FLOWERING PHENOLOGY AND DENSITY-DEPENDENT POLLINATION SUCCESS IN *CEPHAELIS ELATA* (RUBIACEAE)

By

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TABLE OF CONTENTS

Abstract of Dissertation Presented to the Graduate School
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In cloud forest near Monteverde, Costa Rica, the self-incompatible, distylous treelet, *Cephaelis elata* (Rubiaceae), is pollinated by the hummingbird, *Lampornis calolaema*. I investigated the importance of two potentially conflicting relationships affecting pollination service to *C. elata* flowers: (1) positive density-dependence in pollinator visitation, and (2) negative influences of large floral displays and pollinator territoriality on pollen transfer between plants of different floral morphs. I measured effects of floral display size, flower density, and nearest-mate distance on pollen receipt (numbers of stylar pollen tubes) and pollen donation (measured with powdered dye) at two sites during two 7-mo flowering seasons.

Lampornis calolaema males defended feeding territories composed of rich patches of flowers of *C. elata* and other short-corolla species; females foraged mainly at dispersed flowers. Due to the small size of most *C. elata* floral displays (median = 3 flowers/plant), individual territories usually contained many plants. Consequently, compatible

pollen transfer within territories was high, and pollination success of C. elata flowers within territories was often greater than pollination success outside territories.

At each site, the density and dispersion of flowers influenced pollination service to flowers. There was, however, considerable seasonal variation in the strength and, in some cases, even the direction of the relationships examined. (1) Hummingbird visit rates to flowers were often highest during seasonal flowering peaks and at plants with many flowers. (2) Pollen receipt, and occasionally pollen donation, were greatest during flowering peaks. (3) The amount of pollen received by flowers was negatively correlated with the distance to the nearest compatible plant. (4) Presumably due to the spatial segregation of morphs and limited pollen carryover (measured in the lab with captive L. calolaema), flowers in dense patches frequently received fewer compatible pollen grains than isolated flowers. These results suggest pollination service may be highest at plants that do not produce large numbers of flowers per day, that spread out flowering over time, yet still flower in phase with the population.

INTRODUCTION

In hermaphroditic plants, sexual reproduction can occur through seeds sired as a result of pollen dispersed from male structures of the flower, or through seeds set after pollen receipt by female structures. Within a population, variation in the timing and intensity of flower production by plants can affect both pollen donation and pollen receipt. Considerable recent attention has focussed on the evolution of floral display size (Willson and Rathcke 1974, Schaffer and Schaffer 1979, Stephenson 1979, Willson et al. 1979, Wyatt 1980, Augspurger 1980, 1981, Schemske 1980a,b, Geber 1985). Most of these studies have examined the relationship between the number of flowers displayed by inflorescences or plants and measures of the maternal component of reproductive success. Although flowering characteristics may reflect differing selection on male and female function (Janzen 1977, Charnov 1979, Willson 1979, Stephenson and Bertin 1983, Willson and Burley 1983, Sutherland and Delph 1984, Sutherland 1986), few studies have examined the relationship between floral display size and pollen donation (Schemske 1980a, Bell 1985). The density and spatial dispersion of flowers on neighboring conspecifics may also influence pollen receipt (Richards and Ibrahim 1978, Feinsinger et al. 1986) and pollen dispersal (Levin and Kerster 1969a,b, 1974, Beattie 1978, Handel 1983). Furthermore, because conspecific and heterospecific flower density, pollinator availability, and other environmental factors change

seasonally, the effectiveness of a given plant's floral display in donating and receiving pollen should vary over time. This topic has received little attention (although see Schemske 1977, Willson and Price 1977, Woodell et al. 1977). In this study, I examine the effects of the number of flowers displayed by a plant, conspecific flower density and dispersion, and seasonal variation in all three, on male and female components of pollination service.

In zoophilous plants, the effect of the spatial distribution of flowers on pollination is mediated by the foraging movements of flower-visiting animals. The density-dependent foraging behavior exhibited by many pollinators (Levin and Kerster 1974, Heinrich 1979, Linhart and Feinsinger 1980, Schmitt 1980, Waddington 1980, Real 1981, Zimmerman 1981, Waser 1983a) has several consequences for pollen flow. (1) Visit rates to flowers or inflorescences are often highest in areas of high flower concentration (Willson and Price 1977, Silander 1978, Thomson 1981, Roubik 1982). (2) At many-flowered plants, pollinators may visit large numbers of flowers per plant during each foraging sequence (Frankie et al. 1976, Feinsinger 1978, Pyke 1978, Schemske 1980b). As a result, intraplant pollen flow may increase in relation to interplant pollen flow. For self-incompatible plants, at least, this trend may lead to lower pollination rates at large plants (Kalin de Arroyo 1976, Wyatt 1980). (3) As flower density increases, pollinator flight distances will, on average, decrease (Levin and Kerster 1969a,b, 1974, Beattie 1976, 1978, Zimmerman 1981), and this may result in localized pollen flow (see Handel 1983). The relationship between the movements of pollinators and that of pollen depends on pollen carryover, the

pattern of pollen deposition rom a pollen source on sequentially visited stigmas. Because pollen carryover is often substantial (Thomson and Plowright 1980, Price and Waser 1982, Geber 1985, Thomson et al. 1986), pollen dispersal distances will often exceed pollinator flight distances between flowers (Handel 1983).

In general, pollinator visitation to flowers and pollination service are expected to be positive functions of flower density (Thomson 1981, 1983, Rathcke 1983, Feinsinger et al. 1986). Yet, due to such factors as competition among plant species for pollination service (reviewed by Waser 1983a), sedentary behavior by pollinators at large plants (Frankie et al. 1976, Kalin de Arroyo 1976, Feinsinger 1978, Schemske 1980b), or pollinator satiation due to abundant floral resources (Carpenter 1976, Rathcke 1983), flower visitation and pollination service may sometimes be unrelated, or negatively related, to flower density, particularly during flowering peaks.

I addressed the following major questions:

(1)(a) Does the frequency of pollinator visits to flowers increase with the number of flowers on a plant and with the surrounding density of flowers? (b) How does the number of flowers visited per plant change with floral display size?

(2) What is the extent of pollen carryover, and how does it affect pollen transfer among plants?

(3) What is the effect of the number of flowers displayed by a plant on pollen donation and pollen receipt?

(4) How is pollen donation and pollen receipt affected by the density of flowers on neighboring plants?

The study species, Cephaelis elata Sw. (Rubiaceae), is a distylous treelet with an extended flowering season. This species was chosen for several reasons. First, being self-incompatible, C. elata is completely dependent on pollinators that transfer pollen between plants for sexual reproduction. Evaluation of pollination success is not complicated by geitonogamy and the relative fitness of inbred progeny. Additionally, the pollination system is straightforward. At Monteverde, Costa Rica, the plant is pollinated almost entirely by a single resident hummingbird species. Thus, compared to plants in fluctuating environments or those pollinated by several pollinator taxa, plants face a predictable environment for pollination. This suggests that, at least relative to many other plant species, pollination service to flowers may be a predictable consequence of the spatial arrangement of flowers on plants in a population.

STUDY SITE AND PLANT NATURAL HISTORY

All studies took place in the Monteverde Cloud Forest Reserve, Costa Rica (10°18' N, 84°48' W) from August 1981 through September 1983. The Reserve consists mainly of Lower Montane Rain Forest (Holdridge 1967) along the continental divide in the Cordillera de Tilarán. Due to the broken topography and the influence of weather patterns from both the Atlantic and Pacific, local climates and vegetation in the Monteverde area exhibit great spatial variation (Lawton and Dryer 1980). Mean annual rainfall exceeds 2.5 m. Precipitation declines during the dry season from January through May, but along the continental divide blowing clouds and mist from the northeast trade winds maintain almost continuously wet conditions.

I selected two study locations approximately one km apart in windward cloud forest (sensu Lawton and Dryer 1980) at an elevation of 1540 m. The "dense" site was located 300 m east of the Pantanoso trail adjacent to swamp forest (sensu Lawton and Dryer 1980). The "sparse" site was off a cattle trail approximately 100 m west of the continental divide. The forests at these sites are characterized by epiphyte-laden trees 10 to 20 m in height. Small gaps in the canopy are frequent, and there is a dense understory of shrubs and large herbs. Especially well-represented are the Acanthaceae, Gesneriaceae, Musaceae, Palmae and Rubiaceae. Gap frequency and understory development were greater in the dense plot than in the sparse plot.

Cephaelis elata is an evergreen treelet of moist to wet forests, ranging from Mexico to Colombia and the West Indies at elevations of 1550 m or less (Standley 1938). The plant is typically 2 to 3 m tall, but it occasionally reaches 8 m (Woodson and Shery 1980). At Monteverde, C. elata is common and widespread. Population densities are generally high: most plants have over 10 conspecifics within 10 m (Figure 1). The density of C. elata stems at the two study sites differed strikingly (Table 1). At the dense site, stem densities were an order of magnitude greater than at the the sparse site. The ratio of long-style to short-style stems also varied between sites, but in neither case were the ratios significantly different from one (sparse site: $X^2 = 1.0$, $p > .05$, dense site: $X^2 = 1.5$, $p > .05$). Adjoining stems tend to be of the same floral morph. This spatial segregation of morphs was significant in the dense plot ($X^2 = 39.3$, $p < .001$, $N = 177$, 2 X 2 contingency table), but in the sparse plot, where the sample size was low, it was not ($X^2 = 0.7$, $p > .05$, $N = 35$). Additionally, judging by similarities in morphological features and flowering phenology, adjacent stems of the same morph are often clonal. The mechanism of clonal spread appears to be through rooting of stems broken off by falling canopy debris, not through subsoil propagation. In this study, I defined a plant as all stems of the same morph within 1.5 m (the average canopy radius of C. elata) of one another measured at the stem base. With this definition, plants and genetic individuals should be nearly synonymous.

Flowers are borne in compact red-bracted heads (Figure 2), open shortly before or after dawn, and last a single day. The white tubular

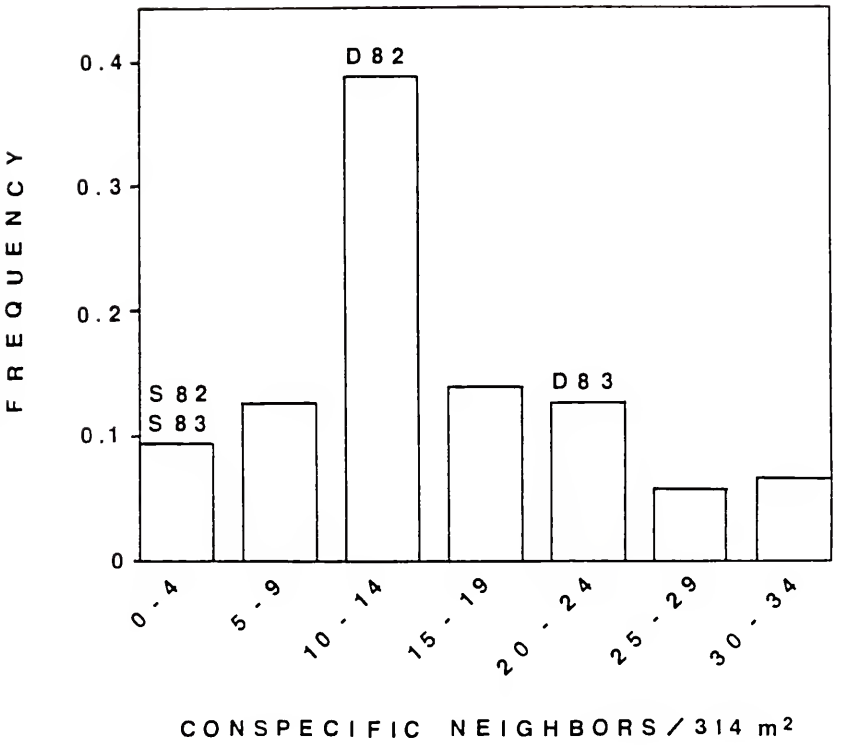

Figure 1. Estimated numbers of flowering conspecifics within 10 m of C. elata plants. Frequencies were calculated from 585 plants censused in 50 randomly selected locations in the Monteverde Cloud Forest Reserve. The mean density of C. elata plants (adjusted to plants/314 m^2) in the sparse (S) and dense (D) study plots in 1982 and 1983 are indicated above appropriate columns.

Table 1. Characteristics of the study sites and of C. elata plants at each site.

Variable	Study site	
	Dense	Sparse
Area (m^2)	3500 (900)[a]	7000
Number of C. elata stems	165	33
Ratio of pin:thrum stems	1.17	0.65
Percent of nearest neighbors of same morph	74.0	60.8
Stems/m^2	0.047	0.0047
Mean[b] number of flowers/m^2		
1982	0.085	0.0069
1983	0.150	0.0077

[a] Subsample of study site sampled in 1983.

[b] Averaged by census date over entire season.

