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THE ECOLOGICAL CONSEQUENCES OF FLOWERING ASYNCHRONY IN MONOECIOUS FIGS: A SIMULATION STUDY[1]

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Abstract. For plants with temporally separate sexual phases to outcross, population-level flowering asynchrony is necessary, but this can decrease the resource base available for pollinators. We developed a simulation model to examine the consequences of such asynchrony for individual reproductive success and long-term pollinator maintenance within monoecious fig populations. In figs, flowering is synchronous within a tree and the specialist pollinators/seed predators can only survive briefly away from trees. Consequently, population-level flowering asynchrony must extend year-round for pollinators to persist locally. In repeated stochastic simulations using phenological traits of one well-studied species (*Ficus natalensis*), a median of 95 trees was required to produce an asynchronous sequence that could maintain local pollinator populations for 4 yr. However, many trees in those simulated populations were either male-sterile (10%) or both male- and female-sterile (35%), because their sexual phases were not well timed with the opposite phases of other trees. Sterility within a population approached zero at 2–3 times the critical population size.

Both the predicted critical population size and frequency of success of the trees within it depended strongly on the duration of reproductive episodes and the intervals between episodes. The level of within-tree reproductive synchrony was also critical: doubling the length of time over which individuals could donate pollen resulted in a 39% decrease in critical population size and a 27% increased likelihood that individuals would achieve at least some reproductive success. These results point to the need for precise phenological data for estimating plant fitness and population structure both in models and in the field.

Key words: asynchronous flowering; Ficus; figs; minimum viable population size; mutualism; phenology; pollination.

INTRODUCTION

Individuals within animal-pollinated plant populations often flower relatively synchronously. The potential benefits of population-level synchrony, such as increased pollinator attraction (Brown and Kodric-Brown 1979, Augspurger 1981) and increased outcrossing frequency (Rathcke and Lacey 1985), have received considerable attention. However, relative costs and benefits of population-level synchrony depend on the reproductive system of the plant in question. In

dichogamous species, i.e., those species with temporally separate sexual phases (Lloyd and Webb 1986), among-plant asynchrony rather than synchrony will promote outcrossing, provided that sufficient numbers of pollinators can be attracted.

We examine here the theoretical consequences of flowering asynchrony for reproductive success and maintenance of a local pollinator pool in populations of monoecious fig trees. Monoecious figs (half of the large genus *Ficus,* Moraceae) provide perhaps the most extreme example of population-level flowering asynchrony. In most species, individuals attract pollinators for a very brief period (Ramirez 1970, Janzen 1979, Bronstein 1989), but unpredictably and out of phase with each other. In large tropical populations, flowering

individuals can be found at all times of the year (Janzen 1979, Newton and Lomo 1979, Wharton et al. 1980, Milton et al. 1982, Baijnath and Ramcharun 1983, Corlett 1984, Michaloud 1988, Windsor et al. 1989).

Many tropical plant species flower year-round (e.g., Gentry 1974, Bullock et al. 1983, De Steven et al. 1987, Marquis 1988), and the Moraceae in particular tend towards long flowering seasons (Windsor et al. 1989). However, most explanations of this phenomenon in *Ficus* revolve around its unique interaction with species-specific pollinators (Hymenoptera, Agaonidae). This relationship is described in detail in Bronstein and McKey (1989) and is particularly well illustrated in Michaloud and Devez (1982). Briefly, the florets of a fig inflorescence (syconium) line an enclosed cavity, attractive and accessible only to the correct agaonid species. Figs are protogynous. Female wasps enter the syconium when the female florets are receptive, oviposit in some of them, and deposit pollen on the stigmas. Seeds and seed-eating wasp offspring mature during the next several weeks. When mature, these wasps mate within their natal syconium. Females then collect pollen from the newly mature anthers and leave the syconium in search of receptive syconia in which to oviposit. Dispersing females do not feed and probably live several days at most. It is therefore critical for them to quickly locate other trees of the same species flowering sufficiently out of phase with their natal tree.

Ramirez (1970) originally suggested that year-round flowering asynchrony evolved in figs to provide a haven for pollinators, guaranteeing the long-term survival of pollinator populations. It is more simply explained in a context of individual selection: trees attracting pollen-carrying wasps while conspecific neighbors are releasing them, and vice versa, should experience higher reproductive success than trees in reproductive synchrony with their neighbors (Janzen 1979, Windsor et al. 1989).

