

BETLE POLLINATION OF DIEFFENBACHIA LONGISPATHA (ARACEAE)¹

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ABSTRACT

Dieffenbachia is an monoecious understory herb of tropical rain forests that exhibits a complex and specialized relationship with its beetle pollinators. The erect protogynous inflorescence has the spadix divided, with the female flowers in the basal half and male flowers in the upper half. *Dieffenbachia longispatha* Engler & Krause is pollinated by scarab beetles in the genera *Cyclocephala* and *Erioscelis*. The enveloping spathe of the inflorescence opens in the evening, but no flowers are sexually functional until the stigmas become receptive about 24 hr later. Beetles fly to the inflorescence in darkness, suggesting that floral odors play a role as an attractant. Beetles remain in the inflorescence for 24 hr, eating protein-rich staminodia that surround the stigmas. On the evening of the third day the anthers dehisce and beetles become covered with pollen as they crawl up the spadix in the process of leaving. Beetles fly an average of 80 m between inflorescences, usually to the nearest female inflorescence, although distances of 400-1,000 m have been observed. Minimal estimate of genetic neighborhood sizes are large for *D. longispatha* (750 to 8,900 plants) and neighborhood areas encompass 41,000 to 67,000 m². Experiments demonstrate that the species is self-compatible and that fruit production is pollinator limited.

THE ARACEAE IS one of the most diverse families (at least 97 species) in the flora of the La Selva Biological Station located in the wet lowlands of northern Costa Rica (Hammel and Grayum, 1982). In spite of its abundance and accessibility, the pollination biology of the family is little studied (Meeuse, 1959; Meeuse and Hatch, 1960; Williams and Dressler, 1976; Bawa and Beach, 1981; and Valerio, 1984). Many species of aroids are beetle pollinated, particularly members of *Philodendron* (Hubbard, 1895; Gottsberger and Amaral, 1984). *Xanthosoma* (L. Goldwasser, pers. comm.; pers. obs.), *Syngonium* (Croat, 1981; pers. obs.), and *Dieffenbachia* (Croat, 1978; Valerio, 1984). Pollination by beetles (cantharophily) is becoming increasingly well-documented in a va-

riety of tropical families, including: Cyclanthaceae (Beach, 1982), Arecaceae (Essig, 1971, 1973; Silbauer-Gottsberger, 1973; Mora Urpi and Solis, 1980; Bullock, 1981; Beach, 1984; Henderson, 1984), Nymphaeaceae (Gottsberger, 1974; Cramer, Meeuse and Teunissen, 1975; Prance and Arias, 1975, Prance and Anderson, 1976; Meeuse and Schneider, 1980; Prance, 1980), Magnoliaceae (Thien, 1974; Gibbs, Semir and Cruz, 1977). Winteraceae (Gottsberger, Silberbauer-Gottsberger and Ehrendorfer, 1980; Thien, 1980). Annonaceae (Gottsberger, 1970; Webber 1981; Schatz, 1985), and Zamiaceae (D. Clark and D. Clark, pers. comm.). These studies, as well as the work presented here, demonstrate that beetles exhibit a complexity and specialization beyond their status as 'mess-and-spoil' pollinators (Faegri and van der Pijl, 1971).

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Beetles are thought to be the earliest animal pollinators of angiosperms (Baker and Hurd, 1968; Crepet, 1979, 1983, 1984; Crowson, 1981). Evidence for this is three-fold: 1) beetles were the most numerous and diverse insects during the Cretaceous, when angiosperms were undergoing their major radiation (Crepet, 1979), 2) primitive angiosperm flowers have a fleshy perianth and an excess of pollen, both of which serve as food for beetles, and 3) a number of extant primitive plants are beetle pollinated: Degeneriaceae (Diels, 1916; Thien, 1980), Winteraceae (Eames, 1961; Gottsberger

et al., 1980; Thien, 1980), Eupomatiaceae (Hotchkiss, 1959; Eames, 1961). However, not all beetle-pollinated plants are primitive. Several advanced families contain genera that are pollinated by beetles: Proteaceae (Faegri, 1965), and Polemoniaceae (Grant and Grant, 1965). These examples of derived beetle pollination may represent 'retrograde' evolution from ornithophily or entomophily to cantharophily (Faegri, 1965; Gottsberger, 1977) with accompanying changes in floral morphology.

A number of floral characters of beetle-pollinated plants have evolved repeatedly in a diversity of families. These include protogyny, i.e., temporal separation of the sexual functions of the flower, with the female parts functioning before the male parts (Bawa and Beach, 1981); epigyny or perigyny (Grant, 1950a); numerous floral parts; and a food reward in the form of pollen, staminodia, or fleshy inner petals (Gottsberger, 1977). Flowers of many beetle-pollinated plants exhibit thermogenic respiration—an increase in metabolic rate that leads to the production of heat (Meeuse, 1975). This temperature increase of the flower acts to volatilize a variety of odors which attract the beetles (Smith and Meeuse, 1966).

In this paper I describe the floral biology of *Dieffenbachia longispatha* Engler & Krause and its pollination by *Cyclocephala* beetles (Scarabaeidae: Dynastinae). Seven species of *Dieffenbachia* occur at La Selva, of which *D. longispatha* is the largest and most abundant. It is visited by 9 species of *Cyclocephala*, as well as by *Erioscelis columbica* Endrödi, another dynastine scarab. All of these beetles are large (1–2 cm). In this paper, I: 1) describe the phenology, floral biology and breeding system of *D. longispatha*; 2) describe the mechanism by which pollination occurs, the species composition of visiting beetles, pollen loads, recapture rates, and flight distances; and 3) discuss the implications of beetles as pollinators on genetic neighborhood sizes of plants.

Dieffenbachia longispatha is a monoecious clonal herb of lowland neotropical rainforests. It occurs in both undisturbed forests and shaded areas of disturbance. Reproductive individuals are 1–1.5 m in ht (Fig. 2a). The inflorescence (Fig. 2b) consists of a tall, slender, leaf-like spathe that encircles a spike (spadix) of unisexual flowers with the female flowers at the base and the male flowers at the tip of the spadix. A reproductive ramet can have from 2 to 7 inflorescences, each maturing sequentially at intervals of 3 to 12 days. The flowering season extends from March through September, with peak flowering occurring in July and early August.

