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SEX DIFFERENTIAL FLORAL LONGEVITY, NECTAR SECRETION, AND POLLINATOR FORAGING IN A PROTANDROUS SPECIES¹

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ABSTRACT

Sex differential nectar production, floral longevity and pollinator foraging were examined in *Lobelia cardinalis*, a self-compatible, protandrous species that is hummingbird pollinated. The staminate phase of the flowers lasts significantly longer and produces significantly more nectar (total sugar) per day than the pistillate phase of the flowers. Additional pollen is presented throughout the staminate phase.

Because inflorescences of *L. cardinalis* mature acropetally, the nectar reward on any given day is greatest at the top of the inflorescence (where staminate phase flowers are located). Hummingbirds appear to be sensitive to this pattern of nectar presentation as they most commonly began foraging in the middle of an inflorescence and proceeded upward. This foraging pattern tends to promote outcrossing and suggests that staminate phase flowers are visited more often than pistillate phase flowers. We conclude that *L. cardinalis* emphasizes the male function at anthesis. Others have hypothesized that the features of this species are a logical consequence of intrasexual selection, but further research is needed before we place great confidence in a sexual selection interpretation of our data.

PLANTS are often depicted as accumulating resources and allocating them to growth, maintenance, and reproduction (see Stearns, 1976; Harper, 1977; Horn, 1978; Evenson, 1983). In hermaphroditic plants, the resources allocated to reproduction are further partitioned between the male and female functions (Charnov, 1979; Willson, 1979; but see Lovett Doust and Harper, 1980). Recently, the allocation of resources to the male and female functions in hermaphroditic organisms has received much attention from experimentalists and theoreticians (Charnov, Maynard Smith and Bull, 1976; Maynard Smith, 1978; Smith and Evenson, 1978; Charnov, 1979; Lloyd, 1979; Lovett Doust and Harper, 1980; Vernet and Harper, 1980; Charlesworth and Charlesworth, 1981; Schoen, 1982; Lovett Doust and Cavers, 1982) because of its relevance to models pertaining to the evolution and cost of sexual reproduction (Williams, 1975; Maynard Smith, 1978; Lloyd, 1980), the evolution of dioecy (Charnov et al., 1976; Charlesworth and Charlesworth, 1978a, b, 1981; Ross, 1982) and the roles of

sexual selection in hermaphrodites (Charnov, 1979; Willson, 1979; Lloyd and Yates, 1982). In regard to the last topic, Charnov (1979) concluded that under the conditions of Bateman's (1948) principle (i.e., fruit and seed production is limited by resources, while reproduction through the male role is limited by access to the ovules of conspecifics), greater fecundity gains are possible through the male function (see also Willson, 1979). Consequently, hermaphroditic plants should evolve traits that increase the transfer of pollen to conspecific stigmas. That is, hermaphrodites should emphasize the male function at anthesis.

It has been suggested that the proportion of resources allocated to each sexual function reflects a plant's emphasis of the respective sexual functions (e.g., Lovett Doust and Cavers, 1982). A relatively straightforward method of examining resource partitioning at anthesis is to collect data on dry weight or inorganic nutrients contained in various floral structures. But, because plants are essentially immobile and commonly dependent upon animal vectors for pollination, other floral features besides dry weight, such as nectar production and the duration of each flower, may be important in the dissemination and reception of pollen. In perfect-flowered plants where both sexes are simultaneously present within a flower, it is difficult to assign the proportion of these traits (nectar production and floral longevity) devoted to each sexual function. However, many

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perfect-flowered plants exhibit dichogamy; that is, the staminate and pistillate phases are separated in time within the same flower. Consequently, dichogamous plants should provide insight into the allocation of nectar and time to the two sexual functions. Furthermore, in dichogamous species, it can be determined if sex differential nectar secretion or floral longevity influences pollinator foraging and thus promotes a particular sexual function.

We report here on a 3-yr study of *Lobelia cardinalis* L., a racemose species with protandrous flowers. Specifically, we asked four questions: 1) Is there a difference in duration between the staminate and pistillate phases in this species? 2) Is there a difference between the staminate and pistillate phases with respect to nectar secretion? 3) Is the pollinator, *Archilochus colubris* (ruby-throated hummingbird), influenced by any difference in nectar reward that might be found in the two sexual phases of the flowers? 4) Are multiple visits by the pollinator required to remove all of the pollen?