Maintenance of a local pollinator pool is, however, a group property, and should be problematic for a species with extremely asynchronous flowering. Pollinators commonly abandon patches when floral resources fall below an acceptable level (Rathcke 1983, Waddington 1983). When pollinators are specialists and can survive only briefly away from the plant, as is the case with fig wasps, a temporary rarity of flowering individuals can lead to the pollinators' local extinction. In these situations, both the success of individual plants and the ability of a pollinator population to persist locally should be frequency-dependent (Fig. 1). The larger the population, the higher the probability that pollen-carriers will be departing from at least one plant near in space and time to others bearing receptive flowers. At some critical population size, there will be no gaps in the flowering sequence, allowing a local pool of pollinators to be maintained indefinitely. However, even in a population large enough to maintain a pollinator pool, individual reproductive failure should be

common, because pollinators will often not be available on the days that a given plant bears receptive flowers. Great variability in pollinator availability over time is in fact evident in the few studies in which fig wasp censuses have been attempted (Balakrishnan Nair and Abdurahiman 1984, Michaloud et al. 1985, Bronstein 1987, Kjellberg et al. 1987).

Quantitatively, the probabilities of persistence for pollinators and reproductive success for trees can be predicted to depend on the interaction of certain plant and pollinator traits. Pollinator longevity and flight ability determine how close trees must be in space and time for successful pollen transfers to occur. Phenological traits of individual plants, such as the interval between successive flowerings, determine how many instances of pollinator departure and pollinator arrival occur within the population each day. While almost no field data are available on the critical fig wasp traits, at least some phenological information is available for a wide range of monoecious figs (Table 1; see also Table 1 in Ramirez 1974, Table 2 in Bronstein 1989). We present here a more detailed and quantitative data set, based on a 4-yr phenological study of an African species, *Ficus natalensis* (Michaloud 1988). Using these data, we develop a computer simulation model of fig phenology to address four ecological questions. (1) How large must a fig population be for a local pollinator population to be maintained? (2) In a fig population large enough to maintain a local pollinator population, how often will trees fail to reproduce? (3) How large a population is required to assure that every tree will reproduce? (4) Which phenological traits are most critical in determining the answers to these questions?

METHODS

Field observations

Ficus natalensis is a hemiepiphytic, riparian species with aerial roots immersed part of the year. Michaloud (1988) studied a wild population located along the Ivindo River at the Makokou field station, south of Makokou, Gabon (0°04' N, 12°52' E), from 1976 to 1980. The habitat is characterized by *Scyphocephalium ochocoa–Pycnanthus angolensis* evergreen rainforest, and belongs to the central African floristic area of Cameroon–Congo–Gabon (Caballe 1978). Rainfall is 1755 mm (10-yr average) and divides the year into two dry and two rainy seasons. Mean monthly temperatures range from 21° to 24°C.

Phenological censuses of *F. natalensis* were made along 12.8 km of shoreline around three islands. This transect was lengthened twice during the study; thus, 58 trees were monitored during 1976–1978, 79 trees were monitored during 1979, and 127 trees were monitored during 1980. Censuses were made at 2-wk intervals. Once syconia were initiated on a tree, a sample was collected every other day. The proportion of syconia containing pollinators (which die trapped within)
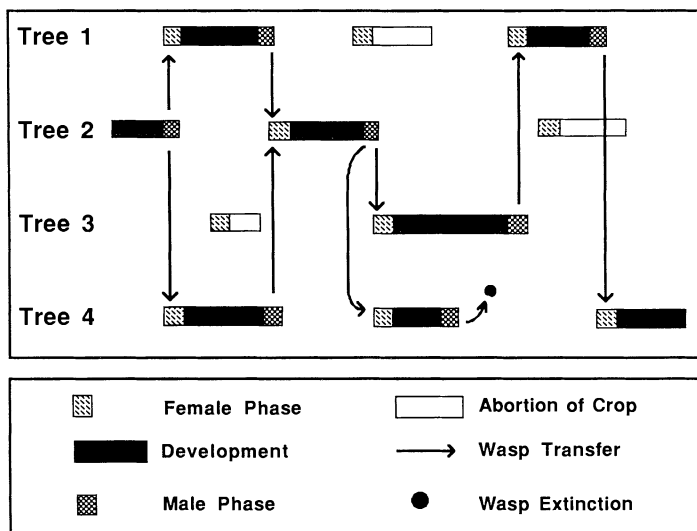
FIG. 1. Schematic diagram of flowering and fertilization in a hypothetical four-tree fig population. Note that: (1) trees flower out of phase, with durations of flowering episodes somewhat variable and intervals between episodes highly variable; (2) episodes frequently fail to obtain any pollinators and thus will be both female-sterile and male-sterile; (3) in some episodes, trees obtain pollinators but fail to donate pollen successfully, and thus will be male-sterile; and (4) the probability of male phase–female phase correspondence will increase with the number of phases of each type each day. Therefore, both the probability of success for individual cycles and the probability of maintaining a local pollinator pool should increase with plant population size. Pollinators can be maintained over the period shown by transferring from 2 → (1, 4) → 2 → 3 → 1 → 4; in the absence of any one of these trees, local wasp extinction would occur during the time period illustrated.

