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FLORAL DISPLAY IN *PHYLA INCISA*: CONSEQUENCES FOR MALE AND FEMALE REPRODUCTIVE SUCCESS

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Abstract.—The inflorescences of *Phyla incisa* consist of flowers in two phases: younger, nectar-containing flowers that have yellow corolla throats and older, nectar-lacking flowers that have dark purple corolla throats. Observations of pollinator visitation patterns to both natural and manipulated inflorescences were made to determine the role of each flower phase in pollinator attraction. The effect of older-phase flowers on male and female reproductive success was determined by comparing stigmatic pollen loads and estimates of pollen removal from inflorescences having different numbers of these flowers.

The pollinators of *Phyla* selected larger inflorescences more often than expected based upon the size distribution of inflorescences available to them. Both younger- and older-phase flowers contributed to the attraction of pollinators, but the latter were less effective in this function. The presence of older-phase flowers significantly increased the visitation rate to inflorescences and the amount of pollen removed but had little effect on pollen deposition on stigmas. The lack of correspondence between pollen deposition and pollinator-visitation rate was not due to stigma saturation, since stigma loads varied greatly. The data indicate that the deposition of pollen on stigmas in this species is a relatively stochastic process, whereas pollen removal from inflorescences occurs at a much more regular rate. Old-phase flower retention appears to contribute to reproductive success through increased pollen donation when pollinator activity is high and may also increase the probability of seed set when pollinators are rare.

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The attraction of pollinators is of primary importance for insect-pollinated plants. One factor that has been shown to be important for the attraction of pollinators is the size of a plant's floral display (Willson and Rathcke, 1974; Willson and Price, 1977; Willson and Bertin, 1979; Schaffer and Schaffer, 1980; Thomson et al., 1982). Increased visitation rates to plants with larger floral displays may affect female reproductive success (pollen receipt) and/or male reproductive success (pollen removal). Species of plants in several families increase the size of their floral display without increasing the number of flowers produced by retaining the corollas of older, nonfunctional flowers that would otherwise be abscised (see Gori [1983] for a review). There are presumably costs involved in the retention of these corollas (e.g., transpirational, respirational), so it is reasonable to suggest that the presence of these flowers confers some advantage to the plant. As early as 1877, Fritz Müller recognized that these old-phase flowers, which lack pollinator rewards and are not typically visited by pollinators, probably function as visual attractants to pollinators (Müller, 1877). This hypothesis has been confirmed for some species (Gori, 1983; Jones and Cruzan, 1988); however, the expected increase in the reproductive success of these plants has been more difficult to demonstrate.

Most studies addressing questions about the characteristics of floral displays and their consequences for the reproductive success of plants have concentrated on measures of female reproductive success (i.e., fruit and seed set). Pollinia removal has been used as an index of male reproductive success in *Asclepias* (Willson and Rathcke, 1974; Willson and Bertin, 1979; Queller, 1983), and a species of orchid (Schemske, 1980), but much less is known about male function for the majority of plant species, which have granular pollen. It has been suggested that male reproductive success may more often be limited by pollinator activity than is female reproductive success (Bell, 1985), and some recent evidence indicates that male

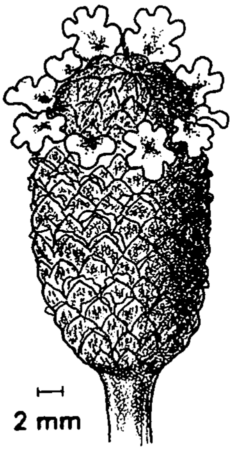


FIG. 1. A schematic representation of a *Phyla incisa* inflorescence. Yellow-throated and purple-throated flowers occur intermixed in a ring around the top of the cylindrical inflorescence. The developing pyrenes occur below the flowers and are concealed by numerous bracts.

function may be more important than female function in the evolution of floral displays (Bell, 1985; Stanton et al., 1986).

It is the purpose of this study to examine the effects of older, nonfunctional flowers that retain their corollas in *Phyla incisa* Small (Verbenaceae), a species with granular pollen. Although inflorescences of this plant represent the reproductive effort of ramets rather than genets, several aspects of this species make it a suitable model system for testing hypotheses associated with old-phase flower retention and the evolution of inflorescence size. We describe the flowering phenology of *P. incisa* and address the following questions: 1) what nectar rewards are available in each flower phase? 2) do pollinators discriminate against less rewarding flowers? 3) are pollinators selective in their visits to inflorescences? 4) to what extent does each flower phase contribute to the attraction of pollinators? and 5) how do patterns of pollinator-visitation rates to different inflorescences affect male and female reproductive success?