Of the ten species of scarab beetles that visit *D. longispatha*, only some are effective as pollinators. This paper concentrates on the eight *Cyclocephala* species that are effective pollinators and essentially ignores *C. kaszabi* Endrödi and *Erioscelis columbica*. The minor effects of the latter two species on the fitness of *D. longispatha* are discussed in a paper concerning the differential effectiveness of beetle species as pollinators (Young, in prep.).

STUDY SITE AND METHODS—This study was carried out at the Estación Biológica La Selva of the Organization for Tropical Studies, located at the confluence of the Ríos Sarapiquí and Puerto Viejo in the Province of Heredia, Costa Rica (10°25'N, 81°1'W; approx. 65 m elevation). Average annual rainfall is 4,000 mm, with a range from 2,900 mm to 5,600 mm. The drier portion of the year occurs between January and April. The vegetation has been described as Tropical Wet Forest and Premontane Wet Forest (Holdridge et al., 1971). For further site descriptions, see Frankie, Baker and Opler (1974) (climate); Bourgeois et al. (1972) (soils); and Hartshorn (1978) (forest structure). Data were collected during the flowering and fruiting seasons of 1982 and 1983, and the flowering season of 1984. I established permanent plots in a cacao plantation abandoned in the early 1970s. It was locally the area of highest population density, reaching some 100–200 'adults' (plants as large as reproductive individuals) per 100 m² of *D. longispatha*. When the plantation was active, the area was kept clear of most herbs and shrubs.

Phenology—All individuals in two populations of *D. longispatha* were marked and mapped ($N = 409$ for Population 1; $N = 288$ for Population 2). These populations were approximately 300 m apart. As each flowering season progressed, additional reproductive individuals were marked along trails at La Selva, for a total of 1,017 plants. Each morning of the flowering season, I checked each reproductive individual and noted if an inflorescence was open and, if so, its sexual stage. Each inflorescence was marked as it opened.

Floral biology—Early in the flowering season, I determined stigma receptivity with peroxidase paper (Macherey-Nagel Co., Germany, distributed by Gallard-Schlesinger Chemical Mfg. Corp., Carle Place, NY) to determine the timing of the onset and duration of the female phase. For several inflorescences, I counted the number of stigmas and the number of synandria (groups of 4 fused stamens).

Staminodia were collected for chemical analysis from inflorescences not visited by beetles. These were dried at 60 C for 24 hr and a proximate analysis on the tissue was performed by Hazleton Laboratories, Madison, WI.

I measured the temperature of two inflorescences in female phase on two evenings in 1984 with a thermistor inserted about 1 cm into the region of the spadix where it becomes attached to the spathe. Ambient temperature was also recorded.

Breeding system—To determine the level of self-compatibility and autogamy in *D. longispatha*, I bagged 129 unopened inflorescences with netting during the 1982 and 1983 flowering seasons. As the inflorescences opened, I either: 1) self-pollinated the inflorescence by waiting until the male flowers released pollen and I applied that pollen to the stigmas, 2) cross-pollinated the inflorescence with fresh pollen from a plant at least 50 m away (to avoid using 'self' pollen from a ramet of the same clone), or 3) left the inflorescence unmanipulated. All bags were removed the day after the inflorescence turned male, when the spathe was tight around the female portion of the spadix.

To investigate the factors that limit fruit set during the 1983 flowering season, I hand-pollinated 7 inflorescences which had previously been visited by beetles (overpollination). Pollen was obtained from plants at least 50 m from the recipient plant. These pollinations were performed in the morning, on inflorescences in female phase. The resulting fruit set and fruit wt were compared with naturally pollinated inflorescences of the same season.

Beetle visitors—During daily censuses of open inflorescences, I marked all *Cyclocephala* and *Erioscelis* beetles found within the spathe by cutting small notches in various positions around the edge of the elytra using a unique pattern of notches for each beetle. Beetles were identified to species and all *Cyclocephala* were sexed, using the morphology of the front tarsi. *Erioscelis* exhibit no sexual dimorphism in tarsal shape and could not be sexed. After marking, the beetles were returned to the inflorescence. Voucher specimens of *Cyclocephala* and *Erioscelis* were sent to the Univ. of Nebraska State Museum, Lincoln, Neb. for identification.

I documented beetle arrivals and departures at 33 inflorescences on 30 evenings in 1983 and 1984. Observations began between 17:15 and 17:45. I stayed at the inflorescence until beetles stopped arriving (~21:00). A miner's lamp with a red filter was used to observe the

beetles after dark. I recorded species identity, sex, and time of arrival and departure of each beetle. I collected 17 *Cyclocephala* as they arrived at inflorescences and 13 *Cyclocephala* as they left the inflorescences. Slides of the pollen being carried by the beetles were made by scraping as much pollen as possible from the elytra and ventral surface of the beetle with a scalpel and mounting the pollen on a slide with fuchsin stained glycerin. I then marked the beetles, and released them within 5 min of their capture.

Fruit set and fruit wt—Infructescences were collected as fruits ripened (9–11 months following fertilization). Female flowers were scored as 1) having undeveloped fruit ("unfertilized"), 2) partially developed fruits, or 3) fully developed fruits. Fruits were weighed individually. Fruit removal rates were estimated by counting fruits remaining on 7 open infructescences for 7 days or until all fruits were gone.

RESULTS—Phenology—The flowering season of *Dieffenbachia longispatha* extends from March through September with large variation between years in date of earliest flowering (Fig. 1). The earliest flowering occurred in mid-March in 1983 and in early July in 1984. A weak, but significant, positive correlation exists between the order of flowering within the flowering seasons in 1983 and in 1984 for individual plants (Spearman rank order correlation $r_s = 0.16$, $N = 25$, $P < 0.005$). For plants that flowered both in 1983 and 1984, those that flowered early in 1983 also flowered early in 1984. Flowering time is important because fruit set is positively correlated with time of flowering within the 1983 season ($r = 0.29$, $N = 169$, $P = 0.015$). Plants which flower early produce few or no fruits. There is no significant correlation between 1982 and 1983 flowering time ($r_s = -0.21$, $N = 19$, $P = 0.39$) or between 1982 and 1984 ($r_s = 0.32$, $N = 22$, $P = 0.14$). There was no effect of spatial location (i.e., habitat) on flowering time, as tested using Tjostheim's index (Hubert and Golledge, 1982).

A large year to year variation in the number of plants flowering was observed. Of 697 plants marked in Populations 1 and 2, 27% (190) flowered at least once between 1981 and 1984; 68% (130) of these flowered in 1981, 17% (33) flowered in 1982, 9% (17) flowered in 1983, and 43% (82) flowered in 1984.

