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DIFFERENTIAL IMPORTANCE OF BEETLE SPECIES POLLINATING *DIEFFENBACHIA LONGISPATHA* (ARACEAE)[1]

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Abstract. *Dieffenbachia longispatha* (Araceae) is pollinated by scarab beetles (*Cyclocephala* spp. and *Erioscelis* sp.) at the La Selva Biological Station, Costa Rica. The relative contributions of each beetle species to female reproductive success of *D. longispatha* were determined by observing inflorescences during the flowering seasons of 1982 and 1983 and recording the number of visiting beetles of each species. Fruit production was determined for each inflorescence as fruits ripened, 9 mo after flowering.

The three most abundant beetle species differed in abundance, recapture rates, pollen loads carried, and behavior at inflorescences. Despite these differences, the effect of a single visit on fruit-set of *D. longispatha* (the "pollinator effectiveness" of each species) did not vary among the beetle species. The "importance" of each pollinator species, estimated in previous studies from the abundance and effectiveness of each species and determined in this study from examining fruit-sets of inflorescences visited by varying numbers of beetles, was not a positive, linear function of beetle abundance. In 1982, when visitation rate of all beetle species was low, fruit-set was positively correlated with the number of beetles in an inflorescence but "per visit" effectiveness decreased with increasing visitation, resulting in a saturation of fruit-set at 42%. Beetle identity (to species) did not explain a significant proportion of the variance in fruit-set in 1982. In 1983, beetle abundance quadrupled relative to 1982 and fruit-set was positively correlated with beetle numbers up to four, but visitation by more than four beetles resulted in a decrease in fruit-set. A high proportion of *Cyclocephala gravis* produced higher than predicted fruit-set, while a high proportion of *Erioscelis* yielded fruit-sets lower than was predicted by total number of beetles. The presence of large numbers of *Erioscelis* within inflorescences in 1983 and the low fruit-sets of those inflorescences explained the significantly negative slope of the regression for inflorescences visited by more than four beetles. Previous models have predicted saturation of fruit-set with increasing pollinator visitation (as seen in 1982) but have not predicted a significant decline in fruit-set with pollinator abundance. The proportion of the variance in fruit-set explained by beetle abundance was low for both years (2–8%), suggesting that other factors contribute to female reproductive success in *Dieffenbachia* (i.e., number of potential mates and the distances to potential mates in the population).

Use of common indices of pollinator contribution to seed set, such as pollinator abundance and the number of seeds produced as a result of a single visit, would lead to erroneous conclusions if applied to *Dieffenbachia* and its beetle pollinators, or to other pollination systems where there is cumulative floral damage with increasing visitation frequencies.

Key words: beetle pollination; Costa Rica; Cyclocephala; Dieffenbachia; Erioscelis; *fruit-set; pollinator effectiveness; pollinator importance.*

INTRODUCTION

The most abundant pollinator is not necessarily the most effective at transferring pollen to conspecific stigmas (Waser 1979, Zimmerman 1980, Arnold 1982, Spears 1983, Schemske and Horvitz 1984, Snow and Roubik 1987). In considering the relative contributions of several animal taxa to the pollination of one plant population, it is useful to distinguish pollinator effectiveness, abundance, and importance. *Effectiveness* measures are based on what is accomplished by a single visit by a particular animal, including effectiveness per visit at removing pollen from anthers, depositing it on stigmas, producing seeds, or influencing other aspects of reproduction (Ornduff 1975, Motten et al. 1981, Parker 1982, Motten 1983, Spears 1983, Schemske and Horvitz 1984, Campbell 1985). Effectiveness has typically been measured for the first visit to a flower. This may lead to erroneous conclusions if estimates of pollinator efficiency are assumed to be the same throughout the range of pollinator abundance, because it assumes that the incremental effect of a pollinator visit is constant.

Indices of pollinator *abundance* are population char-

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acteristics that influence the number of visits that a flower receives from a particular species of visitor. Lastly, the *importance* of a pollinator species to a plant species is often indexed by a combination of the abundance and the effectiveness of that species (Thomson 1978, Thomson et al. 1982, Lindsey 1984, Sugden 1986). A rare species, for example, may deposit many pollen grains per visit and cause as many seeds to be set as a common species that deposits little pollen per visit. These two visitor taxa would be equally important to seed-set. They need not be equally important with respect to other aspects of fitness, such as male reproductive success.

Previous treatments have tended to estimate importance as a linear function of abundance, where the effectiveness measure, considered a constant for each visitor species, is used to weight the abundance measure (Thomson et al. 1982, Lindsey 1984, Sugden 1986). Per-visit effectiveness, however, may not be a constant. Because both male and female reproductive success can be expected to saturate at high visitation rates due to diminishing supplies of pollen, available stigmatic area, or unfertilized ovules, the incremental effectiveness of a single visit could decline with visit number (Silander and Primack 1978, Plowright and Hartling 1981, Snow 1982, McDade and Davidar 1984, Kohn and Waser 1985, Campbell 1986, Snow 1986). In an extreme case, pollinators that cause wear and tear on the flowers may be beneficial pollinators (i.e., have positive effectiveness) at low density, but be detrimental at higher abundances, due to cumulative floral damage. Thus, the relationship between pollinator abundance and pollinator importance is not likely to be linear and may not even be monotonic over certain ranges of abundance.

In this paper I examine the importance of beetle visitors to *Dieffenbachia* c.f. *longispatha* Engler and Krause (Araceae) (specimen number voucher 2225, collected by M. Grayum, Duke Herbarium), a terrestrial clonal herb of neotropical rain forests. It is pollinated by two genera of scarab beetles and is regularly visited by at least seven other taxa of insects (Young 1986*a*). Here I combine estimates of abundance, fidelity, and fertilization efficiency of the three major pollinator species to compare their relative contributions to the female reproductive success of *D. longispatha*. In particular I address the following questions: (1) Are there any mechanistic reasons (behaviors or pollen loads of beetles) why one might expect differences among beetle taxa as pollinators?; (2) Do the major beetle visitors vary in their pollination effectiveness (number of seeds produced as a result of a single visit)?; (3) Do the beetle taxa vary in abundance?; and (4) What is the effect of varying abundances of beetle taxa on the probability of inflorescence success (not aborting) and seed set of *D. longispatha* (pollinator importance), and does the effect vary among beetle taxa?

Pollination by scarab beetles is fundamentally different from pollination by more rapidly foraging animals. For many plant species, beetles arrive at an inflorescence in the evening and remain for 24 h (Prance and Arias 1975, Beach 1982, Gottsberger and Amaral 1984, Valério 1984, Young 1986*a*). In addition, in several beetle-pollinated plants (*Astrocaryum mexicanum*, Búrquez et al. 1987; *Cyclanthus*, Beach 1982; *Dieffenbachia, Xanthosoma, Philodendron, Syngonium*, H. Young, *personal observation*) the phenology of the inflorescences is such that beetles cannot move between inflorescences on the same plant. These features render standard indices of pollinator effectiveness such as number of flowers visited per plant and time spent foraging per flower (Primack and Silander 1975, Thomson et al. 1982) irrelevant for beetle pollinators.

METHODS

Study site

This study was conducted at the La Selva Biological Station in the Atlantic lowlands of Costa Rica (10°26′ N, 84°00′ W). Life zones include Premontane Wet forest and Tropical Wet forest (Holdridge et al. 1971). In this area, *Dieffenbachia longispatha* flowers from March through September and fruits 9 mo later, November through May. I marked and mapped all ramets of *D. longispatha* in a 7-ha area encompassing primary forest, secondary forest, and abandoned cacao plantations. This area was censused during flowering and fruiting periods for 2 yr (March through November, 1982 and 1983) and during flowering in 1984 (March–July). The density of flowering ramets was low in 1983 (0.26 ramets/100 m^2) compared to 1982 (0.59 ramets/100 m^2) and 1984 (0.34 ramets/100 m^2). Pollinator activity was measured in all years and female reproductive success of ramets (fruit-set) was measured in 1982 and 1983.