MATERIALS AND METHODS

General Biology.—*Phyla incisa* is a mat-forming perennial herb with crawling stems that root from the nodes. The erect axillary inflorescences are compact, cylindrical, and have bractlets beneath each flower or fruit (Fig. 1). Inflorescences increase in length as flowering progresses and range from less than one to several centimeters long. The top of the inflorescence forms a landing platform for pollinators, and several small white flowers (2–3 mm wide) form a circle around this platform with their corolla throats oriented upward (Fig. 1). Corolla throats are yellow on the first day after anthesis and change to purple on the following day whether or not flowers have been visited by pollinators. Flowers wilt on the third day after anthesis (Estes and Brown, 1973; pers. observ.). Since new flowers open each day, individual inflorescences are composed of both yellow- and purple-throated flowers irregularly spaced around their tops. Plants are self-compatible, although flowers will not set fruit if they are not visited by pollinators (Estes and Brown, 1973). Fruits are two-seeded pyrenes, which develop within their bractlets (Moldenke, 1973).

Study Site.—We conducted this study during 11–15 February 1985 and 17–22 March 1985 at Palo Verde Reserve, Costa Rica, where *Phyla* formed mats of various sizes along a dirt road and an air strip near the Organization for Tropical Studies field station. Patches of *Phyla* consisted of a nearly continuous cover of leaves, occasionally mixed with grasses, and inflorescences, which were usually elevated several centimeters above the other vegetation. All observations and experiments were conducted in a single patch of *Phyla* approximately 10 × 20 meters, which appeared to be representative of most patches in the area. Observations and experiments on pollinator foraging behavior were made between 7:00 A.M. and 11:00 A.M., when pollinator activity was highest.

Many insects were observed to visit *Phyla,* including introduced honeybees (*Apis mellifera*), several small bees in the family Halictidae, beeflies (Bombyliidae), and several species of lepidopterans in the Nymphalidae, Hesperiidae, and Lycaenidae. Pollinator activity was generally high in the study area. All pollinators were observed to forage for nectar, and none appeared to be actively collecting pollen. Pollinators were grouped into four classes (honeybees, native bees, butterflies, and beeflies) for data collection and analysis.

Fruit Production.—We compared seed set in the presence and absence of pollinators in ten pairs of inflorescences of similar size that were in close proximity to each other. One member of each pair was bagged with fine nylon mesh on 15 February, and fruit set was checked 35 days later. Since flowers were very numerous, fruit set was checked by dissecting the top centimeter of each inflorescence and counting the total number of pyrenes present. Differences between the mean number of pyrenes set in each treatment were compared using a two-sample t test on the $\log_{10}$-transformed data.

Floral Rewards.—We measured nectar volume in two flowers of each phase on ten different inflorescences from which pollinators had been excluded. Small filter-paper wicks (Whatman #1) were inserted into corollas until all of the available nectar had been absorbed. Wicks were then dried and stored on insect pins for sugar assays at a later date. Total sugar for each flower was determined using an anthrone assay for total carbohydrates (McKenna and Thomson, 1988). Data were $\log_{10}$-transformed, and mean total sugar production for the two flower phases was compared in a one-way analysis of variance with flowers from the same inflorescence paired in blocks, using the ANOVA procedure of SAS (SAS Institute, 1982).

Pollinator Behavior.—Over several days we recorded flower phase and inflorescence choice by following individual insects for up to 10 inflorescence visits or until the insect was lost. Flower choice was determined by noting the number of each flower type probed and the number of each type present on the inflorescence. Observations were pooled over several days, and deviation from random flower choice was tested using G tests for each pollinator class.

Inflorescence choice by pollinators was determined by comparing the size distribution of visited inflorescences to the size distribution of available inflorescences in the population with Kolmogorov-Smirnov tests. On each day observations were made, the frequency of inflorescences of different sizes was determined by counting the number of each flower phase present on inflorescences within 2 cm of a 15-m transect line. Inflorescences were assigned to size classes based on total inflorescence size (yellow- plus purple-throated flowers), and the data were pooled across days after they were found to be homogeneous. The relative roles of resource level of inflorescences (number of yellow-throated flowers) and the number of purple-throated flowers in the attraction of pollinators were inferred using multiple regression analysis. Inflorescences were divided into different classes based on the number of each flower phase present. The frequency of each inflorescence class in the population was determined from the transects described above. For each inflorescence class, the visitation frequency by a pollinator was entered as the dependent variable, with availability (relative abundance of that inflorescence size class) in the population, the number of purple-throated flowers, and the number of yellow-throated flowers present as independent variables in regression models for each pollinator class using the REG procedure of SAS (SAS Institute Inc., 1982).