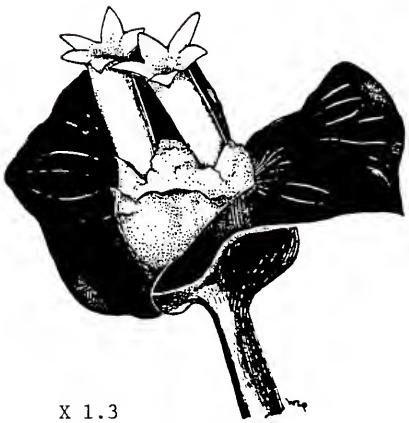

Figure 2. Inflorescence of Cephaelis elata with two 1-d flowers (drawn by W. Z. Pounds).

corollas have a mean length of 18.2 mm (pin: X = 18.0, SD = 1.6, N = 43; thrum: X = 18.4, SD = 1.7, N = 27) and an inside diameter of 3 to 4 mm at the apex. Except for reciprocal location of sexual parts within the corolla, the long-style (pin) and short-style (thrum) flowers have similar morphologies. In short-style flowers the stigma is located an average of 8.2 (SD = 1.5, N = 20) mm from the nectary and the anthers an average of 13.3 mm (SD = 1.6, N = 29). The mean distance from the nectary to the stigma and to the anthers in long-style flowers is 17.2 mm (SD = 1.9, N = 19) and 8.8 mm (SD = 1.1, N = 20), respectively. The ovary contains two ovules. Each flower is simultaneously hermaphroditic; at the time of flower-opening the stigma is receptive and the anthers have dehisced.

Results of controlled pollinations confirm that Monteverde populations of C. elata are completely self- and intramorph-incompatible (Table 2; see also Bawa and Beach 1983). The only compatible or "legitimate" pollen flow is between floral morphs. Only intermorph crosses produced pollen tubes that grew to the base of the style and resulted in fruit production. The few exceptions were styles with single pollen tubes, and these may have resulted from accidental contamination with intermorph pollen. Thrum grains occasionally germinated on thrum stigmas, but pollen tubes did not penetrate into the style. Pin grains on pin stigmas often produced tubes that grew into the style, a few of which penetrated 3/4 the length of the style.

Fruits mature after 4 to 6 months, becoming blue-black berries about 2 cm in length. A variety of bird species, including Myadestes melanops, Chlorospingus opthalmicus, and Turdus plebejus, consume the

Table 2. Results of hand pollinations of C. elata flowers.

A. Pollinated flowers monitored for presence of pollen tubes

Recipient:Donor	Plants	Flowers	Number of flowers with pollen tubes	Percent of flowers with pollen tubes
Short X Self	6	12	0	0.0
Short X Short	6	18	1	5.6
Short X Long	6	16	13	81.3
Long X Self	14	51	1	2.0
Long X Long	14	47	1	2.1
Long X Short	14	57	55	96.5

B. Pollinated flowers monitored for fruit set

Recipient:Donor	Plants	Flowers	Number of fruits	Percent fruit set
Long X Self	4	34	0	0.0
Long X Long	3	23	0	0.0
Long X Short	5	51	26	51.0

fruits and disperse the seeds (Wheelwright et al. 1984; Busby, personal observation).

In Costa Rica, C. elata has an extended flowering season with a peak in the early wet season (Stiles 1978). Plants in a population flower synchronously (Opler et al. 1980). At Monteverde, a few plants with flowers can be found almost year around, but most flowering occurs between March and September (Figure 3). Plants initiate inflorescences synchronously during one to four episodes each year. Each inflorescence produces an average of 21.2 (SD = 8.6, N = 156) flowers over a 30- to 60-d period. As a result, most plants display 1 to 10 flowers each day for 3 to 8 mo per year (Figure 4). Small plants often fail to flower on a given day, while large plants may produce $\geq$ 30 flowers a day.

Flowers of C. elata at Monteverde are utilized by at least 4 species of hummingbirds and a number of insect species, mainly lepidopterans. The great majority of all flower visits are by a single species, the purple-throated mountain-gem, Lampornis calolaema. Lampornis calolaema is the most abundant short-billed hummingbird in the Reserve where it visits numerous species of flowers in the canopy and understory (Feinsinger et al. 1986, Feinsinger et al. in press, Murray et al. in press). Sexes are dimorphic. The brightly colored 5.5 g males (Feinsinger, personal communication) are highly aggressive and frequently defend feeding territories. Females have similar bill morphologies (23 mm total culmen), but are smaller (4.5 g) and less aggressive. Females forage mainly at dispersed flowers. A number of other plant species share pollinators with C. elata at Monteverde. In the Reserve, approximately 30 herbs, shrubs, vines and epiphytes in both

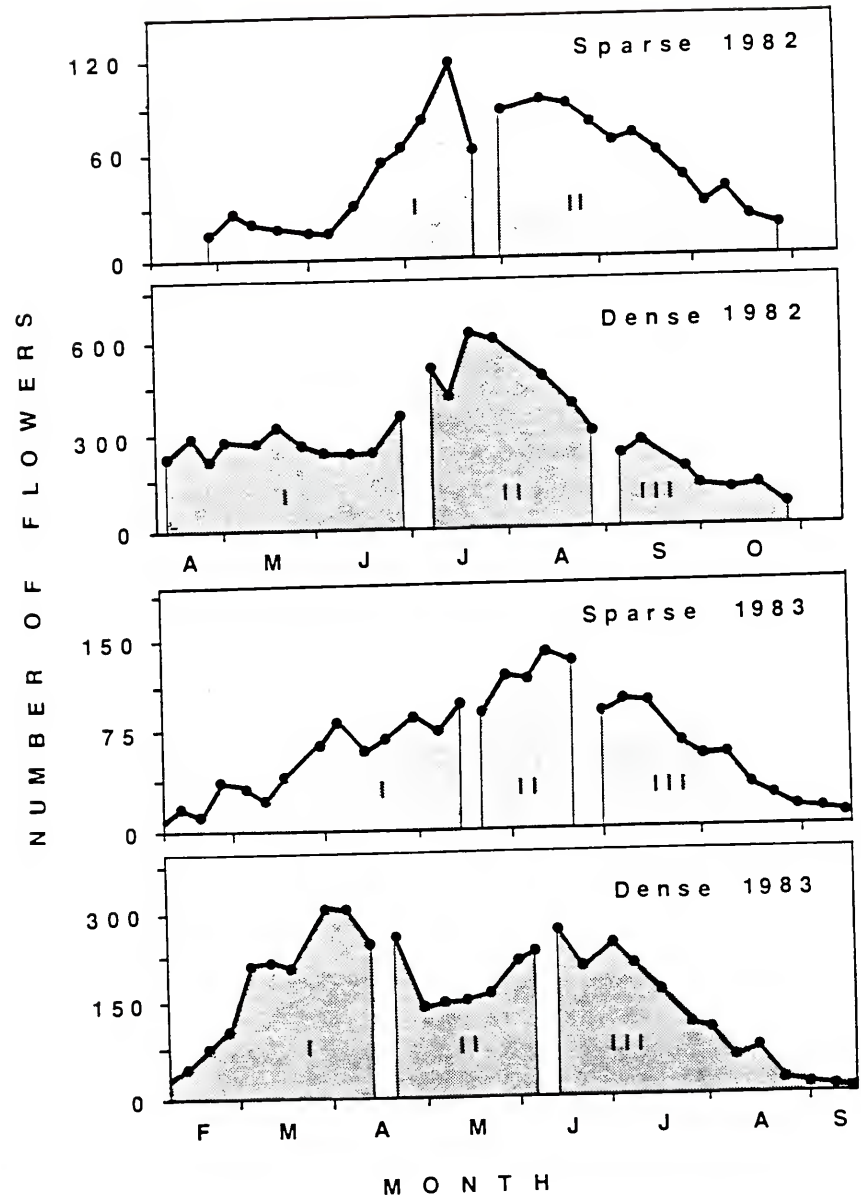

Figure 3. Flowering phenology of C. elata at the sparse and dense study sites in 1982 and 1983. Shaded areas indicate time periods used in analysis of pollen receipt.

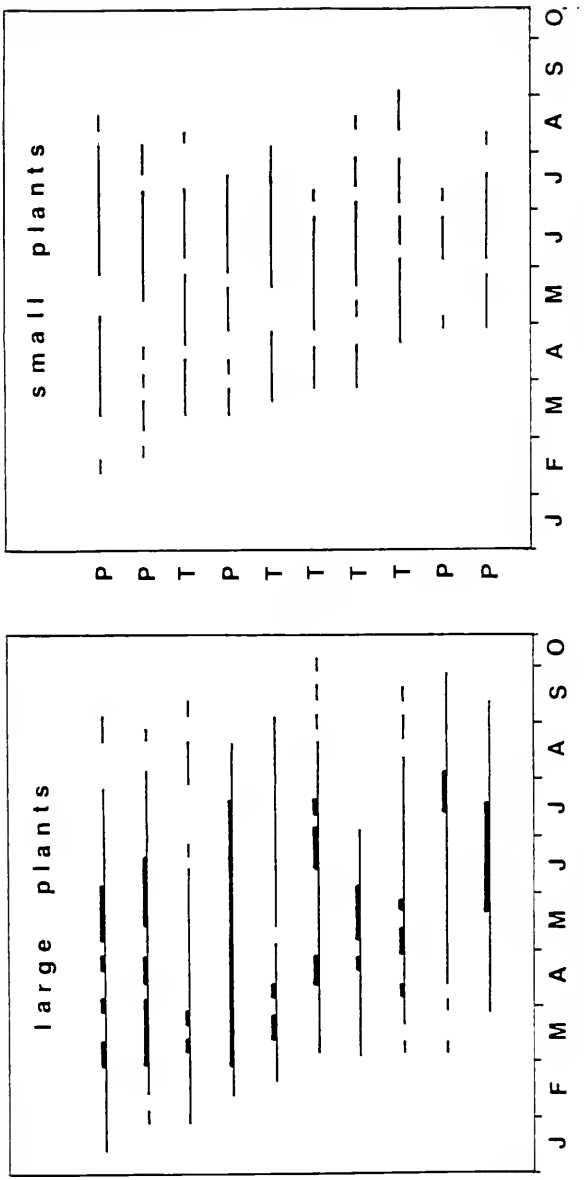

Figure 4. Flowering phenologies of randomly selected pin (P) and thrum (T) C. elata plants from both study sites in 1983. Thin lines indicate plants with 1 to 9 flowers; thick lines indicate plants with more than 9 flowers.

the canopy and the understory produce flowers and are pollinated by short-billed hummingbirds (Feinsinger et al. 1986, Linhart et al. in press). Cephaelis elata is probably the most important nectar resource in the understory for these short-billed hummingbirds, but Besleria triflora (Oerst.) Hanst., Palicourea lasiorrachis Benth. ex Oerst., and Hansteinia blepharorachis (Leonard) Durkee are also common species. A number of species of epiphytic Ericaceae also provide seasonally abundant nectar resources for hummingbirds, but usually flower at different times of year from C. elata (Busby, personal observation).

METHODS

Controlled Pollinations

Hand pollinations were performed to confirm self-incompatibility in C. elata in September 1981 and in August 1983. In 1981, inflorescences with buds were enclosed with Kraft Pollen Tector bags on the day prior to flower opening. Three hand pollination treatments were applied to flowers of each style morph, using 1) pollen from the same flower or from another flower on the same stem, 2) pollen from a different stem of the same morph, or 3) pollen from one or more plants of the other morph. All flowers were pollinated between dawn and 1100 and then were rebagged for at least 5 hours. Later the same day I collected the styles and preserved them in FAA (9:1:1 ethanol:acetic acid:formalin). In 1983, the same procedure was used with flowers on cut inflorescences in the lab. The inflorescences were placed in water-filled glass bottles and covered with plastic bags to minimize desiccation. Flowers are initiated normally for at least three days in this manner. I allowed at least 10 hours for pollen tubes to grow before preserving the styles. The styles were later examined using aniline blue staining and epifluorescence microscopy (Martin 1959). The number of pollen tubes at the base of each style was counted.

Pin pollen grains applied to pin stigmas frequently produced pollen tubes that grew well into the style before gradually losing fluorescence (Bawa and Beach 1983; this study). To determine whether these pollen

tubes actually stopped growing or simply became too faint to detect in the lower part of the style, I conducted additional controlled pollinations on pin plants in 1983 and monitored fruit set. Because I could not permanently mark individual flowers, all flowers on each of 16 inflorescences on 5 plants received one of the three (self, intramorph, and cross) treatments. Approximately 1 mo after all inflorescences had finished flowering, I collected all inflorescences that had not aborted and counted the number of developing fruits.

Plant and Flower Censuses

At each site, all stems of C. elata were marked with numbered metal tags, and the morph of each stem was recorded at the time of flowering. At approximately weekly intervals throughout the flowering season each year, I censused the number of open flowers on all stems at each site.

To determine how the density of C. elata plants in the study plots compared to that elsewhere at Monteverde, I censused numbers of stems per unit area at 50 sites within two km of the study areas. At 50 m intervals along selected trails, I followed a randomly determined compass bearing for a randomly determined distance of 1 to 50 m. The nearest C. elata plant within 20 m (if any) was located, and then the number of conspecific stems within a 10 m radius of the plant was determined. I assumed each plant within the 314 m^2 area had the same number of neighbors within 10 m as the central plant, and therefore weighted each sample by the number of plants within it minus one. Fifty such samples were taken. Because plants not located in the center of a sample area may actually have had differing numbers of neighbors within

10 m than did the central plant, values for numbers of neighbors are estimates.

