, 1988), a decelerating increase (ANDERSSON, 1988), an accelerating increase (KLINKHAMER, & AL., 1989) and an increase followed by a decrease (BELL, 1985). Visits per flower is a measure of pollination efficiency and as such deserves attention. However, for purposes of examining the fitness consequences of increasing inflorescence size one must consider the total reproductive output of a plant. This is potentially related to the total visits received by an inflorescence (visits per flower times number of flowers).

One of the costs associated with increasing inflorescence size has to do with its effect on the quality of visits. More visits may not always translate into more seeds set (female function) or more pollen donated (male function). The larger number of flowers visited per visit to larger inflorescences may result in much intra-inflorescence pollen transfer. This may decrease the contribution of visits to both male and female function. For self-incompatible species the cost may be the loss of pollen that could be transferred to other individuals (male function) or the reduction in available outcross pollen (female function). For self-compatible species, geitonogamous pollination may be disadvantageous in that it may produce low quality offspring (HESSING, 1988). Whether these pollination costs alone are sufficient to limit inflorescence size has yet to be fully explored for any species. Another cost associated with larger inflorescences is the energy involved in making additional flowers and their support structures, and provisioning flowers with nectar. In several studies it has been suggested that pollination benefits keep pace with increasing inflorescence size but that available energy limits the number of flowers that can be produced (WILLSON & PRICE, 1977; DAVIS, 1981).

The purpose of this paper is to begin to explore the adaptive significance of inflorescence size within populations of two closely related species in the family *Ranunculaceae*, *Delphinium nelsonii* Greene, larkspur, and *Aconitum columbianum* Nutt. in T. & G., monkshood. These species are very similar in their pollination biology and their inflorescence architecture but differ markedly in inflorescence size (PYKE, 1978a). The present paper reports on the examination of pollinator visitation patterns to inflorescences of different size within populations of both species.

## MATERIALS AND METHODS

The two subject species were studied in the vicinity of the Rocky Mountain Biological Laboratories (RMBL), Crested Butte, Colorado, USA (elevation 2900 m). Both study species are herbaceous perennials with a racemose inflorescence. *D. nelsonii* blooms in the early spring while *A. columbianum* blooms in mid-summer. In the study area the maximum inflorescence height is 20 cm for *D. nelsonii* vs 150 cm for *A. columbianum*. Flowers of both species are protandrous. Flowers open from the bottom to the top of the flower stalk. Flowers that open are in the male phase for approximately 6 days and in the female phase for approximately 2 days (unpub. data). On average then, the bottom quarter of the inflorescence is in the female phase and the upper 3/4 in the male phase. During each of the days a flower is in the male phase, about 6-7 of the approximately 40 anthers dehiscence; dehiscence is spread over the day (unpub. data). Following dehiscence of all 40 anthers the flower enters the



female phase upon which the tips of the pistils reflex slightly to expose the stigmatic surfaces. Both species are self-compatible (PYKE 1978a).

Pollinator visitation data were obtained for *D. nelsonii* on June 17-19, 1981 at Horse Ranch Park in the Gunnison National Forest (elevation approx. 2743 m). The site is 19.3 km west of

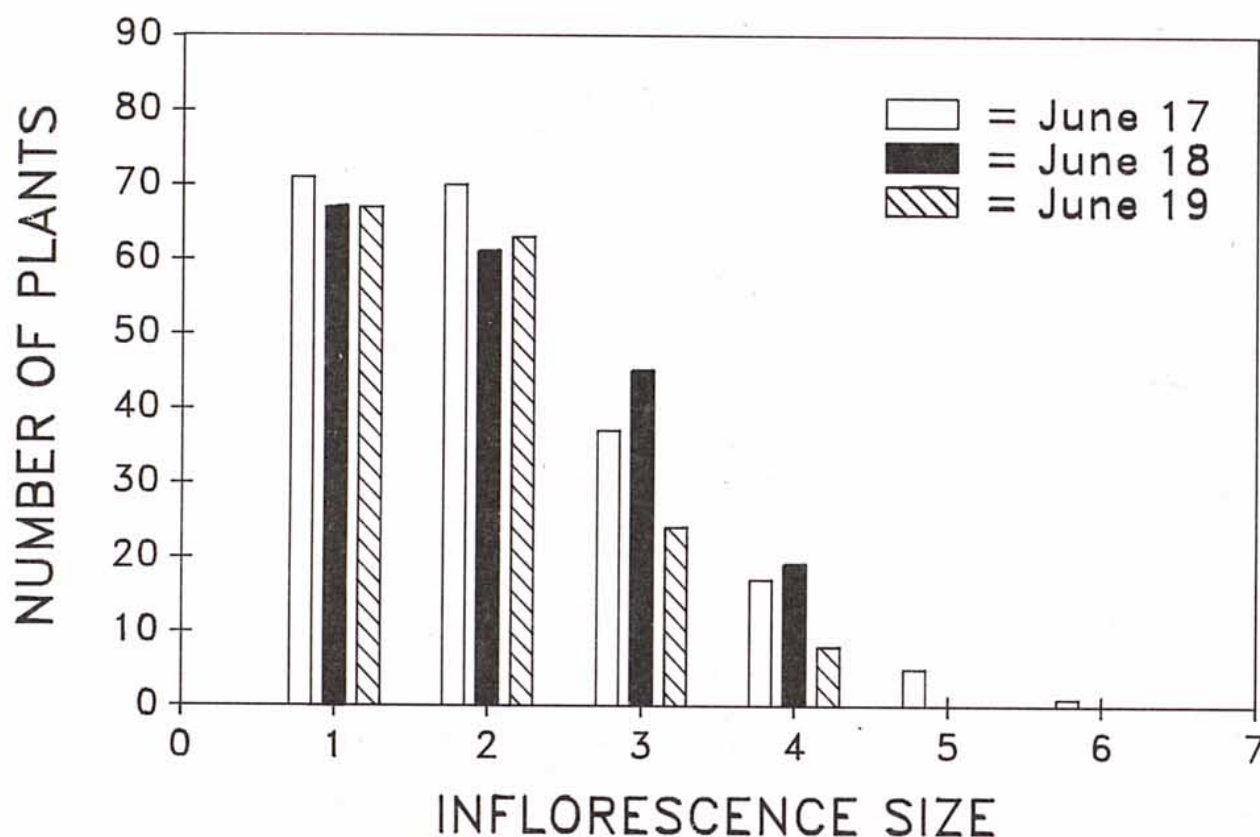


Fig. 1.— Frequency distribution of inflorescence size for *D. nelsonii* on 3 sample dates. Total number of inflorescences for the 3 dates are 201, 192, and 162 for June 17, 18 and 19 respectively.

the town of Crested Butte, Colorado. Each of 205 blooming *D. nelsonii* stalks in a patch approximately  $15 \times 15$  m was tied with colored embroidery thread. Unique color combinations permitted identification of individual plants at a distance and did not influence bumblebee behavior (pers. obs.). The number of open flowers on each stalk (what we will refer to as inflorescence size) was censused on each of the 3 mornings and the total number of flowers produced by each stalk was censused at the conclusion of the study.

During the observation period 2 individuals watched the patch from 0900 to 1800 hrs on each of the 3 days. The primary visitors to this species were queens of *Bombus appositus* and *B. flavifrons* which were collecting nectar. Each bumblebee entering the patch was observed until it left the patch. The number of flowers visited on each plant visited by the bumblebee was recorded. Over the 3 days a total of 1524 bee visits to flowers were observed.

Pollinator visitation data were obtained for *A. columbianum* on July 11, 15 and 18, 1981 in a patch (about  $15 \text{ m}^2$ ) located 1.5 km north of RMBL. The patch contained about 150 inflorescences. Prior to observation all inflorescences in the patch were marked with numbered tags and for each inflorescence a number was painted on each open flower, in sequence, from the



bottom to the top of the inflorescence. During each observation period 3-4 observers monitored the patch and followed every bumblebee that entered the patch until it left. While following a bee, a hand-held tape recorder was used to note every plant and flower visited by the bee. The majority of visitors to *A. columbianum* flowers were workers of *B. flavifrons* with additional visits by workers of *B. appositus*. All visitors were observed to be gathering nectar. For each observation date the number of open flowers on each inflorescence was recorded. The period of observation for each date was: July 11: 1000-1600 hrs; July 15: 0900-1400 hrs; July 18: 1030-1530 hrs. Over the 3 dates a total of 6604 flower visits were observed.

