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Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering

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Summary. Genetic neighborhood size and area were estimated from pollinator movements over 3 years in a scarab beetle-pollinated clonal herb, *Dieffenbachia longispatha* (Araceae) at the La Selva Biological Station, Costa Rica. This species was characterized by low densities of reproductive individuals and asynchronous flowering within the population. The pollinator flight distributions were characterized by relatively long mean distances between consecutive visits to inflorescences (83 m) and movements to the nearest neighboring inflorescence in the appropriate phase of flowering. Pollinator movement distributions between consecutive visits to inflorescences were significantly leptokurtic in 2 of the 3 years. I calculated neighborhood sizes incorporating the levels of kurtosis and found minimal estimates of N_e to be 227–611 ramets and neighborhood area to be 88000–180000 m^2. The three beetle species that made 94% of the visits (*Cyclocephala gravis, C. amblyopsis,* and *Erioscelis columbica*) varied in their flight distributions and in their contributions to the estimates of neighborhood size. *Cyclocephala amblyopsis* exhibited the greatest degree of kurtosis in its movement patterns, and neighborhood size based on its movement was large relative to N_e calculated from movement distributions of the other two beetle species. Long-distance movements of *C. amblyopsis* (>300 m) accounted for 68% of the neighborhood size.

Key words: Genetic neighborhood size – *Dieffenbachia* – *Cyclocephala*

If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees any one of them repeated. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident.

Alfred Russell Wallace (1878)
Tropical Nature and Other Essays

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Low densities of many plant species, whether in the tropics or the temperate zone, will affect not only the species diversity, as Wallace noted, but also play an important role in determining genetic structure. The genetic structure of populations is influenced by the distribution of gene dispersal distances and the density of reproductive individuals (Wright 1943). A convenient measure of genetic structure is Wright's (1946) concept of genetic neighborhoods, the area in which random mating occurs. A neighborhood is defined as the circle within which there is a 85.6% probability of finding the parents of the central individual. In any plant population where densities of reproductive individuals are low, pollinators may move long distances and have a corresponding effect on the size of genetic neighborhoods. Currently, little is known about movement patterns of pollinators in the tropics (but see Linhart 1973; Frankie et al. 1976; Webb and Bawa 1983; Murawski and Gilbert 1986) or the effect of these patterns on neighborhood size of tropical plants. It is generally accepted that gene flow is highly restricted in most plant populations (Levin and Kerster 1974; Levin 1981), leading to adaptation and genetic differentiation on a local scale. In contrast, Ellstrand and Marshall (1985) present evidence for relatively frequent gene flow between widespread populations of wild radish.

I studied the pollination biology of a clonal neotropical herb, *Dieffenbachia* c.f. *longispatha* Engler and Krause (voucher no 2225, M. Grayum, DUKE) (Araceae), at the La Selva Biological Station in the Atlantic lowlands of Costa Rica. The species is characterized by low densities of reproductive individuals in a flowering season, inflorescences that are receptive as females for only 1 day, and a period of several days between flowering of inflorescences on a plant, resulting in very few inflorescences available for pollination each day. *Dieffenbachia* is pollinated by scarab beetles in the genera *Cyclocephala* and *Erioscelis* (Young 1986). In this paper, I estimate neighborhood size for *D. longispatha* from pollinator flight distributions and determine the effect of rare long-distance movements on this estimate.

Reproductive biology of *Dieffenbachia longispatha*

Dieffenbachia longispatha is an understory clonal herb of neotropical lowland rainforests. Each clone is loosely organized due to frequent breaking of the rhizomes from which ramets arise, so the extent of each clone is unknown. Each ramet of *D. longispatha* has from two to seven inflores-

cences that open at intervals of 3–10 days. Each inflorescence (spadix) has female flowers at the base and male flowers at the tip. The entire spadix is enclosed in a spathe until flowering begins. An inflorescence completes flowering in 3 days. The spathe opens in the evening and for the next 24 h the spadix has no sexually functioning parts. On the evening of the second day, the stigmas become receptive and floral odors are volatized by an increase in inflorescence temperature. Scarab beetles arrive at the inflorescence at 1820 h and they remain within the inflorescence for 24 h, eating staminodia that surround the female flowers, and mating. On the evening of the third day, as the male flowers begin to release pollen, beetles leave the inflorescence and, in doing so, become covered with pollen. Pollination takes place when pollen-bearing beetles fly to an inflorescence in female phase. By the time another inflorescence opens on a ramet, the previously open inflorescence has closed, thus preventing pollination between flowers on the same ramet. Detailed information on the pollination biology of this species is given in Young (1986).