Observations of Pollinators

I conducted flower observations at selected plants throughout the flowering seasons at both study sites. To enable individual identification of hummingbirds, I mist-netted at each site 2 to 4 times each season and color-tagged all hummingbirds (Stiles and Wolf 1973). Observations began at dawn or at 3 h after dawn and lasted 3 h, except for several observations in 1982 that were initiated at dawn and lasted 6 h. For all flowers on the observed plant I recorded visitor identity, time of day, number of flowers probed and the occurrence of aggressive behavior. At the distances from which I observed, 4 to 10 m, I could discern insect visits to flowers without affecting hummingbird visitation. Two plants were observed simultaneously if they had non-overlapping canopies and were > 2 m apart. Each month, I conducted four observations, two of each floral morph, in each study plot during the 1983 season. In 1982, the frequency of observations each month was similar to that of 1983 but I did not attempt to equalize observations of pin and thrum plants. Observations were made in conjunction with dye experiments (see below). Consequently, two or more flowers on most observation plants contained powdered dye on the anthers. Judging from pollinator behavior at plants containing both dyed and dye-less flowers, the application of dye to the anthers rarely affected pollinator visitation. I discarded or repeated the few observations where dyed

flowers were avoided by pollinators. In these instances it appeared that an excess of dye contaminated the nectary.

The effectiveness of insects and hummingbirds as pollinators was tested with a 1-d exclusion experiment. On 29 June 1983, I allowed all pollinators to visit a thrum plant in the sparse plot. I collected styles from the plant at 1100, 1400 and 1700 h and preserved them in FAA. The following day I remained near the plant and actively prevented hummingbirds from approaching the plant from just prior to dawn to 1400 h. Insects were allowed to visit flowers on the plant without interference. All insect visits were recorded, and styles were collected in the same manner as the previous day. Later, styles were examined for the presence of pollen tubes (Martin 1959).

Analysis of the Visit Data

The effect of flower density on visit rate was analyzed with stepwise multiple regression. I defined the dependent variable, visit rate, as the number of hummingbird probes per flower each hour. A visit rate was calculated for each plant observed on a given day, then log-transformed. Independent variables were (1) the number of flowers on the observed plant, (2) local flower density (the number of C. elata flowers within 10 m of the observed plant, excluding the observed plant), (3) seasonal flower density (the number of C. elata flowers in the study plot), and (4) heterospecific flower density (the number of all short-corolla hummingbird-visited flowers, excluding those of C. elata, in the understory of the study plot). The number of flowers on the observed plant was recorded at the time of the observation. The

other three variables were derived from weekly flower censuses made on a separate day, and thus were estimates. If a census occurred within 2 d of the observation I used data from that census. Otherwise, I averaged values from the censuses immediately before and after the observation.

I first examined the independent variables for multicollinearity. I removed heterospecific flower density from consideration in the dense plot in both years due to high negative collinearity with seasonal flower density. The stepwise selection option of Proc Stepwise (SAS Institute Inc. 1982) was used with a cutoff value of alpha = .10 for entry of a variable into the model as well as for retention in the model at each step. With stepwise regression procedures, alpha levels used to select variables cannot be used as levels of significance because the partial F-value used at each step is the maximum of several correlated partial F-values (Sokal and Rohlf 1981). For this reason, the significance levels associated with each selected independent variable are approximate.

In the initial stepwise regression models both first-order and second-order (squared) terms were considered for entry into the model. Second-order terms were used to examine possible nonlinear relationships between visit rate and measures of flower density. A second-order term was entered only if it explained a significant amount of the residual variance of the model in the presence of the corresponding first-order term. Because the slope of the relationship between measures of flower density and visitation may decrease as flower density increases (Thomson 1982, 1983, Rathcke 1983), I also evaluated log-transformed independent variables for entry into regression models. In cases where the second-

order term of a variable failed to meet model entry criteria, I used both standard (Proc Reg, SAS Institute Inc. 1982) and stepwise multiple regression procedures to choose between the raw (first-order) and log-transformed versions of each independent variable, retaining whichever one had a higher partial F-value in the presence of the other independent variables (i.e., SAS type III sums of squares).

Flower Removal Experiment

I conducted flower removal experiments to determine the effect of the number of flowers on a plant on pollinator visit rates to flowers. Using 19 x 16 mm mesh plastic netting, I bagged all but a few inflorescences on a large pin plant in the sparse plot. The plant was observed for pollinator visits for 3 or 6 h in the morning on four occasions: 1) the day prior to the manipulation, 2) twice on separate days 2 to 5 d after bagging the plant, and 3) once 2 d after removal of the netting. The experiment was conducted in August 1982 and repeated on the same plant in July and in August of 1983.

Pollen Carryover

I measured pollen carryover in 1983 with caged hummingbirds offered flowers on cut inflorescences. Lampornis calolaema were mist-netted in the field and caged in an outdoor enclosure, 4 x 4 x 3 m, made of nylon mesh. The birds, one male and one female, were maintained on a 20% sucrose solution presented in an artificial feeder, and were kept for up to a week before release. One half hour prior to an experiment, I removed the feeder. Using virgin flowers on inflorescences in water-

filled jars, I offered the bird one or more donor flowers followed immediately by 14 to 20 recipient flowers of the other morph. I recorded the visit sequence to recipient flowers before removing them from the cage. I conducted one to three trials per day and cleaned the bird's bill between runs. A separate series of experiments was made using 1) a single donor flower and 2) six donor flowers in succession. The numbers of pin-to-thrum and thrum-to-pin trials were equalized.

Because pin and thrum pollen grains could not reliably be distinguished, I counted the number of pollen tubes in the styles of recipient flowers (Martin 1959). Styles were picked from inflorescences 12 to 24 h after each experiment and preserved in FAA. Only compatible pollen grains produce pollen tubes that penetrate to the style base (Bawa and Beach 1983; this study); thus, counts of stylar pollen tubes provide a conservative estimate of the number of viable pollen grains deposited on each stigma. Rarely did more than 20 pollen tubes penetrate to the style base regardless of the number of compatible grains on the stigma.

Pollen Receipt

I quantified pollination levels by counting numbers of pollen tubes at the base of floral styles. Plants in both plots were sampled between 1500 h and 1700 h, following flower censuses. The entire style was removed with forceps and pickled in a vial containing FAA. I collected all intact styles from plants with < 6 flowers and a subsample of styles (usually 5) from plants with > 5 flowers. In the sparse plot, I sampled all plants on each census throughout the flowering season. Due to the

large number of plants in the dense plot, I collected styles from a subsample (usually 15 to 30) of plants each census. In the lab, using aniline blue staining and epifluorescence microscopy (Martin 1959), I counted the number of pollen tubes at the base of each style.

Because styles were collected several hours before the end of flower life, some styles may have contained actively growing pollen tubes that had not reached the style base. Thus, actual pollination levels may be somewhat higher than those reported here. Additionally, because the time required for pollen tubes to grow to the base of the longer pin styles (ca. 5 h) was greater than that required in thrum styles (ca. 3.5 h), I was effectively collecting pin styles 1.5 h earlier in the day than thrums. This bias prevents an objective comparison of pollination levels between morphs.

Analysis of Pollen Receipt Data

Weighted stepwise multiple regression was used to analyze the relationship between pollination and measures of flower density and dispersion. I used five independent variables, three of which were previously defined: (1) the number of flowers on the central plant (i.e, a plant from which styles were collected), (2) local flower density, and (3) seasonal flower density. Heterospecific flower density, used in visit analyses, was eliminated because of frequent high negative collinearity with seasonal conspecific density. I used the number of *C. elata* flowers within either 5 m or 10 m of the central plant (exclusive of the central plant) as the measure of local flower density: a 10 m radius was used in the sparse plot, a 5 m radius in the dense plot in

1983, and both a 5 m and a 10 m radius in the dense plot in 1982. These two measures of local density tended, of course, to be highly collinear; where both were evaluated for entry into the model only the more significant of the two was retained. (4) Another variable was the distance to the nearest mate: the number of meters from the central plant to the closest plant of the other morph with one or more open flowers. (5) Lastly, a categorical, or "dummy" variable was included to represent the two morphs (0 = thrum, 1 = pin).

The dependent variable was the mean number of pollen tubes at the base of the style averaged across all styles collected from a plant. Pollen tube counts from individual flowers were not used as the experimental unit since flowers on the same plant are not independent.

Because the sample size generated from each census was small, at each site I pooled censuses into 2 or 3 periods for each flowering season (Figure 3). Criteria for determining break points for the different periods were 1) maximizing the ranges of the independent variables, and 2) equalizing sample sizes among periods. Prior to regression analyses by period, I checked for significant variation among plants in pollination levels by date and style morph with one-way ANOVA. I used raw pollen tube counts from styles of all flowers on each plant. Generally, among plant variation was highly significant.

From this point on, the stepwise multiple regression procedures were as described for the visit data with the following differences: (1) observations were weighted by the number of styles on the plant examined up to a maximum weighting of five; (2) a selection level of alpha = .05 was used for entry and retention of variables in the model;

and 3) first order interaction terms were included as variables in the stepwise process. An interaction term was retained in the model only if it was significant in the presence of both component variables.

To determine whether my definition of a plant influenced results from the analyses, I redefined the dependent variable and repeated regressions for the sparse plot. Instead of using the multi-stem definition of a plant (see above), I used pollen tube values for individual C. elata stem.

Pollen Dispersal

Powdered ultraviolet-fluorescent dyes (Helecon and U.S. Radiant) were used as pollen analogues. The relationship of the dispersal of dye to that of pollen is not well understood; it probably varies among plant species and pollinating agents. Price and Waser (1982) found a close relationship between dispersal of dye and pollen in the hummingbird-pollinated Ipomopsis aggregata. In contrast, Thomson et. al. (1986) showed that dye particles were dispersed farther and in greater quantities than pollen of bee-pollinated Erythronium. Because the relationship between dye and pollen dispersal is unknown for C. elata, I utilized dyes only for comparative purposes. Two types of experiments were conducted. I measured pollen dispersal per flower by placing dye on two flowers of a plant. To quantify pollen dispersal per plant I placed dye on all open flowers of a plant. Dye experiments were conducted on four plants per month, two of each morph, in each study plot during the 1983 season. In 1982 the frequency of experiments each

month was similar to that of 1983, but the numbers of pin and thrum donor plants were not deliberately equalized.

At dawn, I applied the powdered dyes to the anthers of the newly opened flowers at dawn with a toothpick. Experiments using pin and thrum flowers as dye-donors were alternated. Because I was unable (1) to place precise amounts of dye on anther surfaces, and (2) to duplicate effects of possible differences in pollen size and pollen surface features between pin and thrum flowers, I did not make intermorphic comparisons of dye dispersal.

I used two dyes (Helecon green and yellow) that appeared pastel in visible light and one day-glow dye (U.S. Radiant orange-red). In 1982, I used two colors of dye each day, one color per plant. The following year three colors were utilized: one color for two flowers on the first plant, the second color for two flowers on a second plant and the third color for all remaining flowers on one of the two plants. All flowers on each plant were then observed for pollinator visits. Hummingbird behavior was not affected by the color of the dye within flowers. Later that day (1300 to 1500 h), I collected flowers from plants surrounding the donor plant, and pinned them in an insect box for transport to the lab. Only compatible flowers, i.e., those of the other morph from the donor flower, were analyzed for dye receipt. Except in the dense plot in 1982, virtually all compatible flowers were collected on all plants within predefined areas. Using a ladder, I was able to reach all but a few flowers on the tallest plants. At plants containing more than 10 open flowers, I attempted to pick at least half of the flowers. I used the fraction of sampled dye-receiving flowers to estimate the total

number of dye-receiving flowers on the plant. In the sparse plot in 1982, all flowers were collected within the study plot for an effective radius of 50 to 100 m around the donor plant. The following year I expanded collections to all compatible flowers within 100 m, whether within or outside the study plot. In the dense plot in 1982, I collected 1 to 3 flowers from approximately half of the plants within 35 m of the dye source. In 1983, I sampled all flowers on all plants within 25 m or the first 15 nearest neighbors, whichever came first.

In the lab I used a black light with a 10X to 40X dissecting microscope to record the presence and color of any dye on the stigma. Because the size of individual dye particles ranged over several orders of magnitude, rather than count particles I recorded the amount of dye on stigmas using four relative classes. Using maps of the study areas, I calculated the distance from each compatible plant to the dye source.