Inflorescence Visitation.—We determined the effects of inflorescence resource level (number of yellow-throated flowers) and total inflorescence size (yellow- plus purple-throated flowers) on pollinator visitation rate by experimental manipulations on 18 and 19 March. Flowers were removed from inflorescences to produce four treatments as follows: four yellow-throated flowers (4Y/0P), two yellow- with two purple-throated flowers (2Y/2P), four yellow- with four purple-throated flowers (4Y/4P), and four purple-throated flowers (0Y/4P). The number of visits by each pollinator class was recorded for five replicates of the four treatments during two-hour periods by two observers, each at a separate location within the study area. Observed visitation frequencies were tested against expected visitation frequencies from three models of foraging behavior using G tests for goodness of fit for each pollinator class: a resource-level model (i.e., the number of yellow-throated flowers present), which assumes that pollinators make foraging decisions based only upon the total resources available in an inflorescence; a total-inflorescence-size model (yellow- plus purple-throated flowers), which assumes that pollinators make foraging decisions based only upon the size of the floral display; and a random-visitation model, which assumes that pollinators visit inflorescences randomly with respect to the number of yellow-throated flowers and inflorescence size (e.g., move among nearest-neighbor inflorescences).

Reproductive Success. —The effect of old-phase flower retention on male and female reproductive success was assessed by quantifying pollen removal from inflorescences and pollen deposition on stigmas of yellow-throated flowers on 19, 20, and 21 March. Flowers were removed from inflorescences in situ to produce three treatments with four yellow-throated flowers and four, two, or no purple-throated flowers. Such inflorescences were prepared on each day in the early morning, before pollinators became active. Five groups of inflorescences, separated by at least one meter and containing one replicate of each treatment within 20 cm of other members of a group, were prepared on each day. On two of the three days, five additional inflorescences with four yellow-throated flowers were enclosed in fine nylon mesh pollination bags. Both bagged and open-pollinated inflorescences were collected three hours after the initiation of the experiment. Counts of pollen loads on stigmas of yellow-throated flowers were made immediately with a compound microscope at 100× after staining with basic fuschin and squashing the pistils beneath cover slips. The four yellow-throated corollas with attached anthers from each inflorescence were combined and stored in 70% ethanol. After staining with acidified aniline blue, the pollen grains from these flowers were washed into small petri dishes and counted under a stereoscopic microscope at 50×. Estimates of the amount of pollen removed were made by obtaining the difference between the mean number of pollen grains left in the flowers of bagged inflorescences and the pollen left in the flowers of each open inflorescence. Data for stigma loads and pollen remaining in flowers were blocked by groups of treatments and days in an ANOVA using the GLM procedure of SAS (SAS Institute, 1982). Differences between treatment means were tested using Tukey's studentized range test (Box et al., 1978).

RESULTS

Fruit Set. —The mean fruit set for bagged inflorescences (1.3 pyrenes, $N = 10$) was much less than that for open-pollinated inflorescences (13.6 pyrenes, $N = 10$; $t = 6.38$, $P < 0.001$). The number of pyrenes set by open-pollinated inflorescences ranged from four to 37 and was well below full fruit set, since the topmost centimeter of these inflorescences contains approximately 50 to 70 flowers. Nine of ten bagged inflorescences set only two pyrenes or fewer, and four of ten set no fruit at all.

Floral Rewards. —The total available nectar sugar in yellow-throated flowers (mean = 66.33 μg, SD = 24.5, $N = 20$) was significantly greater than that in purple-throated flowers (mean = 2.55 μg, SD = 3.5, $N = 20$; $F_{[1,\ 14]} = 64.91$, $P < 0.0001$). The total carbohydrate content of yellow-throated flowers ranged from 14.5 to 96.5 μg, while half of the purple-throated flowers contained no detectable sugar, and the maximum value measured was only 8.5 μg.

Pollinator Behavior. —Insect visitors to *P. incisa* inflorescences did not forage on the two flower phases equally. All classes of pollinators preferred yellow-throated flowers to purple-throated flowers (Table 1). Honey-bees, native bees, and beeflies probed purple-throated flowers only rarely, while butterflies were much less selective. Kolmogorov-Smirnov tests indicate that honeybees ($D = 0.14$, $P < 0.01$, $N = 84$), native bees ($D = 0.11$, $P < 0.01$, $N = 119$), and butterflies ($D = 0.12$, $P < 0.01$, $N = 53$) selected larger inflorescences than expected from the size distribution of inflorescences available (Fig. 2a–d). Beeflies (Fig. 2e) appeared to select smaller inflorescences than expected ($D = 1.09$, $P < 0.01$, $N = 14$), but the sample size is relatively small.

