

## REPRODUCTIVE SYNCHRONY OF A TROPICAL SHRUB: EXPERIMENTAL STUDIES ON EFFECTS OF POLLINATORS AND SEED PREDATORS ON *HYBANTHUS PRUNIFOLIUS* (VIOLACEAE)<sup>1</sup>

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**Abstract.** This study compares reproductive success of individual plants flowering and fruiting in and out of synchrony with the population. I test the hypotheses that reproductive synchrony enhances a plant's ability to: (1) attract pollinators, and (2) avoid seed predators. The prediction is that an individual in synchrony with its population has higher fruit and ovule set after pollination and has more seeds at dispersal time than an individual out of synchrony.

The test species is *Hybanthus prunifolius* (Schult.) Schulze (Violaceae), a shrub on Barro Colorado Island, Panama. It normally flowers in response to a heavy rain that interrupts a drought in the dry season. An individual produces most of its flowers on a single day. The flowers are self-compatible, but require animal vectors to effect any pollination. To test hypotheses (1) and (2) I used water sprinklers to induce individual plants to flower prior to the normal triggering rain, thereby creating a highly asynchronous population which flowered before the natural population. Peak flowering day for individuals in the experimental asynchronous population spanned 35 d; the natural population spanned 4 d. Measurements included pollination success (ovule and fruit set) due primarily to the social bee *Melipona interrupta*, occupation of fruits by microlepidopteran larvae (Cosmopteriscidae) and dipteran larvae (Lonchaeidae, *Silba* sp.), and final reproductive output (number of mature fruits and seeds).

Individuals in all size categories in the natural synchronous population matured a greater number of seeds than individuals in the asynchronous population. Mean number of mature seeds per individual was 658 in the synchronous population; it was 62 mature seeds per individual in the asynchronous population.

The large difference in seed output occurred primarily because individuals in the synchronous population had greater pollination success than individuals in the asynchronous population (86% vs. 58% fruit set; 78% vs. 40% ovule set). In contrast, fruit infestation by microlepidopteran larvae was greater among individuals in the asynchronous population than in the synchronous population (11% vs. 5%). The combined effects of pollinators and seed predators were thus additive and produced intense selection against temporally isolated individuals.

Similarly low seed output was occasionally observed for the few nonexperimental plants that flowered in response to a light rain during the dry season. Such individuals had lower levels of pollination and mature fruit production than plants that flowered when all others in the entire forest were in flower. The effect of space was similar to that of time. During the natural synchronous flowering period, individuals in sites of low spatial density attracted fewer pollinators and incurred more predation than individuals in sites with high density.

An evolutionary interpretation of these results is that stabilizing selection by both pollinators and seed predators maintains the present low variance in the timing of flowering and fruiting within *Hybanthus prunifolius* populations. Such effects may have been causal in the past in forging the origin of reproductive synchrony in plant populations.

**Key words:** *Cosmopteriscidae*; *Hybanthus prunifolius*; *Melipona interrupta*; Panama; phenology; pollination; reproductive synchrony; seed predation; *Silba* sp.; stabilizing selection; tropical.

### INTRODUCTION

An obligately outbreeding plant must flower with conspecifics for successful reproduction. Indeed, many species, regardless of their breeding systems, have high degrees of flowering synchrony. Several researchers mention the potential for outcrossing as the selective force giving rise to such synchrony, or as the

outcome of such synchrony (Holtum 1954, Moore and Lewis 1965, Whitehead 1969, Stern and Roche 1974, Ashton 1975, Opler et al. 1976). The potential for outcrossing certainly is a result of synchrony, but it need not be a determining selective factor.

Other selective forces proposed for the evolution of flowering synchrony include: isolating mechanisms (Smith 1926, Grant 1949), energetics of pollinators (Heinrich and Raven 1972), and pollinator attraction and seed predator avoidance (Beattie et al. 1973). In fact, no experimental study of the reproductive consequences of flowering synchrony and the selective

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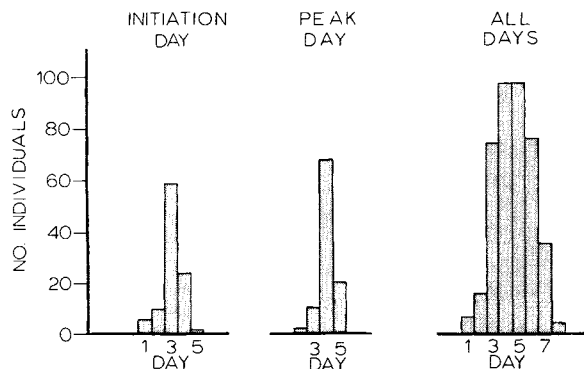


FIG. 1. Frequency distribution of timing of flowering among individuals in natural populations in 1976. Data are combined from five sites ( $n = 93$ ). "Day" for all three histograms refers to the same calendar day. Day 4 is 19 April, the day with the largest number of flowers in the entire forest.

factors influencing synchrony has been previously reported for a natural plant population. In contrast, reproductive synchrony of animal populations has received more attention (Kruuk 1964, Lloyd and Dybas 1966, Dauphine and McClure 1974, Emlen and Demong 1975, Parsons 1975, Estes 1976, Hoagland and Sherman 1976). These studies emphasize the selective roles of predation and social facilitation of mating and feeding of young in giving rise to reproductive synchrony.

Selander (1970) stressed that we know almost nothing about the actual importance of population structure on the evolution of natural populations. Fisher (1958) and Williams (1975) suggested that the individual's reproductive success depends largely upon population structure. In this study I examined the role of the population's temporal structure on the individual's reproductive success.

I experimentally tested two hypotheses:

- 1) Greater synchrony of flowering with the population increases the ability of the individual plant to attract pollinators (Corner 1940, Faegri and van der Pijl 1966, Opler et al. 1976).
- 2) Greater synchrony of fruiting with the population reduces damage to an individual's fruits and seeds by seed predators because the population satiates the seed predators (Darling 1938, Smith 1970, Janzen 1971).

Rejection of these hypotheses requires a demonstration that individuals temporally isolated from the population do not have a higher number of fruits damaged due to predation and do not set a lower number of fruits due to pollination than individuals in synchrony with the population. If both hypotheses are operating concurrently, then pollinators and seed predators act as additive selective forces, both favoring the individual in synchrony with the population. Both hypotheses predict a lower quantitative re-

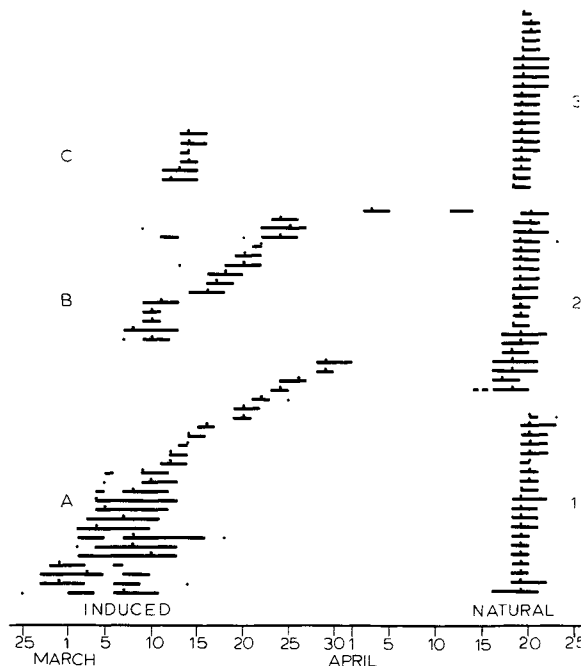


FIG. 2. Time of flowering of individuals in induced asynchronous "population" (A and B) and natural synchronous "population" (1, 2, 3 represent 3 of 4 sites monitored). Individuals in the induced synchronous population (C) serve as a control for differences in timing and location between the other two populations. Each horizontal line indicates the length of time an individual was in flower. A dot level with a horizontal line indicates an isolated day with flowers, but with no flowers on preceding or subsequent days. A dot above each line equals the day of peak number of flowers.

productive success among individuals not in synchrony with the population.