DESCRIPTION OF *LOBELIA CARDINALIS*—*Lobelia cardinalis* L., Lobeliaceae, is an herbaceous perennial that grows in shaded to open, wet sites throughout much of eastern North America (Gleason and Cronquist, 1963). In the autumn each plant produces one or more basal offshoots (rosettes) and overwinters in this state. During the spring and summer the rosettes elongate and eventually produce a single terminal racemose inflorescence of 2 to more than 50 flowers. The number of flowers per inflorescence is correlated with the height and diameter of the stem (unpubl. data). In central Pennsylvania, flowering commences in early August and terminates in mid-September. The inflorescence develops acropetally and the flowers are protandrous. Consequently, in mid-season, a typical raceme will have developing fruits, pistillate flowers, staminate flowers, and flower buds distributed in sequence from the basal to the terminal portion of the inflorescence.

The large, red, zygomorphic flowers of *L. cardinalis* are self-compatible (unpubl. data) and pollinated by hummingbirds (Baker, 1975; Bertin, 1982; Devlin and Stephenson, pers. observ.).

In these flowers, the style is enclosed in a tube formed by the fusion of the five filaments and anthers (anther tube). The anthers shed pollen internally into the distal portion of the tube and pollen is liberated through a ventral valve. A cluster of hairs (a brush) is found directly behind the valve and when these hairs

are pushed back, the valve opens and pollen is released. At the termination of the male phase, the style lengthens until it is exerted from the anther tube. After full extension of the style, the two stigmatic lobes reflex and are then receptive to pollen.

METHODS—All of the field work for this study was performed during the summers of 1980, 1981, and 1982 in a 1.5-ha area of open, wet deciduous forest approximately 5 km east of Alan Seger National Monument in Centre County, Pennsylvania. There are approximately 600 plants at this site.

To determine the duration of each sexual phase, ten plants were randomly selected in the population in 1980 and, in 1982, 24 plants were selected. Each day, from the beginning to the end of the flowering period, the position and sexual phase of each flower were recorded for each plant. Floral development was separated into six phases:

1. immature staminate = flowers recently open but not yielding pollen.
2. mature staminate = pollen present.
3. old staminate = no pollen; style elongating.
4. immature pistillate = stigma exerted but receptive surface not exposed.
5. mature pistillate = receptive surface open.
6. old pistillate = flower wilting.

The sugar content of *Lobelia cardinalis* nectar was examined and the nectar was found to contain mostly sucrose with smaller amounts of fructose and glucose (Devlin and Stephenson, unpubl. data). Because of the refractive index and the caloric value of fructose and glucose are approximately half that of sucrose, the nectar data are reported in terms of sucrose equivalents (henceforth total sugar) in milligrams (Hainsworth and Wolf, 1972). Also, the concentration of the nectar was adjusted from a weight : weight to a weight : volume ratio using a simple regression function (see Cruden, Hermann-Parker and Peterson, 1982). Some flowers produced very small quantities of nectar for which no measurement of concentration could be obtained. These were assigned a reasonable total sugar value of 0.015 mg.

To determine the pattern of nectar secretion as it relates to the location of the flowers within the inflorescence and their sexual phase, 15, 10, and 14 plants were selected in 1980, 1981, and 1982, respectively. In 1980 and 1981, the plants were randomly selected while in 1982 all plants were located in a 4-m² area. Twenty-four hours prior to the start of data collection all flowers were drained of nectar, each inflo-

rescence was enclosed in a cheesecloth bag to prevent hummingbird visitation and a thin stake was pushed into the ground near the plant to support the cheesecloth and prevent damage to flowers. Flowers were sampled in the late morning when most of the nectar for that day had been produced (Devlin and Stephenson, unpubl. data). Nectar was removed with a 5- μ l capillary tube, the quantity read to the nearest 0.5 μ l and the sugar concentration determined with a temperature compensated pocket refractometer. For each plant on each day, we recorded the position of the flower within the inflorescence (these are fixed positions where the lowest flower on the plant is 1, the next highest 2, etc.), the sexual phase (immature male to old female) and the quantity and concentration of nectar present. For a given day this procedure was performed on all open flowers on a plant and for each plant sampled that year.