Floral biology—The inflorescence structure and floral biology have been described previously by Croat (1983) for *Dieffenbachia* in gen-

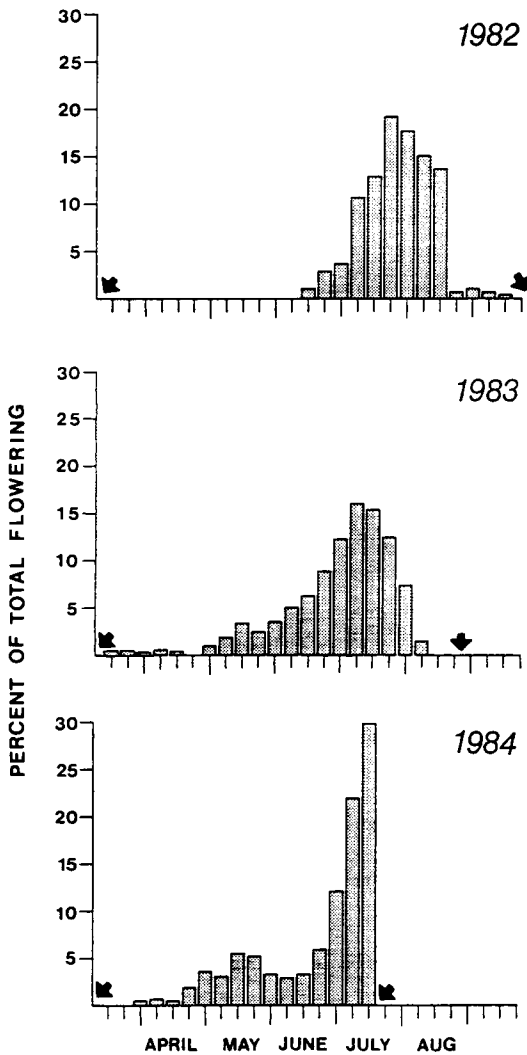


Fig. 1. Phenology of *Dieffenbachia longispatha* for 1982, 1983, and 1984. Percent of plants with inflorescences in female phase is plotted against date. The beginning and end of census periods are marked with arrows. Total numbers of inflorescences are 272 in 1983; 475 in 1983; and 572 in 1984.

eral and by Valerio (1984) for *D. oerstedii* Schott. The floral biology of *D. longispatha* differs from these descriptions in several ways. The flowering of an inflorescence is a 3-day event. The spathe opens in the early evening to reveal the spadix with monoecious flowers:

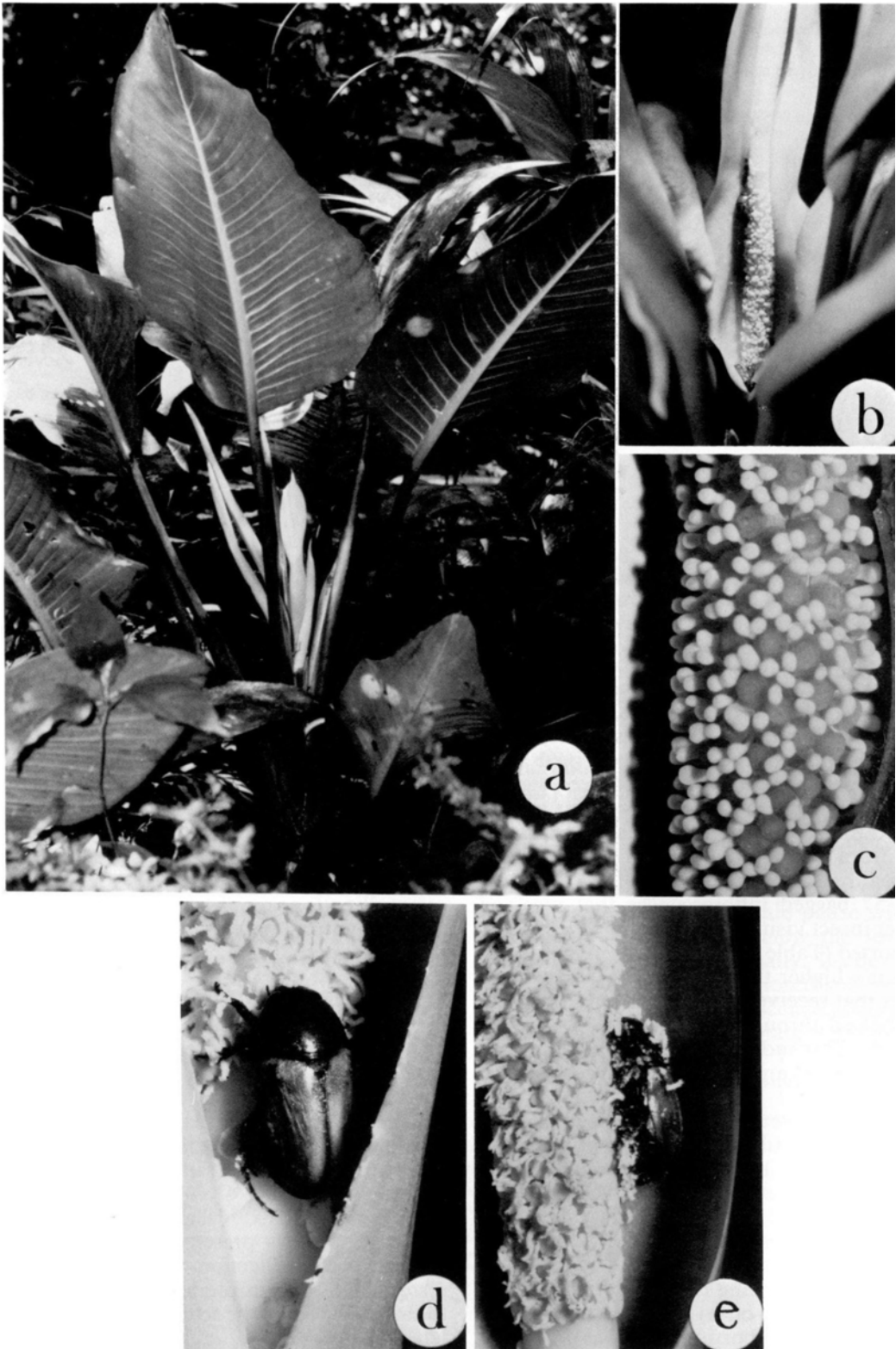
an average of 77 female flowers at the base of the spadix (76.6, SD = 12.0, $N = 84$), and an average of 440 synandria (4 fused stamens) at the distal end (440.3, SD = 81.3, $N = 25$) (Fig. 2b). The stigmas are surrounded by fleshy white staminodia (Fig. 2c), which the visiting beetles eat. From the time of the initial opening of the spathe until 24 hr later, the spadix has no receptive sexual parts, contrary to Croat (1983) and Valerio (1984), who presumed immediate receptivity of female flowers. However, pollen applied to stigmas 12 hr after the spathe opens will germinate 12 hr later, when the stigmas become moist (J. Henny, pers. comm.). Tests with peroxidase paper show that the stigmas become receptive at about 17:30 on the evening of the second day. The relative positions of the spathe and spadix remain unchanged as the anthers release pollen on the evening of the third day at about 17:00–17:30. At this time, the stigmas are still receptive so the potential for self-pollination within an inflorescence exists. As the evening progresses, the spathe closes slowly, first forming a tight constriction around the female portion of the spadix and then closing around the male part. By dawn the next morning, only a small portion of the male spadix is visible.