Floral biology and insect visitors

Reproductive ramets of *Dieffenbachia longispatha* have 2–7 inflorescences during the flowering period. Each inflorescence bears an average of 77 female flowers at the base (SD = 12.0, $N = 84$) and 440 male flowers at the tip (SD = 81.3, $N = 25$). The entire structure is enclosed in a leaf-like spathe except during flowering, when the spathe opens to form a spacious chamber for the beetle pollinators. Consecutive spathes on a ramet open at intervals of 3–12 d; thus there is no potential for pollinators to move between inflorescences on a ramet. Inflorescences are protogynous, female flowers becoming receptive 24 h before the male flowers. No nectar is produced; the rewards for pollinators are fleshy, protein-rich staminodia that surround stigmas. The species is partially self-compatible; selfing by hand resulted in less than one-third the number of fruits produced by outcrossing (Young 1986*a*).

Each inflorescence was checked daily for beetle presence (275 inflorescences in 1982, 423 in 1983, and 578 in 1984). Two genera of dynastine scarab beetles pollinate *D. longispatha*: *Erioscelis* (*E. columbica* Endrödi) and nine species of *Cyclocephala* (*C. gravis* Bates, *C. amblyopsis* Bates, *C. sexpunctata* Cast., *C. conspicua* Sharp, *C. tutilina* Burm., *C. kaszabi* Endrödi, *C. ligyrina* Bates, *C. atripes* Bates, and *C.* sp. nov.). Voucher specimens of all beetles are located at the University of Nebraska State Museum. All beetles encountered at inflorescences were marked with a unique pattern of small notches cut into the elytra, and were returned to the inflorescence. For each inflorescence, the date of flowering and the number and species of visiting beetles were recorded. In this paper, I concentrate on the three species of beetles that made up 94% of the recorded visits: *Erioscelis columbica* (the most abundant scarab visitor), and *C. gravis* and *C. amblyopsis* (which make up 84% of all *Cyclocephala* observed in inflorescences).

Pollination mechanics

Cyclocephala and *Erioscelis* move between inflorescences of *D. longispatha* in the evening. The first beetles arrive at female-phase inflorescences at dusk, between 1800 and 1840. Typically, beetles spend 24 h eating staminodia around the female flowers and mating (if they have the good fortune of the company of a conspecific of the opposite sex). At the end of 24 h, the male flowers of the inflorescence begin to release pollen. At this time, the beetles climb up the spadix, walk over the male flowers, become covered with pollen, and fly off. Beetles depart beginning at 1745 and continue until ≈1930. Pollination occurs when a pollen-bearing beetle flies to an inflorescence in female phase. In many cases, beetles depart from the inflorescence within minutes of arriving or some time during the night; alternatively they can remain within the inflorescence for several days. Because male flowers are not producing pollen when such beetles depart, they do not acquire a pollen load and do not contribute to male fitness of the plant they leave or to female fitness of the plant they visit next.

Because of the rigid timing of stigmatic receptivity and anther dehiscence in an inflorescence, one estimate of beetle effectiveness is the length of time spent at an inflorescence. I observed single inflorescences for 3–5 h on each of 30 evenings (13 in 1983 and 17 in 1984). As beetles flew into the inflorescences, I recorded the number of each species arriving at an inflorescence. Beetles departing during the observation period were also noted, by species. These inflorescences were then observed the next morning; beetles were removed, marked, and replaced. Any beetles not present in the morning were assumed to have departed during the night.

Pollen loads were obtained from beetles arriving at inflorescences in female phase and beetles departing from inflorescences in male phase during evening observation periods. Arriving beetles were captured just before they entered the inflorescence; departing beetles were captured after they had climbed over the male flowers and were departing. Pollen was scraped from their bodies and mounted on a slide with fuchsin-stained glycerin (Beattie 1971). On slides with <200 pollen grains, all grains were counted. For others, pollen grains were counted in three random transects across the slide under 100× power. No beetles were sacrificed because they were involved in a mark-recapture study. Thus, I could not use other standard methods for determining total pollen load, such as rinsing the entire beetle in alcohol (Lindsey 1984). This field technique of removing pollen from pollinators can only be viewed as an estimate of total pollen load due to incomplete removal of all grains. However, similar methods using adhesive tape to remove pollen from hummingbirds (Linhart and Feinsinger 1980) allow comparisons between species. Total pollen loads were estimated as the product of the mean number of pollen grains in three transects and the number of transects on a slide. Individuals of the most common visiting insect taxa (*Drosophila,* mirid bugs, and nitidulid beetles) were collected as they arrived at inflorescences and placed in 70% alcohol. Both the insects and the alcohol solution were examined microscopically for pollen.

Nine months after flowering, when ripe fruits became exposed by the opening of the spathe, all infructescences were collected (N = 146 in 1982, N = 203 in 1983) and fruit-set was determined. Each fruit contains one seed; thus fruit-set is equivalent to seed-set. Many infructescences aborted entirely between flowering and fruit presentation: 47% (N = 129) in 1982 and 52% (N = 220) in 1983. In such infructescences <10% of the ovules had expanded.

Pollinator effectiveness

I defined pollinator effectiveness as the contribution to seed set per individual beetle. Fruit-set was used from inflorescences visited by a single beetle (N = 20 inflorescences visited by one *C. amblyopsis,* N = 27 for *C. gravis,* N = 23 for *Erioscelis*). The probability of abortion and mean fruit-set was calculated for inflorescences visited by single beetles of each of the major beetle species.

Pollinator abundance

The abundance of each beetle species was estimated from daily censuses of flowering inflorescences (during the entire flowering seasons of 1982, 1983, and 1984). Because beetles generally remain within inflorescences for 24 h after arrival, morning surveys of inflorescences supply information on relative abundance of beetle species. Beetles leaving inflorescences before I checked them were assumed to be evenly distributed according to species (see Results: Behavior), so this estimate, although it may underestimate total number of visiting

TABLE 1. Observations of inflorescences at dusk, as beetles arrived, and the following morning. Thirty inflorescences were observed on 30 evenings in 1983 and 1984.*

	Erioscelis columbica		*Cyclocephala amblyopsis*		*Cyclocephala gravis*				
	%	No.	%	No.	%	No.	G	df	P
Individual beetles arriving at inflorescences		78		26		29			
Individuals departing within 30 min.	23	18	0	0	10	3	11.144	2	.004
Expected:		12.32		4.11		4.60			
Individuals departing during the night	31	24	31	8	17	5	1.746	2	.42
Individuals remaining until the following morning	46	36	69	18	72	21	3.621	2	.16

* A 3 × 3 contingency table test for differences between species in their behavior yields $G = 16.25$, df = 4, $P = .003$. G was partitioned into contributions due to species, presented in the row margins. Expected values are presented only where the G value for the row is significant, and are calculated based on the number of beetles arriving at inflorescences.

beetles, is an accurate measure of relative abundance of each species.

Pollinator importance

Pollinator importance estimates the effect of pollinator abundance on female reproductive success. Reproductive success is divided into: (1) the probability that each inflorescence is successful (does not abort), (2) the fruit-set of successful inflorescences, and (3) total female reproductive success (fruit-set of all inflorescences, giving aborted inflorescences a fruit-set of zero). I used logistic regression to predict the probability of inflorescence success as a function of number of visiting beetles (probability of success = $1/[1 + \exp(-a - x_iB_1 - x_i^2B_2)]$; PROC LOGIST in SAS 1986). Logistic regression predicts the probability of occurrence of categorical data (in this case inflorescence success or abortion) from knowledge of a continuous variable (beetle number). Both linear and quadratic logistic regressions were performed. The P value associated with the quadratic term is a measure of the probability that the quadratic term explains significantly more of the variance of the dependent variable than the linear model, and is used to determine the best-fitting regression equation.