Three variables describe dye dispersal: (1) The number of flowers receiving dye was based on all compatible flowers examined that contained dye on the stigma, plus estimates from plants on which I sampled < 100% of the flowers; (2) the dispersal distance and (3) the "plant sequence" are indices of the distance of dye dispersal in meters and in nearest neighbor units, respectively. I first ranked all recipient flowers with dye on the stigma in order of distance from the dye source, then determined the 90th percentile flower from the donor plant. Dispersal distance is the linear distance from the dye source to the plant containing the 90th percentile dye-receiving flower. To calculate plant sequence, all plants for which I had collected flowers that day (i.e., all flowering individuals of the other morph from that

of the donor plant) were ranked in order of distance from the donor plant. Plant sequence is the rank of the plant containing the 90th percentile dye-receiving flower. Dispersal distance and plant sequence are roughly analogous to neighborhood size, N_e, and neighborhood area, N_a (Wright 1969, Levin and Kerster 1971). Neighborhood size and plant sequence both provide an index of the number of interbreeding plants, N_a and the dispersal distance an index to the spatial scale of pollen dispersal. Because neighborhood size and area are based on the variation in dispersal distances, however, their values are especially sensitive to the maximum distances recorded. In this study, I gathered nearly complete data on dispersal events within prescribed areas, but I did not attempt to determine maximum dispersal distances of pollen. Thus, neighborhood size and area could not be quantified.

Fruit Set

Each year, in both plots, I measured percent fruit set on infructescences from pin and thrum plants. Late in the flowering season, I collected a random sample of heads that had flowered during the early to middle portions of the season. Only infructescences that had completed flowering and had not yet matured fruit were collected. Because the ovary remains in the head after corolla abscission, the number of flowers produced by each head could be determined. By dissecting infructescences, I determined the number of developed, undeveloped, and damaged fruits.

RESULTS

Pollinator Identity and Foraging Behavior

The great majority of hummingbird visits to C. elata flowers were made by Lampornis calolaema (Table 3). Other species of hummingbirds made regular visits to flowers only at times when visit rates by L. calolaema were extremely low.

In the dense plot, L. calolaema males established large territories (about 600 to 2000 m^2) early in the flowering season and defended them throughout each day against other hummingbirds and against lepidopterans. Territories in this plot contained approximately 20 to 40 C. elata plants; elsewhere L. calolaema males were occasionally observed defending territories primarily composed of other flowering species, with few C. elata. At the dense site, territory boundaries were well defined. Repeated sightings of individually tagged males indicate that territories were often stable over periods of at least 6 to 8 wk. Territorial behavior included vocalizations and active defense against other flower-visitors. The fact that territory-holders generally moved frequently among perches within their territories suggests they were not able to survey the entire territory from one location. At this site, I estimated that the proportion of all hummingbird visits to flowers made by the territory-holder was over 73% in 1982 and about 84% in 1983. Intruders consisted primarily of L.

Table 3. Identity and behavior of visitors to flowers of Cephaelis elata.

Variable	Sparse site 1982	Sparse site 1983	Dense site 1982	Dense site 1983
Hours of observation	81	81	126	96
Number of plants	23	27	40	32
Number(%) of flower visits:				
Hummingbirds				
Lampornis calolaema, male	209 (17.2)	622 (62.6)	856 (83.0)	1200 (87.9)
L. calolaema, female	854 (70.1)	235 (22.2)	86 (8.3)	48 (3.5)
Eupherusa exima	40 (3.3)	3 (0.3)	0 (0.0)	0 (0.0)
Elvira cupriceps	0 (0.0)	0 (0.0)	2 (0.2)	0 (0.0)
Phaethornis guy	2 (0.2)	0 (0.0)	2 (0.2)	3 (0.2)
Insects				
Heliconius clysonymus	25 (2.1)	91 (8.6)	10 (1.0)	6 (0.4)
Other butterflies	14 (1.1)	23 (2.2)	7 (0.7)	51 (3.7)
Moths	0 (0.0)	6 (0.6)	19 (1.8)	24 (1.8)
Bombus sp.	0 (0.0)	1 (0.1)	15 (1.5)	1 (0.1)
Flies	31 (2.5)	32 (3.0)	19 (1.8)	21 (1.5)
Hummingbird visits/fl·hr				
Mean	1.23	1.39	0.90	1.04
SD	1.21	1.28	0.79	0.76
Total visits/fl.hr				
Mean	1.34	1.87	0.96	1.10
SD	1.21	1.50	0.84	0.76

calolaema females, unmarked males, and marked males from nearby territories.

At the sparse site, both male and female L. calolaema were frequent flower visitors, with relative abundance of each shifting with the abundance of flowers. Flowers on small, isolated plants were visited mostly by females. Individual females often returned to observed plants at regular intervals, but did not appear to follow consistent foraging circuits. Females, therefore, acted as "generalists" (sensu Feinsinger 1976) but did not trapline in the strict sense (Janzen 1971). Foraging areas were typically utilized by a single bird. It was not uncommon, however, for two individuals of either sex to repeatedly return to a plant during an observation. At this site, males were present mainly during periods of high flower availability. Males usually chased other flower-visitors whenever encountered, but presumably due to the spatial dispersal of flowers, rarely defended clearly defined territories. The few well-established territories at the sparse site usually coincided with heavy flowering by other short flowered species adapted for hummingbird pollination, such as Besleria triflora or Palicourea lasiorrachis in the understory and various Ericaceae in the canopy. Territories incorporating flowers in both the understory and canopy, while uncommon, were observed in both study plots.

The most common insect visitors to C. elata flowers were lepidopterans (Table 3). Visits by butterflies were heaviest during dry, sunny weather. Butterflies began visiting flowers by mid-morning and were active throughout the afternoon. Heliconius clysonymus was the most regular insect visitor to C. elata flowers. Individuals of this

species often returned to the same flowers of a plant at frequent intervals throughout the day. Moths were observed visiting flowers at dawn prior to foraging activity by other pollinators.

Flowers suffered few depredations by nectar thieves or robbers. The basal 5 to 10 mm of the flower is embedded within the rigid bracts of the inflorescence, making the nectary inaccessible except through the corolla tube.

In the pollinator exclusion experiment, flowers were not pollinated unless visited by hummingbirds. On the control day (open pollination), six of eight flowers were pollinated; of these, each contained an average of 10.8 (SD = 9.4) pollen tubes. The following day, in the absence of hummingbirds, lepidopterans visited each of the five flowers an average of five times between dawn and 1400 h. None of these styles contained pollen tubes. The presence of heterospecific pollen on four of the five stigmas confirmed, however, that some insect visitors did contact the reproductive parts of the flower.

Effects of Flower Density on Visitation

At each site, the number of flowers on and surrounding observed plants varied greatly (Table 4). Factors characterizing flower density explained 32 to 68% of the seasonal variation in visit rates by hummingbirds (Table 5). Correlations between measures of conspecific flower density and visitation were generally stronger in 1983 than in 1982. As expected, flower visitation was generally positively density-dependent. In all four comparisons, visit rates significantly increased with seasonal flower density. The significant squared term indicates

Table 4. Ranges of the independent variables used in multiple regression analysis of flower visitation.

Site	Year	N	Flowers per plant	Flowers per 314 m^2	Seasonal flower density	Hetero-specific density
Sparse	1982	22	1-60	0-60	15-122	2-210
Sparse	1983	28	1-26	0-34	6-142	4-253
Dense	1982	44	1-16	4-55	79-638	0-311
Dense	1983	43	1-29	0-35[a]	5-280	7-130

[a] A 5 m radius (flowers/78 m^2) was used to compute local flower density at the dense site in 1983.

Table 5. Results of stepwise multiple regression on mean visit rate to flowers on observed plants. Sign of coefficients indicated before F-values. All probability values associated with F-values are estimates (see text).

Site	Year	df	Independent variable: Flowers per plant	Flowers per 314 m^2(a)	Seasonal flower density	SFD X SFD[b]	Heterospecific flower density	R^2
			F values					
Sparse	1982	3,17	+2.79[L] *		+5.42 *		+18.93[L] ***	0.580 ***
Sparse	1983	3,23	+10.14 **		+9.84 **		+13.06[L] **	0.667 ***
Dense	1982	2,40		-3.95	+18.62[L] ***			0.320 ***
Dense	1983	4,37	+5.40[L] *	-5.38 *	+28.67 ***	-12.89 ***		0.684 ***

* $P < .05$, ** $P < .01$, *** $P < .001$.

a Flowers per 78 m^2 used for dense plot analyses in 1983.

b Seasonal flower density squared term.

L Independent variable log-transformed.

that the slope of the relationship between seasonal flower density and visitation was not linear; positive hummingbird responses to increases in flower density were weaker at peak flowering than during either tail of the flowering season. The number of flowers within 10 m of observed plants was not strongly correlated with floral visit rates, although at the dense site, territorial birds did visit flowers in dense patches significantly less frequently in 1983. Flowers on plants with more flowers received more frequent visits in 1983 but not in 1982. The number of heterospecific flowers in the understory was positively correlated with visit rate both years. Due to high negative collinearity with the seasonal density of C. elata flowers, the density of heterospecific flowers was not included in regression analyses in the dense plot.

While multiple regression analysis shows a positive effect of seasonal flower density on visit frequency in all four cases (Table 5), seasonal variation in this relationship was great (Figure 5). In 1983, mean monthly visit rates in both plots rose and fell in accordance with flower density throughout the season. In 1982, the relationship between seasonal flower density and visitation was weak or nonexistent during the first two thirds of the season. Only late in the season was a positive relationship evident. Visit rates were high during the first part of the season, then dropped off abruptly at peak flowering. The cause for the sudden decline remains uncertain, but may be related to a flowering pulse in the canopy. Satyria warscewiczeii and Gonocalyx pterocarpus, two common hummingbird-pollinated epiphytes, bloomed abundantly in July and August 1982 (Busby, personal observation). In

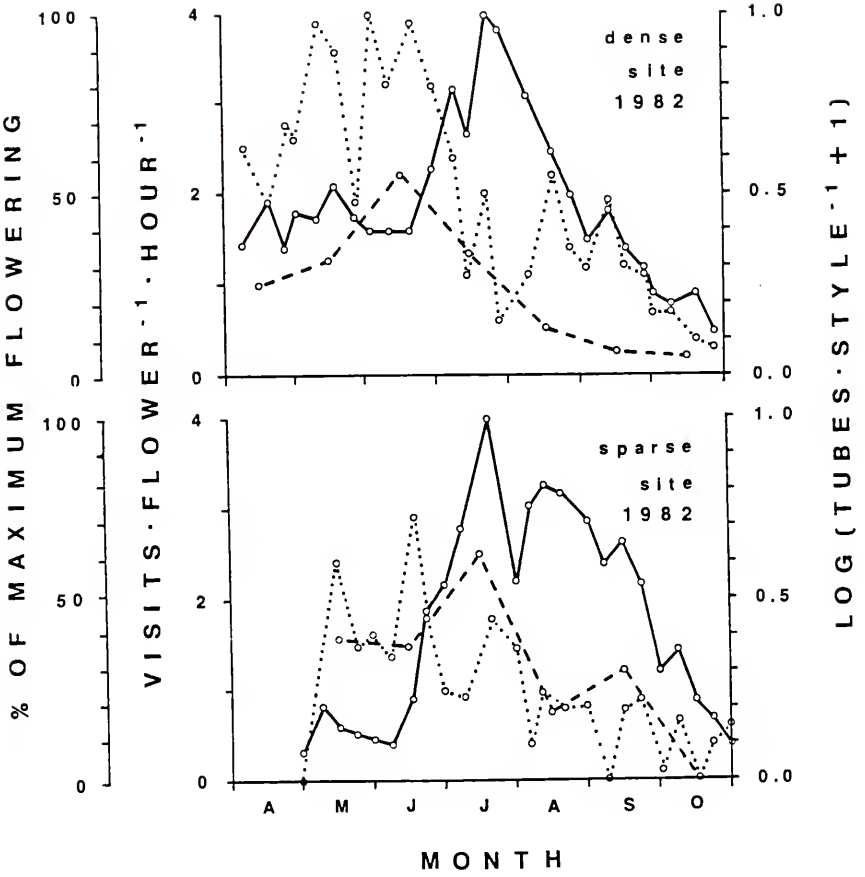

Figure 5. Seasonal fluctuations in total number of C. elata flowers (____), mean monthly visit rates to flowers by hummingbirds (- - -), and pollen receipt (numbers of pollen tubes at the base of the style) (....) at each site in 1982 and 1983.