was then calculated in order to determine the date of peak pollinator arrivals. Sampling was repeated ≈5 wk later to determine the date of peak wasp departures. Mean and variance in duration of reproductive episodes and in interval between successive episodes were then calculated from these peak dates of wasp arrival and departure.

Simulation model

Repeated stochastic simulations were used to determine the number of trees necessary to allow a pollinator population to persist locally for a specified period of time, following a single pollinator immigration event. The variables were five individual-level phenological

TABLE 1. Flowering frequency of monoecious *Ficus* species. All species are tabulated for which census data are available on both duration of reproductive episodes and interval between reproductive episodes, for more than two trees. See also Table 1 in Ramirez 1974 and Table 2 in Bronstein 1989.

| | | Flowering frequency (wk) | | Census information | | | | |
Species	Site	Duration	Interval	Episodes	Trees	Years	Census interval	Reference
F. microcarpa	Singapore	4	2–38	43	8	1.5	1 wk	a
F. vogelii	Kumasi, Ghana	6–7	9–41	29	20	1	nd	b
F. benjamina	Singapore	4	2–34	31	9	1.5	1 wk	a
F. insipida	Barro Colorado, Panama	4–5	4–102	253	39	7	2 wk	c, d
F. yoponensis	Barro Colorado, Panama	4–5	4–101	569	65	7	2 wk	c, d
F. sycomorus	Gobabeb, Namibia	2–13	2–36	38	14	2	4 wk	e
F. pertusa	Monteverde, Costa Rica	7–10	5–80	18	13	2	2 wk	f
F. craterostoma	Makokou, Gabon	5–7	15–117	41	25	4	2 wk	g
F. demisistipula	Makokou, Gabon	7–8	47–189	7	4	4	2 wk	g
F. lingua	Makokou, Gabon	4–5	39–90	12	7	4	2 wk	g
F. ottoniifolia	Makokou, Gabon	6–7	39–203	15	7	7	2 wk	g
F. wildemaniana	Makokou, Gabon	6–8	80–196	9	6	4	2 wk	g
F. variifolia	Makokou, Gabon	5–6	32–80	14	3	5	2 wk	g
F. subcostata	Makokou, Gabon	8–10	16–99	5	3	3	2 wk	g
F. natalensis	Makokou, Gabon	3–8	3–159	244	127	4	2 d	h, i

References: a, Corlett 1984; b, Newton and Lomo 1979; c, Janzen 1979; d, Milton et al. 1982; e, Wharton et al. 1980; f, J. Bronstein, *personal observation*; g, G. Michaloud, *personal observation*; h, Michaloud 1988; i, this study.

TABLE 2. Parameter values used in the simulations. In each simulation, all parameters except the one shown were held at *Ficus natalensis* values (means ± SD: duration = 5.2 ± 0.9 wk, interval = 44.1 ± 24.8 wk). Values were chosen to represent a biologically reasonable range (see Table 1).

Interval between successive flowerings (wk)	Variance in interval
22.0 ± 12.4	0.0
33.0 ± 18.6	24.8*
44.1 ± 24.8*	44.1
55.2 ± 31.0	

Duration of reproductive episode (wk)	Variance in duration
1.3 ± 0.2	0.0
2.6 ± 0.4	0.2
3.9 ± 0.7	0.4
5.2 ± 0.9*	0.9*
6.5 ± 1.3	2.6
10.4 ± 1.8	5.2
20.8 ± 3.6	

* Values used in the *F. natalensis* simulations. Of that simulation 100 replicates were run, and 30 replicates for all other sets of parameters.