I determined the effect of beetle abundance on fruit-set of successful inflorescences by regressing fruit-set on total number of beetles observed visiting the inflorescence. I determined both linear and quadratic regressions for 1982 and 1983 separately. Again, P values associated with terms added to the linear model were used to determine the best-fitting regression model. I investigated the effect of each beetle species on fruit-set by regressing the residual values from the previous best-fitting regression on the proportion of beetles of each species. Functionally, this is equivalent to a multiple regression, with the variation in fruit-set being partitioned into the effect of total number of beetles and the numbers of each species. The beetle numbers were arcsine transformed before analysis. Standardized slopes of these regressions were compared to determine the relative effects of each taxon on fruit-set. Finally, the effect of beetle abundance on total female reproductive success was investigated using regression analyses of beetle numbers on fruit-set of all inflorescences, giving aborted inflorescences a fruit-set of zero. Partitioning the effect of each beetle species was done by analyzing the residual values of this regression.

RESULTS

Differences among beetle species in pollination mechanics

Behavior.—Observations of inflorescences in the evening and the following morning in 1983 and 1984 indicated differences in the length of time *Erioscelis* and *Cyclocephala* species spent in inflorescences (Table 1). *Erioscelis* were more likely to depart the inflorescence within 30 min after arriving than *C. gravis* or *C. amblyopsis* ($G = 11.14$, $P = .004$). There were no differences among the species in the proportions that departed during the night or that remained until the morning. Thus, although more *Erioscelis* departed within several minutes of arriving, the three species were equally likely to remain long enough to remove pollen the following day.

Beetles remaining for an additional 24 h after male flowers released pollen were not effective pollinators because pollen viability was low (24%) after 24 h (fluorescein diacetate test, Heslop-Harrison and Heslop-Harrison 1970). One-third of all recaptures of *Erioscelis* in 1982 and 1983 were from the same inflorescence on consecutive days (127 out of 360 recaptures). Many of these beetles remained on the male portion of the spadix within the constricting spathe, usually eating male flowers. Other *Erioscelis* remained around the female flowers for several days and eventually chewed their way through the spathe tissue. In comparison, only 2.6% (5/192) of the recaptured *C. gravis* and 4.3% (6/139) of the recaptured *C. amblyopsis* remained within the inflorescence for >24 h.

Pollen load differences.—Pollen loads of arriving beetles varied among beetle species (Table 2). A higher

TABLE 2. Pollen loads on arriving and departing beetles (mean ± number of grains). ANOVAs were performed on counts of *Dieffenbachia* or foreign (heterospecific) pollen on arriving beetles and of *Dieffenbachia* pollen on departing beetles. Means with different superscript letters within a given column are different at the .05 level by Tukey's hsd test.

Beetle species	Number of beetles collected	Number of pollen grains of specified type on all beetles (SE)		Number of beetles carrying specified pollen type		Number of pollen grains of specified type on beetles carrying pollen of that type (SE)	
		Dieffenbachia	Foreign	*Dieffenbachia*	Foreign	*Dieffenbachia*	Foreign
Arriving beetles							
Erioscelis	30	2.33 (1.9)^{b}	1.77 (1.2)^{a}	6	4	11.67 (9.1)^{b}	13.25 (7.4)^{a}
Cyclocephala amblyopsis	7	766.14 (246.6)^{a}	93.71 (92.9)^{a}	6	2	893.83 (249.6)^{a}	328.00 (323.0)^{a}
C. gravis	10	252.70 (115.3)^{b}	1.00 (0.5)^{a}	9	3	280.78 (125.0)^{b}	3.33 (0.3)^{a}
		$F = 19.93$ df = 2, 44 $P < .0001$	$F = 3.06$ df = 2, 44 $P = .057$			$F = 7.47$ df = 2, 18 $P = .0043$	$F = 2.27$ df = 2, 6 $P = .184$
Departing beetles							
Erioscelis	11	3.73 (1.4)^{b}		5		8.20 (1.2)^{b}	
C. amblyopsis	7	405.29 (46.0)^{a}		7		405.29 (46.0)^{a}	
C. gravis	6	368.83 (27.8)^{a}		6		368.83 (27.8)^{a}	
		$F = 82.91$ df = 2, 21 $P < .0001$				$F = 35.24$ df = 2, 15 $P < .0001$	

proportion of *C. gravis* and *C. amblyopsis* carried *Dieffenbachia* pollen than did *Erioscelis*. *C. amblyopsis* carried significantly more pollen than the other two species. Small pollen loads on *Erioscelis* can be explained because these beetles frequently left an inflorescence before pollen was released. However, the number of heterospecific pollen grains carried by arriving beetles did not vary among species, probably due to small sample sizes (only nine beetles examined carried foreign pollen). *Erioscelis* carried close to equal numbers of *Dieffenbachia* and heterospecific pollen grains, while the two *Cyclocephala* species had pollen loads dominated by *Dieffenbachia* pollen. Departing individuals of the two *Cyclocephala* species carried significantly more pollen than *Erioscelis*. No pollen was found on the bodies of the three most common nonscarab visitors (13 *Drosophila*, 29 Hemiptera, and 21 nitidulid beetles). Although these taxa were more likely to be found in inflorescences of *D. longispatha* than *Erioscelis* or any species of *Cyclocephala*, they cannot be referred to as pollinators.

Pollinator effectiveness

Single visits by *Erioscelis*, *C. gravis*, and *C. amblyopsis* resulted in 65%, 52%, and 53% abortion of inflorescences (fruit-set = 0), respectively (Fig. 1). This variation in abortion rate among species was not significant ($\chi^2 = 0.92$, df = 1, $P = .34$). In addition, the fruit-sets of successful inflorescences resulting from one visit (Fig. 1) did not vary significantly among species (ANOVA, $F = 1.16$, df = 2,30, $P = .33$). Thus, a single visit by *Erioscelis* was as effective as a single visit by either of the *Cyclocephala* species.

Pollinator Abundance

Beetles were four times as abundant in inflorescences in 1983 as in 1982 or 1984 (Table 3). Beetle numbers within inflorescences ranged from 0 to 15 ($\bar{X} = 1.77$, SE = 0.164, $N = 271$) in 1982, and from 0 to 39 ($\bar{X} = 7.27$, SE = 0.283, $N = 423$) in 1983. Most of the difference between years can be attributed to an increase in *Erioscelis*. The rank order of the three species was constant between the years (*Erioscelis columbica* > *C. gravis* ≈ *C. amblyopsis*). Recapture rates were significantly higher for *C. gravis* and *C. amblyopsis* than for *Erioscelis* in both 1983 and 1984 (Table 3), suggesting smaller population sizes of the former two species. The tremendous difference in beetle numbers between 1982 and 1983 provided a natural test of the effect of beetle abundance on estimates of importance.