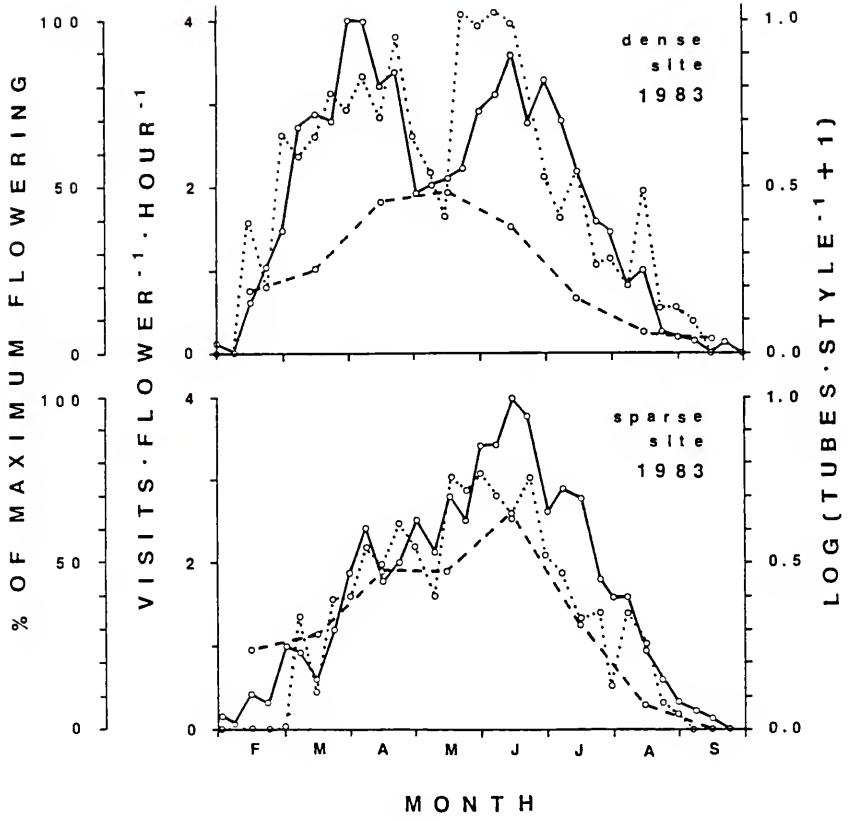

Figure 5--continued.

mid-July a tagged L. calolaema male abandoned a long-held territory in the understory and was sighted in the canopy attempting to defend a profusely-flowering S. warscewiczeii plant against a host of other hummingbirds. This is evidence that flowering in the canopy drew pollinators away from C. elata flowers, and stands in contrast to the positive effects of understory heterospecifics on visit rates to C. elata flowers in the sparse plot (Table 5).

Results of the flower removal experiment are consistent with observations of unmanipulated plants: individual flowers on plants with large floral displays received more visits than those in small displays (Figure 6). In all three replicates, visit rates to flowers consistently dropped when the number of flowers on the plant was artificially reduced, then recovered after removal of netting from the plant.

The relationship between the number of flowers on a plant and the number of flowers probed during each visit by hummingbirds was analyzed with least squares regressions (Table 6). Regression coefficients (slopes) were large, indicating that hummingbirds probed a high proportion of the flowers during typical bouts at plants of all sizes. Birds probed, on average, at least half of the flowers on plants with 10 or fewer flowers and at least one third of the available flowers on plants with > 10 flowers. The results were similar across plots and years, and in all four cases linear models accounted for more of the variance in the number of flowers visited per plant than did logarithmic or exponential models.

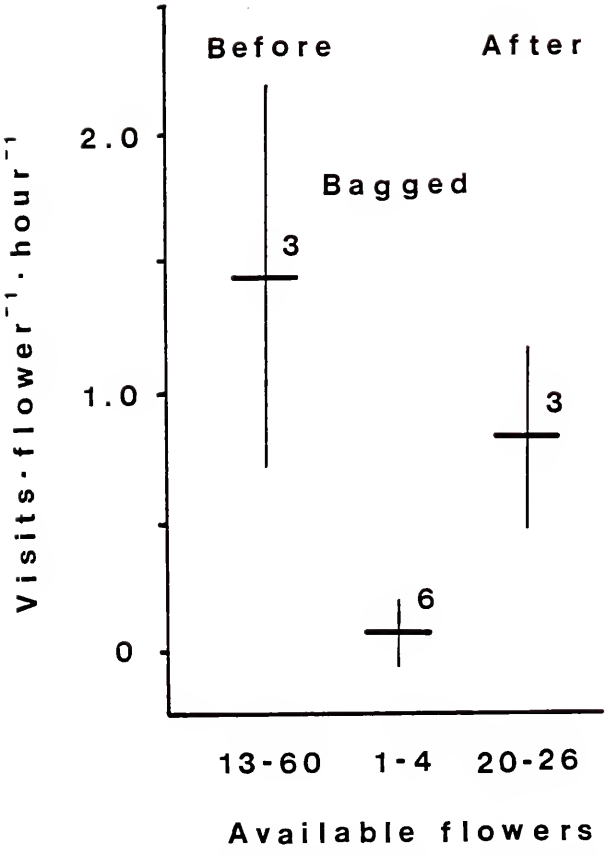

Figure 6. Mean visit rates by hummingbirds to flowers on a C. elata plant before, during, and after bagging the majority of flowers with plastic netting. Vertical lines indicate 1 standard deviation; numbers above each mean indicate sample size.

Table 6. Results of linear regression analysis on the number of flowers visited per foraging bout by hummingbirds as a function of the number of flowers on the plant.

Site	year	intercept	slope	R^2	F(df)	p
Sparse	1982	1.44	0.57	0.76	343.2(1,110)	<<.001
Sparse	1983	0.71	0.48	0.40	151.1(1,166)	<<.001
Dense	1982	1.49	0.45	0.45	134.2(1,230)	<<.001
Dense	1983	1.63	0.36	0.41	161.1(1,232)	<<.001

Pollen Carryover

Results from the pollen carryover experiments for both floral morphs are shown in Figure 7. Pollen from thrum flowers was transferred by hummingbirds to many of the first 20 recipient stigmas. In contrast, pin pollen was dispersed to few thrum flowers; nearly all successful pollen donation by pins was to the first five thrum flowers. Summary values derived from the carryover data quantify these differences (Table 7). In both single and six donor flower trials, thrum pollen was carried to more recipient flowers than was pin pollen. Furthermore, the average amount of pollen transferred from thrum to pin flowers was over twice that transferred from pin to thrum flowers.

In both morphs, the number of donor flowers visited by the pollinator also influenced the pattern of pollen carryover (Figure 7 and Table 7). The major effect of increasing the number of donors from one to six was to increase the amount of pollen donated. The total number of pollen tubes in recipient styles was an average of 2 to 3 times greater in trials where hummingbirds visited six donor flowers rather than one donor. It is less clear if the number of donors affects (1) the number of flowers receiving pollen or (2) the median distance of pollen dispersal. The trends are weak and non-significant.

Variation in Pollen Receipt and Fruit Set

Several sources of variation in pollen receipt by naturally pollinated flowers are shown in Table 8. (1) Variation in the mean number of pollen tubes per style among plants was high. (2) Pollen tube

Figure 7. Pollen transfer by hummingbirds from 1 and 6 donor flowers to sequentially visited flowers of the other morph (recipient flowers 1 to 20). Pollen transfer is measured as numbers of pollen tubes penetrating to the base of recipient styles. Central horizontal lines indicate means; vertical bars indicate 1 standard error (n = 3, shaded bars; n = 5, unshaded bars).

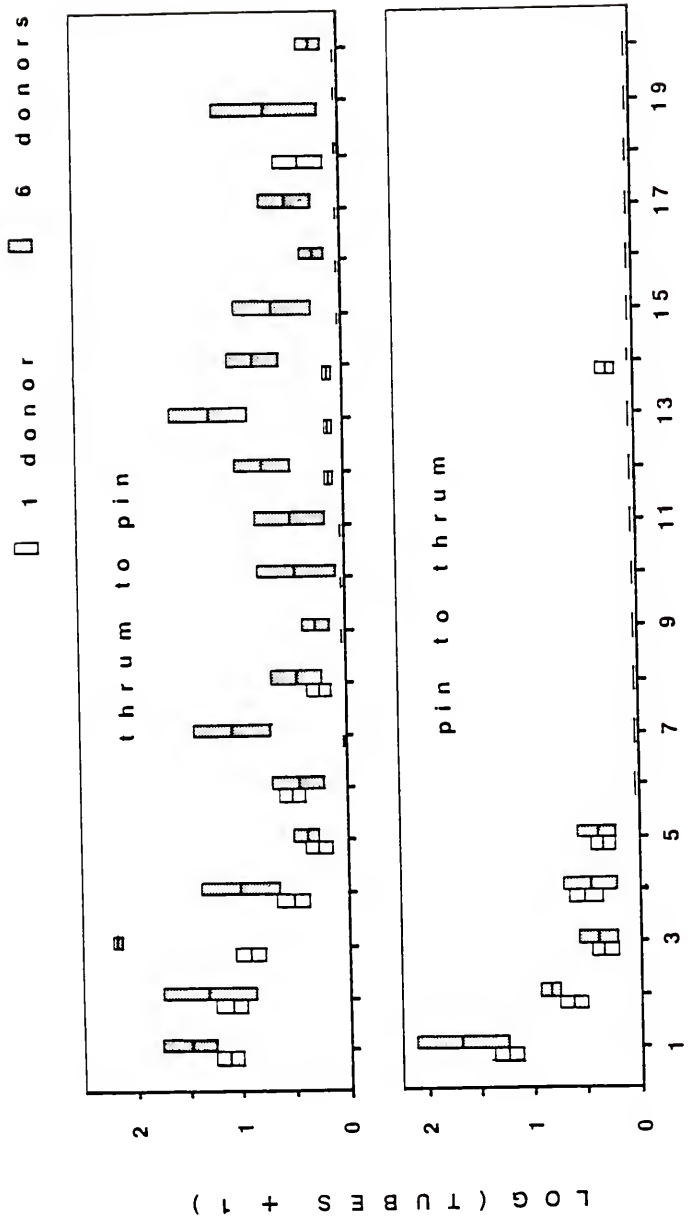
1 donor
6 donors
thrum to pin
pin to thrum
LOG (TUBES + 1)
RECIPIENT FLOWER
0
1
2
1
3
5
7
9
11
13
15
17
19

Table 7. Effect of numbers of donor flowers on pollen transfer between floral morphs. Data are from pollen carryover experiments.

No. Donor Flowers	1 Pin	6 Pin	1 Thrum	6 Thrum
No. Recipient Flowers	16-20 Thrum	17-20 Thrum	14-20 Pin	20 Pin
No. Trials	5	3	5	3
Total donor tubes growing through recipient styles (X ± SD)	7.4±6.0	17.3±5.5	16.0±16.6	48.3±26.2
Mann Whitney U tests (1-tailed)	U = 1	p = .04	U = 1	p = .04
No. recipient styles with >1 donor tube (X ± SD)	2.8±1.8	3.0±1.7	4.4±1.9	9.0±6.1
Mann Whitney U tests (1-tailed)	U = 7	p = .50	U = 4.5	p = .24
Sequence no. of recipient styles receiving median donor tube (X ± SD)	2.7±2.8	1.0±0.0	3.6±2.6	5.3±3.2
Mann Whitney U tests (2-tailed)	U = 4.5	p = .24	U = 3.5	p = .30

Table 8. Numbers of pollen tubes at the base the style averaged across flowers on plants. N = number of plants. The number of flowers is in parentheses.

	Thrum				Pin			
	Mean	SE	N	Percent with >1 tube	Mean	SE	N	Percent with >1 tube
Sparse 1982								
Period 1	2.4	1.7	47(116)	61.2	0.6	1.1	28(161)	16.1
Period 2	0.5	1.1	66(172)	23.3	0.2	0.4	40(330)	5.2
Sparse 1983								
Period 1	2.0	1.7	66(272)	48.5	1.3	1.1	40(136)	40.4
Period 2	4.8	1.7	59(230)	78.7	3.7	1.9	42(181)	53.6
Period 3	1.3	1.6	61(138)	38.4	0.6	1.4	41(162)	9.3
Dense 1982								
Period 1	5.5	1.7	101(258)	80.2	4.8	1.7	114(325)	68.3
Period 2	1.9	1.6	84(322)	43.8	1.1	1.5	114(404)	31.4
Period 3	1.4	1.7	85(236)	40.7	0.4	0.9	89(227)	18.5
Dense 1983								
Period 1	4.8	1.4	64(277)	74.7	1.9	1.8	65(340)	50.6
Period 2	8.0	1.4	83(334)	85.6	4.0	1.6	69(390)	67.4
Period 3	1.1	1.1	74(206)	42.2	1.1	1.6	47(144)	38.9

counts at the base of thrum styles consistently exceeded those at the base of pin styles. This difference is at least partly attributable to the sampling method. (3) Pollination levels varied seasonally. During some periods, most styles contained 10 to 20 pollen tubes, well over the absolute minimum of two needed to fertilize both ovules. At other times, most flowers received no compatible pollen. Pollination levels early in each flowering season were consistently higher than late in the season. In 1983, but not in 1982, flowers produced during mid-season contained more pollen tubes than those in either tail of the season.

The mean percentage of flowers producing fruits varied from 20 to 53% (Table 9). During both years, inflorescences at the dense site set a significantly higher percentage of fruits than at the sparse site. Because of a significant site x morph interaction in 1982, the effect of site on fruit set was examined separately for pins ($t = 7.7$, $p < .001$) and for thrums ($t = 2.2$, $p < .05$). Differences between morphs in fruit set were complex. In 1983, fruit set of thrum inflorescences was higher than that of pins. In 1982, fruit set of pins was higher at the dense site, while thrums set more fruit at the sparse site.

Effects of Flower Density on Pollen Receipt

Using stepwise multiple regression, variation in the density and dispersion of *C. elata* flowers at each site (Table 10) accounted for 12 to 41% of the variation in pollen receipt (Table 11). No single independent variable explained large amounts of the variation in stylar pollen tube counts, yet each variable was significantly correlated with pollination levels in the majority of trials.