Flowering ramets of *D. longispatha* possess from 2 to 7 inflorescences ($\bar{x} = 4.78$ inflorescences per plant). Within a ramet, successive inflorescences of *D. longispatha* open at intervals of 3 to 12 days. The timing of inflorescence opening effectively prevents geitonogamy; by the time a particular inflorescence is female, any earlier inflorescences have ceased to be sexually functional and have become enclosed within the spathe.

The temperature regime of the inflorescence is shown in Fig. 3. The temperature of the inflorescence remains about the same as ambient temperature until 17:50 when it begins to increase as the spadix enters the female phase. Peak temperatures of 3.3 C and 4.1 C above ambient were recorded at 18:55 and 18:43 for two inflorescences.

Breeding system—Although *D. longispatha* is self-compatible (Table 1), self-pollination results in lower fruit set and lower fruit wt than outcrossing. A total of 65 fruits were produced

Fig. 2. 2a. Flowering *Dieffenbachia longispatha*. An open inflorescence is in the center of the plant, surrounded by two closed inflorescences and one bud. This plant is about 1.5 m tall. $\times 0.08$. 2b. Inflorescence of *D. longispatha* showing 3 *Cyclocephala* around the female flowers. When the inflorescence is in female phase, the spathe is closed loosely around the female flowers, the male flowers fully exposed. The photograph was taken on the evening of the second day before beetles had eaten the staminodia. $\times 0.30$. 2c. Stigmas of day 2 spadix surrounded by white, fleshy, club-



shaped staminodia. $\times 1.5$. 2d. *Cyclocephala gravis* crawling out of the enclosed chamber around the female flowers on an inflorescence just beginning to release pollen. $\times 2.0$. 2e. *C. gravis* about one-third of the way up the male part of the spadix, becoming covered with pollen. $\times 1.65$.

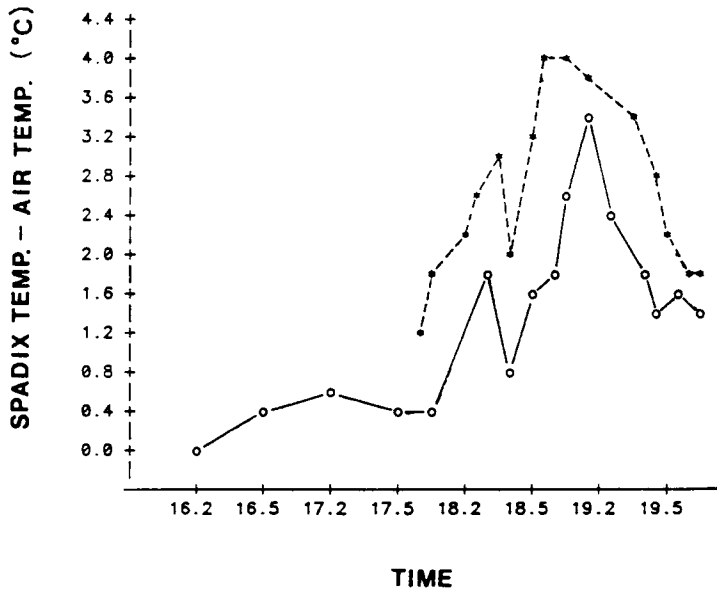


Fig. 3. Temperature elevation of *Dieffenbachia longispatha* inflorescences on the evening the stigmas become receptive. Data are presented for two different inflorescences on two evenings in 1984.

in 14 self-pollinated inflorescences resulting in 4.64 fruits per inflorescence. Cross-pollination produced 2.85 times more fruits than self-pollination (370 fruits in 28 inflorescences; 13.21 fruits per inflorescence). Fruits derived from self-pollinated inflorescences required significantly more time to mature than fruits of outcrossed inflorescences (297 days for fruits derived from self-pollination; 271 days for fruits derived from cross-pollination).

Of 57 bagged inflorescences that received neither insect visitors nor hand applied pollen, 55 aborted (Table 1). This abortion rate is significantly higher than that of bagged inflorescences that received visits by beetles (the beetles chewed through the bagging; 6 out of 20 aborted). This indicates that autogamy is rare and that insects are required for successful fruit set.

Similar fruit set (of inflorescences that produced fruits) resulted from self-pollinated inflorescences and bagged inflorescences which received no beetle visitation (Table 1). Two of the inflorescences which were bagged without beetle visitation may have been self-pollinated through the action of disturbance of the inflorescence (my checking it, an animal bumping it, a branch falling on it). In both cases (selfed and no visitors) abortion rate was high and fruit set was low, resulting in lower overall fitness than outcrossed inflorescences. Each of the 12 inflorescences that were emasculated

and bagged later aborted, suggesting that pollen is required for fertilization.

There is strong evidence for pollinator limitation of fruit set in this species (Table 2). Of the 7 inflorescences that were overpollinated in 1983, all produced fruit. There are significant increases in fruit set and fruit wt for the overpollinated inflorescences in comparison with 169 open pollinated and successful inflorescences of the same year. Fruits derived from overpollination required significantly more time to mature than fruits of open pollinated inflorescences.