Pollinator importance

Probability of inflorescence success.—The probability that an inflorescence matured to produce fruit was a quadratic function of the total number of visiting beetles (Fig. 2). Success rate was lowest for inflorescences visited by few beetles and by many beetles; highest probability of success occurred when inflorescences were visited by intermediate numbers of beetles (8–12). Quadratic logistic regressions were better predictors of inflorescence success than linear (the probability values associated with the slopes of the qua-

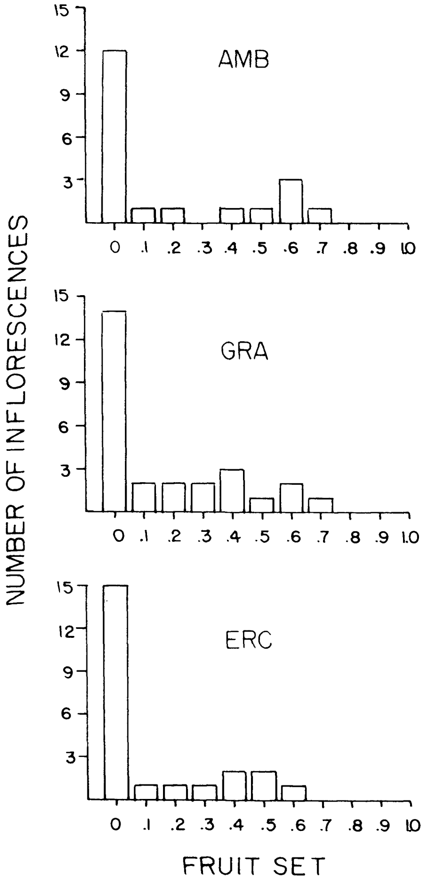

FIG. 1. Effectiveness measures of beetles visiting *Dieffenbachia longispatha.* Frequency distributions of fruit-set of *D. longispatha* resulting from a single visit by *Cyclocephala amblyopsis* (AMB), *C. gravis* (GRA), and *Erioscelis columbica* (ERC). Aborted inflorescences have fruit-set of zero. The percentage of inflorescences setting fruit = 47% for a single visit by AMB; 48% for GRA; 35% for ERC. The mean (SE) fruit-set of successful inflorescences = 51.5% (8.4%) for AMB; 37.5% (5.9%) for GRA; 37.2% (5.8%) for ERC.

dratic terms for total number of beetles in Table 4A were <.05).

The functional relationship between beetle species and inflorescence success varied among species and years. Over the entire range of values, the abundance of *Erioscelis* was positively related to the probability of inflorescence success in 1982 and negatively related in 1983 (Fig. 2, Table 4). In a year when beetles were very abundant (1983), the success rate of inflorescences decreased with increasing numbers of visiting *Erioscelis.* The abundance of *Cyclocephala* was a positive predictor of inflorescence success in 1982. In 1983, the probability of inflorescence success increased with *Cyclocephala* abundance up to six beetles and decreased when inflorescences were visited by more than six *Cyclocephala.*

A simpler way to look at the data is to examine the number of beetles visiting inflorescences that later aborted or set fruit (Table 4B). In 1982, successful inflorescences were visited by significantly more beetles than aborted inflorescences. In 1983, successful inflorescences were visited by significantly fewer beetles (total number of beetles and number of *Erioscelis*), although they had significantly more *Cyclocephala* visits than aborted inflorescences.

Fruit-set of successful inflorescences.—The regressions of fruit-set (including only successful inflorescences) on total number of visiting beetles (*Erioscelis* and *Cyclocephala* combined) showed different relationships between the variables for the two years (Fig. 3). In 1982, fruit-set was positively related to total number of visiting beetles; in 1983, fruit-set declined with increases in beetle numbers. For both years, quadratic regressions did not explain significantly more of the variation in fruit-set than linear regressions (Table 5). The linear regressions explained a limited proportion of the variance in fruit-set, however (1982: r^2 = 0.028; 1983: r^2 = 0.029).

TABLE 3. Summary of differences in beetle abundance (total number of beetles encountered during daily censuses of inflorescences and mean number per inflorescence) and recapture rates during the flowering seasons in 1982, 1983, and 1984.

	1982		1983		1984	
	No.	$\bar{X}$	No.	$\bar{X}$	No.	$\bar{X}$
Total number of beetles observed in inflorescences						
Cyclocephala gravis	132	0.48	570	1.35	164	0.28
C. amblyopsis	116	0.42	387	0.92	201	0.35
Other *Cyclocephala* spp.	77	0.28	91	0.21	134	0.23
Erioscelis columbica	232	0.84	2014	4.76	725	1.25
Total number of beetles	487	1.77	3077	7.27	1131	1.96
Total number of inflorescences censused	275		423		578	
% inflorescences remaining unvisited	31		3		39	
Recapture rates (%)						
Cyclocephala gravis	...*		27		19	
C. amblyopsis	...		22		27	
Erioscelis columbica	...		9		13	

* The beetle marking technique was not perfected until late in the 1982 season so recaptures in that year were rare.

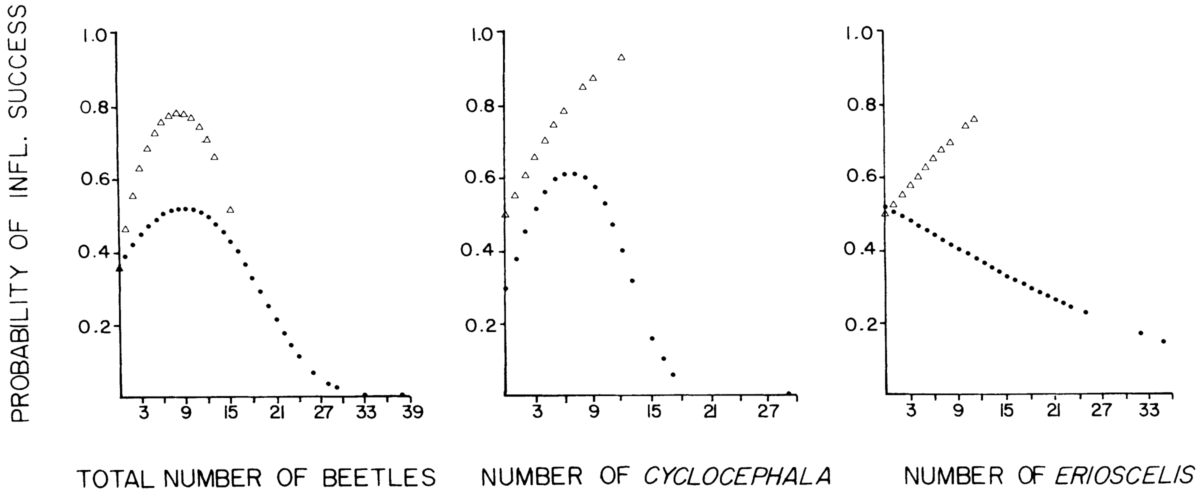

FIG. 2. The probability of inflorescence success (nonabortion) predicted from logistic regressions on beetle number, for total beetles, *Cyclocephala,* and *Erioscelis.* Equations for these regressions are presented in Table 4. 1982 data are represented by triangles; 1983 by solid dots. Note that inflorescences were visited by many more beetles in 1983 than in 1982.

TABLE 4. (A) Linear and quadratic logistic regression equations predicting the probability of inflorescence success as a function of number of beetles visiting inflorescences. Equations are of the form $1/[1 + \exp(-a - x_iB_1 - x_i^2B_2)]$. (B) Mean number of beetles visiting successful and aborting inflorescences. Differences between row means were tested using *t* tests.