Table 9. Fruit set of inflorescences. Analysis of variance performed on arc-sine transformed data.

Morph	Sparse site Mean	SD	N	Dense site Mean	SD	N
1982						
Pin	20.0	12.3	39	52.6	21.4	28
Thrum	35.0	14.8	45	47.8	21.1	10
ANOVA results						
Effect of site	$F_{(1,118)} = 39.13$	$p < .001$				
Effect of morph	$F_{(1,118)} = 2.11$	$p = .149$				
Site x morph interaction	$F_{(1,118)} = 7.75$	$p = .006$				
1983						
Pin	26.9	18.2	29	33.7	18.2	43
Thrum	32.7	21.6	28	43.3	21.4	53
ANOVA results						
Effect of site	$F_{(1,149)} = 6.63$	$p = .011$				
Effect of morph	$F_{(1,149)} = 4.80$	$p = .030$				
Site x morph interaction	$F_{(1,149)} = 0.18$	$p = .674$				

Table 10. Ranges of the independent variables used in multiple regression analyses of pollen receipt. Flowers per plant refers to the central plant from which styles were collected for pollen tube counts. Flowers per 78 and 314 m^2 refer to the two measures of local flower density. Nearest-mate distance is the distance from the central plant to the nearest flowering plant of the other floral morph. Seasonal flower density is the number of C. elata flowers in the study site on the census date.

Site Year	Number of plants	Independent variable: Flowers per plant	Flowers per 78 m^2	Flowers per 314 m^2	Nearest-mate distance	Seasonal flower density
Sparse 1982						
Period 1	75	1-71		0-78	11-122	2-100
Period 2	106	1-59		0-69	21-99	2-60
Sparse 1983						
Period 1	105	1-28		0-21	5-100	6-90
Period 2	101	1-42		0-56	1-34	90-142
Period 3	102	1-42		0-47	1-100	1-102
Dense 1982						
Period 1	215	1-31	0-79	0-119	0.7-13.6	214-364
Period 2	198	1-40	0-110	2-201	1.1-9.7	321-638
Period 3	174	1-24	0-47	1-89	1.1-14.7	79-288
Dense 1983						
Period 1	129	1-40	0-75		1.1-50	1-309
Period 2	152	1-37	0-102		0.5-11.1	147-278
Period 3	121	1-27	0-76		1.1-18.4	6-253

Table 11. Weighted multiple regression results for mean numbers of pollen tubes per style (log-transformed). Signs of coefficients indicated before F-values. All probability values are estimates (see text).

Site Year	df	Independent variable: Flowers per plant	Flowers per 314 m^2	Nearest-mate distance	Seasonal flower density	Morph	R^2
		F values					
Sparse 1982							
Period 1	2,72			-14.45 ***		-22.49 ***	0.343 ***
Period 2	3,103		-11.64[L] ***	-3.53	+4.44 *		0.175 **
Sparse 1983							
Period 1	3,101			-23.76[L] ***	+6.31[L] *	-11.90 ***	0.339 ***
Period 2	3,97	-13.28 ***	-12.54 ***	-23.51 ***			0.358 ***
Period 3	3,98	-9.23[L] **		NE	+7.99[L] **	-3.38	0.220 ***
Dense 1982							
Period 1	2,212	-4.24[L] *		-22.00[L] ***	NE		0.120 ***
Period 2	3,194		-20.17[L] ***	-4.41 *		-10.98 **	0.132 ***
Period 3	4,169	+12.09 ***	-8.67[L] **		+19.75 ***	-23.10 ***	0.272 ***

Table 11--continued

Site	Year	df	Independent variable: Flowers per plant	Flowers per 314 m^2	Nearest-mate distance	Seasonal flower density	Morph	R^2
			F values					
Dense	1983							
	Period 1	5,123	-17.09 ***	-11.42 ***	-8.56 **	+42.35 ***	-9.42 **	0.410 ***
	Period 2[b]	5,146		+5.66 *	+0.30	+19.67[L] ***	-24.26 ***	0.307 ***
	Period 3	2,118	+3.87 *		NE	+7.87[L] **		0.195 ***
			Summary					
No. times H_0 rejected:								
	Positive relationship		2	1	0	7	0	
	Negative relationship		4	5	6	0	7	
No. of trials			11	11	9	10	11	

* $P < .05$, ** $P < .01$, *** $P < .001$.

[a] Number of conspecific flowers per 78 m^2 used in period 3, dense site, 1982.

[b] Model includes interaction term: Mate distance x Seasonal flower density, F = -9.63 **.

[L] Independent variable log-transformed.

NE Variable not evalutated for entry into model (see text).

As expected, the distance from the focal plant to the nearest compatible plant in flower was negatively correlated with pollen receipt (6 of 9 trials, Table 11). In other words, flowers with compatible pollen source nearby received more pollen. The effect of nearest-mate distance was important at the dense site, where potential mates were typically within a few meters, and at the sparse site, where pollen sources were often 30 m or more distant. Of the three measures of density, seasonal flower density was most consistently (7 of 10 trials) and, in general, most strongly correlated with the number of stylar pollen tubes. Local flower density and the central plant's display size each had effects on pollination in 6 of 11 trials, but the direction of the relationship varied; the amount of pollen received by flowers in dense patches was often lower but sometimes higher than that received by isolated flowers.

Does treating all same-morph stems within 1.5 meters as one plant bias the results? To answer this question I re-analyzed the data using mean pollen tube counts of styles from individual stems in the sparse plot (Table 12). Results from these analyses were qualitatively and quantitatively similar to those for multi-stem plants.

Dispersal of Powdered Dyes

All measures of the dispersal of powdered dye from donor flowers are characterized by high variation (Table 13). Little of this variation, however, is explained by the number of flowers on a plant or by seasonal changes in flower density (Table 14). No correlations between the measures of dye dispersal and the number of flowers on the

Table 12. Weighted multiple regression results for the sparse site as in Table 11, except numbers of pollen tubes per style averaged across each stem instead of each plant (see Methods).

Site	Year	df	Independent variable: Flowers per plant	Flowers per 314 m^2	Nearest-mate distance	Seasonal flower density	Morph	R^2
			F values					
Sparse	1982							
	Period 1	2,72			-12.66 ***		-18.55 ***	0.307 ***
	Period 2	3,102		-8.89[L] **	-4.58 *	+2.9		0.157 **
Sparse	1983							
	Period 1	3,101			-20.99[L] ***	+7.95[L] **	-12.65 ***	0.327 ***
	Period 2	3,97	-10.57 ***	-17.08 ***	-21.40 ***			0.357 ***
	Period 3	4,97	-9.06[L] **		8.39[L] **	-3.27[L]	-4.2 *	0.283 ***

* P < .05, ** P < .01, *** P < .001.

[L] Independent variable log-transformed.

Table 13. Measures of the dispersal of powdered dye. Dye was placed on the anthers of two donor flowers per experimental plant. See text for definitions of variables.

Variable	Sparse site 1982			Sparse site 1983			Dense site 1982			Dense site 1983		
	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
Number of flowers receiving dye	4.2	6.4	20	6.8	6.8	24				14.0	10.5	28
Number of plants receiving dye	1.6	1.4	20	2.3	1.9	24	0.20[a]	0.22	31	4.3	2.2	28
Plant sequence	3.4	2.1	14	3.7	2.5	21	0.43[a]	0.29	26	6.9	3.0	28
Dispersal distance	51.9	23.0	14	35.1	12.8	21	15.9	9.4	26	14.2	8.2	28

[a] Values were divided by the number of plants examined to standardize sampling procedure.

Table 14. Spearman rank correlation coefficients between measures of dye movement and floral display size, seasonal flower density, and hummingbird visit rates. Powdered dye was placed on two donor flowers per experimental plant.

	Sparse site 1982		Sparse site 1983		Dense site 1982		Dense site 1983	
	r_s	n	r_s	n	r_s	n	r_s	n
Correlations of the number of flowers on experimental plant with:								
No. flowers receiving dye	-.26	20	+.17	31	+.28	26	+.17	28
Plant sequence	-.02	14	+.13	21	+.25	26	-.05	28
Dispersal distance(m)	-.17	14	+.08	21	+.25	26	+.19	28
Correlations of seasonal flower density with:								
No. flowers receiving dye	+.14	19	+.50**	24	.00	31	+.27	28
Plant sequence	+.40	14	+.22	21	+.16	22	+.32	28
Dispersal distance(m)	+.40	14	-.04	21	+.07	22	+.20	28
Correlations of visit rate per flower with:								
No. flowers receiving dye	+.71***	17	+.44*	23	+.66***	22	+.53**	28
Plant sequence	+.36	13	+.22	21	+.46*	22	+.33	28
Dispersal distance(m)	+.28	13	+.14	21	+.38	22	+.28	28

* $P < .05$, ** $P < .01$, *** $P < .001$.

donor plant were significant, and given the mixture of positive and negative coefficients, no trends are apparent. As the density of surrounding compatible flowers increases over time, one might expect that pollen from a given source would 1) be dispersed to more target flowers, 2) be carried to more consecutive neighbors, and 3) assuming density-dependent foraging movements by pollinators, be transferred shorter distances. Correlations of seasonal flower density with the number of flowers receiving dye and with plant sequence are, in general, positive, but rarely significantly so. Dispersal distance was not clearly related to flower density in any of the four comparisons.

In contrast, all three expected relationships are confirmed in comparing mean values of dye dispersal variables among sites (Table 13). Dye was dispersed to approximately twice as many flowers and plants at the dense site as at the sparse site, while dispersal distances were 2 to 3 times greater at the sparse site. That differences between sites in dye movement are greater than seasonal differences at a single site is not surprising: the ten-fold difference in flower and plant density between the sparse and dense site is substantially larger than the range of densities over which I measured dye dispersal at each site. Inter-site differences must be interpreted with caution due to variation in sampling regimens. Despite differences among sites in the area and number of plants sampled, frequency distributions of dye receipt (Figure 8) indicate that, at least in 1983, the area I sampled for recipient flowers was sufficiently large to capture the majority of flowers that received dye. The proportion of flowers and plants receiving dye at the most distant sampling intervals was generally very low.

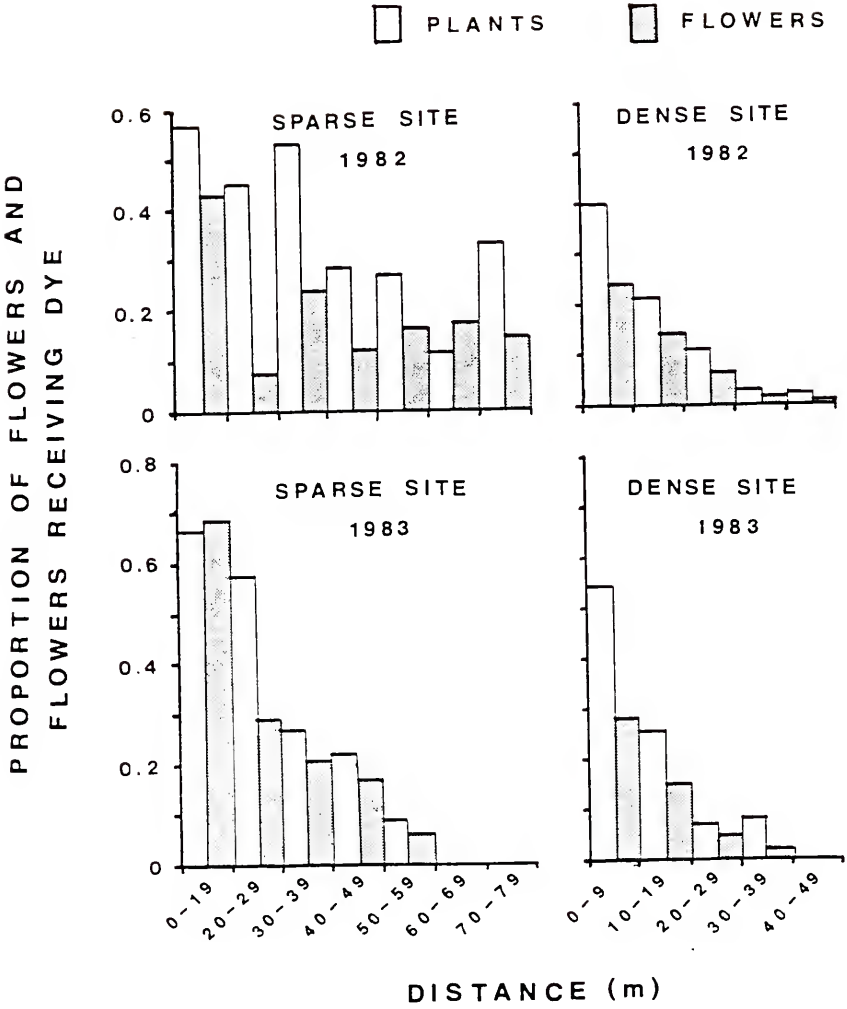

Figure 8. Proportion of compatible flowers and plants receiving powdered dye on the stigma from two donor flowers (see Table 13 for sample sizes).