Insect visitors—No insect visits were observed to the inflorescence during the first 24 hr that the spathe is open and the spadix is exposed. The first visitors are frequently *Drosophila*, which arrive at about 17:30 on the evening of the second day and alight on the male portion of the spadix. Hemiptera (Miridae) arrive next; these insects have been observed visiting all *Cyclocephala*-pollinated flowers at La Selva. A list of insect visitors of *D. longispatha* is presented in Table 3. Examination of a collection of visiting insects (13 *Drosophila*, 29 Hemiptera, and 21 Nitidulidae) indicates that only the scarab beetles carry pollen.

The scarab visitors (*Cyclocephala* and *Erioscelis*) begin arriving just after nightfall (mean time of first arrival = 18:19, $N = 20$ beetles,

TABLE 1. Results of breeding system experiments. All inflorescences were bagged. The effect of treatment on numbers of inflorescences aborted was tested using a 2×2 contingency table and analyzed using Chi-square. Least square means are presented. Means for fruit wt are weighted by the inverse variance of the mean fruit wt for each inflorescence. The paired comparisons were analyzed using analysis of variance. Analyses were performed on arcsin transformed fruit set data

Treatment	# Infl. abort.	# Infl. successful	# of successful inflorescences		
			Mean fruit set % of flowers (S.E.)	Mean fruit wt (g) (S.E.)	Mean # days to maturity (S.E.)
Selfed	11	3	29.72 (7.47)	0.3965 (0.0255)	296.67 (7.56)
Outcrossed	15	13	44.82 (3.97)	0.3382 (0.0122)	271.38 (3.63)
	$P = 0.1158$ ns		$P = 0.1267$ ns	$P = 0.0583$ ns	$P = 0.0093$ **
Bagged but visited by beetles	6	14	35.92 (3.63)	0.3310 (0.0295)	278.64 (6.57)
Bagged and not visited	55	2	29.92 (5.27)	0.2794 (0.0780)	294.00 (17.38)
	$P < 0.001$ ***		$P = 0.6062$ ns	$P = 0.5461$ ns	$P = 0.4225$ ns

SD = 11.8 min, range = 17:57 to 18:41). They easily locate the inflorescence, flying in the darkness and alighting on the spadix within seconds of arriving at the plant. Once on the spadix, they walk rapidly downward into the protected chamber around the female flowers, where they eat the staminodia surrounding the stigmas (Fig. 2c). Removal of staminodia results in beetles leaving earlier than they leave unmanipulated inflorescences (proportion of beetles remaining in inflorescence after 12 hr: 0.00 for removal experiment, $N = 36$ inflorescences; 0.62 for control, $N = 48$ inflorescences).

The majority of the beetles remain in the inflorescence for 24 hr. They frequently mate within the dark closed space provided by the spathe. They begin leaving on the evening of the third day, most of them departing between 17:45 and 19:30. They climb up the spadix as the spathe proceeds to close around the female portion of the spadix. At the same time the anthers are releasing copious pollen which cov-

ers the insects as they crawl over the male flowers (Fig. 2d, 2e). Beetles frequently pause on their upward climb and appear to eat the pollen. However, in most cases the beetles fly off within seconds of leaving the female flowers. *Cyclocephala* captured immediately after leaving an inflorescence carry large amounts of pollen ($\bar{x} = 1,649$ pollen grains, $N = 13$ beetles).

The above description is representative of the majority of beetle species which visit *D. longispatha*. However, 40% of the 'effective' beetle pollinators leave the inflorescence before pollen is released, either min after arriving or sometime during the night. Beetles can also leave an inflorescence in male phase without any pollen by departing below the level of the male flowers. Occasionally, beetles were seen remaining within the closed spathe for 2 and 3 days after the inflorescence turns male. Tests with fluorescein diacetate (Heslop-Harrison and Heslop-Harrison, 1970) show that after 48 hr, only 17% of pollen in anthers is

TABLE 2. Evidence of pollinator limitation in *D. longispatha*. Means are least-square means. The fruit wt mean is weighted by the inverse variance of fruit wts for each inflorescence. Values in parentheses are S.E. All comparisons between overpollinated and open pollinated inflorescences were by analysis of variance. Fruit set was arcsin transformed for statistical analysis

	N	Mean % fruit set	Mean fruit wt (g)	Mean # of days to mature
Overpollinated	7	65.86 (3.74)	0.4152 (0.0386)	312.86 (10.67)
Open pollinated	169	40.54 (1.71)	0.3147 (0.0082)	289.58 (2.18)
		$F = 8.23$ $P = 0.0046$	6.68 $P = 0.0106$	4.57 $P = 0.0339$

TABLE 3. *Insect visitors to inflorescences of Dieffenbachia longispatha*

Coleoptera
Scarabaeidae
<i>Cyclocephala amblyopsis</i> Bates
<i>C. gravis</i> Bates
<i>C. sexpunctata</i> Cast.
<i>C. tutilina</i> Burm.
<i>C. kaszabi</i> Endrödi
<i>C. ligyrina</i> Bates
<i>C. atripes</i> Bates
<i>C. sp. nov.</i>
<i>Erioscelis columbica</i> Endrödi
Nitidulidae
Staphylinidae
Diptera
Drosophilidae
Richardiidae
Hemiptera
Miridae
Dermaptera (earwigs)
Thysanoptera (thrips)

viable, so beetles leaving after such an extended visit carry little viable pollen.

Nine species of *Cyclocephala* and one species of *Erioscelis* visited inflorescences of *D. longispatha* at La Selva (Table 4). Data for each year are presented separately because the number of beetles encountered in 1982 was 3 times that of the other years, with *Erioscelis* primarily responsible for the difference. The average number of beetles of all species present in inflorescences was 3.6 for 1982 and 1984 and 8.7 for 1983 (1983 significantly different from 1982 and 1984 at $P < 0.001$; t -test). The num-

ber of unvisited inflorescences is another indication of differences in beetle densities between years: 31% and 38% of all inflorescences in 1982 and 1984 were not visited by beetles; only 3% of the inflorescences in 1983 were unvisited ($\chi^2 = 165.5$, $P < 0.0001$).

In total, 4,843 beetles were marked. The frequency of recapture of marked *Cyclocephala* (22%) was significantly greater than that of marked *Erioscelis* (10%; Table 5). The low rate of recapture of *Erioscelis* may be explained by large population sizes, by long flight distances between plants (i.e., beyond the areas I checked daily), or by *Erioscelis* being less faithful to *D. longispatha* than *Cyclocephala*.