In the statistical analysis of visitation data, linear regressions ( $y = a + bx$ ) or polynomial regressions ( $y = a + bx + cx^2$ ) were made with inflorescence size as the independent variable and the mean of the visitation parameter for each inflorescence size as the dependent variable. Since sample sizes were limited for some of the larger inflorescence size categories (see Figs. 1 and 2 which show the number of individuals in each size class), several size classes were combined as follows: *D. nelsonii*: June 17: sizes 5-6; *A. columbianum*: July 11: sizes 12-15, 24-26; July 15: sizes 11-13, 14-16, 19-22; July 18: sizes 11-12, 13-16, 19-20.

## RESULTS

*D. nelsonii*: Figure 1 shows the frequency distribution of inflorescence size. The average number of open flowers was 2.01 (S.D. = 0.99,  $n = 555$ ). Inflorescence size, which we have defined as the number of open flowers, is a reflection of the size of the entire plant and not just a transient phenomenon experienced by plants of all sizes. For each of the 3 sample dates inflorescence size was significantly correlated with the total number of flowers the plant produced over its flowering span (June 17:  $r = 0.66$ ; June 18:  $r = 0.62$ ; June 19:  $r = 0.47$ ;  $p < 0.001$ ,  $n = 205$  for all 3 dates).

Figs. 2-4 depict the effect of inflorescence size on 3 aspects of pollinator visitation: the number of visits an inflorescence receives (fig. 2), the number of flowers visited per visit to an inflorescence (fig. 3), and the number of visits per flower (fig. 3). For each of the 3 dates, visits per inflorescence (fig. 2) increases linearly with increasing inflorescence size. Thus larger inflorescences are more attractive than smaller ones. The average probability (across the 3 sample dates) of a plant with 1, 2, 3, 4, 5 or 6 flowers receiving no visits during a day is 0.26, 0.12, 0.04, 0, 0, 0 respectively. For each of the 3 dates, the number of flowers visited per visit to an inflorescence (fig. 3) increases with inflorescence size. The slope of the relationship is less than 1.0, indicating that a smaller proportion of the available flowers is visited on larger inflorescences. The data are slightly better fit by a polynomial regression than a linear regression, suggesting a slowing of the rate of increase in flower visits with increasing inflorescence size. Visits per inflorescence and flowers per visit combine to determine the pattern of visits per flower. For each of the 3 dates, the number of visits per flower increases with inflorescence size (fig. 4) but the pattern of increase varies. On June 17 (fig. 4-A) the increase is linear, on June 18 (fig. 4-B) the increase accelerates with increasing inflorescence size, and on June 18 (fig. 4-C) there is a decelerating increase. All the relationships are best fit by a polynomial regression.

*A. columbianum*: Figure 5 shows the frequency distribution of inflorescence size for each of the 3 sample dates. The average number of open flowers was 7.31 (S.D. = 4.4,  $n = 393$ ). As for *D. nelsonii*, inflorescence size is significantly correlated with the total number of flowers a plant produced over its flowering span (July 11:  $r = 0.76$ ,  $p < 0.0001$ ,  $n = 95$ ; July 15:  $r = 0.40$ ,  $p < 0.0003$ ,  $n = 78$ ; July 18:  $r = 0.51$ ,  $p < 0.0001$ ,  $n = 56$ ).

Figs. 6-8 depict the effect of inflorescence size on the 3 pollinator visitation parameters. All the relationships were best fit by a polynomial regression model. For each of the 3 dates, the number of visits per inflorescence increases with increasing inflorescence size, but at a

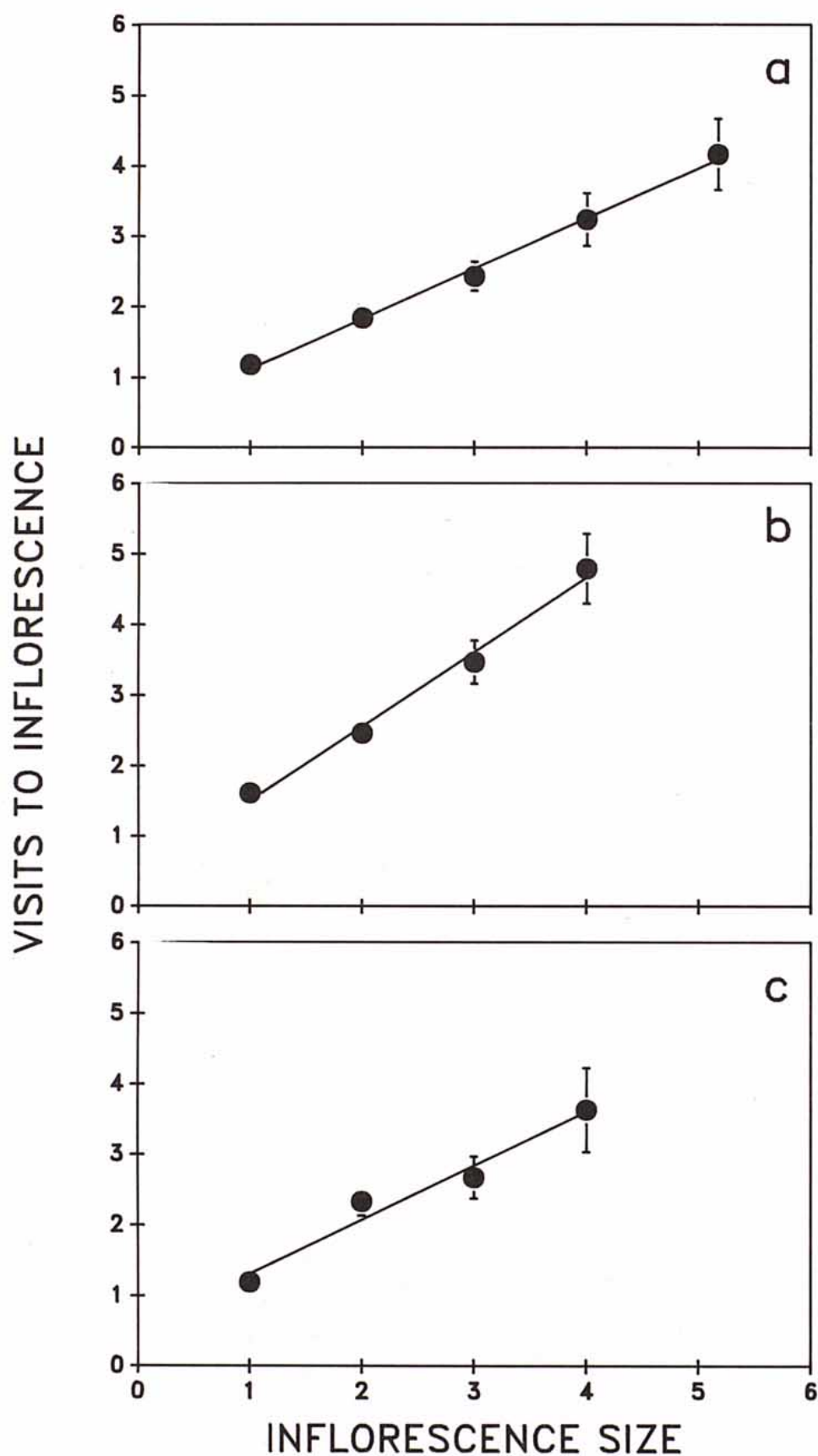


Fig. 2.— *D. nelsonii*. Number of visits received by inflorescences of different size. a) June 17:  $r = 0.998$ ,  $p < 0.01$ ; b) June 18:  $r = 0.995$ ,  $p < 0.01$ ; c) June 19:  $r = 0.982$ ,  $p < 0.01$ . All  $r$  values based on linear regression, sample sizes for each size class can be obtained from Fig. 1.