Methods

Reproductive ramets of *D. longispatha* at the La Selva Biological Station in an area of 27400 m^2 were marked and mapped in 1982. In subsequent flowering seasons, additional reproductive ramets were marked and the census area was enlarged (1983: 50400 m^2; 1984: 70600 m^2). All inflorescences were checked daily during the 1982–1984 flowering seasons. Beetles found visiting inflorescences were marked with a unique series of notches on their elytra (Schatz, Young, and Goldwasser unpublished work). Of the 4843 beetles marked, about 15% were recaptured, either in inflorescences of *D. longispatha* or in inflorescences of the other 60 beetle-pollinated plant species at La Selva. Of those recaptures, 138 represented recaptures on consecutive days between inflorescences of *D. longispatha*. Because beetles remain within inflorescences for 24 h and they generally fly between inflorescences only in the evening, recapture locations on consecutive days were likely to represent direct flights between inflorescences. These recaptures were used to determine flight distances between consecutive visits to inflorescences and to estimate pollen flow distances. The density of flowering ramets was determined by dividing the number of reproductive ramets by the census area for each year.

I calculated neighborhood size (N_e, the number of individuals involved in random mating) and neighborhood area (A, the area of random mating) based only on gene flow by pollen. Although differences exist between the pollination "efficiency" of the three major beetle species (Young 1988), for the sake of simplicity, I assumed that all beetles carry equal amounts of pollen. I inferred pollen flow distance from pollinator movement distances. This assumption may lead to an underestimate of gene flow if pollen carryover is occurring (Schaal 1980; Levin 1981; Smyth and Hamrick 1987). Pollen carryover is unlikely to be important in this system due to low pollen viability after 24 h (the length of time beetles spend in inflorescences) (Young 1986). In the following calculations of N_e, I also assumed that there were no genotypic differences in pollen quantity or quality. This, too, may lead to erroneous conclusions (as mentioned in Harding and Tucker 1969; Schoen and Clegg 1985) because plants may differ in their male component of fitness in ways unpredicted from observations of pollinator movement.

Wright's original (1946) equation for N_e assumed a normal distribution of pollen dispersal distances. If pollinator flight distributions are leptokurtic (with more short- and long-distance flights than expected under a normal distribution), this equation will result in an over- or underestimate of N_e, respectively. The movement distributions of each beetle species and of all beetles for each year were tested for normality using PROC UNIVARIATE in SAS (1985). I tested for deviations from normality by dividing the kurtosis value by the standard error of the movement distributions and comparing it to the t-distribution (Sokal and Rohlf 1981). Incorporating the kurtosis value of the flight distributions, an estimate of N_e was calculated using the following equation (Wright 1977; Beattie and Culver 1979):

$$N_e = \frac{2^{2\alpha}(\Gamma(2\alpha+1)\Gamma(\alpha))}{\Gamma(3\alpha)}\,\pi\sigma^2 d$$

where σ^2 is the variance of dispersal distances (in this case, the variance in beetle movement distances), d is the "genetic effective density" (the density of reproductive ramets), and Γ is the gamma function. Alpha was estimated from the kurtosis value (γ) using the following equation (Wright 1969, equation 12.46):

$$\gamma + 3 = \frac{\Gamma(\alpha)\Gamma(5\alpha)}{(\Gamma(3\alpha))^2}.$$

Neighborhood area (A) is N_e divided by the density of reproductive ramets.

Results

The flowering season of *D. longispatha* extends from March to September. In any given year, few ramets had inflorescences and the total number of inflorescences open on each day was low. The number of inflorescences in female phase (Fig. 1) was even lower due to the temporally changing sex expression of each inflorescence. Most days were characterized by four or fewer inflorescences in female phase within the study area (range = 1.46 per ha in 1982 to 0.57 per ha in 1984), although on some days there were more than 20 (range = 7.30 per ha in 1982 to 2.86 per ha in 1984). The median number of inflorescences in female phase per day was 4 in 1982, 2 in 1983, and 3 in 1984. The density of flowering ramets changed daily and, consequently, so did the distance to the nearest female inflorescence.