Multiple-regression analysis of inflorescence-visitation frequency shows that the availability of each inflorescence class affected inflorescence choice by all three of the most common pollinator classes (Table 2). Pollinators also appeared to respond to both the number of purple-throated flowers, and to the amount of resources present in inflorescences (i.e., the number of yellow-throated flowers) (Table 2). The numbers of yellow- and purple-throated flowers present

TABLE 1. Flower-phase choice by pollinators of *Phyla incisa.* The number of inflorescences visited (*N*), the numbers of yellow- and purple-throated flowers probed, and the total number of yellow- and purple-throated flowers present on inflorescences for the four classes of pollinators (Y = yellow-throated, P = purple-throated). Probabilities are based on *G* tests for the goodness of fit of the number of flowers probed to the number present on inflorescences.

		Probed		Present		
Pollinators	*N*	Y	P	Y	P	*P*
Honeybees	102	254	5	337	258	<0.001
Native bees	120	328	6	386	399	<0.001
Butterflies	18	43	26	67	70	<0.05
Bee flies	35	84	7	129	92	<0.001

in inflorescences were uncorrelated ($r = 0.04$, $P > 0.20$, $N = 681$), allowing us to make independent assessments of the effects of these two variables on visitation rate. Both native bees and butterflies showed positive responses to increasing numbers of purple-throated flowers. For honeybees, the pattern was less clear, although the number of yellow-throated flowers present may have had a stronger effect than the number of purple-throated flowers. Analysis of the pooled visits for the three most common pollinators indicates that the pollinator fauna as a whole responds most strongly to inflorescence availability (relative abundance of an inflorescence size class) and to the number of purple-throated flowers (Table 2).

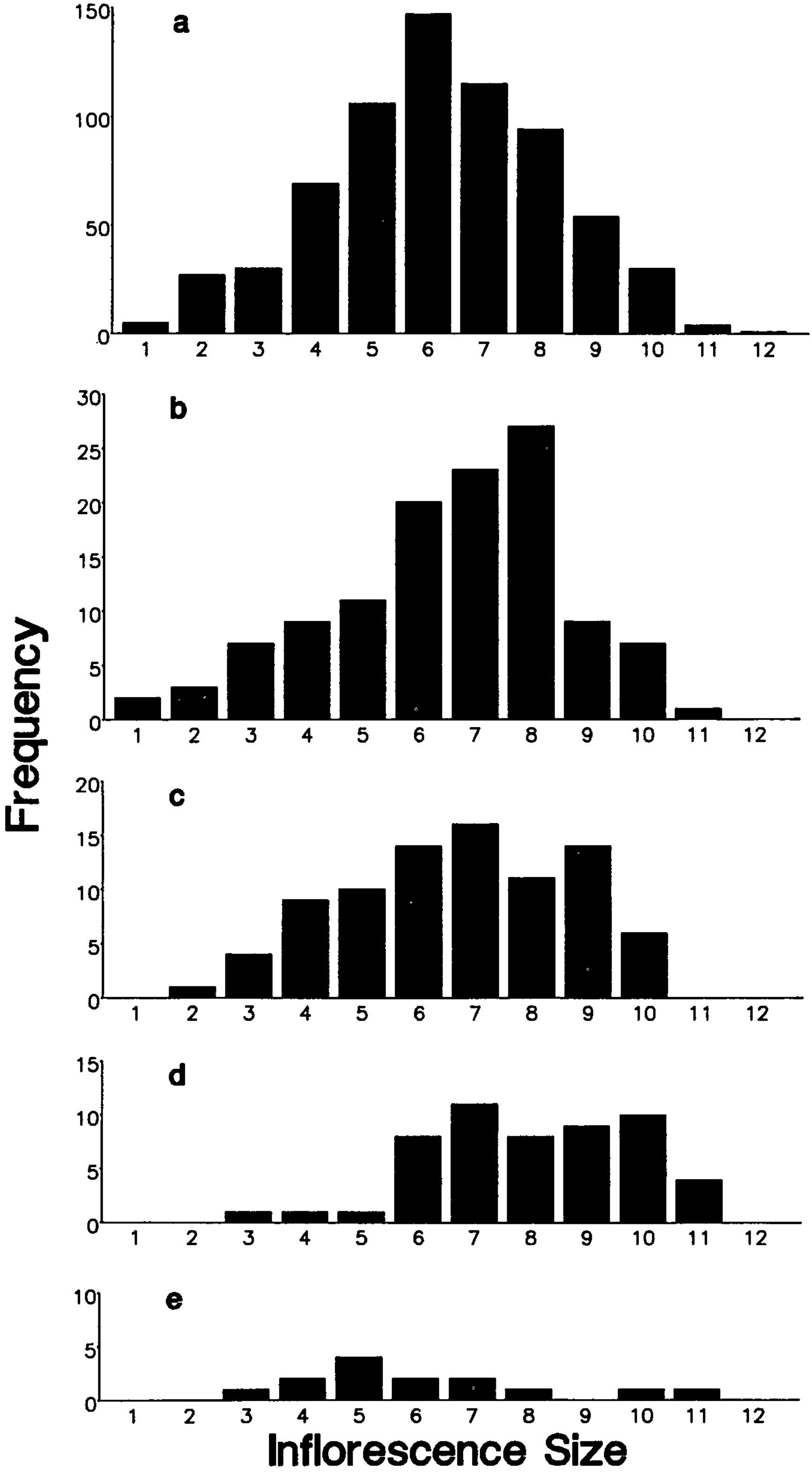
Inflorescence Visitation.—The responses of insect visitors to experimental inflorescences on which we manipulated the number of each flower phase also indicate that both flower types are important for the attraction of insects. Visitation frequencies to manipulated inflorescences and tests for their fit to an inflorescence-size model, a resource-level model, and a random model appear in Table 3. Only honeybees and native bees had high enough visitation frequencies for statistical tests. Visitation frequencies by honeybees do not fit any of the proposed models (Table 3). The pattern of visitation by honeybees to the different treatments most closely resembles that expected from the inflorescence-size model, with the exception of the 0Y/4P treatment. If this treatment is removed there is adequate fit to this model ($G = 2.15$, $P > 0.05$), but not to either the random model ($G = 31.3$, $P < 0.001$) or the resource-level model ($G = 18.00$, $P < 0.001$). Visitation frequencies of native bees appear to fit the model for random inflorescence choice best, although visitation to inflorescences having no rewarding flowers is somewhat less than expected for random inflorescence choice (Table 3).