traits, assumed here to be shared by all individuals within the population: (1) mean interval between successive flowerings (I); (2) variance in interval between successive flowerings ($\sigma^2 I$); (3) mean duration of the reproductive episode, i.e., the time elapsed between arrival of pollinators and departure of their pollen-carrying offspring (D); (4) variance in duration of the reproductive episode ($\sigma^2 D$); and (5) length of male phase (the period over which pollen-carrying wasps leave the tree). Each crop was assumed to be in female phase (chemically attractive to pollinators) only during its 1st wk. To generate the flowering sequence for one tree, its first date of female phase was drawn at random from a uniform distribution between t_0 (the date of wasp immigration) and time $D + I$. The timing of the corresponding male phase was then computed by adding to the female-phase date a number of weeks drawn from a discretized version of a normal distribution of mean D and variance $\sigma^2 D$. The timing of the next female phase was computed by adding to this date a number of weeks drawn from a discretized version of a normal distribution of mean I and variance $\sigma^2 I$, and so on, until t_{max} (usually set at 4 yr) was reached. It was assumed that wasps departing during a given week could reach all female-phase crops in the population during that week only. Once the first tree was added that allowed wasps to be present somewhere in the fig population at t_{max}, the simulation stopped and the number of trees present (the critical population size, or CPS) was recorded. Three measures of individual reproductive success within that population were also recorded: (1) the proportion of all episodes that were sterile (i.e., those in which no pollinators were attracted), (2) the proportion of all episodes successful only in the female

phase (i.e., those in which trees did attract pollinators but failed to donate pollen several weeks later), and (3) the proportion of all episodes successful in both the female and male phases. Note that in figs, for reproduction to succeed in the male phase, an episode has to have succeeded in the female phase first.

The first simulation used the *F. natalensis* traits derived from the field study, with the length of male phase set at 1 wk. One hundred replicates were run. We then doubled male phase to 2 wk and ran another 100 simulations; this allowed us to investigate the effects of relaxing the tight within-tree flowering synchrony often assumed to exist in figs.

Thirdly, we measured the effects of altering phenological traits that control flowering frequency (D, $\sigma^2 D$, I, $\sigma^2 I$) over a range chosen to reflect known values for figs (Table 2; compare Table 1). Male phase length was again set at 1 wk. All parameters other than the one in question were held constant at *F. natalensis* values, except that variances were scaled proportionally to means in the simulations in which the effects of changing means were investigated. We ran 30 replicates using each set of parameters.

Lastly, we investigated how reproductive success of individual trees changed as populations exceeded CPS, the minimum size at which pollinators could persist. To do this, the model was altered to allow final population size to be fixed in advance. *F. natalensis* phenological parameters were used, with male-phase length set at 1 wk. Sets of 100 replicates were run using population sizes progressively 33% larger than the *F. natalensis* CPS value, until individual reproductive success reached a plateau. For each group of simulations, reproductive success was recorded as described above.

For comparing the results of different simulations, we use mean values of the measures of individual success and the median value of CPS (i.e., the population size at which there is a 50% chance that wasps will survive until t_{max}).

Our model makes several assumptions. (1) Wasps arrive at a tree during a 1-wk period only, and can survive 1 wk only between trees. (2) Flowering time is regulated only by the frequency distributions of D and I for the population; thus, the flowering status of neighbors, previous durations or intervals, and previous success or failure have no influence. (3) All times of year are equally favorable for flowering. The consequences of these assumptions are examined in the *Discussion*. We also include no spatial structuring, defining a fig population here as the number of trees within an area in which wasp transfer is possible, provided that wasps are available at the right time.

RESULTS

Field observations

The duration of *F. natalensis* reproductive episodes (Fig. 2) was normally distributed and averaged 5.2 ±
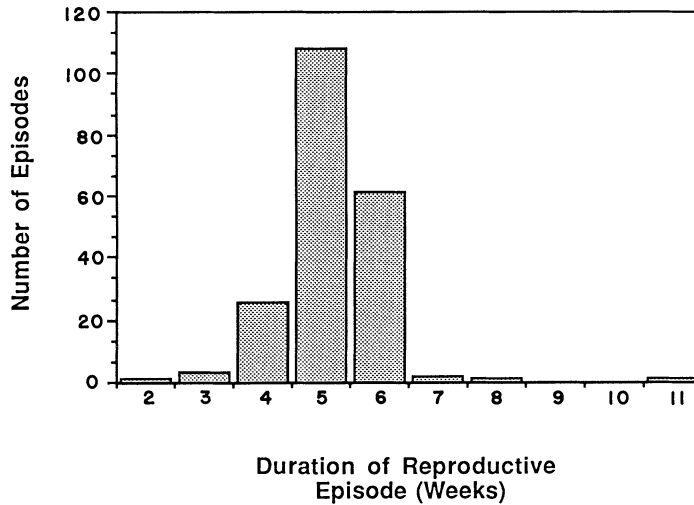
FIG. 2. Distribution of flowering durations in a Gabonese *Ficus natalensis* population. Durations were calculated from the time of peak wasp entry until the time of peak wasp departure from syconia, and averaged 5.2 ± 0.9 wk ($\bar{X} \pm$ SD, $n =$ 203).