To test the hypotheses, I sought a plant species with two characteristics: (1) populations exhibiting a high degree of synchrony with respect to the day of onset of flowering; (2) potential for experimental control of timing of flowering of individuals in a natural forest. I planned to increase the variance in timing experimentally and to produce flowering individuals temporally isolated from other flowering conspecifics. Having experimentally created a highly asynchronous population, I would then compare the ability of the individual to attract pollinators and to avoid seed predators when flowering relatively alone vs. with the population.

#### STUDY SITE AND NATURAL HISTORY OF THE PLANT SPECIES

The study took place in the dry seasons of 1975 and 1976 on Barro Colorado Island (BCI), Panama, a wildlife preserve in Gatun Lake administered by the Smithsonian Tropical Research Institute. Details of the semideciduous lowland forest are described elsewhere (Leigh and Smythe 1978, Leigh et al., *in press*).

TABLE 1. Comparisons of spatial patterns and heights of reproductive individuals in nonexperimental and experimental areas. Values represent means, followed by standard deviations in parentheses.

	Nearest neighbor distance (m)*	Density of reproductives†	Height (m)	Sample size
Nonexperimental area				
Site 1	1.8 (0.8)	6.4	2.7 (0.7)	22
Site 2	1.9 (0.8)	8.0	2.6 (0.5)	31
Site 3	2.8 (1.4)	4.9	2.4 (0.6)	26
Site 4	2.3 (0.7)	6.3	2.7 (0.8)	20
Site 5	4.9 (7.0)	0.9	2.2 (0.5)	17
Total (1–5)	2.6 (2.9)	3.8	2.5 (0.6)	116
Total (1–4 only)‡	2.2 (1.0)	6.6	2.6 (0.6)	99
Experimental area				
Site A§	2.3 (1.6)	4.4	2.9 (0.8)	67
Site B§	2.6 (1.5)	4.9	2.7 (0.7)	41
Site C¹	2.5 (2.5)	6.1	2.5 (0.6)	6
Total (A–C)	2.4 (1.7)	4.5	2.5 (0.8)	114

\* Distance from reproductive individual to its nearest reproductive neighbor.

† Number per 10 m<sup>2</sup>.

‡ Sites 1–4 contain natural synchronous population.

§ Sites A + B contain induced asynchronous population.

¹ Site C contains induced synchronous population.

The test species was *Hybanthus prunifolius* (Schult.) Schulze (Violaceae), a common understory shrub restricted to lowland wet tropical forests of Costa Rica, Panama, Columbia, and Venezuela (Robyns 1967). Details of the floral biology of the species are described elsewhere (Augsburger 1980). The flowers are self-compatible, but no pollination occurs without visitation by insect pollinators. Therefore observations of fruit and ovule set directly reflect pollinator activity.

Three temporal and spatial characteristics of the shrub contribute to its production of a very brief but highly abundant floral resource. First, the individual shrub has a high degree of flowering synchrony. Although total flower production of a shrub averages 226 flowers (SD = 199,  $n = 87$  individuals with more than 25 flowers), 62% of those flowers are open on 1 peak d. A flower lasts 1 d, and an individual shrub produces flowers for an average of 4.2 d (SD = 1.0,  $n = 87$ ).

Second, the local population has a high degree of flowering synchrony, with the majority of individuals initiating flowering on 1 common d (Fig. 1). "Local population" refers to reproductive individuals sampled in a specific study site (see Methods). The mean variance in timing of peak day of flowering among 20 individuals in a local population is very low (SD = 0.83 d,  $n = 8$ ). The local population is in flower for an average of 6.5 d (range = 5–8,  $n = 9$ ). Because minor variance in timing of flowering occurs from one site on the island to another (Fig. 2), there are some flowers on the island as a whole for 8–10 d ( $n = 2$  yr).

Third, the population occurs in high spatial density. Spatially isolated individuals are rare. The mean distance from one reproductive individual to its nearest reproductive neighbor is 2.6 m (SD = 2.9,  $n = 116$ ).

The flower buds of *H. prunifolius* are formed in the wet season. Flowering occurs in the following dry season and begins 6–7 d after a heavy rain subsequent to a period of drought (see Augspurger 1982 for experimental results of cue requirements of *H. prunifolius*). Such a triggering rain can occur any time from January to May. In the experimental year of 1976, the rain occurred on 10 April.

#### METHODS

Four populations of *Hybanthus prunifolius* were selected in different areas of the forest. Sites with comparable spatial density were chosen to eliminate effects of variation in space on attraction of pollinators and seed predators (Table 1). Mean area sampled at these four widely separated populations (sites 1–4) was 1152 m<sup>2</sup>. The actual population at each site extends beyond the sampled individuals. A fifth site (site 5) was chosen because of its low spatial density (Table 1).

Prior to flowering, 20–30 individuals of reproductive size (1–4 m tall) were selected at each study site. Individuals were selected to provide a wide range of crown diameters. Only individuals with >25 flowers were ultimately used in the analysis. When making comparisons with individuals experimentally induced to flower (see below), individuals at sites 1–4 were lumped and comprised the natural synchronous "population" ( $n = 87$ ) (Fig. 2).

To create the highly asynchronous population, I selected plants in two additional sites (A and B) which are adjacent to one another in the forest, but separated by a large ravine. These two experimental sites are not contiguous with sites 1–4, which are scattered at various locations across the island.

TABLE 2. Comparison of number of flowers per individual in experimental and nonexperimental areas, in asynchronous and synchronous populations, and in high and low spatial density sites.

		Mean	SD	Range	N
Experimental area					
A + B	Induced asynchronous	187	212	25–709	41
C	Induced synchronous	483	450	25–997	6
D	Natural synchronous, low density	248	243	34–891	11
Subset of A + B compared with C					
		375	212	92–709	12
Total (A–D)					
		228	259	25–997	58
Nonexperimental area					
Sites 1–4	Natural synchronous, high density	226	199	25–1188	87
Site 5	Natural synchronous, low density	92	67	25–217	8
Other					
Sites 5 + D	Natural synchronous, low density	182	205	25–891	19

From mid-February onward, I could experimentally induce flowering in an individual either by pointing a water sprinkler directly at the ground at the base of the trunk for as little as 5 min, or by misting the entire foliage of the plant. For consistency, and for more direct simulation of the natural rains, I chose to sprinkle the entire foliage for a 7-h period. This long a period resulted in the soil becoming fully saturated and ensured adequate soil moisture for subsequent flowering and fruit development. A plant began to flower 5–6 d after sprinkling.