Reproductive Success.—The mean total number of pollen grains produced per four flowers in the bagged inflorescences was 963.7 (SD = 331.9, $N = 10$). A relatively small proportion of this pollen was found on stigmas. Stigmas of most bagged flowers had either no pollen (63%) or fewer than ten pollen grains (77%), suggesting that autogamy is rare. The mean number of pollen grains per stigma of bagged flowers of 15.7 (SD = 39.3, $N = 10$) is inflated by a minority of larger pollen loads.

The presence of old-phase flowers affected pollen removal from inflorescences more strongly than it affected pollen deposition on stigmas (Fig. 3). The patterns of pollen deposition and removal found were consistent for all three days the experiment was run ($P > 0.05$ for the effect of day in both ANOVAs). Means for each inflorescence type were significantly different for pollen removal ($F_{[2,26]} = 8.05$, $P < 0.01$) and tended to increase with the addition of old-phase flowers (regression slope = 52.97, $P < 0.0001$). Pollen removal was relatively low when no purple-throated flowers were present, and it increased significantly for inflorescences having two purple-throated flowers. Pollen removal was greater for the treatment with four purple-throated flowers than for the treatment with two purple-throated flowers, but this difference was not significant (Fig. 3). Pollen deposition on stigmas did not differ among the three treatments ($F_{[2,152]} = 1.68$, $P > 0.19$) and did not show a significant increase with the addition of old-phase flowers (regression slope = 2.97, $P > 0.30$). Pollen-load sizes on stigmas varied greatly but were generally between 50 and 100 grains with larger pollen loads being more rare (Fig. 4).

DISCUSSION

The retention of older flowers with associated morphological changes is known to


Frequency
a
150
100
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1 2 3 4 5 6 7 8 9 10 11 12
Inflorescence Size

TABLE 2. The influence of inflorescence availability (relative abundance), the number of yellow-throated flowers, and the number of purple-throated flowers on visitation frequency by the three most common types of pollinators of *Phyla incisa*. Slopes and intercepts from multiple regression analyses for visitation frequency by each pollinator class are given. Probabilities (in parentheses) are from *t* tests of differences from zero for each slope and intercept.