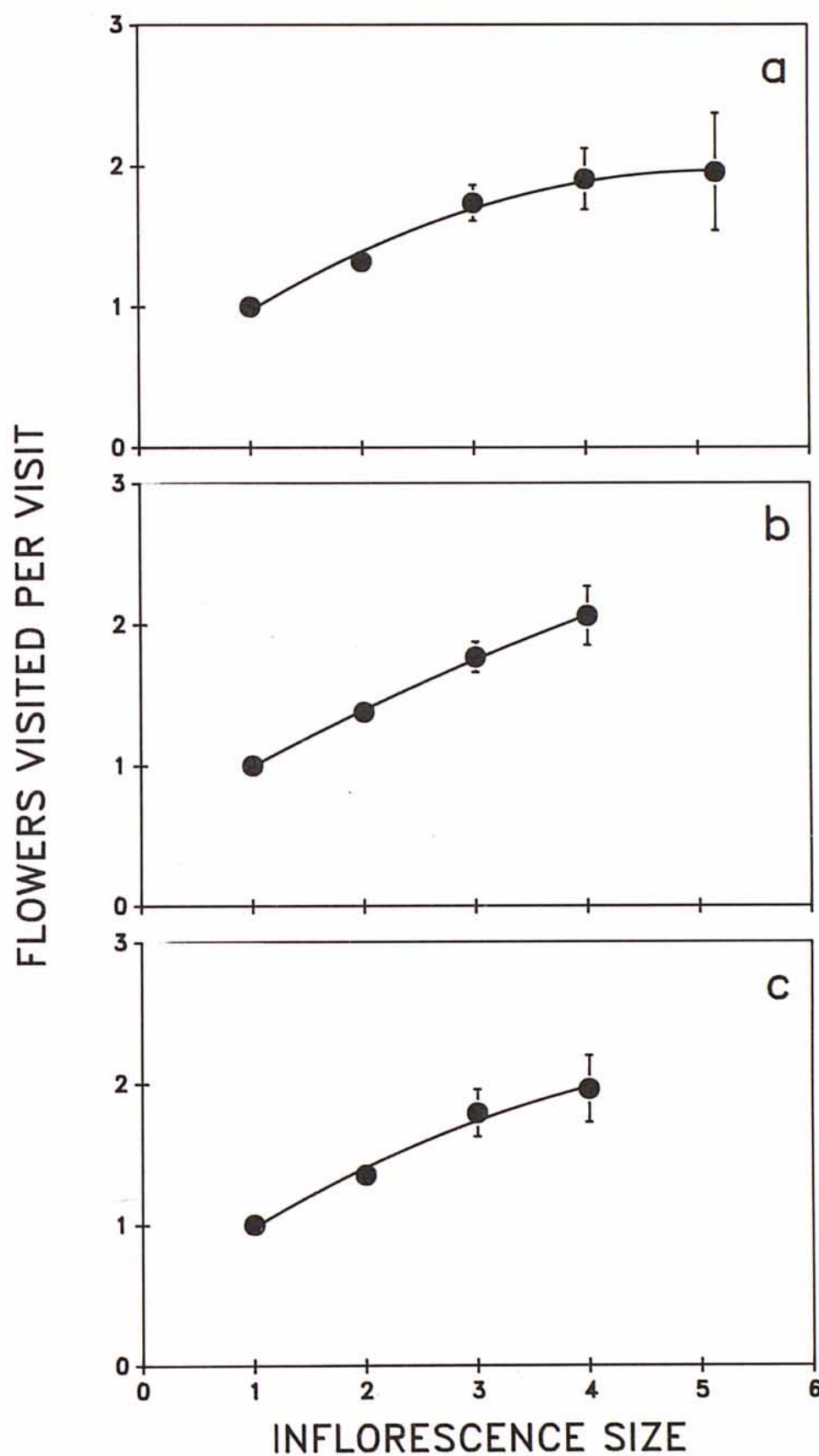


Fig. 3.— *D. nelsonii*. Number of flowers visited per visit to inflorescences of different size. a) June 17:  $r = 0.994$ ,  $p < 0.01$ ; b) June 18:  $r = 0.999$ ,  $p < 0.01$ ; c) June 19:  $r = 0.994$ ,  $p < 0.01$ . All  $r$  values based on polynomial regression, sample sizes for each size class can be obtained from Fig. 1.

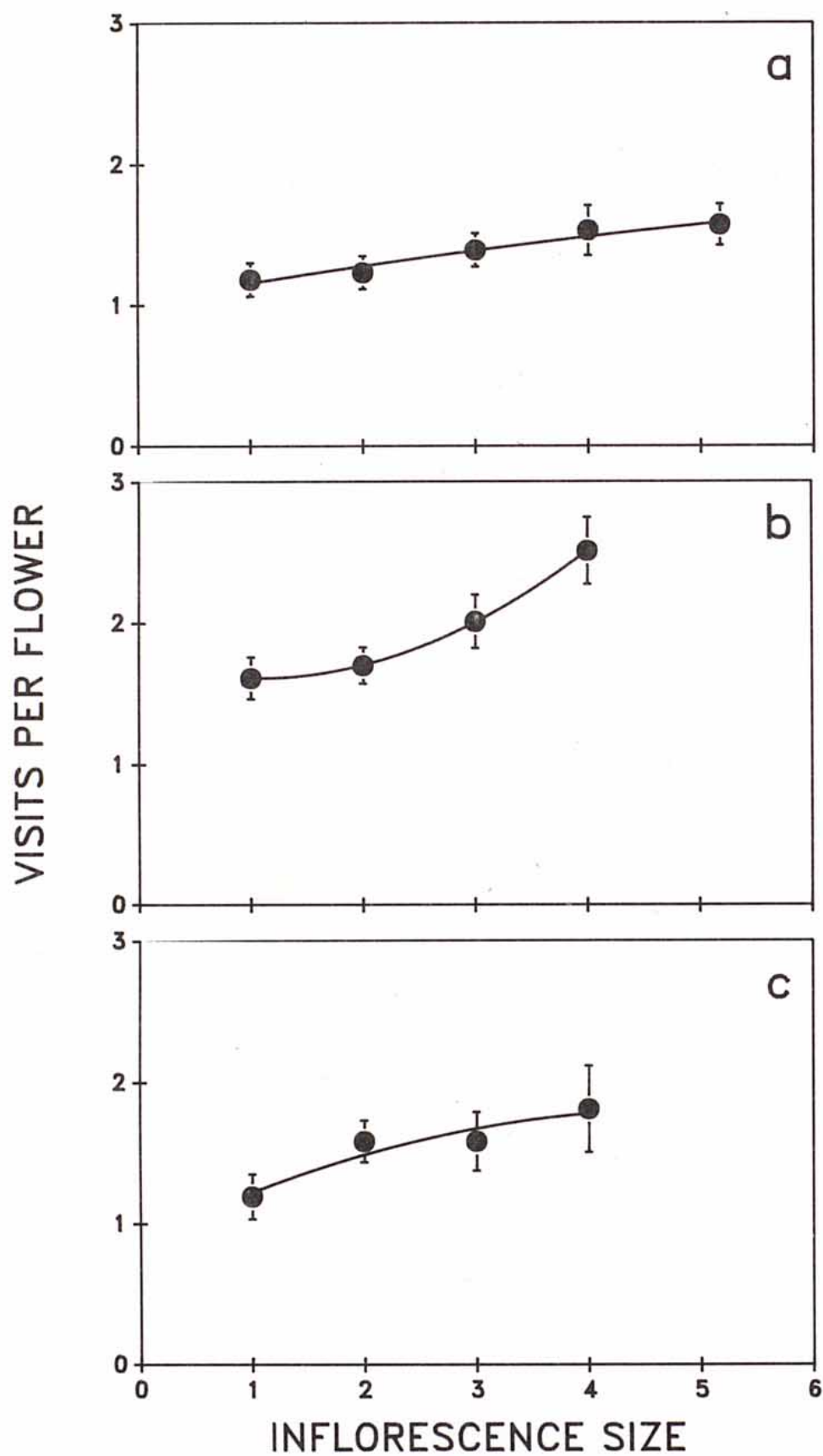


Fig. 4.— *D. nelsonii*. Number of visits per flower for inflorescences of different size. a) June 17:  $r = 0.999$ ,  $p < 0.01$ ; b) June 18:  $r = 0.999$ ,  $p < 0.01$ ; c) June 19:  $r = 0.95$ ,  $p < 0.01$ . All  $r$  values based on polynomial regression, sample sizes for each size class can be obtained from Fig. 1.