0.9 wk ($\bar{X} \pm$ SD, $n = 203$; median $= 5$ wk). Interval between successive flowerings (Fig. 3) was left skewed and showed a bimodal tendency. Intervals averaged 44.1 ± 24.8 wk ($\bar{X} \pm$ SD, $n = 115$; median $= 42$ wk). This figure is necessarily an underestimate because it was calculated from observed intervals. Thus, it does not include intervals that began before censuses started, those that finished after censuses ended, or those that extended throughout the 4-yr census. Thirty-four trees on the 127-tree transect in fact never flowered during this study.

Flowering was evenly spread throughout the year. Michaloud (1988) found no predictability of flowering with month or rainfall, and a weakly significant correlation with river level in only 2 of 4 yr, suggesting that flowering is endogenously controlled.

Simulation using F. natalensis measured phenological parameters

Median critical population size (CPS) was 95 trees ($n = 100$ runs, time $= 4$ yr) (Table 3). Variation among runs was large (Fig. 4); in one case 294 trees were required to maintain a wasp population. Similar outliers occurred in all simulations. Although CPS calculated over only 4 yr will underestimate the median number of trees required to maintain a wasp population for longer periods, we have no evidence that this bias would be large. Median CPS increased by only 22% in simulations ranging from 0.5 to 4 yr (Fig. 5).

Table 3 lists three measures of reproductive success of individuals within 100 simulated *F. natalensis* populations of critical size. On average, trees failed to at-
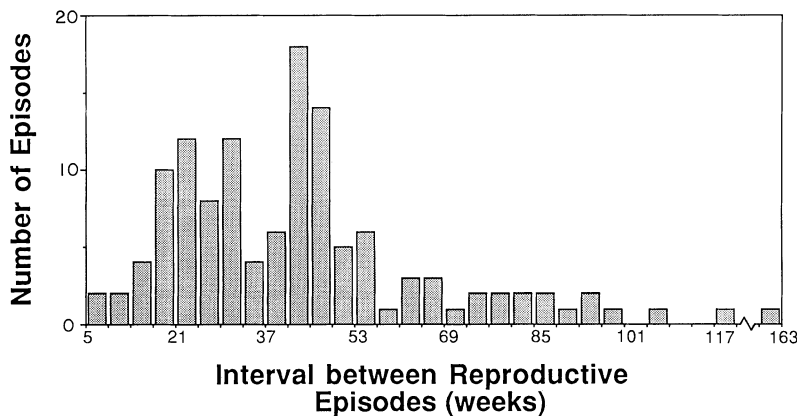

FIG. 3. Distribution of intervals between flowering episodes in a Gabonese *Ficus natalensis* population. Intervals were calculated from the time of peak wasp departure from syconia until the next peak of wasp entries, and averaged 44.1 ± 24.8 wk ($\bar{X} \pm$ SD, $n = 113$).
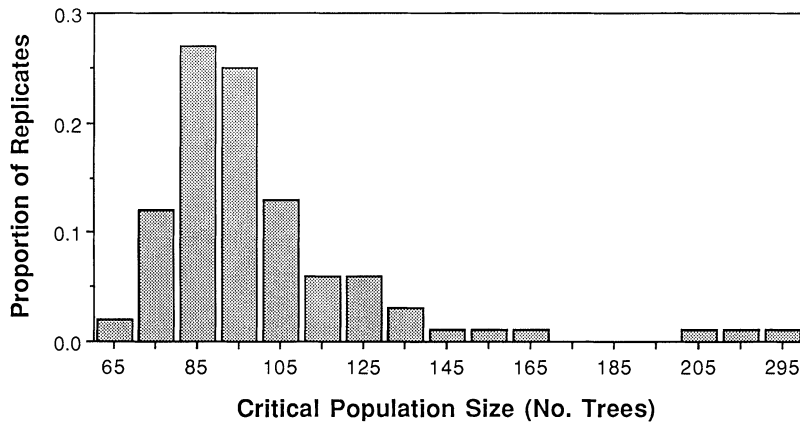
FIG. 4. Distribution of values of critical population size in 100 4-yr runs of the model, using *Ficus natalensis* phenological parameters.

tract pollinators in 35% of all episodes, and these were consequently sterile in both the female and male phase. In another 10% of episodes, trees attracted pollinators but could not successfully donate pollen to other trees, and thus were functionally female (i.e., male-sterile). In each population a few trees were sterile (2%) or male-sterile (3%) for the full 4 yr of the simulation.