Variable	Pollinator Native bees	 Honeybees	 Butterflies	Total
Number of yellow-throated flowers	−0.95 (0.01)	0.66 (0.11)	−0.17 (0.64)	−0.16 (0.48)
Number of purple-throated flowers	0.50 (0.01)	0.09 (0.66)	0.48 (0.05)	0.26 (0.04)
Inflorescence availability	0.17 (<0.01)	0.08 (0.01)	0.08 (<0.01)	0.11 (<0.01)
Intercept	0.40 (0.73)	−1.37 (0.40)	−2.21 (0.18)	−0.27 (0.76)
Sample size	119	84	54	247

occur in a large number of species (Gottsberger, 1971; Casper and La Pine, 1984; Jones and Buchmann, 1974; Schemske, 1976; Schaal and Leverich, 1980; Gori, 1983; Delph and Lively, 1985; Jones and Cruzan, 1988). The change in corolla color from yellow to purple in *Phyla incisa* occurs on the evening of the first day that flowers are open and does not require pollination. Similar patterns have been found for other species (Gori, 1983; Casper and La Pine, 1984), but morphological changes induced by pollination are also known (Gori, 1983; Jones and Cruzan, 1988). Old-phase flowers in *Phyla* and other species lack pollinator resources, and pollinators apparently learn to discriminate against them (cf. Jones and Buchmann, 1974; Casper and La Pine, 1984).

Several hypotheses have been proposed to explain the occurrence of old-phase flower retention in other species. Barrows (1976) suggested that the presence of old-phase flowers in *Lantana* may discourage nectar thieves from perforating younger flowers. This is probably not the case in *Phyla*, since old-phase flowers occur adjacent to nectar-containing flowers rather than encircling them as in *Lantana*. The corolla tubes in *Phyla* are enclosed by bracts, which may help discourage nectar thieves. It has also been suggested that old-phase flowers increase pollination efficiency or constancy (see Gori, 1983), but these hypotheses address the reason for morphological changes in old-phase flowers rather than the reason for their retention. After being unable to demonstrate any advantage of old-phase flower retention in *Lupinus argenteus* in terms of seed set, Gori (1983) concluded that the higher visitation rates resulting from the retention of old-phase flowers must increase pollen donation, but he made no test of this hypothesis. As suggested by Müller (1877), the primary function of old-phase flower retention is probably to increase the number of pollinator visits received by a plant. Implicit assumptions of this hypothesis are that pollinators visit larger inflorescences more frequently and that old-phase flowers contribute to the attraction of pollinators. Increases in the visitation rate may translate into increases in plant fitness through male or female reproductive function. However, each of the two sexual functions is likely to bear a different relationship to visitation rate, and neither of these relationships is likely to be linear. Visitation rate is therefore an unreliable index of either kind of reproductive success; it is preferable to use indices that are more tightly correlated with the variables of interest. By measuring pollen removal and deposition to estimate male and female reproductive

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FIG. 2. Frequency distributions of total inflorescence size (yellow- plus purple-throated flowers) present in the population and visited by each pollinator class for *Phyla incisa*: a) frequency of inflorescences in the population and visitation by b) native bees, c) honeybees, d) butterflies, and e) beeflies.

TABLE 3. Expected and observed pollinator-visitation frequencies for experimentally manipulated inflorescences of *Phyla incisa.* A) Expected proportion of visits for the inflorescence-size, resource-availability, and random-visitation models. B) observed proportions of visits by each pollinator type. C) Fit to each model was tested for honeybees and native bees using *G* tests. An asterisk indicates that visitation frequencies are significantly different than expected ($P < 0.05$) based upon the model being tested. Treatments are listed as the number of yellow-throated/purple-throated flowers.

	Treatment			
	4Y/0P	2Y/2P	4Y/4P	0Y/4P
A. Model:				
Inflorescence size	0.20	0.20	0.40	0.20
Resource level	0.40	0.20	0.40	0.00
Random	0.25	0.25	0.25	0.25
B. Pollinator:				
Honeybees (*N* = 351)	0.25	0.22	0.42	0.11
Native bees (*N* = 92)	0.29	0.32	0.25	0.14
Butterflies (*N* = 15)	0.13	0.27	0.47	0.13
Beeflies (*N* = 12)	0.25	0.00	0.75	0.00

C. *G* tests:

	Model		
Pollinator	Inflorescence size	Resource level	Random
Honeybees	22.0*	18.0*	67.4*
Native bees	16.4*	12.1*	7.3

success, we obtain a more direct estimate of male success and an estimate of female success that includes the potential for modification of female success through gametophytic competition (Mulcahy et al., 1975; McKenna and Mulcahy, 1983).