Beetles recaptured on successive days provide data on flight distances between inflorescences (Table 6). One-night movement distances are not significantly different between years (analysis of variance, $F = 0.03$, $df = 2, 135$; ns). Beetles move an average of 83 m between successive plants. Half the beetles recaptured on consecutive days moved to the nearest inflorescence in female phase (Fig. 4). Beetles moving to the nearest female inflorescences reflect flight distances of 1 to 400 m. The mean distance to the nearest plant in female phase on the nights these beetles moved was 38 m ($N = 138$, S.E. = 8.79). The difference between the mean distance moved by beetles and the mean distance between female inflorescences can be attributed to beetles that flew long distances between inflorescences. Two beetles were recaptured in inflorescences of *Xanthosoma undipes* C. Koch (Araceae) 1.5 km from where they had been seen the previous night in *D. longispatha*.

TABLE 4. *Numbers of individuals of each beetle species and mean number of beetles per inflorescence encountered in 1982, 1983, 1984. Means are determined using only inflorescences which received visits by each particular beetle species*

Species	1982		1983		1984	
	Total # beetles	Mean # per infl.	Total # beetles	Mean # per infl.	Total # beetles	Mean # per infl.
<i>Cyclocephala gravis</i>	132	0.54	570	2.06	164	0.4
<i>C. amblyopsis</i>	116	0.19	387	1.33	201	0.6
<i>C. sexpunctata</i>	73		45		26	
<i>C. kaszabi</i>	0		2		93	
<i>C. ligyrina</i>	0		23		3	
<i>C. tutilina</i>	0		6		7	
<i>C. atripes</i>	0		10		0	
<i>C. conspicua</i>	4		1		3	
<i>C. sp. nov.</i>	0		4		2	
<i>Erioscelis</i>	232	1.18	2,014	5.08	725	1.8
Total <i>Cyclocephala</i>	325	1.99	1,048	3.62	499	1.3
Total beetles	557	3.21	3,062	8.69	1,224	3.1
# Inflorescences	275		423		578	
% Inflorescences without beetles	30.91		3.31		39.06	

TABLE 5. Percent of marked beetles recaptured. All comparisons were analyzed using a 2 × 2 contingency table and a Chi-square test

Beetle species	1983	1984
<i>C. gravis</i>	26.85%	18.90%
<i>C. amblyopsis</i>	21.82	26.87
<i>C. sexpunctata</i>	6.67	11.54
<i>C. tutilina</i>	—	14.29
<i>C. ligyrina</i>	0	0
<i>C. kaszabi</i>	0	7.53
<i>C. sp. nov.</i>	0	0
<i>Erioscelis columbica</i>	*** 8.89	*** 13.10 **
Total		
<i>Cyclocephala</i>	23.13	ns 19.20
All species	13.74	ns 15.59

Fruiting biology—Fruit maturation inside the closed spathe takes 8–11 months. The fruits change color from green to white to yellow to orange-red. Upon fruit ripening, the spathe tissue senesces, turning bright orange and eventually splitting as the entire infructescence arches backwards, revealing the orange-red drupes. The single seed makes up approximately 77% of the fresh wt of a drupe. Fresh fruits weigh from 0.2 g to 0.75 g.

Abortion of whole inflorescences is common (52% for 1982, 47% for 1983). These inflorescence abortion rates are low in comparison with the 81% abortion rate in *D. oerstedii* reported by Valerio (1983).

Fruit set of 82 naturally pollinated inflorescences collected outside of the study area during the 3 seasons ranged from 3 to 90%, with a mean fruit set of 48% (Table 7). This is similar to fruit set in *D. oerstedii* (\bar{x} = 48.6%, N = 28) (Valerio, 1983). A nested analysis of variance was used to measure the relative effects of year and treatment (unmanipulated vs. beetles removed, marked, and replaced) on fruit set and

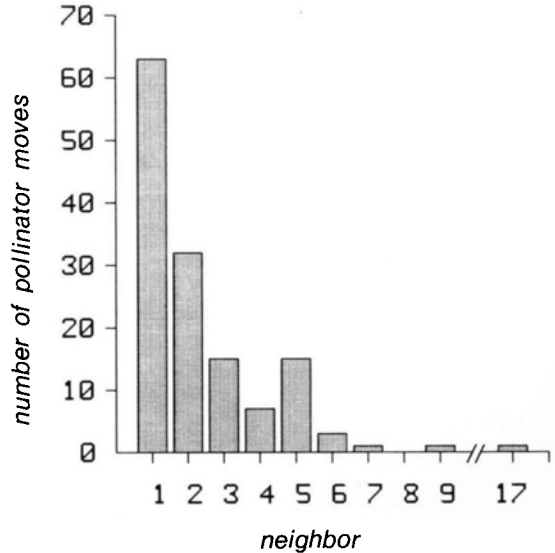


Fig. 4. The number of times *Cyclocephala* were recaptured on consecutive days in the first, second, third, etc. nearest neighbor of the inflorescence they visited first. N = 138 beetle movements.

fruit wt. There is a significant effect of year on fruit set (fruit set was higher in 1983 than 1982) but not on fruit wt. There are no significant effects of treatment on either variable. This indicates that removing beetles from inflorescences to mark them did not significantly affect fruit-set or fruit weight in inflorescences that did not abort.

Fruit removal rates were variable, from all fruits removed within 48 hr after the infructescence opened to gradual removal of fruits over a period of 7 days. No fruits were found on the ground below the plants. Animals observed removing fruits from infructescences include a squirrel, *Sciurus* sp. (G. Schatz, pers. comm.) and a bird (scarlet-rumped cacique), *Cacicus uropygialis* (J. Trainer, pers. comm.).

TABLE 6. Mean distances beetles travelled in one night for each year. The mean distance to nearest females calculated to plants that were female on the nights these 1-day recaptures occurred. Densities of flowering plants were calculated from Populations 1 and 2 and include all flowering individuals within these areas (regardless of date of flowering). Differences between years were analyzed using analysis of variance for beetle movement distances and distances to nearest female plants; using a 3 × 1 contingency table for density of flowering plants

	N	Beetle movement distance		Distance from males to females on same date		Density of flowering plants (per 100 m ²)
		Mean distance (m)	S.E.	Mean distance (m)	S.E.	
1982	15	78.06	(22.188)	45.48	(12.730)	7.44
1983	99	84.03	(8.327)	38.49	(5.368)	1.72
1984	24	81.85	(25.391)	32.08	(6.252)	13.16
		F = 0.03 ns		F = 0.34 ns		$\chi^2 = 66.66$ P < 0.001

TABLE 7. Fruit set and fruit wts of unmanipulated inflorescences and manipulated inflorescences (beetles within them were removed, marked, and replaced). Nested analyses of variance were performed to test the effect of year and treatment on fruit set and fruit wt. Fruit set data were arcsin transformed before analysis. Mean fruit wts were weighted by the inverse of the variance of the mean fruit wt for each inflorescence

	Fruit set (as percent of female flowers)					
	Unmanipulated inflorescences			Inflorescences with beetles removed, marked, and replaced		
	N	Fruit set	S.E.	N	Fruit set	S.E.
1982	32	53.36	4.18	135	47.20	1.86
1983	32	44.77	4.39	169	40.54	1.71
1984	18	42.61	4.16	—	—	—

ANOVA results $F = 3.15$, $df = 4$, $P < 0.05$, significant year to year variation in fruit set.