Sprinkling plants appeared adequately to mimic a natural rain. Sprinkling for 7 h raised soil mass due to moisture by 7–10% ( $n = 4$ ). Soil before sprinkling was 28% water by mass (range = 26–30% for four sites); after sprinkling it was 37% water by mass (range = 36–39% for four sites). The soil before the 10 April rain of 40 mm that induced natural flowering was 27% water by mass (range = 23–32% for six sites); after the rain it was 32% water by mass (range = 30–37% for six sites). Development of flowers and fruits on sprinkled individuals showed no apparent differences with individuals naturally triggered to flower. Nectar production sampled every hour from 0630–1730 was similar in both types of plants (natural: mean =  $8.4 \mu\text{L} \cdot \text{flower}^{-1} \cdot \text{d}^{-1}$ , SD = 2.1,  $n = 9$ ; induced: mean =  $7.8 \mu\text{L} \cdot \text{flower}^{-1} \cdot \text{d}^{-1}$ , SD = 2.4,  $n = 11$ ).

From late February to early April 1976, I induced plants to flower with the use of sprinklers. This group of 41 plants comprised the induced asynchronous "population" (Fig. 2A and B). The peak flowering days of these individuals spanned 35 d; there was almost no overlap of peak days of individual plants. On any one day a maximum of three plants had coincident flowering peaks. Coincident individuals were chosen

so as to be >30 m apart. Most temporal overlap that occurred represented a very low number of flowers.

It was necessary to test for underlying differences, other than degree of synchrony, between the plants in the experimental area (Sites A and B) and in the nonexperimental area (sites 1–4). Plants in the two areas were similar in these aspects: (1) density (Table 1); (2) distance to nearest reproductive neighbor (Table 1); (3) height (Table 1); (4) number of flowers per individual (but see below) (Table 2); and (5) nectar production (see above). The first four comparisons were made using all reproductive individuals in the experimental area, and were not restricted to individuals subsampled for inclusion in the induced flowering treatment. These fundamental similarities make it likely that differences in fruit, ovule, and seed set between experimental and control plants are due to differences in degree of synchrony rather than to pre-existing resource and microenvironmental differences between sites. A direct test of this hypothesis was not included, however, in this experiment.

The mean number of flowers per individual was not significantly different when all 58 individuals in the experimental area were compared with the plants in the nonexperimental areas ( $t = .29$ ,  $df = 143$ , NS, Table 2). However, only 41 plants in the experimental area were used for the experiment. These 41 plants did have a significantly lower mean number of flowers than the individuals in the natural synchronous population ( $t = 1.78$ ,  $df = 126$ ,  $P < .05$ , Table 2). This sampling error occurred because individuals were selected before it was known how many flowers they would produce. The error thus precluded direct overall comparisons between populations, irrespective of number of flowers per individual, requiring that comparisons between populations be made by categories based on number of flowers.

The two populations also differed in their time of flowering. To control for this difference I induced a small population to flower synchronously in the experimental area (Fig. 2C). These individuals also served as a control for possible but unknown differences due to induction of flowering by sprinkling rather than by rain. This population was small ( $n = 6$ ) and the mean number of flowers was larger than in the induced asynchronous population (Table 2). Therefore, I compared individuals in this induced synchronous population with a subset of individuals in the induced asynchronous population which (1) had a comparable number of flowers (Table 2), (2) flowered in the same general location, and (3) flowered at the same general time (relative to the individuals in the natural synchronous population).

I estimated pollinator activity in two ways. First, I made direct observations of visitors to the plants (details of observations are in Augspurger 1980). Twenty days of observation were made at 17 individuals in the induced experimental area. Eight days of observation

were made at 8 individuals flowering during the natural synchronous periods in 1975 and 1976. One individual shrub was observed per day. Observations occurred from 0700 to 1600 in alternating 15-min intervals, giving 4½ h of observation per day. Since a flower is open on only 1 d from dawn to dusk, no night observations were necessary.

Second, I recorded fruit and ovule set for each individual plant. The flowers require external agents to effect pollination, so measurements of fruit and ovule set can be used directly to indicate pollinator activity. To measure fruit set I color-tagged each flower up to a maximum of 100 flowers/individual<sup>-1</sup>/d<sup>-1</sup>; >100 flowers rarely occurred except on peak days. I then made observations of fruit set 5 d after each flower was open. This method provides an accurate measure of the level of pollination because the entire unpollinated flower falls off the shrub within 5 d, while ovaries of pollinated flowers remain on the shrub. After this initial 5-d period, developing fruit may abort despite pollination. Abortion may occur due to predation, low number of pollinated ovules within the fruit, and unknown reasons (see below).

Ovules swell following pollination. Thus, the number of swollen ovules per fruit (ovule set) is an additional measure of the effectiveness of pollination. Ovule set was measured by counting the number of ovules swollen per fruit per individual (maximum sample = 20 fruits/d<sup>-1</sup>/individual<sup>-1</sup>). To avoid destructive sampling of fruits, determination of ovule set was delayed until the fruit was mature. Both swollen and unswollen ovules remain intact throughout maturation. Not all swollen ovules remain intact throughout maturation. Therefore the number of mature seeds per fruit was also measured. Thus in one fruit I could record both ovule set, a measure of pollination success, and seed set, a final measure of reproductive success. Ovule set was also determined in samples of aborted fruits.

Number of aborted fruits was monitored at weekly intervals over the 4-wk development period. Total number of mature fruits was recorded for each plant. All aborted fruits and flowers and the above sample of mature fruits were examined for evidence of insect damage and/or presence. This examination was used to quantify the number of flowers and fruits with predation per individual.

All data are summarized at the level of the individual plant. Summaries of percentages of fruit set, ovule set, and predation per individual allow direct comparisons among plants irrespective of differences in the number of flowers. These comparisons determine if the proposed mechanisms of pollinator attraction and seed predator avoidance are contributing to any observed differences in reproductive success of individuals in the two populations. A summary is also made for an individual's reproductive success, measured in absolute number of offspring (seeds) produced. This sum-

mary comes closest to being a measure of an individual's fitness and thus is essential for evaluating whether selection acts against asynchronous individuals.

Nonparametric statistics are used in the percentage comparisons because these data do not meet assumptions of normality and equality of variance. Therefore median values accompanied by 95% confidence intervals are shown for these comparisons rather than mean values.

## RESULTS

### *Seed production*

Individuals in the natural synchronous population had far greater seed production than individuals in the induced asynchronous population. All synchronous individuals produced some mature seeds; the mean number of seeds per individual was 658 (SD = 661, range = 8–3409). By contrast, 20% of the asynchronous individuals produced no mature seeds; the mean number of seeds per individual was 62 (SD = 153, range = 0–866).

This large difference in seed production may have been somewhat exaggerated because the number of flowers per individual in the natural synchronous population was greater than that in the induced asynchronous population (see Methods). However, this wide discrepancy in seed production was manifested at all size categories of plants (Table 3). This categorical analysis thus demonstrates that the large difference in seed production is not attributable primarily to the initial difference in number of flowers.

The difference in seed production accrued from two sources: (1) number of fruits matured, and (2) number of seeds per fruit (Table 3). Differences in number of mature fruits contributed much more to the differences in total number of seeds than did differences in number of seeds per fruit.

Having established this large difference in seed production between individuals in the two populations, I now examine three factors possibly responsible for the difference: (1) fruit and ovule set due to pollination, (2) abortion due to seed predation, and (3) abortion due to causes other than seed predation.