The number of open flowers in a raceme changes throughout the flowering period and the number of open flowers on different racemes on a particular day is quite variable. To analyze sugar production within the raceme on a daily basis, we classified open flowers on a given day as belonging to the top, middle or bottom third of their inflorescence. Racemes with less than three flowers open on a given day were eliminated from this analysis. A mean total sugar production per day was then calculated for each third of the raceme. Finally, these data were examined for the following patterns:

T = Top third	M = Middle third	B = Bottom third
1. T > M > B	3. B > M > T	5. T > B > M
2. M > T > B	4. M > B > T	6. B > T > M

We interpret the first two patterns as showing apical emphasis, the middle two patterns as showing basal emphasis, and the last two patterns as showing no emphasis. Mean daily sugar production per third was tested for significant differences using the Bonferroni test for multiple pairwise comparisons within a one-way ANOVA (Neter and Wasserman, 1974).

To quantify the foraging pattern of hummingbirds on each inflorescence the following data were collected on five separate days in 1981 and in 1982. As a hummingbird foraged on an inflorescence, we recorded where it began (top, middle, bottom with respect to open flowers), the direction of movement (up, down, out (= left plant)) and whether or not it reversed its direction of movement after visiting one or

more flowers. We discontinued these observations after the bird had visited 30 inflorescences or after it left the site. On 19 days in 1982 (intermittently from 7 August to 8 September), we recorded the number of flowers visited per inflorescence. All observations of hummingbird foraging reported in this study were made during the first foraging period in the morning.

To quantify pollen production, 15 flowers were selected in 1982 and emptied of all pollen on each day from anthesis until stigma emergence. Pollen was collected by inserting the anther tube into a vial and brushing the hairs against the vial wall. A flower was determined to be empty of pollen when no pollen was shed when the hairs were brushed along a clear area on the vial wall. The pollen was then suspended in 25 μ l of a 0.1% solution of NaCl and counted using a Coulter counter (Model Z_B; 140 μ m diameter orifice). Five samples (0.5 μ l) were counted from each vial and the median value multiplied by 50 to obtain the number of pollen grains produced per day.

RESULTS—The immature staminate, old staminate, and immature pistillate phases of the flowers each lasted less than 1 day on average. Old pistillate phase flowers (wilting) lasted from one to several days. In 1980, the mature staminate phase of the flowers lasted 5.5 ± 1.8 day (mean \pm SD) which is significantly longer ($t = 11.5$; $df = 178$; $P < 0.0001$) than the mature pistillate phase (2.8 ± 1.3 day). In 1982, the duration of the mature staminate phase was 4.7 ± 2.0 day while the duration of the mature pistillate phase was 3.1 ± 1.5 day. Again, these differences are significant ($t = 9.6$; $df = 464$; $P < 0.0001$). A comparison across years reveals that the staminate phase was significantly longer in 1980 than in 1982 ($t = 3.3$; $df = 321$; $P < 0.0001$) but there were no significant differences in the pistillate phases ($t = 1.6$; $df = 321$; $P > 0.05$).

Differences in daily sugar production between mature staminate and mature pistillate phase flowers were found in all 3 years (see Table 1) with staminate flowers yielding substantially greater nectar rewards (Mann-Whitney U , $P < 0.0001$). The nectar data for 1981 and 1982 were also analyzed to determine if there was a relationship on a daily basis between the sugar reward per flower and the relative position of the open flowers on the raceme (1980 data are not reported because the inflorescences had a low number of open flowers per day). To standardize variable inflorescence size, the open flowers on a raceme were divided into thirds and the mean total sugar per third

TABLE 1. Mean daily nectar production in the male mature and female mature phases (mg total sugar) [$\bar{x} \pm SD$ (N)]

Year	Male mature phase	Female mature phase	P ^a
1980	0.88 \pm 0.96 (235)	0.49 \pm 0.65 (143)	<0.0001
1981	1.53 \pm 1.12 (445)	1.04 \pm 1.05 (144)	<0.0001
1982	0.88 \pm 0.86 (838)	0.29 \pm 0.57 (605)	<0.0001

^a Mann-Whitney *U* Test.

was then calculated. Table 2 presents the results. A pattern of decreasing nectar reward from the top to the bottom of the inflorescence ($T > M > B$) occurred most frequently in both years, and collectively it is most common to find higher nectar reward in the upper two-thirds of the inflorescence.

In both years there were differences in the total sugar produced per day by the flowers located in the top, middle, and bottom of the inflorescence (Table 3). The middle and top thirds of the inflorescence have significantly more sugar than the bottom third. In 1982, the top third had significantly more sugar in the open flowers than the middle third. In 1981 the same trend was apparent but the differences were not significant. These data reveal a pattern within the inflorescence in relation to the total sugar that is available to the pollinators.