Of the beetles recaptured on consecutive days, the majority flew to the nearest inflorescence in female phase within the study area (Fig. 2). The flight distances of the two most abundant *Cyclocephala* species (*C. gravis* and *C. amblyopsis*) were correlated with distance to the nearest female inflorescences (for *C. amblyopsis*, $r = 0.56$, $n = 49$, $p < 0.0001$; *C. gravis*, $r = 0.40$, $n = 68$, $p = 0.0008$) but the flight distances of *Erioscelis columbica* showed no significant relationship ($r = 0.37$, $n = 12$, $p = 0.23$). The absence of significance of the correlation coefficient for *E. columbica* may be partly attributed to the small number of recaptures of this species.

The mean distance moved by beetles on a single night was 83 m (S.E. = 12.80 m, $N = 138$) with a range of 1–529 m. One flight of 1350 m was observed between visits to *D. longispatha* (one of the plants visited was out of the study

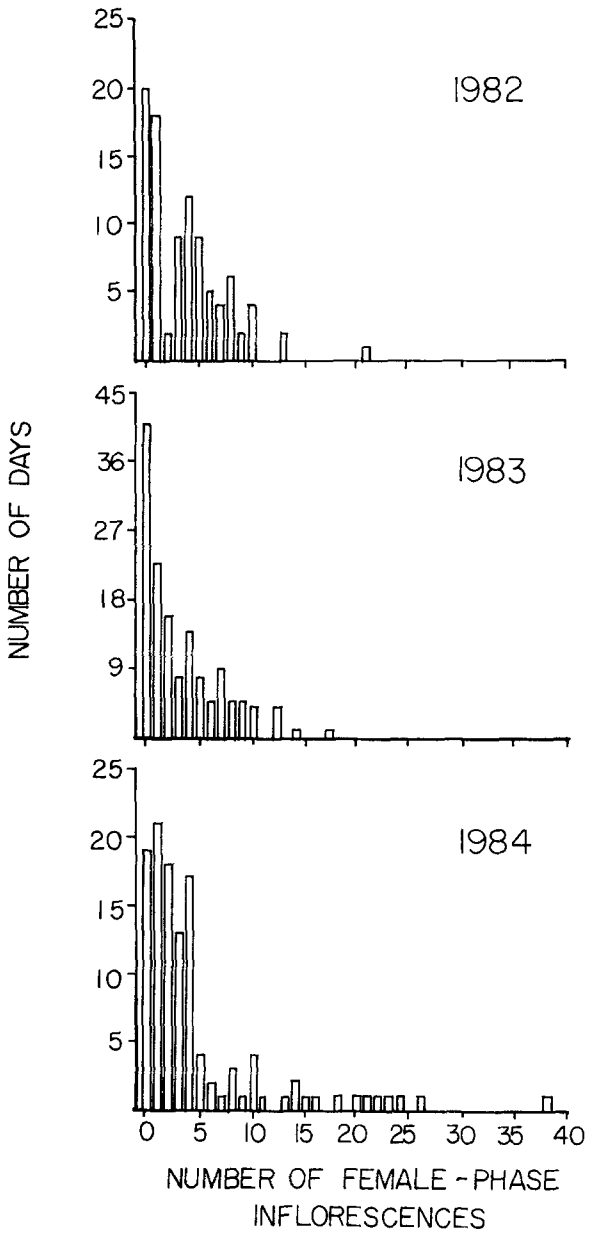

Fig. 1. Frequency distributions of the number of inflorescences in female phase for three flowering seasons (1982–1984). The total number of inflorescences in 1982 = 355; 1983 = 472; 1984 = 570

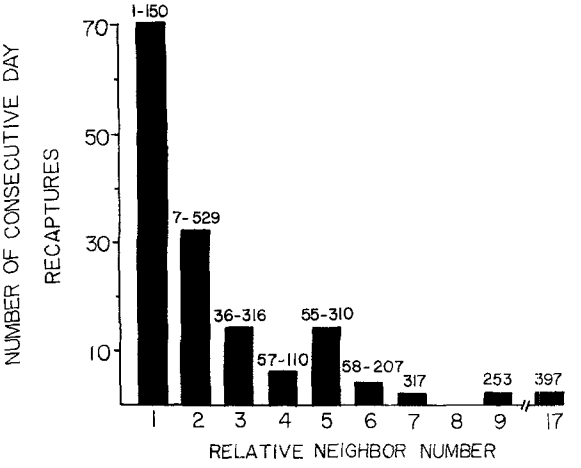

Fig. 2. Number of beetles recaptured on consecutive days at plants of differing distances from the central plant (neighbor 1 is the closest female-phase inflorescence to the inflorescence that the beetle departed from, neighbor 2 is the next closest, and so on). Ranges for movement distances (m) are given above each bar of the histogram

area). This flight distance was not included in the analysis above but it does demonstrate the existence of extremely long distance movements of these beetles.