decelerating rate (fig. 6). Thus larger inflorescences are more attractive but not as attractive as would be expected if attractiveness was proportional to the number of open flowers. Beyond about 15 flowers there appears to be no further increase in attractiveness. The number of flowers visited per visit (fig. 7) increases with increasing inflorescence size, but also at a decelerating rate. This is most evident for July 11 (fig. 7-A), but is less pronounced for the

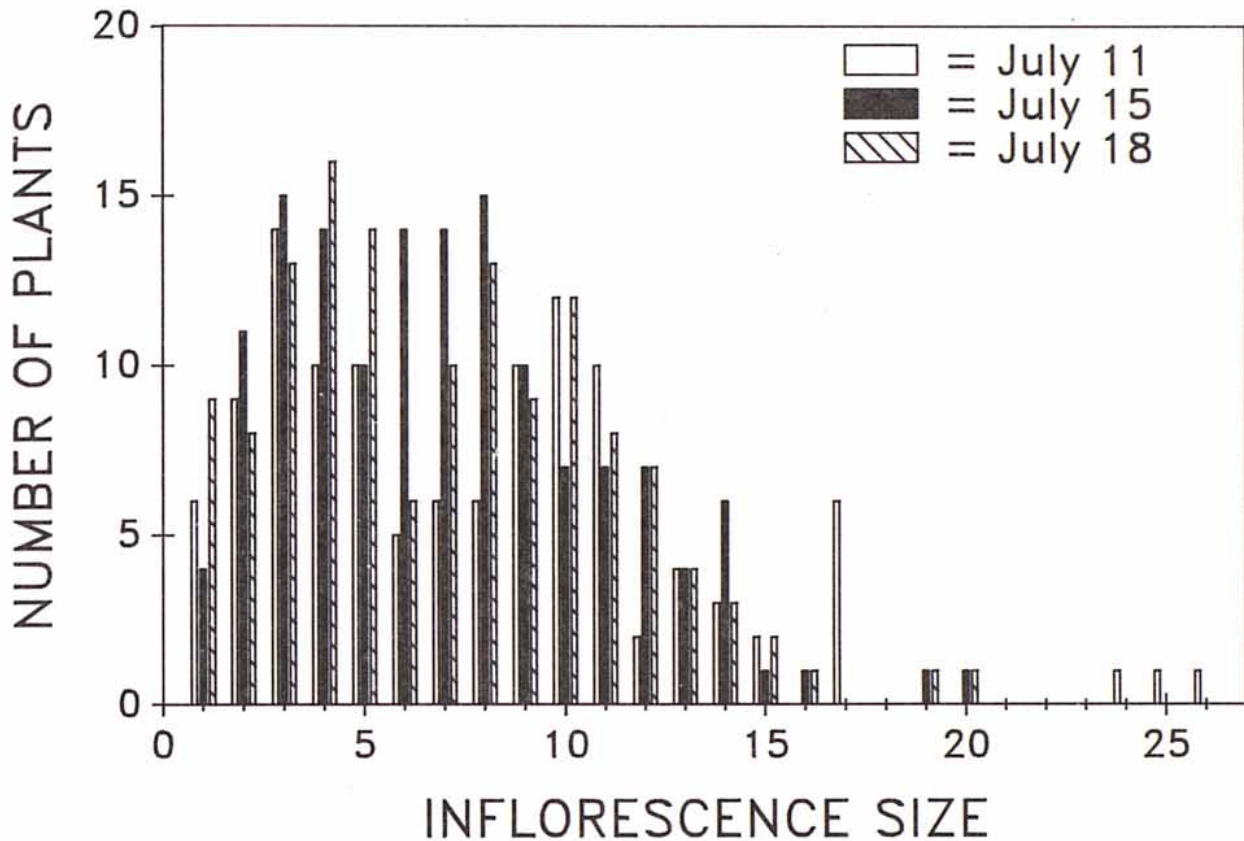


Fig. 5.— Frequency distribution of inflorescence size for *A. columbianum* for 3 sample dates. Total number of inflorescences for the 3 dates are 114, 142, and 137 for July 11, 15 and 18 respectively.

other 2 dates (figs. 7-B and 7-C) although the regression relationship for these latter two is still best described by a polynomial. The number of visits per flower (fig. 8) reflects the decelerating increase in both visits per inflorescence and flowers per visit with increasing inflorescence size; the combination results in the largest inflorescence size class having fewer visits per flower for 2 of the sampling dates (figs. 8-A and 8-B). Thus larger inflorescences generally have more visits per flower but this trend is reversed for the largest inflorescences.