### *Pollination hypothesis*

The median percentage of fruit set in the natural synchronous population was significantly greater than the median in the induced asynchronous population (Fig. 3). The difference between individuals in the two populations diminished as the number of flowers increased, but for all size categories, median percentage of fruit set was significantly greater in the natural synchronous population (Table 4). Likewise, a greater absolute number of fruits was set in natural synchronous individuals in all five size categories (Table 3).

A similar pattern emerged in the individuals serving as controls for differences between the two popula-

TABLE 3. Comparison by size category of total number of flowers and ovules, number of flowers and ovules pollinated and matured to fruits and seeds, and number of fruits with predation. Values represent means and (SD) of absolute numbers (not percentages) per individual plant. (S) indicates natural synchronous population and (A) indicates induced asynchronous population.

Size category: range of number of flowers	Sample size		Flowers		Flowers pollinated		Aborted Fruits*		Mature fruits†		Seeds per mature fruit‡		Total seeds‡	
	S	A	S	A	S	A	S	A	S	A	S	A	S	A
25–49	9	11	35 (8)	33 (4)	29 (7)	13 (8)	7 (6)	11 (8)	22 (8)	2 (1)	6.5 (1.8)	4.0 (1.0)	146 (74)	5 (5)
50–99	17	10	75 (11)	71 (14)	60 (15)	38 (20)	26 (20)	33 (17)	34 (18)	5 (7)	6.3 (1.7)	4.2 (1.6)	229 (162)	24 (34)
100–199	22	9	143 (28)	144 (32)	120 (32)	85 (30)	38 (21)	78 (25)	82 (33)	7 (11)	5.9 (1.4)	3.7 (1.8)	487 (268)	25 (33)
200–399	27	4	284 (50)	316 (59)	237 (55)	200 (102)	93 (48)	168 (91)	144 (56)	32 (25)	5.4 (1.4)	3.1 (1.4)	811 (387)	133 (146)
400+	12	7	613 (219)	615 (102)	530 (205)	436 (109)	210 (95)	357 (124)	320 (176)	79 (90)	4.8 (1.3)	4.8 (3.2)	1631 (1071)	290 (311)
Total	87	41	226 (198)	187 (210)	190 (175)	105 (146)	70 (77)	89 (121)	120 (120)	16 (44)	5.7 (1.6)	3.9 (2.0)	658 (661)	62 (153)

Size category	Ovules per fruit		Ovules pollinated per fruit				Fruits with predation by:			
			Aborted		Mature‡		Microlepidoptera		Diptera	
	S	A	S	A	S	A	S	A	S	A
25–49	27 (3)	26 (2)	10.5 (4.0)	3.4 (3.0)	20.8 (4.3)	11.4 (3.6)	3 (4)	5 (7)	0.4 (1.2)	5 (5)
50–99	25 (2)	27 (2)	11.8 (4.7)	6.0 (6.2)	17.2 (8.0)	11.2 (4.8)	4 (5)	15 (15)	0 ...	14 (13)
100–199	26 (3)	27 (2)	10.1 (4.5)	4.0 (3.3)	20.3 (4.6)	9.9 (5.4)	11 (8)	19 (17)	1 (4)	41 (31)
200–399	26 (2)	24 (2)	11.1 (3.3)	6.9 (5.8)	19.1 (3.4)	11.4 (6.6)	18 (12)	40 (25)	0.6 (1.6)	47 (30)
400+	28 (3)	28 (2)	12.9 (5.9)	6.6 (5.0)	19.3 (1.3)	11.6 (8.3)	35 (23)	109 (91)	0 (1)	90 (88)
Total	26 (2.6)	27 (2.1)	11.1 (4.4)	5.0 (4.6)	19.8 (4.1)	11.0 (5.4)	14 (15)	31 (53)	0.6 (1.6)	33 (50)

\* Includes abortion due to all causes including predation.

† Represents mean of all individuals, with or without any mature fruit.

‡ Represents mean only of individuals bearing some fruit to maturity.

tions in their time of flowering, location, and method of inducing flowering (see Methods). An individual in the induced synchronous population had a significantly greater percentage of fruit set than an individual of comparable size in the induced asynchronous population (Fig. 3). The difference between the two synchronous populations was not significant.

An individual in the natural synchronous population also had a significantly greater percentage of ovules set per fruit than an individual in the induced asynchronous population. This relationship held both for aborted and mature fruits (Fig. 4). Likewise, for all size categories, a greater absolute number of ovules were set per fruit in synchronous individuals than in asynchronous individuals (Table 3).

Results from direct observations of pollinators par-

allel these results of fruit and ovule set. The details of pollinator attraction and movement patterns at this mass-flowering shrub are discussed in detail elsewhere (Augspurger 1978, 1980) and are only briefly summarized here. A social bee, *Melipona interrupta*, which actively recruits other colony members to newly found resources, was the major effective pollinator. Individual shrubs that attracted visits from this bee had a significantly higher percentage fruit set and ovule set than individuals receiving no visits from this bee.

Attraction of the bee was highly erratic in the asynchronous population. The bees were attracted to an individual in the asynchronous population on only 4 of 17 observation d. The number of flowers on those individuals attracting the bee ranged from 41–209; individuals not attracting the bee had 18–274 flowers.

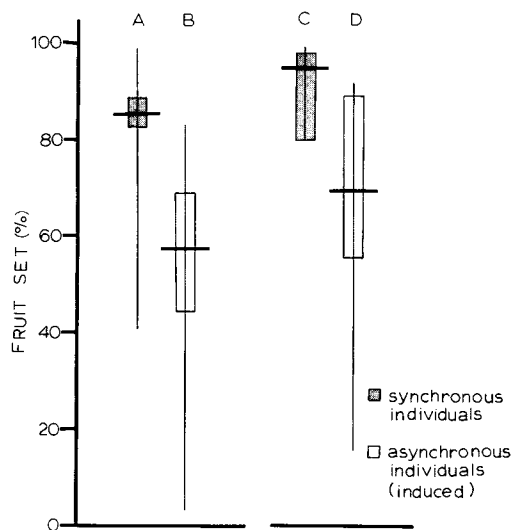


FIG. 3. Percentage fruit set 5 d after flowering for individuals in the natural synchronous population (A,  $n = 87$ ) and individuals in the induced asynchronous population (B,  $n = 41$ ). C ( $n = 6$ ) equals individuals in the induced synchronous population and D ( $n = 12$ ) equals individuals with a comparable number of flowers in the induced asynchronous population. Horizontal line = median, rectangle = 95% CI for median, and vertical line = range. Statistical test for differences between A and B: Mann-Whitney  $U = 537.0$ ,  $P < .0001$ ; between C and D: Mann-Whitney  $U = 9.0$ ,  $P < .002$ ; between A and C: ns.

*Melipona interrupta* was attracted to all observed individuals in the synchronous populations. It foraged on 8 observation d of eight individuals in the natural synchronous population; the number of flowers per individual ranged from 34–267. It also foraged on 3 observation d of three control individuals in the induced synchronous population. Thus, in contrast to asynchronous individuals, attraction to synchronous individuals was consistent.