Neighborhood size

I calculated N_e and A for 1982, 1983, and 1984 based on movement distances of all beetle species combined (Table 1). The density of flowering ramets, the level of kurtosis, and the variance of pollinator flight distributions varied among the three years. As a consequence of these differences, N_e varied greatly between years. The lowest value of N_e (227 ramets) was for 1983 (a year characterized by a small variance of pollinator movements and low densities of flowering ramets) and the highest value (611 ramets) was for 1984 (with large variance in movements of pollinators and a higher density of reproductive ramets).

Table 1. Neighborhood size (N_e) and neighborhood area (A) of *Dieffenbachia longispatha* for 3 years calculated using the kurtosis values (γ) of beetle movement distributions. N_e is based on pollen dispersal distances alone, inferred from pollinator flight distances. N is the number of 1-day beetle recaptures each year. P is the probability of significant kurtosis, using a t-test with standard errors given by Sokal and Rohlf (1981). The standard deviations of beetle movement distances are given (S.D.). Alpha (α) is calculated from values of kurtosis using equation in text

Year	N	Density (per m^2)	γ	P	α	S.D. (m)	N_e	A (m^2)
1982	15	0.0059	1.54	N.S.	0.802	85.9	556	94227
1983	99	0.0026	1.97	>0.99	0.867	82.8	227	87308
1984	24	0.0034	8.39	>0.99	1.449	124.4	611	179848

The three most common species of scarab beetles visiting *D. longispatha* had different flight distributions, as represented by the kurtosis values and the variance in movement distributions of each species (Fig. 3, Table 2). The flight distance distributions of *C. gravis* and *C. amblyopsis* exhibited significant leptokurtosis, whereas the movement distribution of *Erioscelis* showed no significant kurtosis. Although the shapes of the movement distributions of the three species appeared different, the variation was not statistically significant (ANOVA, $F = 2.29$, d.f. = 2,126, $p = 0.106$).

Calculating N_e on the basis of flight distributions of each beetle species separately showed that, despite the nonsignificant variation in flight distance among the species, they contributed to neighborhood sizes quite differently (Table 3). *Erioscelis* had flight distances that were normally distributed and, calculating N_e from its flight distances alone resulted in a value of 82 ramets. Neighborhood sizes based on the flight distances of the two *Cyclocephala* species were substantially larger (228 and 711 ramets). *C. amblyopsis* had flight distance patterns showing the most kurtosis, due to the long distance flights of this species, and the