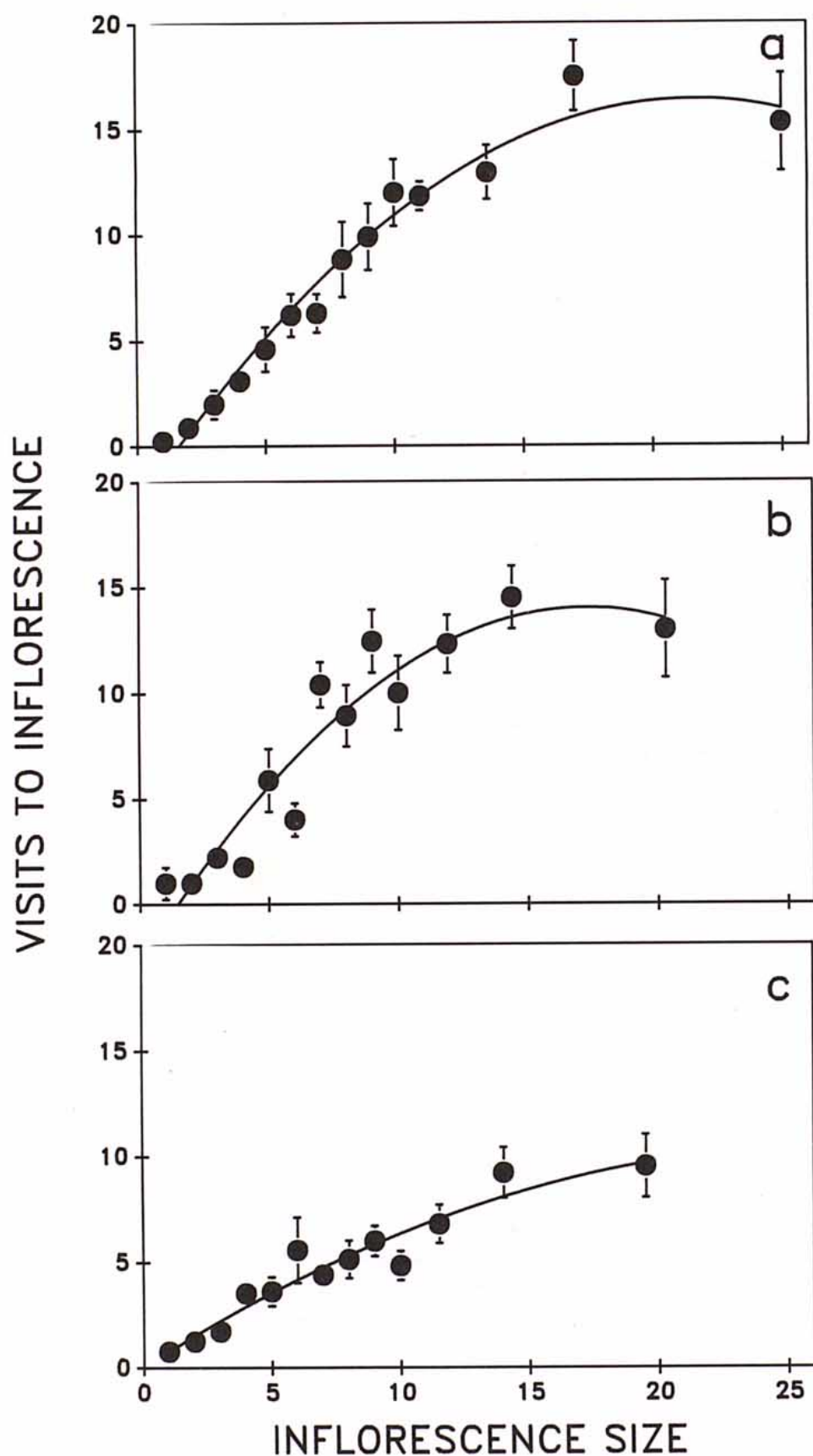


Fig. 6.— *A. columbianum*. Number of visits received by inflorescences of different size. a) July 11:  $r = 0.987$ ,  $p < 0.01$ ; b) July 15:  $r = 0.949$ ,  $p < 0.01$ ; c) July 18:  $r = 0.962$ ,  $p < 0.01$ . All  $r$  values based on polynomial regression, sample sizes for each size class can be obtained from Fig. 5.



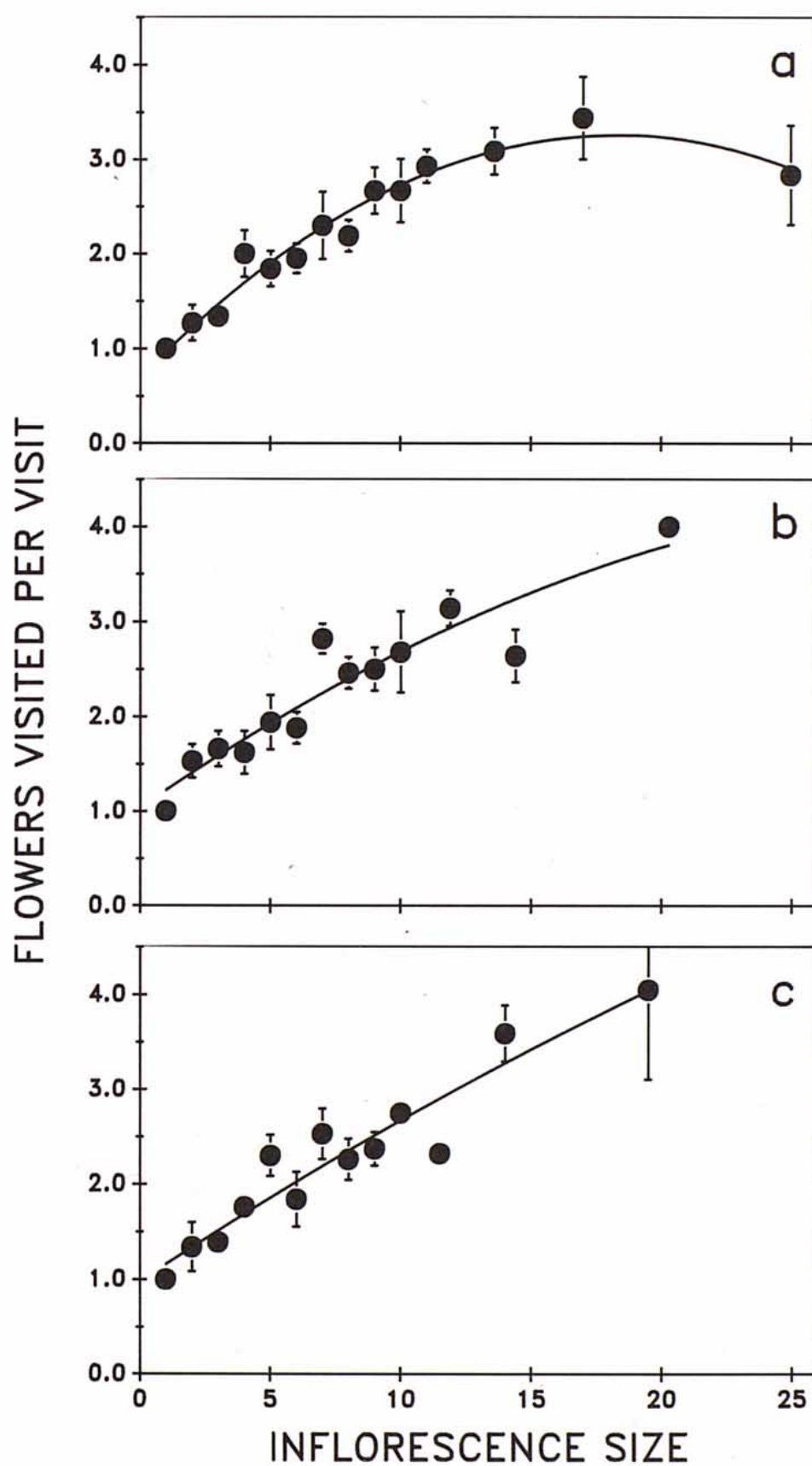


Fig. 7.— *A. columbianum*. Number of flowers visited per visit to inflorescences of different size. a) July 11:  $r = 0.981$ ,  $p < 0.01$ ; b) July 15:  $r = 0.939$ ,  $p < 0.01$ ; c) July 18:  $r = 0.95$ ,  $p < 0.01$ . All  $r$  values based on polynomial regression, sample sizes for each size class can be obtained from Fig. 5.