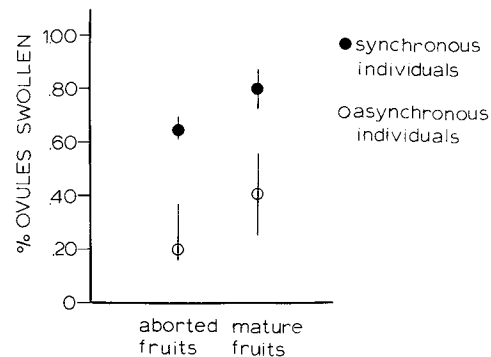


FIG. 4. Percentage of ovules swollen per aborted fruit and per mature fruit per individual. Circles = median; vertical line = 95% CI for median. Statistical tests for differences between the two populations: mature fruits:  $n_1 = 34$ ,  $n_2 = 29$ , Mann-Whitney  $U = 51.0$ ,  $P < .0001$ . aborted fruits:  $n_1 = 87$ ,  $n_2 = 41$ , Mann-Whitney  $U = 204.0$ ,  $P < .0001$ . Statistical tests for differences between the two types of fruits: natural synchronous population:  $n = 34$ , Wilcoxon Rank Sum of Differences = 558.0,  $P < .0001$ ; induced asynchronous population:  $n = 29$ , Wilcoxon Rank Sum of Differences = 389.0,  $P < .0001$ .

The combined evidence from both pollinator observations and fruit and ovule set indicates that the individual flowering in synchrony with the population was more effective in consistently attracting pollinators than the individual flowering alone. What population size of synchronously flowering individuals is required to attract the pollinator? Although *H. prunifolius* flowers synchronously over the entire forest, the data show that a small population size (e.g.,  $n = 6$  in the induced synchronous population; total number of flowers in this population was 2909) is as effective as the entire forest with respect to pollination level (Fig. 3). The discrepancy between pollination of synchronous and asynchronous individuals decreases as number of flowers per plant increases (Tables 3 and

TABLE 4. Comparison by size category of levels of pollination and predation by microlepidopteran larvae in natural synchronous population (S) and induced asynchronous population (A). Values represent median percentage and (95% CI) per individual. Statistical test = Mann-Whitney; \* =  $P < .05$ , \*\* =  $P < .01$ , \*\*\* =  $P < .001$ .

Size category Number of flowers	Flowers pollinated		Fruits with predation		Sample size	
	S	A	S	A	S	A
25–49	88.6 (70.4–92.0)	27.8** (9.5–69.0)	5.7 (0–11.4)	0 n.s. (0–44.4)	9	11
50–99	82.3 (76.3–86.9)	44.6** (33.8–88.1)	2.4 (0–9.0)	14.6** (8.5–41.0)	17	10
100–199	85.1 (82.4–91.0)	61.0*** (47.7–71.9)	6.9 (3.2–10.8)	10.7* (1.2–27.0)	22	9
200–399	84.5 (80.3–90.3)	57.5* (...)	5.6 (3.0–7.8)	5.6 n.s. (...)	27	4
400+	90.1 (82.3–94.4)	75.7** (>55.7)	4.5 (2.6–8.3)	11.4* (1.7–40.7)	12	7
Total	85.5 (82.7–88.6)	57.6*** (44.6–69.0)	5.4 (3.5–6.9)	11.4** (5.2–22.7)	87	41

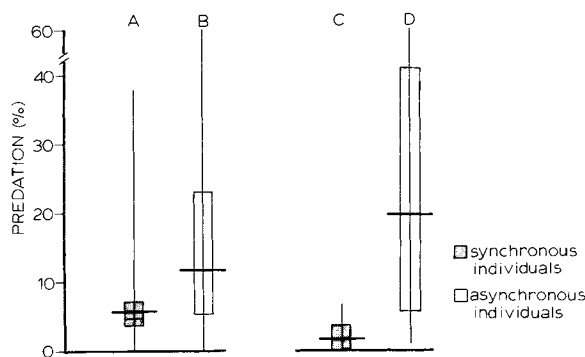


FIG. 5. Percentage of fruits with predation by microlepidopteran larvae for individuals in the natural synchronous population (A) and the induced asynchronous population (B). C equals individuals in the induced synchronous population and D equals individuals of comparable number of flowers in the induced asynchronous population. See Fig. 3 for symbols. Statistical test of differences between A and B: Mann-Whitney  $U = 1206.0$ ,  $P < .005$ ; between C and D: Mann-Whitney  $U = 0$ ,  $P < .005$ .

4). For the largest category of plants there is only a 14% difference in pollination level between individuals in the two populations (Table 4). Thus, it appears that the addition of a small number of synchronous and spatially close individuals to one temporally isolated individual is sufficient to attract pollinators at levels comparable to the entire synchronous forest.

#### Seed predator hypothesis

**Microlepidopteran predator.**—The major seed predator of *Hybanthus prunifolius* in natural flowering and fruiting periods of both 1975 and 1976 was a microlepidopteran larva (Family Cosmopterididae, Chrysopoleiinae, probably new genus, new species; identification by R. W. Hodges, United States Department of Agriculture). Its biology is largely unknown, but if judged from allied genera, it is predicted to be relatively host specific (R. W. Hodges, *personal communication*); it is also found in fruits of the shrub *Rinorea sylvatica* (Violaceae) on BCI.

Predation occurs prior to dispersal. The adults lay eggs during the flower or early fruit stages. The larva feeds on the endosperm of the developing ovules. Pupation occurs outside of the fruit. In the laboratory the entire life cycle of the moth from adult to adult requires about 4–5 wk.

Fruits incurring predation by this moth larva commonly drop from the shrub during the 2nd wk after flowering, which is also the major time when abortion of noninfested fruits occurs (see below). Some mature fruits contain predators that have damaged most, but not always all, of the mature seeds. In both populations aborted fruits of an individual had a significantly greater percentage of predation than mature fruits of an individual (Wilcoxon matched-pair rank-sum test: natural synchronous, rank sum of differences = 3107,

$n = 87$ ,  $P < .0001$ ; induced asynchronous, rank sum of differences = 418,  $n = 30$ ,  $P < .0001$ ).

The overall level of predation by microlepidopteran larvae was relatively low. However, median percentage of predation in the natural synchronous population was significantly lower than in the induced asynchronous population (Fig. 5). Likewise, a lower absolute number of fruits incurred predation in synchronous individuals than in asynchronous individuals. An individual in the induced synchronous population had a significantly lower percentage of predation than an individual of comparable size in the induced asynchronous population (Fig. 5).

As an additional control for the difference in time of flowering between the two populations, I also allowed 11 widely scattered individuals to flower naturally in the experimental area (=population D). I used those individuals, in part, to check whether or not the microlepidopteran predator was still active by the later time of flowering in the natural synchronous population. Those individuals incurred a median of 12.6% predation; that level was comparable to a median of 11.4% predation for individuals in the induced asynchronous population in the same experimental area. This predator was thus clearly still active at the time of the natural flowering. Therefore, the lower level of predation in the natural synchronous population than in the induced asynchronous population was most likely due to differences in synchrony rather than differences in time of flowering and activity periods of this seed predator.