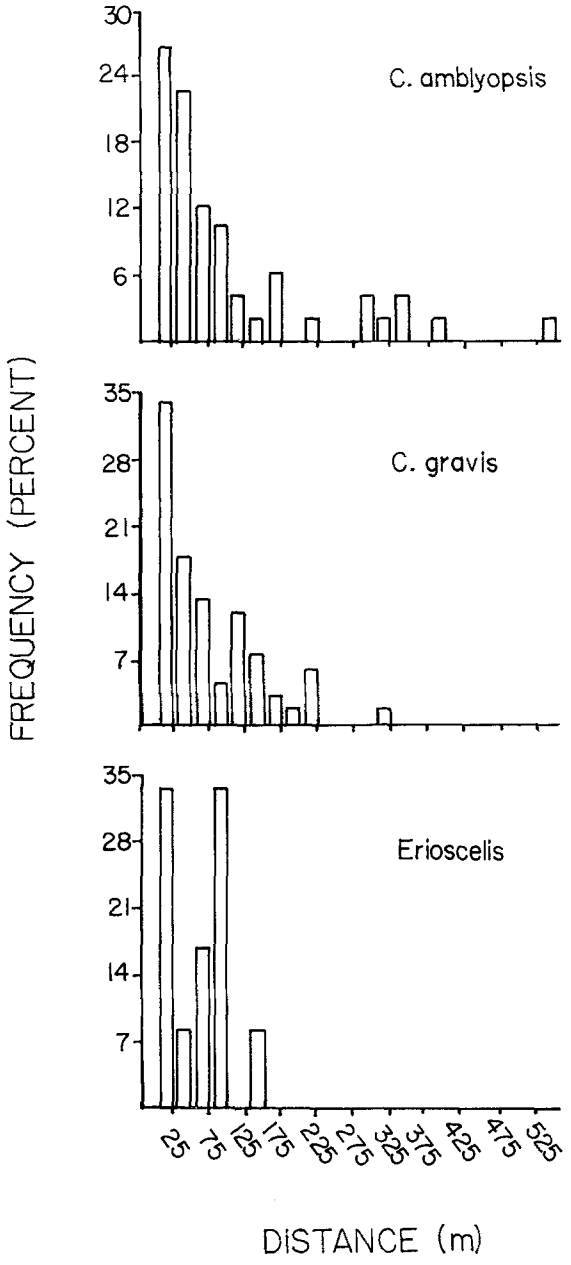

Fig. 3. Frequency distributions of flight distances of the three major pollinators of *Dieffenbachia longispatha* obtained from consecutive day recaptures. Each bar represents a 25 m distance class. $N=49$ for *Cyclocephala amblyopsis*; $N=68$ for *C. gravis*; $N=12$ for *Erioscelis*

result was a large contribution to neighborhood size and area.

How important are long distance movements of the pollinators to the genetic structure of this plant population? By removing the longest 5% of the beetle flights from the calculation of N_e (flights over 300 m), N_e was reduced by two-thirds for *C. amblyopsis* (from 711 to 229 ramets), reduced only slightly for *C. gravis* (from 228 to 182) and not at all for *Erioscelis* (this genus exhibited no flights over 300 m). Thus, the long distance flights made by *C. amblyopsis* and *C. gravis* accounted for 67.7% and 20.1% of the neighborhood size estimate, respectively.

Table 2. Parameters of flight distributions of scarab-beetles visiting *D. longispatha*. *P* (the probability of significant kurtosis) is determined as in Table 1

Species	*N*	Kurtosis	*P*	Range of flights (m)
Cyclocephala amblyopsis	49	3.13	>0.999	2.3–529.0
C. gravis	68	1.82	>0.99	1.4–317.0
Erioscelis	12	−0.96	N.S.	2.2–135.5

Table 3. Neighborhood size based on the movement distances of each beetle species alone, including the kurtosis value of the flight distribution of each. Alpha (α) is calculated from the value of kurtosis (see text). The mean density of reproductive ramets for the three flowering seasons (0.004/m^2) is used to calculate N_e and area

Species	Mean movement distance (m)	S.D. of movement distances (m)	α	N_e	Area (m^2)
Cyclocephala amblyopsis	101.9	119.0	1.015	711	177713
C. gravis	69.8	67.0	0.845	228	57108
Erioscelis	57.9	42.8	0.186	82	20601

Discussion

Unlike many temperate plant species whose flowering seasons are relatively short, and where individuals within a population are synchronous in their phenology, *Dieffenbachia* is characterized by a long flowering season, asynchronous flowering within the population, and a temporal separation of sexual functions, resulting in a low density of inflorescences available for visitation by pollinators. Consequences of this flowering behavior are long distance movements by beetles between visits to inflorescences and extensive potential pollen movement. Neighborhood sizes estimated here (230–610 ramets) are within the range of, or greater than, values of N_e reported for temperate herbaceous species (Levin and Kerster 1968; Beattie and Culver 1979; Schaal 1980; Schmitt 1980; Antlfinger 1982; Waser 1982; Zimmerman 1982; Tonsor 1985; Bos et al. 1986; Smyth and Hamrick 1987) and are of an order of magnitude such that random genetic differentiation (drift) is unlikely (Wright 1943). Neighborhood area of *D. longispatha* (9–18 ha), however, is several orders of magnitude larger than that reported for temperate species, due to the low density of reproductive ramets.

In a population of asynchronously flowering plants, the available mates for a plant on any day represent only a subset of the total number of plants it will mate with in a flowering season. Each day that its inflorescences are open, its potential mates will vary in number and identity. This same phenomenon occurs within the lifetimes of perennials that do not reproduce annually. The mates available in a flowering season may be a completely different set from those available in the subsequent or previous flower-

ing seasons. Over an individual's lifetime, it may have the chance to mate with nearly every plant in the population. A more accurate estimate of N_e will be obtained if the density of reproductive individuals includes all plants with which an individual could mate in its lifetime. Although *D. longispatha* individuals have a reproductive life of more than 3 years (Young, pers. obs.), I have calculated N_e based on the total number of flowering ramets in 1982–1984 within the area censused yearly (the area established in 1982): density = 0.0099/m^2, S.D. of total pollinator movements = 90.0 m, gamma = 5.24, alpha = 1.223; N_e = 995. This value of N_e is 63% larger than the largest value calculated in Table 1 (1984: N_e = 611). The relationship between N_e and the reproductive lifespan of a *Dieffenbachia* individual is represented by a decelerating curve, with N_e saturating when all possible mates within the population have flowered.