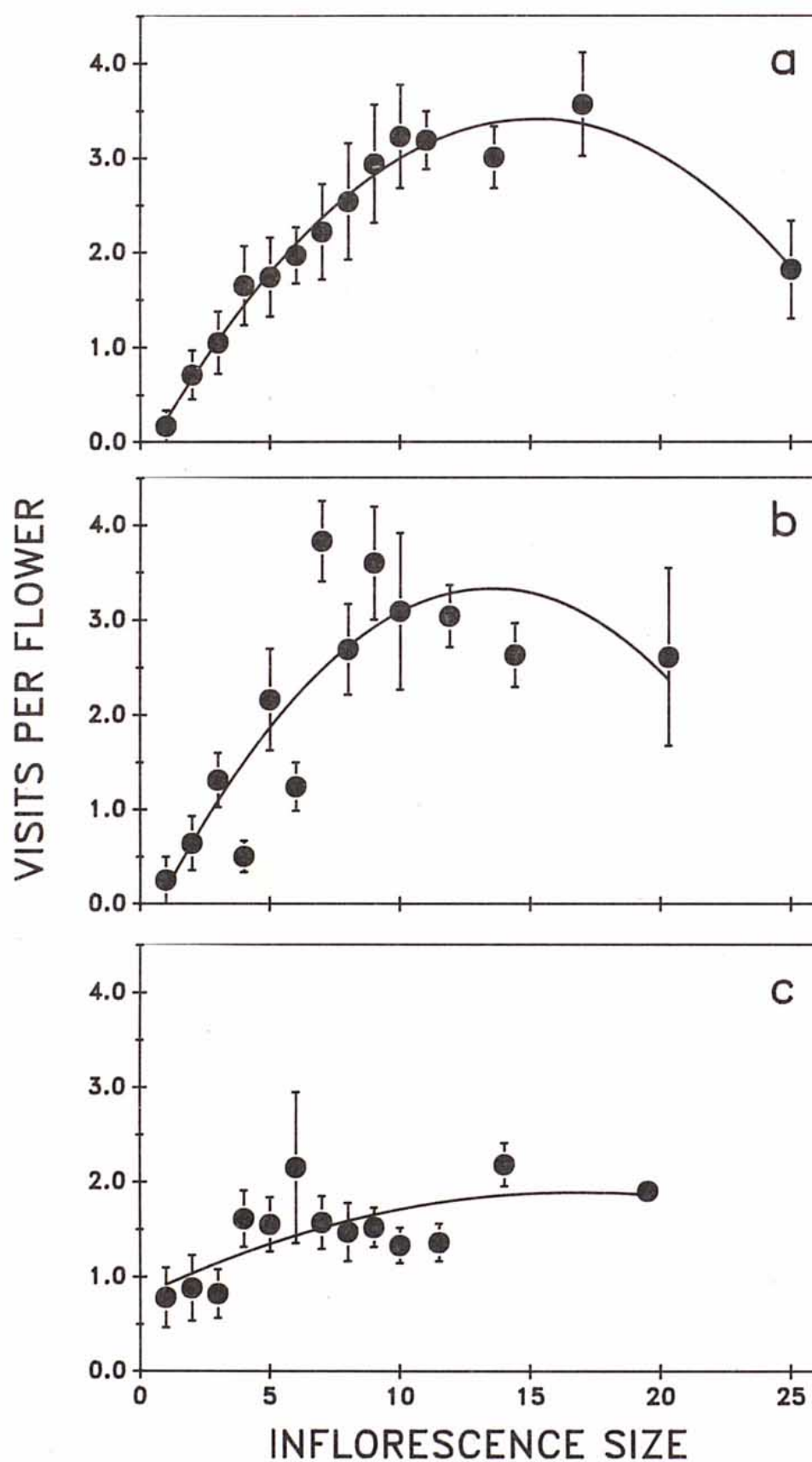


Fig. 8.— *A. columbianum*. Number of visits per flower for inflorescences of different size. a) July 11:  $r = 0.987$ ,  $p < 0.01$ ; b) July 15:  $r = 0.85$ ,  $p < 0.01$ ; c) July 18:  $r = 0.69$ ,  $p < 0.001$ . All  $r$  values based on polynomial regression, sample sizes for each size class can be obtained from Fig. 5.



## DISCUSSION

**Visits per inflorescence:** For *D. nelsonii* the relative attractiveness of inflorescences is directly proportional to their size, but for *A. columbianum*, while larger inflorescences are also more attractive than small inflorescences, they are proportionately less so. Although a number of studies have found a positive correlation between inflorescence size and attractiveness, few have explored the functional relationship between the two. ANDERSSON (1988) found that attractiveness did not continue to increase proportionally for plants with larger numbers of inflorescences. The data presented in PYKE (1981), CRUZAN & AL. (1988) and SCHMID-HEMPEL & SPEISER (1988) can also be interpreted this way, although the authors never addressed this point. In general, it appears that increments in inflorescence size have a relatively smaller beneficial effect on attractiveness as inflorescence size increases.

These results can best be explained by the concept of just noticeable difference. Two inflorescences that differ in size by 1 flower will be more readily perceived as different by bumblebees when both inflorescences are small, as would be the case for inflorescences of *D. nelsonii*, than when both inflorescences are large, as would be the case for inflorescences of *A. columbianum*.

That pollinators should be attracted to larger inflorescences makes sense from a foraging economics standpoint (PYKE, 1981); larger inflorescences represent a more concentrated patch of resources. Once a bee is on an inflorescence, another resource point (a flower and its nectar) on the same inflorescence is not as far away as a resource point on a new inflorescence. For *A. columbianum* it takes 5.6 s to travel to and obtain the nectar from the next flower on the same inflorescence but 8.2 s to travel to a flower on a new inflorescence and obtain the nectar (PLEASANTS, unpub. data). For *D. nelsonii* it takes 0.7 s to travel to the next flower on an inflorescence and 1.7 s to travel to a new inflorescence (HODGES, 1981). Minimizing flight time on larger inflorescences will only yield a higher nectar energy intake rate if the average standing crop of nectar on larger inflorescences is at least the same as that for smaller inflorescences. For *A. columbianum*, nectar standing crop has been found to be the same (PYKE, 1982) or greater (PLEASANTS, unpub. data) on larger inflorescences.

**Flowers visited per inflorescence:** For both *D. nelsonii* and *A. columbianum*, the number of flowers visited did not increase in direct proportion with increasing inflorescence size, i.e. a smaller proportion of the available flowers was visited on larger inflorescences. This phenomenon has been observed in a number of other studies (GEBER, 1985; CIBULA & ZIMMERMAN 1987; MORSE, 1986; ANDERSON, 1988; SCHMID-HEMPEL & SPEISER, 1988). The functional relationship between inflorescence size and number of flowers visited has rarely been explored (PYKE, 1978b). When there is a linear relationship between the two, a smaller proportion of flowers visited with increasing inflorescence size will be obtained whenever the slope of the regression is less than 1. We found not only a slope less than 1 but a lower slope for larger inflorescence sizes (nonlinear relationship). Thus larger inflorescences have an even lower proportion of their flowers visited than would be expected on the basis of a linear relationship. It should be mentioned that PYKE (1982), in another study on *A. columbianum*, described the relationship between flower visits and inflorescence size as linear. However, the largest inflorescence size he examined was 14, compared to 25 in the present study, and his data points (his fig. 1) would be better fit by a non-linear relationship such as ours.

No attempt has previously been made to explain the cause of the phenomenon of a diminishing proportion of available flowers visited as inflorescence size increases. For *D. nelsonii* and *A. columbianum*, inflorescence architecture and pollinator movement patterns on an inflorescence might suggest that the number of flowers a bee visits on an inflorescence could be proportional to the number available. Both species have a racemose inflorescence which means their flowers can be visited systematically. Several studies have shown that bees tend to start at the bottom of such inflorescences and move progressively upward, rarely