Hummingbird foraging was observed many times during the 3 years of this study, but only in 1982 did we record the number of flowers visited per inflorescence and only in 1981 and 1982 did we attempt to quantify movements of birds within an inflorescence. There was a mean of 4.6 ± 2.3 ($N = 322$) flowers open per inflorescence on those inflorescences visited by hummingbirds during the 19 days of observation in 1982. It should be noted that all of the observations were made during the first foraging period of the day and that the obser-

vation days ranged from early to late in the flowering season. The data from these observations are summarized in Table 4. On 58% of the inflorescences that were foraged upon, a bird visited more than three quarters of the open flowers and on 80% of the inflorescences a bird visited more than half of the flowers.

The foraging movements of hummingbirds on inflorescences of *L. cardinalis* in 1981 and 1982 are summarized in Table 5. In both years, the first flowers visited in an inflorescence tended to be located in the middle third of the open flowers in an inflorescence. Because of the speed with which hummingbirds forage, it was often difficult to precisely assign a visit to the top, middle or bottom of an inflorescence (especially in borderline situations). Consequently, we present no statistical analysis of our best estimates of the location of first visitation. Over 90% of the time that a bird visited the bottom third of the inflorescence first, it foraged up the inflorescence. In the few instances in which a bird started to forage downward, it always reversed its direction and began to forage upward. The opposite pattern is true for a bird that visited one of the flowers near the top of the inflorescence first. That is, it usually foraged downward and in the few instances in which it began to forage upwards it always reversed its direction. When a bird first visited the middle of an inflorescence, it was significantly more likely to forage upward than down-

TABLE 2. Number of occurrences of each possible pattern of nectar production (total sugar) per day

Pattern	1981		1982	
	No. of occurrences	Freq.	No. of occurrences	Freq.
Apical emphasis ($T > M > B$) ($M > T > B$)	46 (27) (19)	0.66	218 (187) (31)	0.83
Basal emphasis ($B > M > T$) ($M > B > T$)	13 (5) (8)	0.18	16 (12) (4)	0.06
No emphasis ($T > B > M$) ($B > T > M$)	11 (10) (1)	0.16	29 (23) (6)	0.11
Total	70	1.00	263	1.00

TABLE 3. The total sugar secreted per flower per day by the open flowers in the bottom, middle, and top thirds of each inflorescence of *Lobelia cardinalis*. Mean \pm SD. Sample sizes: $N = 70$ in 1981; $N = 277$ in 1982

Inflorescence position	Year	
	1981 ^a	1982 ^{ab}
Bottom third	0.8 \pm .63 mg	.27 \pm .56 mg
Middle third	1.42 \pm .82 mg ^a	.54 \pm .77 mg ^a
Top third	1.56 \pm .83 mg ^a	.75 \pm .65 mg ^{ab}

^a One-way ANOVA, $F = 22.85$; $P < 0.0001$.

^{ab} One-way ANOVA, $F = 82.96$; $P < 0.001$.

^a Significantly greater than bottom third; Bonferroni Multiple Pairwise Comparisons with an overall $\alpha < 0.05$.

^b Significantly greater than middle third; Bonferroni Multiple Pairwise Comparisons with an overall $\alpha < 0.05$.

TABLE 4. Percent of open flowers visited per inflorescence. The data were collected by observing hummingbird foraging on 19 separate days from 7 August to 9 September 1982

No. of inflorescences (%)	% of open flowers visited per inflorescence			
	≤25	26–50	51–75	>75
	16 (5%)	47 (15%)	72 (22%)	187 (58%)

TABLE 5. Foraging movements of hummingbirds on inflorescences of *L. cardinalis*

Year	Location of first flower visited on the inflorescence	N (%)	Direction of movement from 1st flower	N (%)	No. of reversals in the direction of first movement (%)
1981	Top	28 (20)	Down	20 (71)	2 (10)
			Up	2 (7)	2 (100)
			Out	6 (22)	—
	Middle	75 (54)	Down	23 (31)	18 (77)
			Up	49 (65)	9 (19)
			Out	3 (4)	—
	Bottom	35 (26)	Down	1 (3)	1 (100)
			Up	32 (91)	2 (6)
			Out	2 (6)	—
1982	Top	15 (12)	Down	12 (80)	2 (13)
			Up	1 (7)	1 (100)
			Out	2 (13)	—
	Middle	69 (55)	Down	14 (20)	13 (93)
			Up	49 (71)	8 (16)
			Out	6 (9)	—
	Bottom	41 (33)	Down	2 (5)	2 (100)
			Up	38 (93)	3 (8)
			Out	1 (2)	—