The three major beetle pollinators differ not only in their effect on female reproductive success of *Dieffenbachia* (Young 1988), but also in their relative contribution to neighborhood size. *Erioscelis* demonstrates few long distance flights and contributes less to estimates of N_e than the *Cyclocephala* species, paralleling the results of Zimmerman (1982) where differences in N_e between two herbaceous plants were found, due to the different patterns of flight distances of bumble bees visiting them. Neighborhood size in *Dieffenbachia* is likely to be strongly influenced by the relative abundance of each beetle species because each species demonstrates different flight distance distributions and each contributes differently to seed set (Young 1988). *Erioscelis* is the most abundant pollinator but carries the smallest quantity of pollen; *C. amblyopsis* is the least abundant pollinator but carries significantly more pollen than *Erioscelis*. N_e could be estimated more accurately by incorporating coefficients of beetle species abundance and contribution to seed set.

Admittedly, these estimates of N_e are based on a number of simplifying assumptions: I have not considered the effects of vegetative reproduction, seed dispersal, or self-fertilization on neighborhood size. The clonal structure of the populations of *D. longispatha* will reduce N_e because some of the pollinator flights may be between ramets of the same genotype. This is made less likely by the staggered flowering of ramets in the population. With a median of three inflorescences in female phase per day in a 70000 m^2 area, the probability that these represent inflorescences of the same genet is small. The average beetle movement distance of 83 m reduces the likelihood that pollen is travelling within a genet.

Seed dispersal is likely to be extensive as a result of removal by squirrels and understory birds (Young 1986). I have measured fruit removal rates of 12 infructescences and found that all fruits are actively dispersed (no fruits were found on the ground below the infructescences). Including seed dispersal would increase estimates of N_e substantially. I have also assumed that all seeds produced are the results of cross-pollination. Experimental evidence (from bagged inflorescences) demonstrates that self-pollination is rare in this species (Young 1986).

Lastly, I have ignored potential long distance pollen flow caused by beetles leaving the study area and visiting a *D. longispatha* inflorescence some distance away. Beetles do not always fly directly from one inflorescence to the nearest inflorescence in female phase of *D. longispatha,* as suggested by the low number of recaptures on consecutive days (2.8% of the total beetles marked). Because the three most common scarab visitors exhibit high floral constancy (82%–96% of all recaptures represent movements between conspecific plants; Schatz and Young, in prep.), it is likely that many of the 97.2% of marked beetles that I did not recapture on consecutive days flew to inflorescences of *D. longispatha* out of the study area. Due to the censored nature of these data, all estimates of neighborhood size based on 1-day movement distances are underestimates. Of these considerations, the last is likely to be the most important. Rare long-distance flights can dramatically affect genetic structure of populations (Antonovics 1968; Gillespie 1975). If long-distance flights are common (a condition met if beetles are moving to *D. longispatha* inflorescences outside of the study area), then N_e will be substantially larger than estimated above.

Long distance gene flow does not necessarily result from long distance pollinator movements if pollinators are consistently moving to the nearest neighbors (Slatkin 1985). Nearest neighbor pollinations and restricted seed dispersal will result in small neighborhood sizes, increased inbreeding and homozygosity, and substructuring of the population (Rohlf and Schnell 1971; Turner et al. 1982). This outcome is supported by estimates of small neighborhood sizes in plants that experience nearest neighbor pollination (Levin and Kerster 1968; Schmitt 1980), and in species that have low outcrossing rates (Schaal 1974, 1975; Ennos and Clegg 1982). Slatkin (1985) states that "true" long distance gene flow can only result if pollen carryover is common or if pollinators move beyond nearest neighbors. Yet *D. longispatha,* with its asynchronous flowering, experiences relatively large neighborhood sizes despite pollinator movements between nearest neighbors of the appropriate sexual phase. These beetles are exhibiting "nearest available neighbor" pollination: they are flying past a large number of reproductive, but not flowering, individuals in their search for a female-phase inflorescence. This flowering behavior is likely to result in low levels of geitonogamy, low levels of inbreeding, and large areas over which random mating occurs.

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