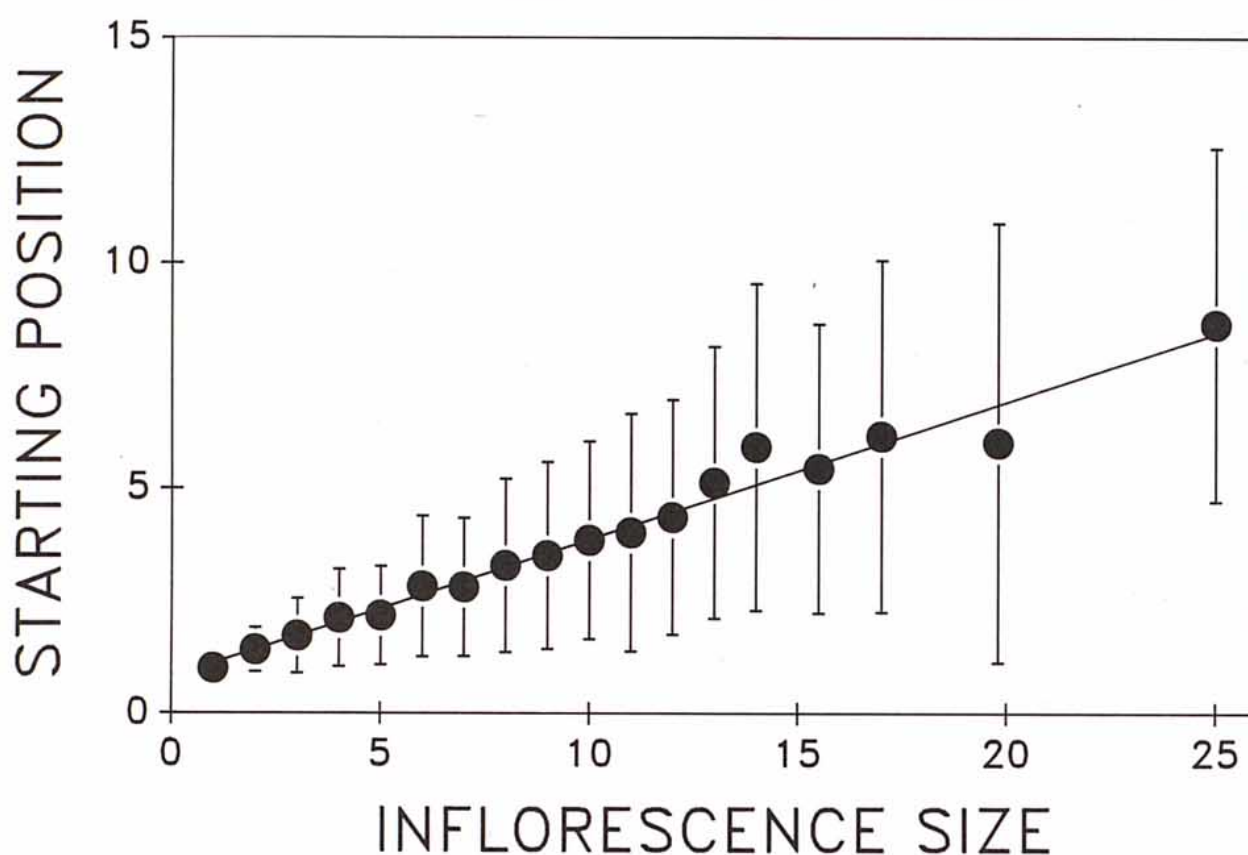


Fig. 9.— Starting position on *A. columbianum* inflorescences (means  $\pm$  1 S. D. are shown). Sample sizes for each inflorescence size are as follows 1-8, 2-29, 3-89, 4-99, 5-136, 6-114, 7-203, 8-244, 9-272, 10-260, 11-246, 12-137, 13-162, 14-130, 15-5-93, 17-104, 19-8-56, 25-43. Linear regression:  $r = 0.995$ ,  $p < 0.0001$ .

revisiting flowers (PYKE, 1982; HODGES, 1985b). There is a general pattern of decreasing standing crop of nectar proceeding from the bottom to the top of the inflorescence (PYKE, 1982; HODGES, 1985a). Because bees are likely to depart from an inflorescence when a low reward is encountered (PLEASANTS, 1989), we might expect the average departure position relative to the number of positions available (inflorescence size) to be similar for all inflorescence sizes. This would produce a constant proportion of flowers visited for all inflorescence sizes.

The fact that this is not the case can be explained by considering bumblebee foraging behavior, in particular the probability of a bee visiting another flower on an inflorescence. For both *A. columbianum* and *D. nelsonii* that probability is on average 0.65 (unpub. data). We propose a model of bee behavior on an inflorescence which consists of the following 4 rules: 1) a bee arrives at some position on the inflorescence; 2) a bee always moves upward; 3) if more flowers are available above the first position visited on the inflorescence the bee will visit the next closest flower; and 4) after visiting a flower the probability of visiting another flower is 0.65. The predicted number of visits per inflorescence is thus given by the sum of  $(1 + 2x + 3x^2 \dots nx^n)$ , where  $x$  is the average probability of going to the next flower and  $n$  is the number of flowers available).

Before presenting the results of this foraging model it is important to discuss the validity of each of these rules. **Rule 1:** Although it has been shown that bees tend to start at the bottom of racemose inflorescences (PYKE, 1978a; HODGES, 1985b), the actual starting point is usually not the bottommost flower. For *A. columbianum* the starting point increases linearly with increasing inflorescence size (fig. 9). Consequently, if bees tend to move upward, the number of flowers available to be visited will be fewer than the number of open flowers. **Rule 2:** The



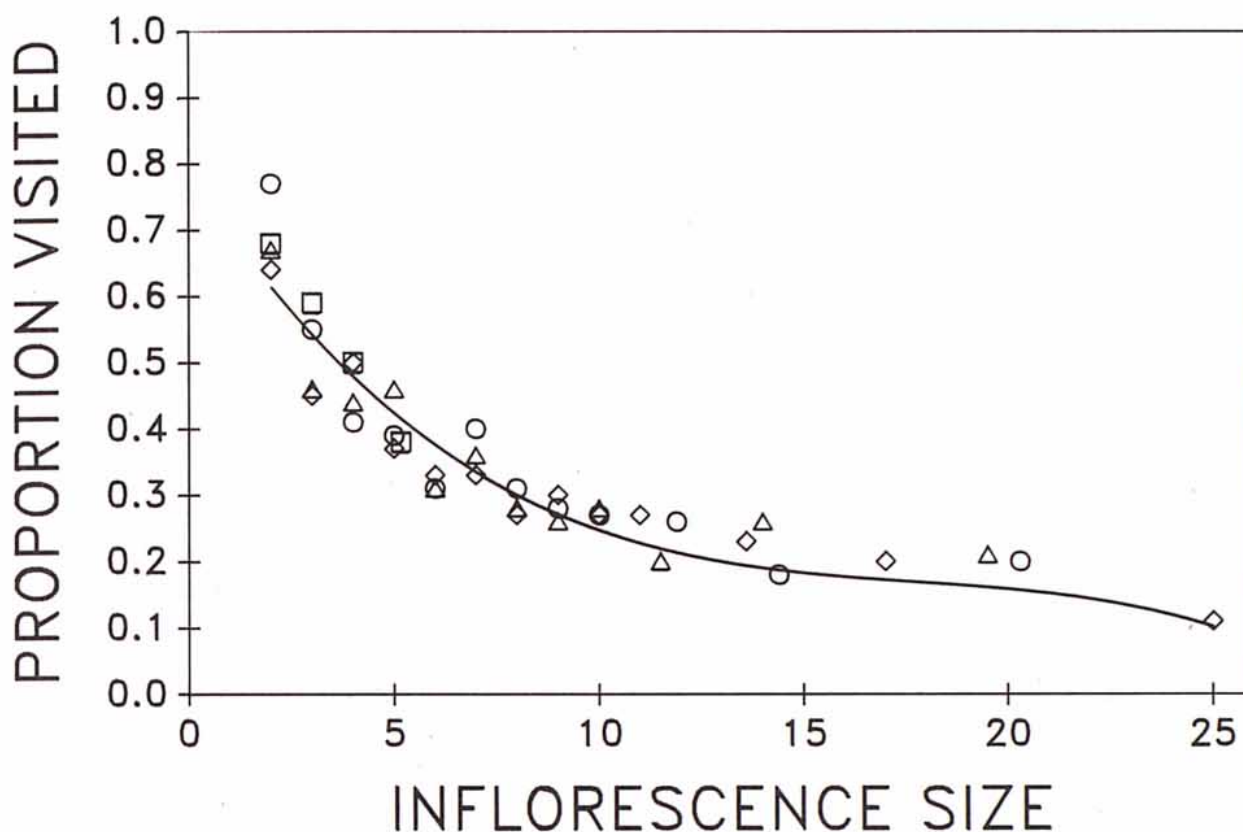


Fig. 10.—Proportion of flowers visited per visit to an inflorescence. Symbols: *A. columbianum*: diamonds = July 11, circles = July 15, triangles = July 18; *D. nelsonii*: squares = average over 3 dates. The line is based on a model of pollinator visitation (see text).

assumption that bees always move upward is a simplification. For *A. columbianum* the probability of upward movement is 0.74 (PLEASANTS, unpub. data) and for *D. nelsonii* 0.80 (HODGES, 1985b). Including the possibility of downward movements is not likely to change the results of the model. **Rule 3.** That bees go to the next nearest flower on an inflorescence has empirical support (PYKE, 1979). Because of the angle of placement of successive flowers on both *A. columbianum* and *D. nelsonii* inflorescences, the nearest flower may not always be the next higher one, consequently flowers will be missed (PYKE, 1978a, 1979). For *A. columbianum* about 30 % of flowers are missed between the arrival position and the departure position (PLEASANTS, unpub. data) and a comparable percentage is found for *D. nelsonii* (PYKE, 1978a). This means that not all of the flowers above the starting position will be available to be visited. **Rule 4:** the probability of moving to another flower is in reality not fixed but is larger or smaller depending on whether the reward received at the present flower is higher or lower than average, respectively (PLEASANTS, 1989; PLEASANTS unpub. data). This decision behavior reflects the fact that the nectar amount in the next flower is correlated with the amount in the present flower (PYKE, 1982; PLEASANTS, 1989). However, for any particular flower the reward it has when visited will vary from one visit to another. Thus on average, the probability that a bee will go from this flower to another will be 0.65 and we will consider this to be a fixed probability for the model.