	Fruit wt (g)					
	Unmanipulated inflorescences			Inflorescences with beetles removed, marked, and replaced		
	N	Mean wt	S.E.	N	Mean wt	S.E.
1982	31	0.3513	0.0195	135	0.3204	0.0086
1983	30	0.3520	0.0201	169	0.3147	0.0082

ANOVA results $F = 1.89$, $df = 3$, $P = 0.1285$, no effect of treatment or year on fruit wt.

DISCUSSION—*Dieffenbachia* as an exemplar of cantharophily—The floral biology of *Dieffenbachia* exemplifies the beetle pollination 'syndrome.' The inflorescence produces heat, it is protogynous, the ovaries are inferior, the flowers are nectarless but food bodies exist in the form of fleshy staminodia, and the timing of the changes in sexual expression indicate visitation by a nocturnal pollinator.

The heat produced by *D. longspatha*, although slight in comparison with the reported heat production of 20 C above ambient temperature of *Philodendron selloum* C. Koch (Nagy, Odell and Seymour, 1972), may increase odor volatility. Beetles arrive at the inflorescence in darkness, when visual stimuli are limited. Beetles fly directly to inflorescences, suggesting that they must be using olfactory cues to locate the flowers. In particular, beetles do not land on an inflorescence which is in its first night and not producing heat, implying that they are using more than just visual cues. Floral odor has also been implicated in attracting beetles to flowers of *Talium* (Magnoliaceae; Gibbs et al., 1977), and *Victoria* (Nymphaeaceae; Prance and Arias, 1975).

It is important to consider the morphology of the inflorescence (i.e., female flowers in the basal half and male flowers in the upper half of the spadix) and the behavior of the beetle pollinators to understand the benefits of protogyny. Bawa and Beach (1981) suggest that protogyny in beetle pollinated plants has co-evolved with several specific life-history aspects of the beetle pollinators, particularly the long residence time of the beetles within the flowers and the timing of flight behaviors. *Cy-*

clocephala are nocturnal insects, arriving at an inflorescence in the evening and spending 24 hr in the vicinity of the female flowers. The timing of changes in sexual expression indicates an adaptation to a nocturnal pollinator: female and male flowers become functional on consecutive evenings. Nocturnal opening of flowers has been observed for many beetle pollinated plants (Prance and Arias, 1975; Gibbs et al., 1977; Beach, 1982; Henderson, 1984). A study of two species of *Nymphaea*, one pollinated by beetles and the other pollinated by bees, revealed numerous differences between them (Prance and Anderson, 1976). The beetle pollinated species, *N. rudgeana* G.F.W. Meyer, was protogynous, was primarily cross-pollinated, had nocturnally opening flowers, and produced a strong odor. The bee pollinated species, *N. ampla* (Salisb.) DC., had simultaneously functioning sexes, was primarily self-pollinated, had diurnal flowers, and a weaker odor. This suggests that a strong association exists between pollinator behavior and floral characters. Considering the morphology of the inflorescence of *Dieffenbachia* and the behavior of the *Cyclocephala* beetles, protogyny is an effective sexual system for promoting outcrossing in *Dieffenbachia*.

Protection of ovules is important for *Dieffenbachia* because beetles spend 24 hr eating in the vicinity of the female flowers. Grant's (1950a) survey of plants with different classes of pollinators reveals that 80% of cantharophilic species have protected ovules in contrast to species pollinated by long-tongued insects, of which only 28% have some sort of protection for the ovules. Most descriptions of beetle pollination emphasize that beetles do very little

TABLE 8. Composition of food tissue of 3 *Cyclocephala* pollinated plants. Values presented are percent of dry wt for each constituent. Analyses were performed by Hazleton Labs, Madison, WI

	<i>Dieffenbachia longispatha</i> (Young)	<i>Cyclanthus bipartitus</i> (Beach 1982)	<i>Cymbopetalum torulosum</i> (Schatz, pers. comm.)
Source	Staminodia	Inner bract	Inner petal
Protein	24.5%	19.3%	14.8%
Lipid	8.3	48.8	2.5
Ash	5.4	—	—
Carbohydrates	55.7	14.4	40.6
Calories (per 100 g)	396	567	244

damage to the ovules of the flowers they visit (Grant, 1950b; Prance and Arias, 1975; Gibbs et al., 1977), usually because the beetles are offered more accessible and higher quality food in the form of staminodia or fleshy petals. However, accessibility appears to be less important than quality; beetles arriving at an inflorescence than has had the staminodia removed do not eat the ovaries.

A proximate analysis of the staminodia which surround the stigmas of *Dieffenbachia* reveals that they are high in protein and carbohydrate content and low in lipids (Table 8). The inner petals of *Cymbopetalum* are similar in composition (Schatz, pers. comm.). The carpellary appendages of the beetle pollinated *Victoria amazonica* (Poepp.) Sowerby are high in carbohydrates (Knoch cited in Prance and Arias, 1975). In contrast, Beach (1982) reports that lipids account for nearly half (by wt) of the inner bract of *Cyclanthus* and lower levels of protein and carbohydrates. Although quantitative, an analysis of the beetle food of another beetle pollinated plant, *Calycanthus* (Calycanthaceae), revealed that it is rich in protein but has low levels of lipid and starch (Rickson, 1979). Concentrating on analyses of food rewards of *Cyclanthus*, *Cymbopetalum*, and *Dieffenbachia* (all analyses performed by the same company), three trends are worth emphasizing: 1) high carbohydrate concentration in *Dieffenbachia* and *Cymbopetalum* vs. low in *Cyclanthus*; 2) high protein concentration in all three genera; and 3) high lipid concentration in *Cyclanthus* resulting in very high caloric value.