ward ($\chi^2 = 9.38$; $df = 1$; $P < 0.005$ in 1981; $\chi^2 = 19.44$; $df = 1$; $P < 0.001$ in 1982). When a bird began to forage downward (from the middle of an inflorescence), it was significantly more likely to reverse its direction than a bird that first foraged upward ($\chi^2 = 24.10$; $df = 1$; $P < 0.001$ in 1981; $\chi^2 = 28.41$; $df = 1$; $P < 0.001$).

In summary, on an average day there are about five open flowers per inflorescence and most of the time a bird visits 50 to 100% of the open flowers on an inflorescence. In general a bird is most likely to begin foraging on the middle third of an inflorescence and to forage upward.

In the study in which all of the pollen was completely removed from the anther tube of mature male phase flowers, nine of the flowers produced appreciable amounts of pollen for 3 days and six of the flowers produced pollen for 4 days. The flowers produced an average of $120,154 \pm 25,791$ pollen grains over their lifetime. More pollen was produced on the second day of the mature staminate phase than on the other three days (Table 6). These data suggest that *L. cardinalis* produces and releases mature pollen into the anther tube over several con-

secutive days. Furthermore, in order to remove the pollen it was necessary to repeatedly stroke the hairs at the distal end of the anther tube. Consequently, it may take more than one visit to a flower to remove all of the pollen present in the anther tube on a given day.

DISCUSSION—Recently, Lloyd and Yates (1982) have argued that intrasexual selection (competition among potential pollen donors for access to the ovules of conspecifics) should lead “to the evolution of features which in-

TABLE 6. Mean daily pollen production of staminate phase flowers (anthesis until stigma emergence)

Day	Pollen quantity ^a	N
1	34,553 ± 31,748	15
2	57,313 ± 31,464 ^b	15
3	21,918 ± 15,919	15
4	16,175 ± 10,777	6

^a One-way ANOVA: $F = 5.95$; $P < 0.001$.
^b Significantly greater pollen production than days 1, 3, 4. Bonferroni Multiple Pairwise Comparison with an overall $\alpha < 0.05$.

crease the number of occasions during which pollinating agents can pick up pollen." For dichogamous flowers, they predicted that the staminate phase should last longer than the pistillate phase and that pollen should be presented in such a way that it is deposited onto pollinators over a number of visits. Others have suggested that staminate flowers on monoecious and dioecious species should secrete more nectar than pistillate flowers as a result of intrasexual selection (Bawa, 1980; Bullock and Bawa, 1981). The data presented here are consistent with these predictions generated by the male competition component of the theory of sexual selection. In *L. cardinalis*, the staminate phase of the flowers lasts significantly longer and secretes significantly more sugar per day than the pistillate phase of the flowers (Table 1). In addition, there are two floral features that may function to increase the number of floral visits that are necessary to remove all of the pollen. Because we had to repeatedly stroke the hairs at the distal end of the anther tube in order to empty all of the pollen it is unlikely that the pollinator, the ruby-throated hummingbird, would completely remove the pollen from an anther tube during a single visit. We have examined flowers after pollinator visitation and found pollen still present (Devlin and Stephenson, pers. observ.). Furthermore, *L. cardinalis* presents appreciable amounts of pollen over a 3–4-day period (Table 6). Consequently, even if a bird does remove all of the available pollen during a single visit, more pollen would be present on succeeding days.

It is of interest that the staminate phase on open-pollinated plants lasted 1 to 2 days longer than the staminate phase on the plants in which we manually removed the pollen. In another study, which will be reported in more detail elsewhere (Devlin and Stephenson, 1984), we described the factors that influence staminate and pistillate duration. In that study, we showed that staminate duration is inversely related to pollen removal from the anther tube and that 3–4 days can be viewed as the minimum duration of the staminate phase. Also, we determined that pistillate duration is shortened by pollination. In the present study, the duration of the staminate and pistillate phases falls between the minimum and maximum duration found in the study cited above. Consequently, we conclude that staminate and pistillate durations are controlled by pollinator foraging. In the previous study, we also showed that the pistillate duration of unpollinated flowers is less than the minimum staminate duration (Devlin and Stephenson, 1984). Furthermore, the durations cited above would oc-

cur in nature only if hummingbirds visited staminate phase flowers frequently but never (or rarely) visited pistillate phase flowers. Therefore, we conclude that there are consistent differences in the duration of the sexual phases in *L. cardinalis*.