A) Terms in equation†	Intercept			Linear term			Quadratic term		
	a	χ^2	P	B_1	χ^2	P	B_2	χ^2	P
1982									
TOT	−0.352	4.50	.034	0.205	13.39	.0003			
TOT,(TOT)^2*	−0.568	8.84	.003	0.444	14.55	<.0001	−0.027	6.07	.014
CYC*	−0.021	0.03	.869	0.216	3.86	.049			
CYC,(CYC)^2	−0.041	0.09	.758	0.329	2.65	.104	−0.018	0.49	.485
ERC	−0.005	0	.969	0.105	2.03	.155			
ERC,(ERC)^2	−0.035	0.06	.809	0.194	1.32	.251	−0.012	0.35	.552
1983									
TOT	0.062	0.13	.718	−0.030	3.06	.080			
TOT,(TOT)^2*	−0.598	4.89	.027	0.158	6.18	.013	−0.009	8.49	.004
CYC	−0.367	6.98	.008	0.055	3.40	.065			
CYC,(CYC)^2*	−0.884	23.10	<.0001	0.402	21.84	<.0001	−0.030	14.83	<.0001
ERC*	0.069	0.28	.598	−0.053	8.10	.004			
ERC,(ERC)^2	−0.139	0.77	.381	0.069	1.47	.226	−0.008	4.51	.034

B) Abundance measure†	Successful			Aborted				
	N	$\bar{X}$	SE	N	$\bar{X}$	SE	t	P
1982								
TOT	141	1.78	0.23	130	1.20	0.20	1.90	.029
CYC	141	0.78	0.15	130	0.51	0.13	1.35	.089
ERC	141	1.00	0.17	130	0.68	0.14	1.47	.071
1983								
TOT	192	7.89	0.34	231	8.83	0.43	1.66	.049
CYC	192	3.86	0.21	231	3.19	0.25	1.99	.024
ERC	192	4.03	0.31	231	5.64	0.43	2.93	.002

* The best fitting regressions are plotted in Fig. 2; for the quadratic regression to be significantly better than the linear, the *P*-values associated with both B_1 and B_2 must be $<.05$. Neither of the logistic regressions with *Erioscelis* in 1982 is significant; the linear regression is plotted in Fig. 2. The levels of significance of the estimated intercept (a) and slope parameters (B_1 and B_2) were tested with chi-square statistics (PROC CATMOD in SAS 1985).

† TOT = total no. beetles visiting each inflorescence; CYC = total no. of visiting *Cyclocephala*; ERC = total no. of visiting *Erioscelis.*

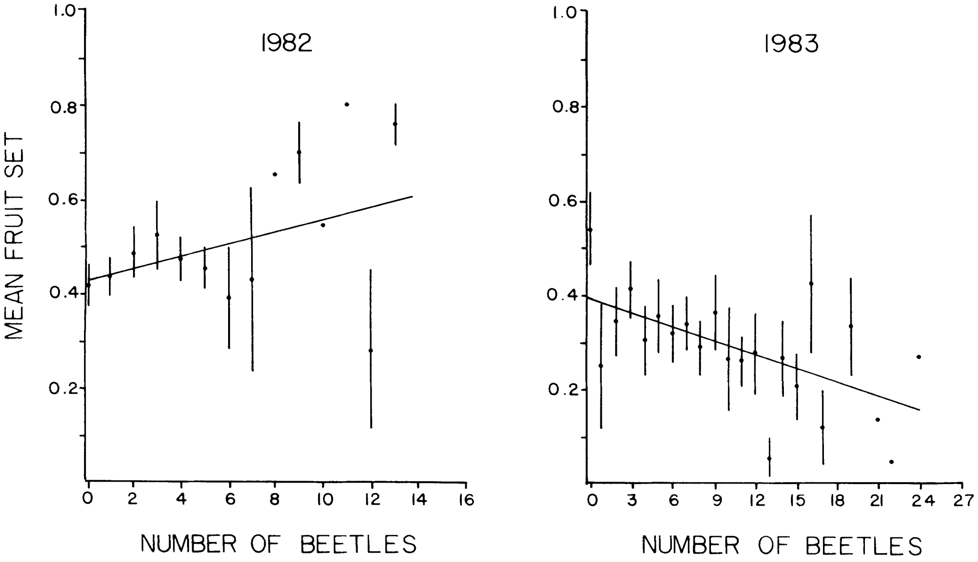

FIG. 3. Regression of fruit-set on total number of beetles visiting inflorescences for 1982 and 1983. Aborted inflorescences are not included. Mean fruit-set (±SE) is plotted against number of visiting beetles. The best fitting regressions are represented with solid lines and given in Table 5.

In 1983, the regression of the relative abundance of *Cyclocephala gravis* on the residual fruit-set values of the above regression had a significant positive standardized slope (Table 5). Increases in the relative abundance of *C. gravis* within the inflorescence can account for the fruit-set values above the values predicted by the total beetle regression. The regression of the residuals on the proportion of *Erioscelis* within inflorescences had a significant negative standardized slope. Thus, as *Erioscelis* became relatively more abundant within inflorescences, their presence explained the fruit-sets below the predicted values. The standardized slope of the regression with *C. amblyopsis* was not significant, and therefore its relative abundance did not explain a significant amount of the residual variance of fruit-set. Thus, for 1983, when the effect of the total numbers of beetles on fruit-set was removed (by the linear regression), the overall effect of increases in proportions of *C. gravis* on fruit-set was positive and the overall effect of increases in proportions of *Erioscelis* on fruit-set was negative. Variation in beetle species abundance within flowers clearly contributed to the unexplained portion of the fruit-set variance in the overall regression analysis.

In contrast, analysis of the residual values of fruit-set for 1982 showed that relative abundance of each beetle species had no significant effect on female reproduction (Table 5). No single beetle species explained the variance of fruit-set around the predicted values, which indicates that each species was contributing in the same manner to the predicted fruit-set. In 1982, *Erioscelis* was not detrimental to fruit-set when its relative abundance was high (any more than the two *Cyclocephala* species). This is probably because no species was particularly abundant in 1982, when the greatest number of beetles in an inflorescence was 15, in contrast to 1983, when beetle numbers reached 39 in an inflorescence and 66% of all beetles were *Erioscelis* (42% were *Erioscelis* in 1982).

Total female reproductive success.—Inflorescences that abort are not contributing to the maternal success of plants possessing them, yet they represent a significant cost to the plant. Total female success is a function of the number of inflorescences aborting as well as the fruit-set of successful inflorescences. Regressions of fruit-set on beetle number that include the zero fruit-set of aborted inflorescences revealed an interesting relationship between beetle abundance and *Dieffenbachia* reproductive success (Fig. 4). In 1982, a linear regression of log beetle number explained more of the variance in fruit-set than a linear, untransformed model (Table 6A). Fruit-set increased with beetle number but saturated at a beetle abundance of ≈12, where the predicted fruit-set is 47%. The per-beetle effectiveness decreased with increasing number of visiting beetles. In 1983, the best-fitting regression was a quadratic regression of log beetle numbers. The per-visit contribution to fruit-set was large and positive for the first four beetles; increases in beetle abundance above four beetles resulted in decreased fruit-set. Both years showed profound deviations from the a priori expectation of a positive linear relationship between pollinator abundance and importance. The *y* intercepts of the regressions in Fig. 4 are significantly greater than zero, predicting that fruit-set associated with no visitation would be 16 and 20% for 1982 and 1983, respectively. Observed fruit-set from bagged, unvisited inflorescences was 29% (Young 1986*a*), suggesting that, even in the

TABLE 5. (A) Linear and quadratic regressions of fruit-set on total number of beetles visiting inflorescences in 1982 and 1983 (untransformed and log-transformed). Beetle number was the independent variable, and fruit-set the dependent variable. (B) Regressions of residual values from the linear regressions above on proportion of each beetle species. Proportion of each beetle species was the independent variable, and the dependent variables were residual values from the untransformed linear regressions. Aborted inflorescences are not included. Proportion of each beetle species was arcsine transformed.