The number of pollinator visits received by donor flowers had a strong effect on the dispersal of fluorescent dye (Table 14). In all four comparisons, dye reached significantly more compatible stigmas where visit rate was higher. Correlations of seasonal flower density with dispersal distance and plant sequence were also consistently positive, but usually not significantly so.

Lastly, dye dispersal per plant varied markedly with floral display size (Table 15). When dye was placed on the anthers of all the flowers of a plant, dye from plants with more flowers was transferred to more stigmas on plants spread over a wider area. This relationship was pronounced at the dense site each year but absent at the sparse site in 1983.

Table 15. Spearman rank correlation coefficients floral display size (number of donor flowers/plant) and measures of dye dispersal. Dye placed on the anthers of all open flowers of each experimental plant.

Variable	Sparse site 1982		Dense site 1982		Dense site 1983	
	r_s	n	r_s	n	r^s	n
Number of flowers receiving dye	+.04	22	+.63***	17	+.70***	18
Plant sequence	-.01	22	+.48*	16	+.55*	18
Dispersal distance(m)	.00	22	+.34	16	+.48*	18

* $p < .05$, ** $p < .01$, *** $p < .001$

DISCUSSION

Effect of Floral Display Size on Pollinator Behavior and Pollination Success

Two aspects of hummingbird behavior varied with the number of flowers on C. elata plants: visit rates to individual flowers and the numbers of flowers probed per plant during each hummingbird visit. Other studies have shown that visit frequencies to plants increase with the size of the floral display (Willson and Rathcke 1974, Willson and Bertin 1979, Wyatt 1980, Schemske 1980b). Visit rates to individual flowers may also increase with the number of flowers on a plant (Augspurger 1980, Geber 1985). In this study, hummingbird visit rates to flowers increased significantly with floral display size in field experiments (Figure 6), and in natural populations during one of the two years (Table 5).

For plants with large floral displays, the benefits of providing rich resources for pollinators has a potential disadvantage. The tendency of pollinators to visit many flowers at large floral displays, and to move less often between plants, may increase within-plant (geitonogamous) pollen transfer and result in reduced rates of outcrossing (Linhart 1973, Carpenter 1976, Feinsinger 1978, Augspurger 1980, Stephenson 1982). This reduction in visit quality with increasing numbers of flowers on a plant may select for an upper limit on floral display size, particularly for obligate outcrossers (Schemske 1980b,

Wyatt 1980). This argument may apply especially to hummingbird-pollinated plants: hummingbirds generally forage in a density-dependent manner, often probing many of the available flowers on a plant during each foraging trip (Stiles 1975, Feinsinger 1978, Schemske 1980b). In this study, at C. elata plants of all sizes, hummingbirds probed a large proportion, usually > 50%, of the flowers each visit (Table 6).

The extent to which outcrossing is limited by long pollinator foraging sequences at individual plants depends on pollen carryover. If all pollen picked up at a flower is deposited on the next flower--i.e., a carryover of 1.0--only pollen from the last flower visited on a plant could potentially cross-pollinate flowers on other plants. In carryover experiments with hummingbirds, I found that the median pollen grain was deposited on the first to sixth recipient flower, but that some pollen reached as far as the 14th consecutive thrum stigma and at least as far as the 20th pin stigma (Table 7). Such high variation in pollen deposition has been found in most studies of pollen carryover (Thomson and Plowright 1980, Waser and Price 1982, Lertzman and Gass 1983, Geber 1985). With the carryover values reported here, hummingbirds can effectively transfer pollen to and from C. elata plants with large floral displays despite long within-plant visit sequences. A bird arriving at a plant carrying compatible pollen, for instance, would typically deposit that pollen on 3 to 9 flowers during a foraging sequence of 20 flowers (Table 7).

The amount of pollen dispersed per flower from the plant, however, should be inversely related to the number of flowers probed per plant. In the carryover experiments, as the number of flowers probed per plant

increased from one to six flowers, the average number of pollen tubes attributed to each donor flower declined from 7.4 to 2.9 in pin flowers and 16.0 to 8.1 in thrums (Table 7). As the number of flowers probed per plant increases beyond six, average amounts of pollen donated and received per flower each visit probably continue to decrease. In summary, moderate pollen carryover in C. elata promotes outcrossing despite multiple-flower visits by pollinators to plants with many flowers, but visit effectiveness nonetheless drops markedly as intraplant pollinator flights to flowers increase relative to interplant flights.

Were differences in foraging behavior by hummingbirds at plants with many and few flowers reflected in pollination? In the field, the number of flowers on a plant had no effect on pollen donation per flower (Table 14) and often had no effect on pollen receipt (5 of 11 trials, Table 11). Occasionally, pollen receipt per flower was positively (2 of 11 trials) or negatively (4 of 11 trials) correlated with floral display size. These results imply that factors influencing pollination success are complex. Often, the advantage of large floral displays (pollinator attraction) may simply cancel out the disadvantage (sedentary pollinator behavior), resulting in no net effect of floral display size on pollination. Alternatively, pollen carryover may mask slight differences in pollinator behavior at many- and few-flowered plants. For a plant, the effects of displaying a given number of flowers may also shift seasonally. At times when pollinator visitation limits pollination and seed set, plants will compete for pollinator attention (Zimmerman 1980). Under these conditions, the greater attractiveness of

plants with large numbers of flowers to pollinators may result in a positive correlation between floral display size and pollination success of flowers. Alternatively, at peak flowering, sedentary behavior by pollinators at large floral displays may result in low rates of pollen flow among plants. If visit rates to flowers vary little with floral display size, which was often the case where plant density was high, pollen donation and receipt by flowers on few-flowered plants may be higher due to low levels of geitonogamous pollen flow. In any event, while pollination success of flowers often varies with the number of flowers on in C. elata plants, no single floral display size consistently receives better pollination service (Tables 11 and 14). In studying these same relationships, Geber (1985) found that despite subtle differences in visit patterns by bees to Mertensia plants of differing sizes, flowers on all plants received similar amounts of pollen from conspecifics and had similar reproductive outputs.

Reproductive performance in plants can be evaluated at the level of the plant, the inflorescence, or individual flowers. This study evaluates visitation and pollination per flower, and in doing so, provides a measure of the efficiency of pollination service to plants. The importance of the efficiency of resource utilization for reproduction should depend on the degree to which a plant is resource-limited. Located in forest understory, most C. elata plants appear to be strongly limited by light. Flower production, for example, clearly increases with the amount of available light, and plants growing in dense shade sometimes fail to flower altogether (Busby, personal observation; see also Schemske 1977, Motten et al. 1981, Campbell 1985).

Thus, the pollination success of individual flowers should be a biologically important measure for C. elata plants. For those plants located in treefall gaps or other high-light environments, however, reproductive efficiency may be less important than total reproductive output. Conditions in treefalls are generally favorable for plant reproduction (Linhart et al., in press). Cephaelis elata plants in forest gaps often flower profusely. High light availability is generally temporary, however, because the canopy closes over and light levels return to near pre-perturbation levels within a very few years (R. Lawton, personal communication). For these plants, the importance of maximizing short-term reproductive output may make pollination success of the plant a more appropriate measure than pollination success per flower.

Regardless of how individual flowers fared on plants of differing sizes, plants with many open flowers generally donated and received more compatible pollen than plants with few open flowers. The dye experiments showed that many-flowered plants dispersed their pollen not only to more compatible flowers but also to more plants and, in some cases, to greater distances (Table 15). It is not clear which of these measures--flowers, plants, or location of plants--is most directly related to male reproductive success (see Janzen 1977, Stephenson and Bertin 1983). In any event, all three were positively correlated. Pollen receipt per plant is simply the sum of the pollen received by individual flowers. Thus, unless pollen receipt per flower decreases sharply with increasing floral display size, plants with more flowers will receive greater total amounts of compatible pollen. At times when

pollination is not limiting to fruit set, potential fruit set per plant will simply be equal to the number of flowers produced by the plant.

Flower Density and Visitation

Optimal foraging theory predicts that pollinators should concentrate foraging efforts in rich patches of flowers (see Heinrich and Raven 1972, Pyke 1978, Heinrich 1979, Thomson 1981, Zimmerman 1981). While the positive effects of floral display size on flower visitation support the theory, effects of local flower density (the number of conspecific flowers within 10 m of the central plant) on visitation did not. Local flower density had little detectable effect on hummingbird visit rates to flowers (Table 5). The absence of an effect of local flower density is not surprising where plant density is high, pollinator flights short, and pollinator foraging behavior complicated by territoriality, as in the dense plot. However, in the sparse plot, where pollinators often had to traverse long distances between plants, theory predicts isolated plants should have received fewer visits than those in clumps. The lack of such an effect may be due to confounding effects of heterospecific flowers. Alternatively, hummingbird responses may be more closely keyed to resource dispersion on a larger scale. Thomson (1981) found that correlations between insect visitation and flower density varied markedly with spatial scale.

Over the course of the blooming season, hummingbird visit rates to flowers often tracked changes in seasonal flower density. In general, mid-season visit rates exceeded those earlier and later in the season (Figure 5). Increases in pollinator activity during seasonal peaks in

flowering have been shown for a number of plants (Zimmerman 1980, Thomson 1982, Schmitt 1983a, Motten 1986), but exceptions are not uncommon (Thomson 1982). In this study, the consistency of the correlation between flower density and visitation across 7 mo of flowering in 1983 demonstrated the extent to which floral resource levels of a single species can produce consistent pollinator responses in a complex community. On the other hand, the sudden decline in visit rates at mid-season the preceding year indicates that seasonal trends in pollinator visitation can be strongly influenced by other environmental factors.

One such factor affecting visitation to C. elata flowers was the availability of heterospecific flowers. At the sparse site, flowering by other hummingbird-pollinated species in the understory was positively correlated with seasonal changes in visit rates to C. elata flowers (Table 5). Circumstantial evidence suggests flowering by canopy species had just the opposite effect: hummingbirds abandoned territories in the understory to forage at rich nectar sources in the canopy. Such variable effects of heterospecifics on visitation are consistent with a model proposed by Thomson (1982, 1983). He suggests that as spatial intermingling of two species decreases, the effects on visitation switch from mutualistic to competitive. If spatial proximity does underlie these complex effects of pollinator-sharing species, their effect on visitation to C. elata flowers should vary among plants depending upon location. Consequently, only species that occupied different habitats or forest strata should have a consistent competitive relationship with C. elata in terms of visitation.

Effects of Neighbors on Pollination Success

For a self-incompatible plant the presence of flowering conspecifics is necessary for sexual reproduction. It is surprising, therefore, to find the density of surrounding conspecific flowers often (5 of 11 trials, Table 11) had a significant negative effect on pollen receipt by C. elata flowers. The explanation may lie in the distribution of pin and thrum plants. Spatial aggregation of morphs (Table 1) increases the chance that pollinator flights will be between stems of the same morph. Consequently, intramorphic pollen transfer should increase relative to legitimate pollen transfer, resulting in lower pollination of flowers in such clumps. This may be the cause underlying the negative correlations between local flower density and pollen receipt. Similarly, Price and Barrett (1984) proposed that legitimate pollination in tristylous Pontederia cordata is limited at some sites by spatial segregation of floral morphs in combination with density-dependent pollinator movements. Clumped distributions of morphs have been reported for several other heterostylous species as well (Levin and Kerster 1974, Wyatt and Hellwig 1979, Hicks et al. 1985, Nichols 1985). Additional evidence that the local distribution of morphs is important to pollination is provided by the effect of the distance to the nearest mate. As expected, the distance to the nearest compatible plant in flower was inversely related to pollen receipt by flowers in most cases (6 of 9 trials, Table 11). Only at times where pollination levels were extremely low or extremely high was mate distance non-significant. Although it is generally expected that the

distance to mates should affect pollination and reproductive success (Levin and Kerster 1974, Richards and Ibrahim 1978, Bawa 1983, Handel 1983), several studies have failed to detect an effect of the proximity of neighbors on pollen receipt (Bell 1985) or fruit set (Willson and Rathcke 1974; see also Keegan et al. 1979, Wyatt and Hellwig 1979).

Seasonal increases in flower density were often positively correlated with pollen receipt (7 of 10 trials, Table 11), but less often with pollen dispersal (1 of 4 trials, Table 14). Higher pollination rates at mid-season may be a function of 1) the generally high number of visits flowers received at such times, 2) the increased effectiveness of pollinator visits with increasing flower density, or 3) a combination of these two factors. I did not measure visit effectiveness, but the correspondence between visit rates and pollination levels over a wide range of values (Figure 5 and Table 14) suggests that visitation is an important factor in determining both male and female components of pollination success. The amount of variation in pollen donation from flowers explained by visit rate ranged from 19 to 50% (Table 14). In two other neotropical, hummingbird-pollinated plant species relationships between visitation and measures of female reproductive success were not strong. Hummingbird visitation was only weakly related to stigmatal pollen loads in Passiflora vitifolia (Snow 1982). Similarly, McDade and Davidar (1984) found the number of hummingbird visits received by Pavonia dasypetala flowers was not a good predictor of fruit set or seed set.