Very small individuals (<25 flowers), in both populations, had a higher probability than larger individuals of escaping predation completely (natural synchronous:  $\chi^2 = 26.4$ , 1 df,  $P < .0005$ ; induced asynchronous:  $\chi^2 = 27.6$ , 1 df,  $P < .0005$ ). Above this small size, however, in both populations, simple linear regression showed that percentage of predation per individual was not dependent on abundance of flowers (natural synchronous:  $Y = .202 + .005X$ ,  $r^2 = .001$ , NS; induced asynchronous:  $Y = .18 + .036X$ ,  $r^2 = .021$ , NS). For three of five size classes the median percentage of predation was significantly lower in the natural synchronous population than in the induced asynchronous population (Table 4). The differences between the other two size classes were not significant. The absolute number of fruits with predation per individual was greater in the induced asynchronous population in all five size categories (Table 3).

In summary, unlike the major pollinator, this seed predator was more likely to be attracted to temporally isolated individuals. These plants therefore had both higher percentages and absolute numbers of fruit with predation than individuals flowering and fruiting in synchrony with the population. The population in toto appears to have satiated this seed predator.

**Dipteran predator.**—A second seed predator, a dipteran larva (Lonchaeidae, *Silba* sp.), also damages the



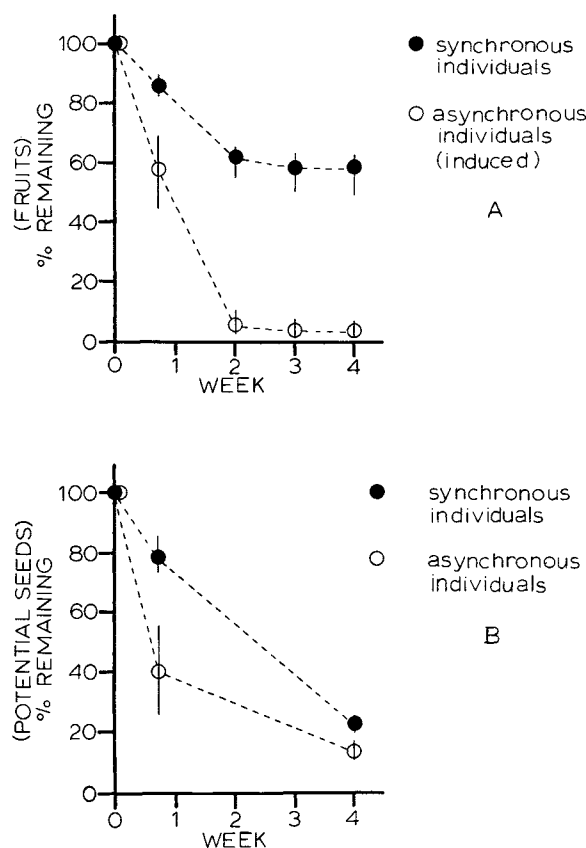


FIG. 6. A. Maturing fruits remaining over time as a percentage of total number of flowers. Percentage 5 d after flowering equals pollination level per individual plant; 4 wk after flowering equals dispersal level. Differences between individuals in the two populations at all time intervals after flowering are statistically significant (Mann-Whitney,  $P < .0001$ ). See Fig. 4 for symbols.

B. Maturing seeds remaining over time as a percentage of total number of ovules. The values represent ovules only in fruits that reached maturity at 4 wk and do not include ovules in aborted fruits (see Fig. 4). Percentage 5 d after flowering equals pollination level of ovules per individual plant; 4 wk after flowering equals dispersal level of mature seeds per individual plant. Differences between individuals in the two populations at both time periods after flowering are statistically significant (Mann-Whitney) ( $P < .0001$ ). See Fig. 4 for symbols.

developing seeds of *Hybanthus prunifolius*. Fruits containing larvae generally drop from the shrub during the 2nd wk following flowering. This seed predator was not discovered in 1975; it was very rare in 1976 in the natural synchronous population (0.5% of all fruits in the population contained this predator; median percent predation per individual was 0). This predator was much more common in individuals in the induced asynchronous population (Table 3); median predation was 15.2% per individual. Individuals in the induced synchronous population had a significantly lower level of predation (median = 7.7% per individual) than individuals of comparable size in the induced

asynchronous population (median = 20.4% per individual) (Mann-Whitney  $U$  test = 11.0,  $P < .01$ ). Therefore flowering and fruiting synchrony contributed toward satiation of this seed predator, at least within the experimental area.

The extremely low level of dipteran predation in the natural synchronous population could also be ascribed to synchrony resulting in predator satiation. An additional possibility is that population levels of this predator were quite variable spatially throughout the forest. However, additional evidence indicates that the low level was primarily due to inactivity of the dipteran predator by the later time of the natural synchronous flowering. Widely scattered individuals in the experimental area allowed to flower later, but naturally (population D), had a very low level of predation (median = 0% per individual).

Thus it appears that while the microlepidopteran predator was still active during natural flowering, the dipteran larva essentially was not. The dipteran predator may also have switched to another host plant by the later time of flowering of *Hybanthus prunifolius*. This difference in time of activity of the dipteran predator at fruits of *H. prunifolius* complicates any direct comparison of the final reproductive success between individuals in the natural synchronous and induced asynchronous populations (see below).

#### Other causes of abortion

**Fruit abortion.**—The already large differences in fruit set, measured 5 d after pollination, were even further exaggerated during the fruit maturation period of 4 wk (Fig. 6A). Fruit abortion was heavily concentrated in the 1st 2 wk and was negligible in the remaining 2 wk. A significantly greater percentage of fruits aborted per individual in the induced asynchronous population than in the natural synchronous population (Fig. 6A). Absolute number of fruits aborted was also greater for individuals in the asynchronous than in the synchronous population (Table 3).

Abortion of a given fruit may have occurred in response to several different factors: (1) seed predation, (2) low ovule set, (3) selective brood reduction based on genetic quality of potential offspring, and (4) resource availability. It is impossible to designate amounts of abortion due to specific factors, in part because a fruit with predation may have aborted for other reasons, such as inadequate pollination of its ovules. Not all fruits with predators eventually aborted; some mature fruits contained larvae. It is clear, however, that the major cause of abortion was not predation. The total amount of fruits aborted far exceeded the amount aborted with evidence of predation (Table 3).

Individuals in the induced asynchronous population had a significantly lower percentage of ovules swollen per fruit (Fig. 4). Aborted fruits in both populations had a significantly lower percentage of swollen ovules

TABLE 5. Comparison between major and minor flowering periods of flowers pollinated (equals 5-d fruit set) and flowers producing dispersed fruits. Values represent mean per individual plant, followed by standard deviation in parentheses.

Major flowering	Number of flowers	Fruit set		Fruits dispersed		Sample size
		Number	Percentage	Number	Percentage	
1975	178 (143)	160 (147)	90 (12)	59 (44)	33 (21)	50*
1976	197 (190)	164 (161)	83 (10)	106 (99)	54 (15)	50*
Minor flowering						
1975—1	112 (108)	22 (18)	20 (17)	9 (8)	8 (8)	9
1975—2	43 (17)	7 (4)	16 (13)	0 ...	0 ...	3

\* Same set of individuals followed in both years.

than did mature fruits (Fig. 4). These results support the hypothesis that a major factor causing abortion in both populations was inadequate pollination of ovules in a given fruit. Asynchronous individuals had more of their fruits inadequately pollinated and hence aborted a greater percentage of their pollinated flowers (95% vs. 27%). My direct observations of pollinator activity revealed that a large proportion of 5-d fruit set in asynchronous individuals was due to activity by smaller ineffective bees and not by *Melipona interrupta*, the major effective pollinator (Augspurger 1980). Individuals not visited by *Melipona* had 7% of their ovules swollen, while individuals with visits by *Melipona* had 49% of the ovules swollen. Individuals without visits by *Melipona*, although initially setting some fruit, developed almost no fruits to maturity. Therefore it appears that a large amount of the abortion in asynchronous individuals was related to the low number of ovules swollen due to the plants' inability to attract the major effective pollinator.