A) Independent variable: beetle number
Dependent variable: fruit-set

			Linear term		Quadratic term					
	Intercept	*P* intercept ≠ 0	Slope	*P* slope ≠ 0	Slope	*P* slope ≠ 0	*F*	df	*P*	r^2
1982:										
Linear*	0.424	<.0001	0.0129	.04			3.98	1, 139	.04	0.028
Quadratic	0.428	<.0001	0.0097	.57	0.0003	.84	1.99	2, 138	.14	0.028
Linear log	0.409	<.0001	0.0479	.06			3.59	1, 139	.06	0.025
Quadratic log	0.418	<.0001	0.0170	.82	0.0143	.66	1.88	2, 138	.16	0.026
1983:										
Linear*	0.388	<.0001	−0.0095	.01			6.25	1, 205	.01	0.029
Quadratic	0.411	<.0001	−0.0157	.24	0.0003	.63	3.23	2, 204	.04	0.031
Linear log	0.469	<.0001	−0.0768	.01			6.15	1, 205	.01	0.029
Quadratic log	0.424	.0005	−0.0218	.86	−0.0150	.65	3.16	2, 204	.04	0.030

B)

	Standardized slope†	*F*	df	*P*	r^2
1982:					
Proportion *Cyclocephala gravis*	−0.059	0.49	1, 139	.48	0.004
Proportion *C. amblyopsis*	0.098	1.35	1, 139	.25	0.010
Proportion *Erioscelis*	0.098	1.33	1, 139	.25	0.010
1983:					
Proportion *C. gravis*	0.127	3.39	1, 205	.05	0.016
Proportion *C. amblyopsis*	0.075	1.17	1, 205	.27	0.006
Proportion *Erioscelis*	−0.133	3.72	1, 205	.05	0.018

* The best fitting regression, which is plotted in Fig. 3.
† Standardized slope = slope/[(SD of fruit-set) ÷ (SD of beetle number)].

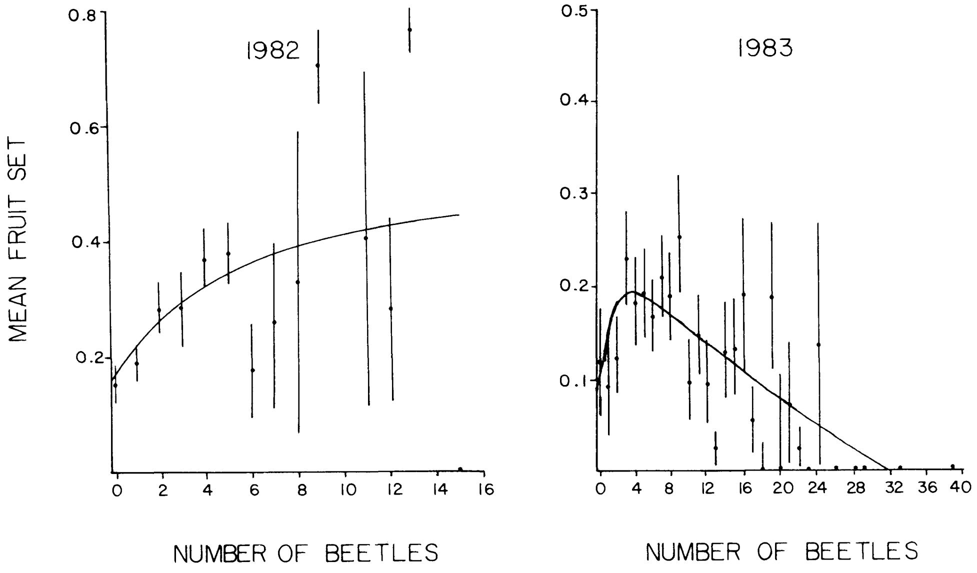

FIG. 4. Regression of fruit-set on total number of beetles visiting inflorescences for 1982 and 1983. Aborted inflorescences are included, assigned fruit-sets of 0. Mean fruit-set (±SE) is plotted against number of visiting beetles. The best fitting regression lines are represented with solid lines and given in Table 6. Note the different scale for the *y* axis between years.

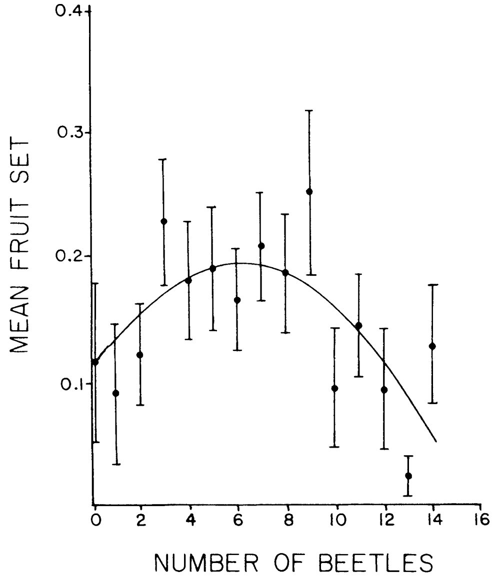

FIG. 5. Regression of fruit-set on total number of visiting beetles for inflorescences visited by fewer than 15 beetles in 1983 (to make the abundance of beetles similar to 1982). Aborted inflorescences are included, given a fruit-set of zero. Mean fruit-set (±SE) is plotted against beetle number (see Table 7 for regression equation).

absence of beetle visitors, self-pollination may take place.

Again, in partitioning the effect of beetle abundance on fruit-set among beetle species, the relative abundances of *C. gravis*, *C. amblyopsis*, and *Erioscelis* did not explain a significant portion of the residual fruit-set values in 1982 (Table 6B). Thus, all species were contributing in the same functional manner to the asymptotic fruit-set curve in Fig. 4. For 1983, the relative abundance of *C. gravis* explained the fruit-sets above those predicted by total beetle number; *Erioscelis* was significantly related to the fruit-set values below those predicted; and *C. amblyopsis* did not explain a significant portion of the residual fruit-set values.

The negative relationship between fruit-set and beetle numbers >4 in 1983 could explain the low fruit-sets of inflorescences visited by >15 beetles. Inflorescences with >15 beetles in 1983 contained an average (±SE) of 70 ± 4.17% *Erioscelis* (N = 60; compared with 46 ± 1.9% *Erioscelis* in inflorescences with <15 beetles, N = 349), suggesting that the high relative abundance of *Erioscelis* in these inflorescences reduced fruit-set. To test directly the effect of high numbers of beetles on fruit-set, I performed a regression of fruit-

TABLE 6. (A) Linear and quadratic regressions of fruit-set on beetle abundance (beetle number, both untransformed and log-transformed). Aborted inflorescences were given fruit-set of zero. (B) Residual values of fruit-set were regressed on proportion of total beetle numbers that were composed of each beetle species (arcsine transformed).

A)

			Linear term		Quadratic term					
	Intercept	P intercept ≠ 0	Slope	P slope ≠ 0	Slope	P slope ≠ 0	F	df	P	r^2
1982										
Linear	0.177	<.0001	0.0278	<.0001			20.55	1, 269	<.0001	0.071
Quadratic	0.153	<.0001	0.0529	<.0001	−0.0026	.041	12.14	2, 268	<.0001	0.083
Linear log*	0.142	<.0001	0.1093	<.0001			24.29	1, 269	<.0001	0.083
Quadratic log	0.138	<.0001	0.0972	.126	0.0060	.839	12.12	2, 268	<.0001	0.083
1983										
Linear	0.196	<.0001	−0.0051	.011			6.48	1, 421	.011	0.015
Quadratic	0.191	<.0001	0.0001	.975	0.0002	.278	3.83	2, 420	.022	0.018
Linear log	0.199	<.0001	−0.0229	.172			1.87	1, 421	.172	0.004
Quadratic log*	0.072	.189	0.1526	.010	−0.0496	.0021	5.72	2, 420	.003	0.026

B)

1982: Dependent variable: residuals of linear log regression

	Standardized slope†	df	F	P	r^2
Proportion *C. gravis*	−0.0292	1, 269	0.23	.63	0.0009
Proportion *C. amblyopsis*	+0.0855	1, 269	1.98	.16	0.0073
Proportion *Erioscelis*	−0.0394	1, 269	0.42	.52	0.0016

1983: Dependent variable: residuals of quadratic log regression

	Standardized slope	df	F	P	r^2
Proportion *C. gravis*	+0.1482	1, 421	9.46	.002	0.022
Proportion *C. amblyopsis*	+0.0418	1, 421	0.74	.39	0.0017
Proportion *Erioscelis*	−0.1286	1, 421	7.09	.008	0.017

* The best fitting regression, which is plotted in Fig. 4.