Effect of lengthening male phase

Lengthening the male (pollen-donor) phase of all reproductive episodes from 1 to 2 wk had striking effects for critical population sizes and reproductive success of the trees within them. As shown in Table 4, median CPS decreased by 37%, from 95 to 58 trees, when male phase was doubled. As a rule, for a given parameter set in this model, individuals within smaller CPS populations experienced more frequent reproductive failure (J. L. Bronstein, *personal observation*); however, extending male phase *decreased* reproductive failure as it decreased CPS. In particular, the proportion of trees succeeding at least in the female phase increased by

27%. Effects were similar whether male phase was set to start 1 wk earlier than in the *F. natalensis* simulation (results in Table 4), or whether it was set to extend 1 wk longer (J. L. Bronstein, *personal observation*).

Effect of manipulating duration and interval of reproductive episodes

Ultimately, the factor determining the likelihood of pollinator persistence in a simulated population can be shown to be the total number of crops experiencing wasp arrivals and departures each week, which decreases as (duration + interval) increases. The effects on CPS of the four phenological parameters considered individually are shown in Fig. 6. CPS increased linearly when mean interval between flowerings was increased from 22 to 55 wk (Fig. 6A). Manipulating variance in interval while holding other parameters constant at *F. natalensis* values had no effect on CPS (Fig. 6B). CPS decreased sharply as mean duration of flowering increased, until near the *F. natalensis* value of 5.2 ± 0.9 wk, at which point it plateaued (Fig. 6C). The initially high CPS can be shown to be partially a consequence of the low variance, scaled to the smallest mean durations used in the simulation, rather than of low mean durations per se. Similar CPS values resulted when variance in duration alone was manipulated (Fig. 6D).

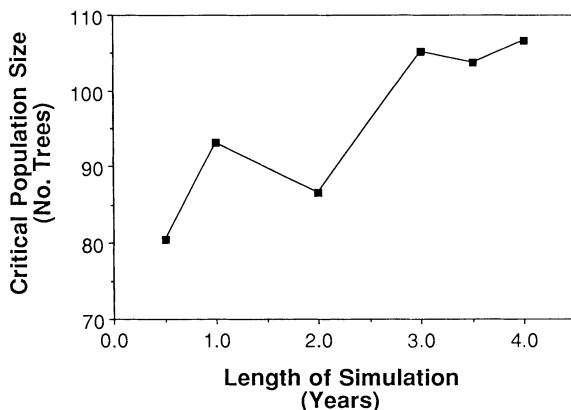Fig. 7 shows the frequency of reproductive failure of

FIG. 5. Critical population size of simulated *Ficus natalensis* populations followed from 6 mo to 4 yr. Medians of 30 replicates are shown.

TABLE 3. Simulation results: *Ficus natalensis* phenological parameters (duration = 5.2 ± 0.9 wk, interval = 44.1 ± 24.8 wk, female phase length = 1 wk, male phase length = 1 wk). Data from 100 replicates of a 4-yr period.

Critical population size (no. trees)	
Median:	95
Range:	65–294
Reproductive success (%, $\bar{X} \pm 1$ SD)	
Episodes female-fertile and male-fertile:	54.7 ± 13.4
Episodes female-fertile only:	10.2 ± 2.7
Episodes sterile:	35.1 ± 12.6

TABLE 4. Simulation results using *Ficus natalensis* pheno-logical parameters (see Table 3) but doubling male phase length to 2 wk. Data from 100 replicates of a 4-yr period.