The probability that different resource levels in the two populations affected abortion was not specifically tested in this study. Resource differences appear unlikely, given the similarities between the nonexperimental and experimental area in height, density, number of flowers, soil moisture, and nectar production (see Methods).

Whether individuals selectively aborted self-pollinated relative to cross-pollinated fruits is unknown. Sample sizes of self-compatibility studies were too small to warrant any conclusion regarding selection for genetic quality. Synchronous individuals experienced more cross-pollination than asynchronous individuals which were temporally isolated from other pollen donors; all the fruit set in the latter resulted from self-pollination. However, the amount of cross-pollination experienced by the synchronous individuals was estimated to be as low as 10% (Augspurger 1980). Hence selection for genetic quality is not likely to have contributed much to the differences in abortion levels between individuals in the two populations.

*Abortion of pollinated ovules.*—Not all swollen ovules developed into mature seeds in the fruits that did mature (Fig. 6B). Individuals in the induced asyn-

chronous population had a lower percentage of pollinated ovules per fruit but aborted a significantly lower percentage of those pollinated ovules per fruit than did individuals in the natural synchronous population (59% vs. 69%; Mann-Whitney  $U = 313.0$ ,  $P < .01$ ). Causes of abortion of pollinated ovules and the differences in percentages of abortion between the two populations remain unknown. It is possible that abortion of pollinated ovules was less pronounced in asynchronous individuals because their resources were being used to mature far fewer fruits and/or fewer ovules per fruit. Despite their higher percentage of abortion of pollinated ovules, the synchronous individuals nevertheless matured a larger absolute number of seeds per fruit than the asynchronous individuals (Table 3).

In summary, the combined effects of differential pollination and subsequent abortion, only partly due to seed predation, produced a 10-fold difference in mean seed output for individuals in the two populations. Individuals flowering and fruiting in synchrony with the population gained a significant advantage in reproductive fitness.

#### *Evidence from natural flowering periods*

Thus far comparisons have been between an experimental population and a natural population. Is there any supporting evidence from an entirely natural situation?

Multiple flowering periods by *Hybanthus prunifolius* can occur within one dry season although there is usually only one major flowering period. If the rain triggering flowering is very near the minimum required to evoke a response, only a few individuals in a population may flower. These are often widely spaced individuals. A minor response may include individuals which have not flowered in a major period and which have numbers of flowers per individual comparable to a major period. It may also include a few of the same individuals as in the major flowering period, but they commonly have many fewer flowers per individual. A minor flowering period may occur before or after a major period.

I compared fruit set at 5 d and at maturity for two

major and two minor responses. Individuals included in the analysis for minor responses had not flowered in the major response. An individual in a major response had more flowers pollinated and more flowers becoming mature fruits than an individual flowering in a minor response (Table 5).

A similar analysis was not possible for predation. The very low fruit set in minor responses (Table 5) due to low pollinator attraction yielded very low quantities of fruit for seed predators. Sample sizes per individual were inadequate for analysis. An analysis was done only on total fruit, without summarizing on the individual plant level. Of 81 aborted fruits examined in minor responses, 42% had predation by microlepidopteran larvae. Of 9886 aborted fruits examined in the 1976 major response, 9.3% had such predation by microlepidopteran larvae. Any interpretation of these results is complicated, however, because of the possibility of a buildup of the predator population during a major response. In 1975, the two minor responses occurred after the major response.

The results from the minor responses are exactly as one would predict from the experimental results, and thus support the earlier results. An individual flowering and fruiting in low temporal density in the population, whether naturally or experimentally, attracts fewer pollinators and less easily avoids predators than an individual flowering and fruiting in synchrony with large numbers of spatially-close individuals.

#### *Influence of spatial density*

A prediction that arises from these results is that similar patterns of pollination and predation will emerge if the variable distinguishing populations is space instead of time. Individuals in populations with high spatial density should attract pollinators and avoid seed predators more easily, thus contributing to a higher reproductive success, than individuals in populations with low spatial density (Gentry 1974a, 1974b, Vandermeer 1975). This prediction holds only until some unknown spatial density is reached which satiates pollinators.

An analysis testing the effect of space was done, comparing individuals in populations which differed spatially and which flowered naturally. The time variable was largely controlled because populations at all sites had approximately the same high degree of flowering synchrony.

Populations at the study sites were grouped into two categories of spatial density: high and low. The four high-density sites had roughly similar densities (Table 1). These sites (1-4) were lumped in the earlier analysis to become the natural synchronous population. In contrast, site 5 had a much lower spatial density (Table 1). A second population (D) of low spatial density occurred in the experimental areas (sites A and B). Very widely scattered individuals in this area were allowed to flower naturally after the experimental induction of

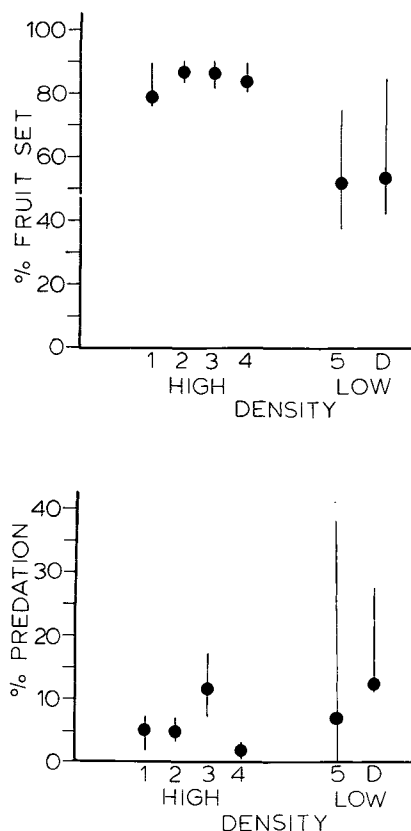


FIG. 7. Percentage fruit set 5 d after flowering (level of pollination per individual plant) and percentage predation by microlepidopteran larvae per individual plant at high spatial density (1-4) and low spatial density (5 + D) sites. See Fig. 4 for symbols.

flowering had been completed ( $n = 11$ ). Site 5 and the population D in the experimental area were designated as the two low-density sites. Comparisons were made first, among the sites designated high density, and second, between the composites designated high and low density. No significant differences in number of flowers per individual were found among the four high-density sites or between the low- and high-density composites. Therefore, comparative analyses using percentages of pollination and predation were used to test for differences due to space.

Spatial variation had a larger and clearer effect on pollination than on seed predation (Fig. 7). No significant differences in percentage of fruit set per individual occurred among the four high-density sites (Kruskal-Wallis statistic = 2.5, 3 df, ns). In contrast, there was a significantly lower percentage of fruit set among individuals at the two sites with low spatial density than among individuals at the four high-density sites (Mann-Whitney  $U = 187$ ,  $P < .0001$ ).

Comparisons of predation by microlepidoptera were more complex. First, there were significant differences in percentage of predation per individual among the

TABLE 6. Comparisons of the effect of time vs. space on pollinators vs. seed predators. Values represent median percentage per individual plant, followed by 95% CI in parentheses.