† Standardized slope = slope/[(SD of fruit-set) ÷ (SD of beetle number)].

TABLE 7. (A) Regression of fruit-set on beetle number for inflorescences visited by fewer than 15 beetles in 1983. Aborted inflorescences are included, given fruit-set of zero. (B) The residual values of the quadratic regression on untransformed beetle number, regressed on the proportion of each beetle species (arcsine transformed).

A)

			Linear term		Quadratic term					
	Intercept	P intercept $\neq 0$	Slope	P slope $\neq 0$	Slope	P slope $\neq 0$	F	df	P	r^2
Linear	0.189	<.0001	−0.004	.239			1.39	1, 361	.239	0.004
Quadratic*	0.108	.008	0.028	.028	−0.002	.009	4.17	2, 360	.016	0.027
Linear log	0.124	.0006	−0.003	.894			0.02	1, 361	.894	0
Quadratic log	0.110	.0009	0.175	.015	−0.059	.010	3.32	2, 360	.037	0.018

B)

	Standardized slope†	df	F	P	r^2
Proportion *C. gravis*	+0.1463	1, 361	7.89	.005	0.021
Proportion *C. amblyopsis*	+0.0377	1, 361	0.51	.47	0.001
Proportion *Erioscelis*	−0.1243	1, 361	5.67	.02	0.016

* The best fit regression, which is plotted in Fig. 5.

† Standardized slope = slope/[(SD of fruit-set) ÷ (SD of beetle number)].

set on total number of beetles only for inflorescences visited by <15 beetles in the 1983 flowering season, which represented a range of beetle numbers comparable to 1982. The resulting quadratic regression equation had a positive linear component and a negative quadratic component (Table 7A, Fig. 5). Highest fruit-set resulted from visitation by six beetles. The regressions of the residuals on the proportion of beetles of each species showed that *Erioscelis* had a significant negative slope, *C. gravis* had a significant positive slope, and *C. amblyopsis* had a slope that was not significant (Table 7B). Thus, when the range of beetle numbers for 1983 was made to equal that of 1982: (1) fruit-set was positively related to beetle numbers up to six beetles (when the predicted fruit-set was 19%), but negatively related to beetle number at higher beetle abundance, and (2) *Erioscelis* still exhibited a negative effect on fruit-set, in contrast to the positive effect of low numbers of *Erioscelis* in 1982.

DISCUSSION

These results show that the contributions of several beetle taxa to the female success of *Dieffenbachia longispatha* cannot be predicted from their behavior, pollen loads, abundance, or from fruit-set resulting from a single visit (effectiveness). Of equal importance, the incremental effect of beetles on fruit-set (the per-visit effectiveness) is not positive and linear over the natural range of abundance of the beetles.

The effectiveness measures (effect of a single visit on fruit-set and probability of inflorescence abortion) of the three major scarab pollinators are not significantly different. Previous studies have calculated the importance of various pollinator taxa as the product of effectiveness and abundance of a particular taxon (Thomson et al. 1982, Lindsey 1984, Sugden 1986). Taxa with the largest products are the "most important" pollinators. By such measures, *Erioscelis* would be the most important pollinator of *D. longispatha* by virtue of its high relative abundance. Such calculations assume a positive linear relationship between the abundance of a pollinator and its relative contribution to the reproductive success of the plant. The system illustrated by *Dieffenbachia* and its beetle pollinators provides evidence that such importance values can be misleading.

The fate of inflorescences visited by varying numbers of *Erioscelis* suggests that this genus contributes little to the female reproductive success of *D. longispatha* (their abundance contributes to inflorescence abortion and low fruit-sets of inflorescences that do not abort). The detrimental effects of *Erioscelis* in 1983 may be explained by their high relative and absolute abundance.

The relationship between beetle abundance and female reproductive success of *Dieffenbachia* was neither positive nor linear in either year. In 1982, when abundance of all beetles (particularly *Erioscelis*) was low, all species were positively related to fruit-set, but their effect on fruit-set declined with increasing beetle abundance. In 1983, the relationship between beetle number and fruit-set is positive for inflorescences visited by fewer than four beetles, but fruit-set declines when visitation exceeds four beetles. There are two reasons that such a nonlinear relationship may exist. First, because fruit-set is constrained to level off at 100%, the per-visit effectiveness of pollinators may decrease with increasing abundance, as in 1982 (Gori 1983). Motten et al. (1981) and Plowright and Hartling (1981) consider this when they predict, through models, the probability of fruit formation or seed-set as functions of pollinator abundance. However, these models do not predict a decline in fruit-set with high pollinator abundance.

A second explanation for the nonlinear relationship is that per-visit effectiveness may be dependent on the number of previous visits, such that increasing pollinator abundance results in cumulative floral damage. Because I have seen only one instance of beetles damaging ovaries of *D. longispatha,* it is difficult to explain the decrease in fruit-set with increased beetle numbers. Beetles spend 24 h feeding, mating, and walking around the stigmas. In the presence of abundant beetles, these actions may dislodge more ungerminated pollen from stigmas than is deposited (see Gori 1983), or beetle waste products may accumulate that could reduce pollen germination and thereby cause reduced fruit-set. In addition, foreign pollen grains may accumulate when beetles are abundant, effectively blocking the stigmatic surface. The phenomenon of pollinators being detrimental at high densities may be especially likely in plant species that offer an enclosed chamber where pollinators remain for relatively long periods.

These results lend quantitative support to earlier qualitative evidence of density-dependent pollinator effects. Prance and Arias (1975) previously showed that the number of beetles present in flowers of *Victoria* was qualitatively associated with low numbers of seeds produced, while Búrquez et al. (1987) found that increased exposure of *Astrocaryum mexicanum* inflorescences to insects (mostly scarab beetles) resulted in decreased fruit-set. Therefore, the descriptive function of beetles varies with their abundance: they can be beneficial pollinators at low densities but harmful parasites at high densities. This is in contrast with Schemske and Horvitz's (1984) observation that the ineffective pollinators of *Calathea ovandensis* in Panama were merely commensals in the system (they did not have a negative effect on fruit-set). Scarab beetles pollinating *Dieffenbachia* clearly demonstrate density-dependent pollinator importance.

Some animal visitors may be detrimental at all levels of abundance, but the damage is usually restricted to anthers, pollen, or the gynoecium without affecting seed-set, or the damage is attributed to a separate stage in the life cycle. There are reports of the larvae of pollinators causing damage to floral or fruit structures: *Yucca* and *Tegeticula* moths (Powell and Mackie 1966); *Ficus* and wasps (Wiebes 1979); *Silene* and *Hadena* moths (Brantjes and Leemans 1976); *Davilla* and a curculionid beetle (Gottsberger 1977); *Nuphar lutea* and *Donacia,* its beetle pollinator (Schneider and Moore 1977). Beetles frequently damage floral structures of the plants they pollinate: anthers (*Drimys,* Gottsberger et al. 1980; *Philodendron selloum,* Gottsberger and Amaral 1984; Clusiaceae, Gottsberger 1977); and stigmas (*Victoria amazonica,* Prance and Arias 1975; *Zygogynum,* Thien 1980; *Magnolia tripetala* and *M. grandiflora,* Thien 1974; *Talauma,* Gottsberger 1977). Gibbs et al. (1977) emphasize that in none of the reported examples of beetle pollination does damage seriously affect ovules.

The number of beetles visiting inflorescences explains only a limited portion of the variance in fruit-set ($r^2 = 0.02 - 0.08$). Factors other than pollinator abundance may limit female reproductive success, such as resources available for maturation of fruits (reviewed in Stephenson 1981), the number and sizes of pollen-donating plants in the population (Thomson and Barrett 1981, Young 1986*b,* Devlin and Stephenson 1987, Ennos and Dodson 1987), or the spatial distribution of potential mates (Young 1986*b*). Although female success may not increase with increasing numbers of pollinators in *D. longispatha,* male success may be a positive function of visitation frequency (as demonstrated by Stanton et al. 1986 for *Raphanus raphanistrum*). If this is true for *Dieffenbachia,* selection may be acting differently on male and female reproductive success through selection on the physical parameters affecting pollinator visitation rate (such as inflorescence size, floral odor, time of flowering). Determining that intermediate numbers of pollinators result in highest female success, in addition to being an unexpected observation, is the first step in correlating phenotypic characters with fitness in this species.