The inflorescences of *Dieffenbachia* offer at least three rewards for visiting beetles. First, the inflorescence is a source of food. Beetles will leave an inflorescence on the same night they arrive if there are no staminodia present, as demonstrated by staminodia removal experiments. Second, beetles frequently mate within the inflorescence. *Cyclocephala* have also been reported as mating within the inflorescences of *Cyclanthus* (Beach, 1982) and within the flowers of *Cymbopetalum* (G. Schatz, pers.

comm.) and *Talauma* (Gibbs et al., 1977). Third, beetles gain protection against predators by remaining within the inflorescence during daylight hr. Vertebrate predators of *Cyclocephala* include lizards (Beach, 1982), jacanas (Prance and Arias, 1975), and toucans (Beach, 1982; pers. obs.). The enclosing spathe of many beetle pollinated plants (Araceae, *Cyclanthus*) offers the insects a protected place to feed and mate.

All of the scarab beetle species that visit *D. longispatha* were also seen in inflorescences of other beetle pollinated plant species, minimizing the importance of species specific co-evolution between plant and pollinator. However, there are degrees of specialization; for example, *Cyclocephala gravis* Bates has only been observed visiting 6 species of *Dieffenbachia* and one species of *Philodendron*, *P. grandipes* Krause. This philodendron species is the only terrestrial species in the genus at La Selva, making it more similar to *Dieffenbachia* than the epiphytic species of *Philodendron*. In addition to sharing similar habitats and life forms, *Dieffenbachia* and *P. grandipes* share a floral odor compound that is not found in most other *Philodendron* species (G. Schatz, pers. comm.). Even greater pollinator specificity occurs in other beetle pollinated species. Gibbs et al. (1977) report that the beetle species that pollinates *Talauma ovata* St. Hil. (Magnoliaceae) in Brazil was never found in inflorescences of the numerous *Philodendron* in the area, and vice versa, even though both beetle species were making their flights at the same time of the evening.

Influences on reproductive success—Very few plants flowered in 1983, yet more beetles were observed in 1983 than any other year. The result is that there were more beetles per inflorescence and more inflorescences visited in 1983 than in other years. Surprisingly, fruit set of successful inflorescences was significantly lower in 1983 than in 1982. I attribute this phenomenon of higher beetle visitation rate

but lower fruit set to the detrimental effects of *Erioscelis* (Young, unpubl.). Few *Erioscelis* carry pollen and those that do, carry less than *Cyclocephala*. Fruit set in *D. longispatha* appears to be limited by the number of effective pollinators because hand-pollinated plants produced more seeds than naturally pollinated controls (an operational definition of "pollinator limitation" as proposed by Bierzychudek, 1981). Without further information, the high abortion rate observed by Valerio (1983) in *D. oerstedii* cannot be attributed with certainty to pollinator limitation, although Valerio proposes that lack of pollinator specificity accounts for inflorescence abortion in this species.

Gene flow—Pollinator flight distances and seed dispersal distances influence gene flow. Reported mean pollinator flight distances range from 0.58 m to 12.4 m for bees and butterflies in the temperate zone (Levin and Kerster, 1968, 1969; Pyke, 1978; Schaal, 1980; Schmitt, 1980; Levin, 1981; Waddington, 1981; Antlfinger, 1982; Waser, 1982). An average pollen movement distance of over 50 m has been found in a bee-pollinated *Miconia* species (Melastomataceae) in Peru (D. Stratton, pers. comm.). Linhart (1973) has documented pollen movement by nonterritorial hummingbirds visiting *Heliconia* species in Costa Rica. Assuming that 20 flowers were checked at each distance in his fig. 2, I calculate that pollen is moving an average of 51 m in *H. acuminata* (*H. mathiasiae*; J. Kress, pers. comm.) but pollen is also moving as far as 265 m. However, absolute movement distances typically depend on plant spacing, and in all of these studies, the majority of pollinators are moving to nearest neighbors. Beetles visiting *D. longispatha* are moving predominantly between nearest flowering neighbors but they are occasionally flying 400 m to 1,000 m between plants. Pollen carryover is unlikely to be important in *Dieffenbachia* so pollinator movement distances may equal pollen flow. I have calculated genetic neighborhood size from the data in Table 6 using the equation by Wright (1943, 1946):

$$N_e = 2\pi r d \frac{\sum p^2 + \sum s^2}{2N}$$

where r = the proportion of seeds produced by outcrossing, $\sum p^2$ and $\sum s^2$ are the sum of squares of the observed flight distances and seed dispersal distances, N = the number of observed flight distances and seed dispersal distances, and d = the density of flowering plants. Following Schmitt (1980), I have assumed that $r = 1$ (no selfing) and have calculated N_e based

on pollinator distances alone (assuming no seed dispersal). Neighborhood sizes for 1982, 1983, and 1984 are 3,035, 749, and 8,900 individuals, respectively. Including seed dispersal would increase these values. The level of random differentiation for $N_e \geq 1,000$ is essentially the same as under conditions of panmixia (Wright, 1943). Therefore, at least in 1982 and 1984, and probably in other years, very strong selective pressures would be needed to maintain adaptive differentiation within a *D. longispatha* population. Neighborhood area, $A = N_e/d$, for each year are 40,979 m², 43,535 m², and 67,632 m². These values are underestimates because: 1) on any given night that beetles travel between plants, the density of available inflorescences (inflorescences in female phase) is lower than the total density of flowering plants and 2) seed dispersal is excluded. Estimates of N_e for *D. longispatha* are comparable to those for butterfly pollinated *Senecio integerrimus* (Schmitt, 1980) (maximum $N_e = 6,153$), yet neighborhood area for *D. longispatha* is at least 20 times that of *Senecio*, because density of flowering *D. longispatha* is much lower than that of *Senecio*. Although beetles are usually travelling to the nearest *D. longispatha* in female phase, these plants are far apart. The beetles will transport substantial amounts of pollen across microhabitat boundaries, reducing the likelihood of small-scale adaptation and differentiation in *Dieffenbachia* compared to *Senecio* or other herbs with greater densities and more conventional pollination systems.

It is becoming clear that beetles are often far from being 'mess and spoil' pollinators, and that the specialized morphology, physiology, and behavior of both beetles and beetle-pollinated plants can be highly co-evolved, and to a degree exceeding that of many more commonly studied pollination systems.

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