The suggestion that plants can increase pollen donation by providing greater nectar rewards in staminate phase flowers assumes that the pollinators are sensitive to the variations in the rewards available among individual flowers. Consequently, we examined the relationship between the pattern of sugar secretion on inflorescences of *L. cardinalis* and the pattern of pollinator foraging. In both 1981 and 1982, the bottom third of the open flowers on an inflorescence secreted significantly less nectar than the flowers on the top of the inflorescence. In both years there was a tendency for total sugar secretion to be greater on the top third than on the middle third of the inflorescence, although only in 1982 were the differences significant (Table 3). In addition, the hummingbirds most frequently began foraging in the middle of an inflorescence and were significantly more likely to forage upward (Table 5). Consequently, the pollinators appear to be influenced by the pattern of nectar presentation as they most often foraged on that portion of the inflorescence that had consistently higher nectar rewards. This foraging pattern has two very important consequences. First, it would tend to promote outcrossing. The first flower visited on an inflorescence could be in either the staminate or pistillate phase depending upon the location of the first flower visited but later flowers visited on the inflorescence would be in the staminate phase. As a result, when a bird forages upward, either outcrossing occurs before additional pollen is picked up or merely staminate phase flowers are visited. However, because a few visits proceed downward, it is also reasonable to predict that pollen is occasionally transferred within an inflorescence. Second, the foraging pattern of the hummingbirds suggests that staminate phase flowers are visited more often than pistillate phase flowers. In addition, this outcome should be enhanced by the increased duration of the staminate phase.

From our data on the longevity of the flowers in each sexual phase, nectar secretion in each sexual phase and their effects on pollinator foraging, it is reasonable to conclude that, at anthesis, *L. cardinalis* emphasizes the male function. Moreover, it appears that this emphasis influences pollen dissemination. Most empirical studies of the allocation of resources to the sexual functions at anthesis have examined dry

weight or inorganic nutrients (Smith and Even-son, 1978; Lovett Doust and Harper, 1980; Lovett Doust and Cavers, 1982; Schoen, 1982; Bookman, 1983). Typically, resource allocation to the male function is greater than the female function at anthesis. For example, Lovett Doust and Harper (1980) found that in *Smyrniolum olusatrum* dry matter allocation to the male function at anthesis was 1.5 times greater than to the female function. Our findings, which focus on energy allocation in the form of time and nectar, further accentuate the male emphasis. Also, our data indicate a possible problem with dry weight or inorganic nutrient analyses. Because these measurements are, in a sense, instantaneous and because both pollen and nectar production occur throughout the duration of the staminate phase in *L. cardinalis*, any instantaneous measurement is likely to underestimate allocation to the male function.

Although the data we have obtained are consistent with the predictions generated by the theory of sexual selection (Bawa, 1980; Bullock and Bawa, 1981; Lloyd and Yates, 1982), we are not altogether convinced that the reproductive features of *L. cardinalis* discussed in this paper are the consequences of sexual selection. Additional types of data are warranted. First, in order for sexual selection to operate in hermaphroditic plants, fruit and seed production must be limited by resources rather than pollination (see Bateman, 1948; Charnov, 1979; Willson, 1979). Because pollen transfer is mediated by an external agent, resource limited fruit and seed production cannot be assumed (see Bierzychudek, 1981 and references therein). Second, if sexual selection is influencing the evolution of male reproductive traits in *L. cardinalis*, the variance in the number of offspring sired by the individuals in a population should exceed the variance in the number of seeds produced (Bateman, 1948; Wade, 1979; Wade and Arnold, 1980; Bertin and Stephenson, 1983). In highly self-fertilizing species there would be little opportunity for sexual selection (variance in the sexual functions would be equal) but the opportunities for sexual selection would increase with an increasing level of outcrossing (Stephenson and Bertin, 1983). Because *L. cardinalis* is self-compatible and because our data indicate that some geitonogamous pollinations do occur, there may be an a priori reason to question the intensity of sexual selection on this species. Whether or not sexual selection has been a potent force in the evolution of reproductive traits in *L. cardinalis* (or any other species) awaits further study.

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