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LITERATURE CITED

Arnold, R. M. 1982. Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). American Midland Naturalist **107**:360–369.

Beach, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). American Journal of Botany **69**:1074–1081.

Beattie, A. J. 1971. A technique for the study of insect-borne pollen. Pan Pacific Entomologist **47**:82.

Brantjes, N. B. M., and J. A. A. Leemans. 1976. *Silene otites* (Caryophyllaceae) pollinated by nocturnal Lepidoptera and mosquitos. Acta Botanica Neerlandica **25**:281–295.

Búrquez, A., J. Sarukhán, and A. L. Pedroza. 1987. Floral biology of a primary rain forest palm, *Astrocaryum mexicanum* Liebm. Biological Journal of the Linnean Society **31**:161–174.

Campbell, D. R. 1985. Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. Ecology **66**: 544–553.

———. 1986. Predicting plant reproductive success from models of competition. Oikos **47**:257–266.

Devlin, B., and A. G. Stephenson. 1987. Sexual variation among plants of a perfect-flowered species. American Naturalist **130**:199–218.

Ennos, R. A., and R. K. Dodson. 1987. Pollen success, functional gender and assortative mating in an experimental plant population. Heredity **58**:119–126.

Gibbs, P. E., J. Semir, and N. D. Cruz. 1977. Floral biology of *Talauma ovata* St. Hil. (Magnoliaceae). Ciência e Cultura **29**:1436–1441.

Gori, D. F. 1983. Post-pollination phenomena and adaptive floral changes. Pages 31–45 *in* C. E. Jones and R. J. Little, editors. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, New York, USA.

Gottsberger, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. Plant Systematics and Evolution, Supplement **1**:211–226.

Gottsberger, G., and A. Amaral. 1984. Pollination strategies in Brazilian *Philodendron* species. Berichte der Deutschen Botanischen Gesellschaft **97**:391–410.

Gottsberger, G., I. Silberbauer-Gottsberger, and F. Ehrendorfer. 1980. Reproductive biology in the primitive relic angiosperm *Drimys brasiliensis* (Winteraceae). Plant Systematics and Evolution **135**:11–39.

Heslop-Harrison, J., and Y. Heslop-Harrison. 1970. Evaluation of pollen viability by enzymatically induced fluorescence: intracellular hydrolysis of fluorescein diacetate. Stain Technology **45**:115–120.

Holdridge, L. R., W. C. Granke, W. H. Hatheway, T. Liang, and J. A. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon, Oxford, England.

Kohn, J. R., and N. M. Waser. 1985. The effect of *Delphinium nelsonii* pollen on seed set in *Ipomopsis aggregata*, a competitor for hummingbird pollination. American Journal of Botany **72**:1144–1148.

Lindsey, A. H. 1984. Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. American Journal of Botany **71**:375–387.

Linhart, Y. B., and P. Feinsinger. 1980. Plant-hummingbird interactions: effects of island size and degree of specialization on pollination. Journal of Ecology **68**:745–760.

McDade, L. A., and P. Davidar. 1984. Determinants of fruit and seed set in *Pavonia dasypetala* (Malvaceae). Oecologia (Berlin) **64**:61–67.

Motten, A. F. 1983. Reproduction of *Erythronium umbilicatum* (Liliaceae): pollination success and pollinator effectiveness. Oecologia (Berlin) **59**:351–359.

Motten, A. F., D. R. Campbell, and H. E. Alexander. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology **62**:1278–1287.

Ornduff, R. 1975. Complementary roles of halictids and syrphids in the pollination of *Jepsonia heterandra* (Saxifragaceae). Evolution **29**:371–373.

Parker, F. D. 1982. Efficiency of bees in pollinating onion flowers. Journal of the Kansas Entomology Society **55**:171–176.

Plowright, R. C., and L. K. Hartling. 1981. Red clover pollination by bumblebees: a study of the dynamics of a plant-pollinator relationship. Journal of Applied Ecology **18**:639–647.

Powell, J. A., and R. A. Mackie. 1966. Biological interrelationships of moths and *Yucca whipplei* (Lepidoptera: Gelechiidea, Blastobasidae, Prodoxidae). University of California Publications in Entomology **42**:1–46.

Prance, G. T., and J. R. Arias. 1975. A study of the floral biology of *Victoria amazonica* (Poepp.) Sowerby (Nymphaeaceae). Acta Amazonica **5**:109–139.

Primack, R. B., and J. A. Silander. 1975. Measuring the relative importance of different pollinators to plants. Nature **255**:143–144.

SAS Institute. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

———. 1986. SUGI supplemental library user's guide, version 5 edition. SAS Institute, Cary, North Carolina, USA.

Schemske, D. W., and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science **225**:519–521.

Schneider, E. L., and L. A. Moore. 1977. Morphological studies of the Nymphaeaceae. VII. The floral biology of *Nuphar lutea* subsp. *macrophylla*. Brittonia **29**:88–99.

Silander, J. A., and R. B. Primack. 1978. Pollination intensity and seed set in the evening primrose (*Oenothera fruticosa*). American Midland Naturalist **100**:213–216.

Snow, A. A. 1982. Pollination intensity and potential seed set in *Passiflora vitifolia*. Oecologia (Berlin) **55**:231–237.

———. 1986. Pollination dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. American Journal of Botany **73**:139–151.

Snow, A. A., and D. W. Roubik. 1987. Pollen deposition and removal by bees visiting two tree species in Panama. Biotropica **19**:57–63.

Spears, E. E. 1983. A direct measure of pollinator effectiveness. Oecologia (Berlin) **57**:196–199.

Stanton, M. L., A. A. Snow, and S. N. Handel. 1986. Floral evolution: attractiveness to pollinators increases male fitness. Science **232**:1625–1626.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics **12**:253–279.

Sugden, E. A. 1986. Anthecology and pollinator efficacy of *Styrax officinale* subsp. *redivivum* (Styracaceae). American Journal of Botany **73**:919–930.

Thien, L. B. 1974. Floral biology of *Magnolia*. American Journal of Botany **61**:1037–1045.

———. 1980. Patterns of pollination in the primitive angiosperms. Biotropica **12**:1–13.

Thomson, J. D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. American Midland Naturalist **100**:431–440.

Thomson, J. D., and S. C. H. Barrett. 1981. Temporal and spatial variation of gender in *Aralia hispida* Vent. (Araliaceae). Evolution 35:1094–1107.

Thomson, J. D., W. P. Maddison, and R. C. Plowright. 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). Oecologia (Berlin) **54**:326–336.

Valério, C. E. 1984. Insect visitors to the inflorescence of the aroid *Dieffenbachia oerstedii* (Araceae) in Costa Rica. Brenesia **22**:139–146.

Waser, N. M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). Oecologia (Berlin) **39**:107–121.

Weibes, J. T. 1979. Coevolution of figs and their insect pollinators. Annual Review of Ecology and Systematics **10**:1–12.

Young, H. J. 1986*a*. Beetle pollination of *Dieffenbachia longispatha* (Araceae). American Journal of Botany **73**:931–944.

———. 1986*b*. Pollination of *Dieffenbachia longispatha*: effects of beetles on reproductive success, gene flow, and gender. Dissertation. State University of New York, Stony Brook, New York, USA.

Zimmerman, M. 1980. Reproduction in *Polemonium*: competition for pollinators. Ecology **61**:497–501.