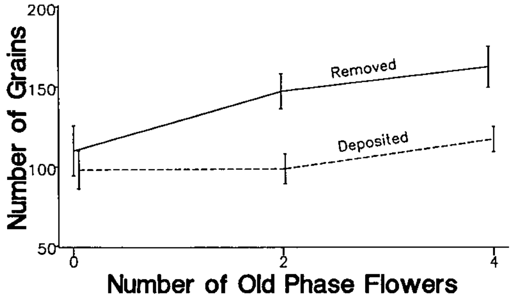

FIG. 3. The effect of the number of purple-throated flowers present on pollen removal from inflorescences and deposition on stigmas of *Phyla incisa.* Inflorescences had four yellow-throated flowers with zero, two, or four purple-throated flowers. Vertical bars represent the standard errors of the means.

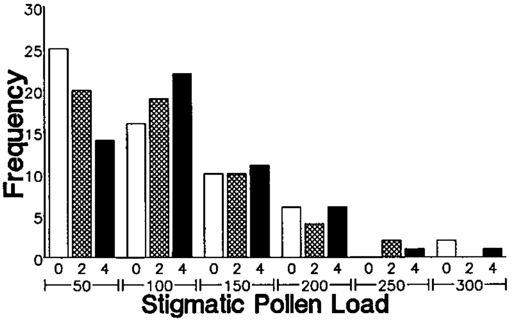

FIG. 4. Frequency distributions of stigmatic-pollen-load sizes for open-pollinated flowers of *Phyla incisa.* Data are the same as those presented in Figure 3. Inflorescences had four yellow-throated flowers with zero (open bars), two (cross-hatched bars), or four (solid bars) purple-throated flowers. Each pollen-load size class is represented by the median number of grains for the range of pollen-load sizes.

Pollinators of *Phyla* tend to select inflorescences with larger displays, and thus, old-phase flowers contribute to the attraction of pollinators. Old-phase flowers have also been shown to contribute to the attraction of pollinators in *Lotus* (Jones and Cruzan, 1988) and *Lupinus* (Gori, 1983); however, Casper and La Pine (1984) found no decrease in visitation rate by several species of bees and flies when old-phase flowers had been removed from plants of *Cryptantha humilis.* Old-phase flowers in *Phyla* function for long-distance attraction of pollinators (Tables 2, 3) but apparently are less attractive than nectar-containing flowers, since visitation to inflorescences having only purple-throated flowers was lower than expected (Table 3). Judging from the visitation rates to the 4Y/4P (185 total visits) and the 4Y/0P (121 total visits) treatments, inflorescences having only four yellow-throated flowers should receive 0.75 visits per hour (121 visits/18 inflorescences/9 hr) and would receive an additional 0.40 visits per hour (185 − 121 = 64 visits/18 inflorescences/9 hr) by retaining four purple-throated flowers.

The different classes of pollinators of *Phyla* appear to respond differently to the number of flowers of each phase present in inflorescences. Honeybees appear mostly to cue in on total inflorescence size but are less attracted by purple-throated flowers than by yellow-throated flowers. Native bees also appear mostly to choose large inflorescences but may be more likely to move to nearest-neighbor inflorescences than honeybees, since their visits to manipulated inflorescences were apparently random.

Pollinators of *Phyla incisa* that choose inflorescences according to total inflorescence size should not lose much foraging efficiency. Total inflorescence size (number of yellow- plus purple-throated flowers) was a fairly good predictor of inflorescence resource availability (number of yellow-throated flowers) in this study ($r = 0.58$, $P < 0.0001$, $N = 681$). Pollinators would obviously increase their foraging efficiency if they could detect resource levels of inflorescences but are apparently not able to discriminate purple-throated flowers at a distance. The throat color differences between the rewarding and nonrewarding flowers allow pollinators to forage relatively efficiently once they have landed on an inflorescence. If a plant retained its corollas beyond the period of sexual function and nectar production but did not have associated morphological changes to indicate nonrewarding flowers, it would be perceived as relatively unrewarding, and pollinators would be expected to avoid those individuals (Heinrich, 1975). The lack of a cue to indicate nonrewarding flowers might also reduce the amount of time pollinators spend on individual plants (Gori, 1983) and may result in the wastage of male gametes due to superfluous visits to nonfunctional flowers (Schaal and Leverich, 1980; Gori, 1983).