	Flowers pollinated	Fruits with predation by		Sample size
		Microlepidoptera	Diptera	
Time*				
Natural synchronous	86 (83–89)	5 (4–7)	0 ...	87
Induced asynchronous	58 (45–69)	11 (5–23)	15 (7–24)	41
Space†				
High density	86 (83–89)	5 (4–7)	0 ...	87
Low density	59 (47–63)	12 (6–20)	0 ...	19

\* Space is controlled by having both populations with comparable densities and distances to nearest reproductive neighbors.

† Time is controlled by having both density groups with comparable flowering synchrony.

four high-density sites (Kruskal-Wallis statistic = 37.5, 3 df,  $P < .0001$ ) (Fig. 7). For unknown reasons, Site 3 had a particularly high level of predation; this site did have the lowest spatial density of the four high-density sites (Table 1).

Second, the two low-density sites combined had a significantly higher percentage of predation per individual than the four high-density sites (Mann-Whitney,  $U = 406$ ,  $P < .0005$ ). However, Site 5 had a predation level statistically indistinguishable from the high-density sites. The low-density population D in the experimental area had the highest level of predation of all sites. That population had the lowest spatial density of flowering individuals of all sites during the natural flowering period. However, these results from this experimental site could be confounded if there was an increase in the population size of the predator during the prolonged 2-mo asynchronous flowering period in the experimental area. There was no evidence for this, however, as there was no significant difference in predation by microlepidoptera in the experimental area among the induced and the naturally flowering individuals. Analysis of spatial effects by the dipteran larva were impossible given the very low level of their predation in the natural synchronous population.

In summary, the data illustrate that high density in both time and space is important in attraction of pollinators and in avoidance of seed predators. Thus isolation from the population is the overall critical factor influencing the reproductive success of the individual. Temporal and spatial isolation appear to be equally important factors, at least for the particular densities tested (Table 6). The pollinators, rather than the seed predators, appear to play the dominant role in determining the large differences in reproductive success due to differences in temporal and spatial density (Table 6).

#### DISCUSSION

In this system, variation in timing of reproduction can be correlated with seed output, a major component of fitness. The system thus permits strong inferences about the processes of selection occurring in a field setting. The results suggest the following evolu-

tionary interpretation. The reproductive output of an individual which is out of synchrony with the population is reduced because its pollination level is decreased and its seed predation is increased. The experimental population demonstrated lower seed production among individuals which flowered well before the natural population flowering peak. In 1975 similarly low reproductive output was demonstrated for individuals flowering in the minor responses which occurred well after the major population flowering peak. Synchronous flowering in *Hybanthus prunifolius* is associated with nearly as synchronous fruiting (Augspruger 1978); plants which flowered asynchronously also fruited asynchronously. Low reproductive output resulted both from low pollination levels and high seed predation levels. Thus both pollinators and seed predators can potentially impose stabilizing selection for maintenance of the present low level of variance in timing both of flowering and fruiting in the population, and may have operated in the past to reduce variation to this level.

These evolutionary statements rest on the assumption that the timing of flowering is heritable. I have not directly tested the heritability of this character in *H. prunifolius*. Numerous studies from the crop and agricultural literature illustrate that timing of flowering is heritable (Cooper 1960, Paterniani 1969, Stern and Roche 1974). Furthermore, selection on flowering response to proximate cues can produce dramatic changes in a population in only a few generations (McNeilly and Antonovics 1968). Therefore, it is likely that the response to a flowering cue by *H. prunifolius* is heritable. However, the specific mechanisms that produce the flowering response and that are affected by selection remain unclear (but see Augspruger 1982). The physiological limitations of this highly precise timing are also unknown.

In this study differences in Darwinian fitness have not been directly measured. The evolutionary interpretation thus also rests on the assumption that the observed quantitative differences in seed output between individuals in the two populations are translated into differences in reproducing adults arising from those seeds.

The data show that flowering synchronously with the population is of greatest importance to the smallest individuals. This finding further illustrates the importance of the temporal structure of the population on an individual's reproductive success. Furthermore, it predicts that flowering synchrony influences selection on the size (and presumably age) of first reproduction. If flowering synchronously with the population, an individual may begin reproducing successfully at an earlier age than if the individual were flowering asynchronously.

Flowering in synchrony with the population may lead to disadvantages affecting an individual's offspring. If a high density of seedlings accrues from synchronous flowering, this may increase the number of seedlings dying (Hett 1971), due to density-dependent processes such as herbivory (Connell 1971, Root 1973), competition (Yoda et al. 1963), or spread of pathogens in dense seedling stands (Gibson 1965, Burdon and Chilvers 1974).

A large resource appears to be required to activate colony recruitment of the major pollinator to a specific area. During 2 yr of observation of *Hybanthus prunifolius* and other understory shrubs, I had only rare encounters with *Melipona interrupta*, except at mass-flowering individuals which flower for a very restricted part of the year. This suggests that the bee, which is active year-round, generally forages in the canopy and thus is attracted en masse only to very dense patches of shrub flowers. High flower densities are achieved by three mechanisms: mass-flowering within each individual shrub, a high degree of population flowering synchrony, and a high spatial density of plants. Selection, therefore, would favor the individual mass-flowering shrub that is closest to its conspecifics in both time and space.

Evolutionary responses may occur more readily to selection for timing of reproduction than for spacing in *H. prunifolius*. Direct genetic control of time is possible but the location where an individual becomes established spatially cannot be controlled as directly. Some control may occur over the distance a seed is dispersed, i.e., by acting on the explosive dispersal mechanism of *H. prunifolius*, but dispersal distance does not directly determine the individual's ultimate spatial relation to other individuals.

The evolutionary significance of reproductive synchrony for the population is that it delimits effective population size (Wright 1946). A higher degree of synchrony may result in potential for pollen flow between a larger number of individuals and thus potentially leads to a larger effective population size. The consequences of this for individual fitness are unknown. Disruptive selection on local variation in timing may subdivide the population and result in very local genetic differentiation.

Data reported elsewhere (Augspurger 1978, 1980) indicate that in *H. prunifolius* the potential for very

extensive pollen flow arising from a high degree of reproductive synchrony may not be realized. This is because pollen flow in this self-compatible species is restricted in amount and in distance.

A distinction must be made between the potential for pollen flow and outbreeding, and its actual occurrence and significance. The ecological and evolutionary consequences of outbreeding in *H. prunifolius* are not yet known. A temporally isolated individual can only experience self-pollination, and then only if it is self-compatible. Flowering in synchrony with the population increases the potential number of plants with which an individual can exchange genes; furthermore, synchrony may influence mate selection. Information on the contribution of outcrossing to individual fitness will help to determine whether this may serve as a supplementary selective force yielding a high degree of reproductive synchrony.

This study demonstrates the selective role of pollinators and seed predators in influencing flowering and fruiting synchrony. In this system they act as additive forces, both favoring the individual in synchrony with the population. This is because the pollinator behaves in a density-dependent manner, being more attracted to higher abundances of flowers. The bee is responsive to three levels of floral density: mass-flowering of the individual plant, high degree of reproductive synchrony within the population, and high spatial density of the population. Conversely, the predator is more attracted than the pollinator to lower abundances of flowers and fruits. It should be emphasized that, in other systems, it is possible for the two groups to be in conflict in their selective roles.

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