Territoriality and Pollination Success

Territorial hummingbirds restrict pollen flow by confining the bulk of foraging movements within the boundaries of defended feeding areas (Schlissing and Turpin 1971, Linhart 1973, Stiles 1975, Feinsinger 1978). A plant producing sufficient nectar to support a territorial hummingbird may encounter few opportunities for outcrossing due to sedentary pollinator behavior. This may set an effective upper limit on floral display size for self-incompatible plants dependent on hummingbirds for pollination (Stiles 1975, 1978, Feinsinger 1978, Schemske 1980b). Evidence presented here supports this idea. The floral displays of most plants were small. At peak flowering the average plant produced only 5 to 10 flowers each day. The most reproductively active plants I observed contained approximately 70 flowers. A floral display of this size produces an estimated 812 calories in nectar per day (based on 11.6 calories/flower·day; Busby, personal observation). Energy budgets of other territorial hummingbirds indicate that this is slightly less than the amount of nectar necessary to support a L. calolaema male (Hainesworth and Wolf 1972, MacMillen and Carpenter 1977, Ewald and Carpenter 1978). Assuming a territorial L. calolaema male requires 1160 calories per day, the nectar from several profusely-flowering plants or approximately 15 plants with average floral display sizes would be needed to support one bird. In the field, territories composed primarily of C. elata generally contained at least 15 plants.

How does the pollination service provided by territorialists compare with that of non-territorial hummingbirds? At the dense site,

where L. calolaema males defended territories through most of the flowering season, both maternal and paternal components of pollination success were consistently higher that at the sparse site where generalists pollinators predominated (Tables 8 and 13). I have no evidence, however, that territoriality per se affected pollination success either positively or negatively. In all likelihood, the cause of higher pollination levels at the dense site was the greater availability of mates associated with high flower density. Regardless, this study demonstrates that territorial hummingbirds can provide highly effective pollination service to obligately outbred plants.

Genetic Implications of Plant Density

Evidence suggests gene flow through both pollen and seeds is high. Dispersal of powdered dyes indicates that pollen is commonly transported 15 to 50 m by pollinators (Table 13). Frugivorous birds may carry seeds much further. Murray (1986) estimated bird-generated seed shadows of three understory shrub species at Monteverde and found median dispersal distances of 35 to 60 m. Some of the same bird species he studied also consume C. elata fruits (Wheelwright et al. 1984, Busby personal observation). The high mobility of pollen and seeds leads to the prediction that neighborhood area in C. elata is large.

Differences between sites in dye movement indicate flower density plays an important role in pollen flow. At the dense site, the average distance of pollen transport was lower than at the sparse site, but pollen was dispersed to more flowers on greater numbers of plants (Table 13). This increased interplant pollen exchange suggests the pollen

component of gene flow is greater at higher plant density despite shorter pollinator flights. Beattie (1976, 1978) found a similar relationship between plant spacing and pollen-mediated gene flow in Viola, and concluded that plants in high density colonies contained greater evolutionary flexibility (cf. Levin and Kerster 1969a).

In contrast to differences between sites, seasonal changes in pollen flow at each site were surprisingly modest. Neither the distance nor the amount of interplant pollen transfer was significantly related to seasonal fluctuations in flower density. A confounding factor was floral visit rate. Visitation, which was strongly tied to pollen dispersal itself (Table 14), generally rose with flower density and may have counteracted any effect of decreasing pollinator mobility on pollen dispersal during flowering peaks. Richards and Ibrahim (1978) point out that changes in visitation due to flower density bias calculations of genetic neighborhoods. Thus, while flower density clearly influences pollen flow, other factors that change seasonally in natural populations may complicate the density--pollination relationship.

Implications of Pollination for Reproductive Success

Considerable debate exists over the importance of pollination events for plant reproductive success (Stephenson 1981, Bawa and Beach 1981, Bierzychudek 1981, Willson and Burley 1983). Certainly, where numbers of pollen grains reaching stigmas are insufficient for fertilization of all ovules, pollination potentially limits seed set. In C. elata, substantial numbers of styles contained fewer than the two pollen tubes required for full seed set (Table 8). The proportion of

flowers receiving no compatible pollen varied among seasons from 14.4 to 76.7% for thrums and from 32.7 to 94.8% for pins. Because styles were collected prior to the end of flower life, pollen tube numbers reflect only pollination events of the first half of the day. The bulk of pollination should occur during this time: anthers dehisce about dawn, and both nectar secretion and pollinator visits are greater earlier than later in the day. In any event, failure to receive any compatible pollen limits potential reproductive success of many C. elata flowers to male function.

That pollination events influenced fecundity is supported by the fruit-set data (Table 9). During both years, pollen receipt and fruit set at the sparse site were lower than at the dense site. This indicates that pollination at the sparse site limited fruit set. Pollination may also have limited fruit set at the dense site where the proportion of flowers with stylar pollen tubes (Table 8) was not substantially greater than the proportion of flowers setting fruit (Table 9). Many factors other than pollination, however, are potentially important in determining fruit-set (Primack 1978, Stephenson 1980, 1981, Udovic 1981, Udovic and Aker 1981, Wiens 1984, Sutherland and Delph 1984).

While some flowers received no pollen, many others received pollen loads greatly exceeding the number of ovules. Furthermore, because pollen from a plant was often dispersed to many different neighbors (Table 13), it is likely that the reverse is true: pollen arriving at stigmas often came from different individuals. Growing evidence suggests that where large numbers of pollen grains from different

sporophytes reach the stigma, resulting seed fitness may be enhanced through pollen tube competition or maternal selection (Mulcahy and Mulcahy 1975, Mulcahy 1979, Schaal 1980, Bertin 1982, Marshall and Ellstrand 1985). Variation in pollen tube growth rates and the frequency of pollen arrival at stigmas (Busby, personal observation) indicate that competition among pollen grains for access to ovules may occur in some C. elata flowers . As a consequence, high pollen loads may result in improved seed quality (Stephenson and Winsor 1986).

The relationship between paternal pollination success and reproductive success as a male should depend on levels of pollen receipt. When the number of pollen grains reaching stigmas is less than the number of available ovules, every compatible pollen grain arriving at a stigma stands a good chance of fertilizing an ovule, and paternal reproductive success should be a linear function of the number of successfully dispersed pollen grains. Where pollen loads on stigmas are high, pollen grains will compete for access to ovules and factors such as the timing of pollen arrival at the stigma, pollen tube growth rate (Mulcahy et al. 1983), and genetic compatibility of the haploid genomes (Stephenson 1981, Stephenson and Bertin 1983, Wiens 1984) come increasingly into play. Few successfully dispersed grains will fertilize ovules when pollen loads are high. Consequently, male fitness per successfully-dispersed pollen grain should decrease, on average, as stigmatal pollen loads increase. Because pollen donation per flower tended to be highest exactly at times when pollen receipt was also high, the implications for reproductive success of high pollen donation may be limited. Extensive pollen dispersal by flowers under conditions of

heavy competition among males for ovules may enhance male fitness no more than moderate pollen dispersal at times when competition is weak. This being the case, male reproductive success may be just as high during times of low to moderate pollinator visitation (when pollen donation and receipt are lower) as at peak flowering (when pollen donation and receipt are higher).

Floral Display Size and Sexual Function

There has been considerable interest in the role of intersexual selection in the evolution of flowering characteristics of hermaphroditic plants (Janzen 1977, Charnov 1979, Willson 1979, Stephenson and Bertin 1983, Sutherland 1986). Among monoecious and dioecious plants, flowering by males and females may differ in timing, duration and intensity of flowering (Thomson and Barrett 1981, Bullock and Bawa 1981, Lloyd and Webb 1977; see Stephenson and Bertin 1983). Presumably due to the difficulties of quantifying pollen donation, little is known about how variation in flowering characteristics in bisexual plants affects both pollen donation and receipt. In this study, I found little evidence that floral display size or the seasonal timing of flower production affected pollen donation differently than pollen receipt. Floral display size had no consistent effect on maternal or paternal measures of pollination success of flowers (Tables 11 and 14). Pollen receipt was more often significantly related to the seasonal changes in flower density than was pollen donation, but this may be an artifact of the smaller sample sizes for pollen donation. The frequency of pollinator visits to flowers strongly influenced pollen

donation (Table 14), yet the same appears true for pollen receipt (Figure 5).

Is there evidence in C. elata of gender specialization in pin and thrum flowers? In other heterostylous species, differences among morphs have been observed in pollen loads on stigmas (Levin 1968, Ornduff 1970, 1975a,b, 1980, Ganders 1976, Barrett and Glover 1985), fruit set (Ganders 1975, Philipp and Schou 1982, Wyatt 1983, Hicks et al. 1985), and pollen donation (Nichols 1985). In this study, two different indices of reproductive success have contrasting implications for the relative gender of the two morphs. In pollen carryover experiments, hummingbirds transferred larger amounts of pollen to more recipient flowers from thrum donors than from pin donors (Figure 7 and Table 7). This implies that thrums function more as males and pins function more as females. However, thrum inflorescences had higher fruit set than pin inflorescences in 1983, indicating thrums were more successful as females than were pins. Unfortunately, the techniques used in this study for measuring pollen receipt and donation by flowers in the field were not designed to make intermorphic comparisons. Asymmetries among floral morphs in gender may be an important feature of the pollination system of C. elata, but additional studies are needed to address this topic.

Conclusions

Patterns of flower presentation can influence plant reproductive success through effects on pollinator foraging movements. Mass-flowering is frequently an effective means of recruiting large numbers

of pollinators to plants (Gentry 1974, Augspurger 1980, Frankie and Haber 1983), whereas extended flowering, the production of few flowers per day over long periods of time, is thought to maximize outcrossing (Janzen 1971, Frankie 1976, Bawa 1983). The problem of balancing attraction of pollinators with maintaining high rates of interplant pollen transfer appears to a central one for C. elata. In this study, visit frequency, closely tied to both male and female components of pollination success, was often highest during seasonal blooming peaks. Flowers on plants with many flowers also often received more hummingbird visits. Nevertheless, because of lower rates of legitimate pollen transfer, pollen receipt by flowers within large pin or thrum clumps was frequently lower than pollen receipt by isolated flowers. Thus, benefits of flowering in synchrony with the population were partly offset by negative effects of high local densities of unimorphic flowers. These results suggest that pollination service may well be highest at plants that do not present large numbers of flower per day, spread out flowering over time, yet still flower in phase with the population.

The optimal size of floral display in terms of pollination success may vary with the plant's resource state. Pollen donation and receipt per flower were often highest at plants that contained few flowers. This means that the small floral displays, typically produced by small or resource-poor plants, frequently receive the best pollination service per unit investment in flowers. Nevertheless, the pollination data suggest that over the range of floral display sizes monitored, the total number of embryos potentially sired or set is a monotonic increasing

function of the number of flowers produced. In other words, at a small cost in the "efficiency" of pollination, profusely flowering plants gain considerably in potential reproductive output. The drop in pollination efficiency on plants with many flowers might be offset by prolonging the flowering season and producing fewer flowers each day, as described above. Still, differences in resource availability among plants are likely to outweigh weak effects of floral display size on the pollination success of flowers.

In any event, it is questionable how finely tuned floral displays in C. elata can be. First, while the seasonal timing of flower initiation may have a genetic basis, size of floral display may be very plastic (cf. Primack 1980, Schmitt 1983b). It is also not clear what consequences differential pollination success has for plant fitness. Second, although this study documents frequent, and sometimes strong, density-dependent effects on pollen donation and receipt by plants, few of the independent variables I examined consistently affected pollination success. Often, the strength and even direction of relationships showed marked seasonal and annual variation. Any evolutionary consequences of such variable influences would be as likely to increase as to decrease the natural variation in the size and timing of floral displays. Existing flowering phenologies, where flowering by all plants is extended but the magnitude of flower production varies greatly among plants with available resources, may be in part a consequence of conflicting ecological events and selective pressures over space and time.

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BIOGRAPHICAL SKETCH

William Huntoon Busby was born in Santa Monica, California, on February 2, 1955. Fleeing the growing congestion and smoggy skies of the Los Angeles Basin early in his second year, he moved to northern California. In subsequent years, summers were passed hiking the trails of the Sierra Nevada; winters, learning New Math or running with the Tamalpais High School cross country team.

In 1973, Bill entered Colorado College. Despite unpleasant memories of mitochondria and DNA structure from high school, he found he enjoyed biology and majored in that field. Bachelor of Arts in hand, he spent two years studying peregrine falcons with the Colorado Division of Wildlife, teaching environmental science to 6th graders in coastal California, and painting houses.

In the fall of 1979, he began graduate studies at the University of Florida. After an Organization for Tropical Studies course in 1980, he became fascinated with tropical ecology. Two and a half years were spent in the cloud forest near Monteverde, Costa Rica, where he studied the pollination ecology of "hot lips" (Cephaelis elata). There he met his future wife, Anna Fortenbaugh. They were married in Bayhead, New Jersey, in 1986.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Peter Feinsinger, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John Ewel
Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Richard Kiltie
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1987

Dean, Graduate School