Critical population size (no. trees)	
Median:	58
Range:	39–227
Reproductive success (%, $\bar{X} \pm 1$ SD)	
Episodes female-fertile and male-fertile:	59.4 ± 14.2
Episodes female-fertile only:	23.3 ± 0.7
Episodes sterile:	17.3 ± 10

individual flowering episodes in fig populations of crit-ical size characterized by different phenological param-eters. Neither mean nor variance in flowering interval had important effects on frequency of episode failure (Fig. 7A, B): consistently, ≈30% of all episodes failed in both the female and male phase and 10% succeeded in the female phase only. Mean and variance in flow-ering duration had similarly little effect on male-phase failure, but influenced total failure of episodes very strongly (Fig. 7C, D). More episodes were sterile when mean flowering durations were long and when variance in flowering duration was small.
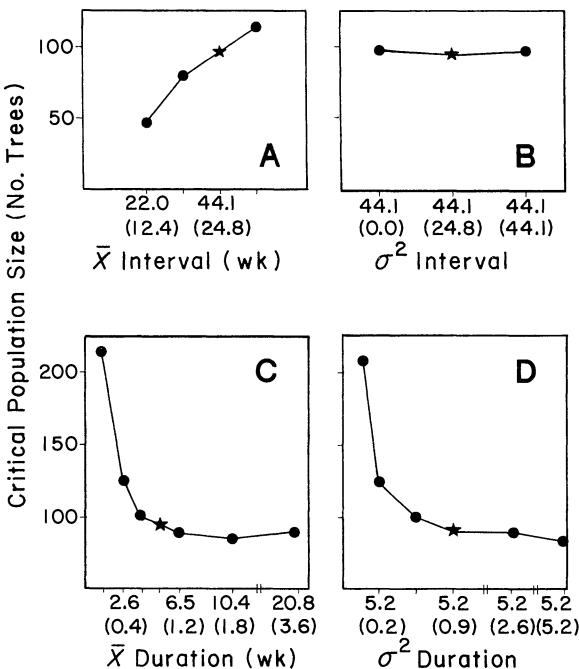

FIG. 6. Critical population size (CPS) as a function of phenological parameters. In each case, ★ represents CPS of the simulated *Ficus natalensis* population. Medians of 30 rep-licates are shown. Each simulation was run for 4 yr, holding all phenological parameters other than the indicated one con-stant at *F. natalensis* values; phenological parameters are shown as mean ± 1 standard deviation. (A) CPS as a function of mean interval between flowerings; variance was scaled in pro-portion to the mean. (B) CPS as a function of variance in interval. (C) CPS as a function of mean duration of repro-ductive episode; variance was scaled in proportion to the mean. (D) CPS as a function of variance in duration.
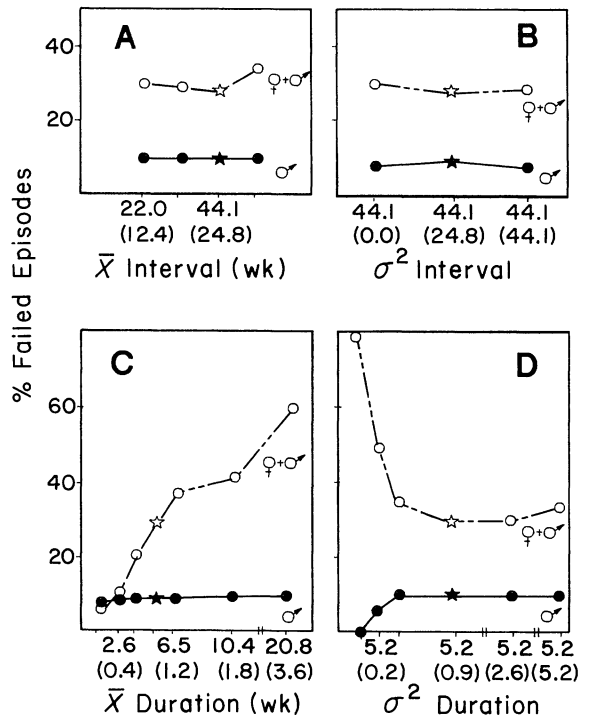

FIG. 7. Reproductive failure of individual flowering epi-sodes as a function of phenological parameters. Each point = mean of 30 runs; in each case, ★ represents value for the simulated *Ficus natalensis* population. ●——● proportion of all flowering episodes successful in the female phase only. O-·-·-O proportion of all episodes sterile. Each simulation was run for 4 yr, holding all phenological parameters other than the indicated one at *F. natalensis* values; phenological parameters are shown as mean ± 1 standard deviation. (A) Failure as a function of mean interval between flowerings; variance was scaled in proportion to the mean. (B) Failure as a function of variance in interval. (C) Failure as a function of mean duration of reproductive episode; variance was scaled in proportion to the mean. (D) Failure as a function of vari-ance in duration.