A pollinator fauna that favors larger inflorescences would put selective pressures on plants to increase inflorescence size and may be responsible for the evolution of old-phase flower retention in *Phyla incisa* and other species. Inflorescence size has been shown to influence both pollinia removal (Willson and Rathcke, 1974; Willson and Price, 1977; Willson and Bertin, 1979; Schemske, 1980; Queller, 1983; Wolfe, 1987) and fruit production (Willson and Price, 1977; Schaffer and Schaffer, 1980; Schemske, 1980) in several other studies. The increase in inflorescence size by retention of old-phase flowers in *Phyla* strongly affects pollen removal from inflorescences, while having little effect on pollen deposition on stigmas (Fig. 3). Old-phase flower retention was found to affect seed set in *Lotus scoparius* (Jones and Cruzan, 1988), but Gori (1983) found no effects on fruit or seed set in *Lupinus*. Male reproductive success was not examined in either of these two studies. The consequences of increased inflorescence size for male and female reproductive success may depend to some extent upon pollinator activity. If pollinator activity were low enough that not all flowers received a visit, then increases in the reproductive success of larger inflorescences might be expressed through both seed set and pollen dispersal. Pollinator activity during this study was relatively high, so that individual inflorescences were likely to receive one or more visits per hour. However, lower levels of pollinator activity may occur at other times during the flowering season.

Pollen deposition for most open-pollinated flowers was probably great enough to ensure the fertilization of both of the ovules (Fig. 4). Pollen loads larger than the minimum size required for full fertilization may modify female reproductive success through increases in seed quality. In single-donor crosses, pollen-load size is known to affect seedling vigor in some species (Mulcahy et al., 1975; McKenna and Mulcahy, 1983). In addition, pollen arriving on stigmas from individual insect visitors probably consists of pollen from several donors (Marshall and Ellstrand, 1985), due to pollen carryover (Thomson and Plowright, 1980). Larger stigmatic loads would therefore also represent an increase in the probability of receiving at least some "higher quality" pollen. Since the higher visitation rates to inflorescences with old-phase flowers (Table 3) did not appear to affect the amount of pollen deposited on the stigmas of *Phyla incisa*, mechanisms of gametophytic competition were probably not important in the evolution of old-phase flower retention in this species.

The amount of pollen removed from an inflorescence is indicative of the opportunity for reproduction through male function. Larger amounts of pollen were removed from inflorescences with old-phase flowers, due to increases in their pollinator-visitation rates (Table 3, Fig. 3). Increases in pollen removal represent increases in the number of pollinators dispersing pollen from an inflorescence and increases in the probability of more pollen being deposited on receptive stigmas. Once pollen has left a flower, its probability of being deposited on a stigma may be relatively high. A comparison of the mean numbers of pollen grains removed from inflorescences and deposited on stigmas indicates that 75% of the pollen removed reaches stigmas. Such high pollen-transfer efficiency is probably partly due to a large amount of within-flower and within-inflorescence transfer of pollen in *Phyla* (Estes and Brown, 1973). However, geitonogamous transfer of pollen explains relatively little of the variation in pollen removal and deposition, since there was only a weak correspondence between the amount of pollen removed from an inflorescence and the amount of pollen it received ($r = 0.26$, $P > 0.05$).

The patterns found for pollen removal and deposition in *Phyla* suggest that pollen is taken from inflorescences at a relatively constant rate, whereas pollen deposition on stigmas is a much more stochastic process. The increase in pollen removal for treatments with old-phase flowers present was apparently due to increased visitation by pollinators. An estimate of the average amount of pollen removed during each pollinator visit in the 4Y/4P treatment can be made by using the pollinator-visitation rate (3.42 visits/inflorescence/3 hr; Table 3) and the pollen removal rate (650.3 grains removed/inflorescence/3 hr; Fig. 3). These data indicate that, on the average, 190 pollen grains of an average of 963.7 available in each inflorescence were removed with each visit. Pollen deposition for inflorescences having old-phase flowers apparently was not affected by the increased visitation rate (Fig. 3). This lack of correspondence between visitation rate and pollen deposition was apparently not due to stigma saturation, since stigmatic pollen loads were highly variable (Fig. 4). These patterns of pollen deposition and removal may be due to the positioning of the reproductive organs within the flower. Anthers in this species are located in the top of the corolla throat, so pollinators are very likely to contact them with their mouth parts as they probe for nectar. The stigma is located in the bottom of the corolla, so pollinators may contact it less frequently, and the amount of pollen deposited may be dependent on pollinator behavior.

We have shown that pollen-removal rate, which is an important component of male reproductive success, may more often be limited by pollinator visitation rate than is female reproductive success (as measured by pollen deposition on stigmas) in *Phyla incisa*. If the high pollinator visitation rates and the preference of pollinators for larger inflorescences that were observed in this study have existed over long periods of time, they may have been responsible for selection through male function for old-phase flower retention. These findings corroborate results from several recent studies (Sutherland and Delph, 1984; Bell, 1985; Stanton et al., 1986) that also suggest that selection through male function may be more important than female function in the evolution of floral displays.

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