The proportions of flowers visited on *A. columbianum* inflorescences of different size are shown in Fig. 10. Because bee foraging behavior on *D. nelsonii* is expected to be similar, data for this species are also included (see also CIBULA & ZIMMERMAN, 1984). Also included in this figure is a line representing the expected proportion of flowers visited on inflorescences of



different size if bees forage according to the four rules listed above. The agreement between observed and expected is close, supporting the validity of the model.

One of the predictions of the model is that the average number of flowers visited on an inflorescence will reach an asymptote at about 3 flowers with increasing inflorescence size. This is somewhat smaller than the observed number of flowers visited on large inflorescences of *A. columbianum* (3.44, 4.0 and 4.05 for the 3 sampling dates). This is because the probability of visiting another flower is actually higher than 0.65 (average 0.75) for larger inflorescences (and correspondingly lower for smaller inflorescences). This higher probability translates into a maximum of 3.7 flowers visited per inflorescence, closer to that observed.

The higher probability of moving to another flower on larger inflorescences could be due, in part, to the higher average standing crop of nectar on large inflorescences (PLEASANTS, unpub. data). But for the same nectar reward in the present flower, the probability of visiting another flower is also higher for larger inflorescences (PLEASANTS, unpub. data). This behavior could be due to the fact that the standing crop declines less precipitously for larger inflorescences (PLEASANTS, unpub. data). Thus for any given reward obtained from the present flower, the reward expected from the next flower, on average, will be greater for larger inflorescences. Bees have been shown to forage as if they were aware of different reward expectations for flowers in different positions on an inflorescence (PLEASANTS, 1989).

The model may also be applied to other species with racemose inflorescences. The predicted limit to the average number of flowers visited of 3-4 is found for several species despite some of them having a larger average inflorescence size than *A. columbianum*. For *D. barbeyi*, which has an average number of open flowers of 17.0 (PYKE, 1978a), the number of flowers visited on large inflorescences is about 4 (CIBULA & ZIMMERMAN, 1987). In a study on *D. virescens* (WADDINGTON 1981), the largest inflorescences, which can have more than 9 open flowers, averaged 3.7 flower visits. *Epilobium* (= *Chaemaenerion*) *angustifolium* which has an average of 12.3 open flowers (PYKE, 1978a) has between 3.5 and 4.5 flowers visited on large (16 flower) inflorescences (SCHMID-HEMPEL & SPEISER, 1988).

For plant species that do not have a racemose inflorescence, or any other inflorescence architecture that allows pollinators to visit flowers in a systematic fashion, a different explanation may be necessary for the observed pattern (GEBER, 1985; MORSE, 1986; ANDERSSON, 1988) of a diminishing proportion of flowers visited as inflorescence size increases. Non-systematic visitation means that bees will leave a spatially haphazard trail of empty flowers after visiting an inflorescence. The cumulative effect of such visits may be that the larger the inflorescence the smaller the proportion of flowers visited by a bee before a low reward flower is encountered, causing the bee to leave. This explanation will have to be verified by foraging studies of bees on species with such inflorescence types. To date no such studies have been done.

**Visits per flower:** Visits per flower decreased or reached a plateau for the largest inflorescence sizes of *A. columbianum* while for *D. nelsonii* visits per flower continued to increase. Several other studies found no difference in visits per flower between larger and smaller inflorescences (GEBER, 1985; MORSE, 1986; SCHMID-HEMPEL & SPEISER, 1988) but these studies did not look at a range of inflorescence sizes, only two or three size classes. One study found an increase in visits per flower with increasing size (KLINKHAMER & AL., 1989), another study found a plateau effect (ANDERSSON, 1988) while still another study found lower visits per flower for the largest size (BELL, 1985).

For *D. nelsonii*, the fact that visits per flower increases with inflorescence size in the present study suggests that pollinator visitation does not place limits on inflorescence size in this species. Larger plants not only have more visits per flower but more total visits. It is unlikely that visit quality will suffer for larger inflorescences because of the increased amount of intra-inflorescence movement. When an inflorescence is visited, the number of flowers



visited is so small relative to the pollen carryover in this species (WASER, 1988) that a sufficient amount of outcross pollen is likely to be available (no loss in female function) and the amount of self pollen lost in self-pollination is likely to be small (no loss in male function).

It seems probable then that available energy limits inflorescence size in *D. nelsonii*. That energy limits exist for this species is apparent from ZIMMERMAN's (1983) study in which natural seed set declined from bottom to top flowers. The fact that hand pollination did not significantly increase seed set indicates that the seed set decline is a reflection of energy limits and not pollinator activity differences. Seed set is near 0 for the top flowers (position 6) indicating that further increases in inflorescence size would not contribute to the female component of plant fitness although there could be a contribution to the male component.

For *A. columbianum* the possibility exists that diminishing returns in pollinator visitation may be a factor in limiting inflorescence size. In this species the number of visits per flower is reduced for the largest inflorescences. This suggests that seed set per flower will be reduced as well because for the 3 sample dates seed set is positively correlated with visits per flower (results at or near statistical significance for 2 dates) (July 11:  $r = 0.31$ ,  $p = 0.06$ ,  $n = 27$ ; July 15:  $r = 0.34$ ,  $p = 0.02$ ,  $n = 37$ ; July 18:  $r = 0.19$ ,  $p = 0.17$ ,  $n = 27$ ).

As pointed out earlier, however, the total number of flower visits an inflorescence receives, rather than visits per flower, is the most appropriate indicator of the fitness, and thus the value of inflorescence size. The 3 largest plants in the study (avg. inflorescence size = 25, July 11) actually have a lower total number of flower visits than 17-flower plants from the same date (45.5 vs 60.7). However, the largest inflorescence class on July 15 and 18 (avg. 20 open flowers) has more total visits than the next largest class on those dates (July 15: 52.9 vs 37.9; July 18: 37.1 vs 30.5). It is tempting to say that beyond an inflorescence size of about 20 flowers further increases in inflorescence size are disadvantageous. However, because of the small sample size (3 plants) we must be cautious in our interpretation. This points out the dilemma of studying the effects of inflorescence size using the natural range available. If plants are pursuing the optimal strategy we should not find inflorescences that are larger than the optimal size, making it difficult to identify the suboptimal inflorescence size. We can only say at this point that inflorescence size in *A. columbianum* may be limited by pollination. It is interesting to note that large plants of this species typically have side branch inflorescences (PLEASANTS pers. obs.). This indicates that there is sufficient energy to make an even larger inflorescence. The fact that plants do not simply add more flowers to the main inflorescence implies that there is a disadvantage in doing so.

We have not examined possible changes in visit quality with increasing inflorescence size in *A. columbianum*. To do so would require examining different inflorescence sizes and obtaining data on the amount of pollen picked up per visit to a male-phase flower that is donated to female-phase flowers on other inflorescences (male function), and the amount of outcross pollen deposited per visit to a female-phase flower (female function). A study using fluorescent dye particles to track pollen dispersal and electrophoresis to determine parentage is currently in progress.

We have also not investigated the cost to the plant of producing additional flowers. Although the caloric value of floral structures and nectar could be obtained, the costs must be described in the same currency as the benefits (seed set) to make a valid assessment of the net gain of adding flowers. Caloric values would have to be converted to their effect on present or future seed set, which is a difficult task.

The purpose of the present study was to begin to explore the costs and benefits of different sized inflorescences. Clearly more studies investigating not only the quantity but also the quality of visits as a function of inflorescence size are needed to answer more fully the question of what limits inflorescence size.



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