Reproductive success in larger populations

The likelihood of reproductive success for individ-uals within a population rose asymptotically as pop-ulations increased beyond their critical size. Success in both sexual phases exceeded 95% at 2–3 times CPS regardless of the phenological parameters used in the simulation. Fig. 8 illustrates the results on one such simulation using *F. natalensis* parameters.

DISCUSSION

Temporal separation of sexual phases in hermaph-roditic plants decreases the frequency of interference between the male and female reproductive functions in hermaphrodites (Lloyd and Webb 1986). However, for outcrossing to result from it, some degree of flow-ering asynchrony within a population is necessary; oth-erwise, all individuals will be in the same sexual phase simultaneously. One consequence of such asynchrony
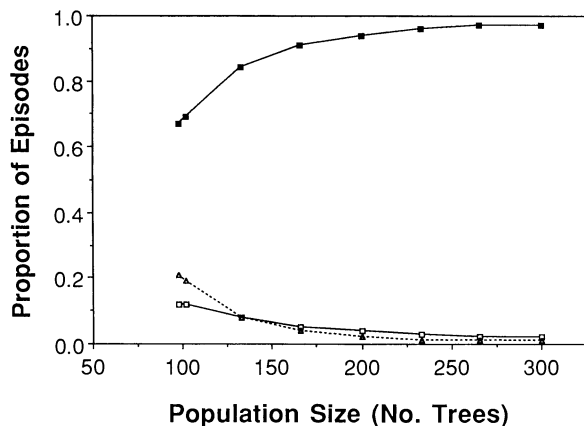
FIG. 8. Reproductive success in simulated *Ficus natalensis* populations larger than critical size. ■——■ proportion of all reproductive episodes successful in both reproductive phases. □——□ proportion of all reproductive episodes successful in the female phase only. ▲– – –▲ proportion of all reproductive episodes sterile. The first point on each line represents values at CPS; other points represent values at population sizes progressively larger than CPS. Reproductive success approaches 100% at population sizes 2–3 times larger than CPS.

is that within populations, flowering will be scattered and sporadic. This should have major implications for individuals, especially in small populations. Mate diversity should be low, and pollinator visitation as well; animals commonly abandon patches when floral resources fall below an acceptable level (e.g., Heinrich 1979, Augspurger 1981, Frankie and Haber 1983).

These effects should be particularly striking for monoecious figs. In this case, asynchronous flowering must extend year-round, since the species-specific pollinators cannot survive in the absence of a flowering individual. A gap in the flowering sequence therefore leads to local extinction of pollinators, rather than simply a temporary abandonment; wasp recolonization is necessary before any tree can reproduce again.

Population consequences of flowering asynchrony

Our model was formulated in part to examine how large a fig population must be for a pollinator population to be maintained indefinitely; that is, for no gap in the flowering sequence to arise that would cause all pollinators to die before reproducing. We found that this population size was highly sensitive to certain flowering traits but averaged ≈95 trees when flowering of one species, *Ficus natalensis*, was simulated. However, since simultaneity of male and female phases among plants is a probabilistic process, very large numbers of trees were sometimes required to maintain wasps (Fig. 4). Periodic loss of wasps may therefore be inevitable, even in populations considerably larger than the median "critical size." These results have clear consequences for conservation of figs and of the diverse organisms dependent upon them in tropical forests (e.g.,

see Morrison 1978, Janzen 1979, Milton 1980, Leighton and Leighton 1983, Terborgh 1986, Bronstein and Hoffmann 1987). The relationship between minimum viable population size (Shaffer 1981, Soule 1987) and CPS in figs has recently been discussed in detail by McKey (1989).

It should be pointed out, however, that there are as yet no field data available to test whether the likelihood of maintaining pollinators is in fact a function of fig population size. This is in part because accurate measures of population size depend on information about pollinator flight distance, which is still poorly known (Bronstein 1989). An island situation would provide a useful test of this hypothesis. For example, the pollinators of *Ficus microcarpa*, an Asian species commonly planted as an ornamental in the neotropics, unexpectedly appeared and established at certain neotropical sites during the 1970s (McKey 1989). It would be of interest to determine whether *F. microcarpa* population size is now an effective predictor of pollinator presence on New World islands.

Individual reproductive consequences

Flowering asynchrony should also have strong consequences for the breeding structure of plant populations. The more asynchronously that flowering occurs within a population, the fewer are the individuals with which a plant can potentially exchange genes in a given reproductive episode. For example, Primack (1980) calculated that in populations of four relatively synchronously flowering shrub species, individuals could on average exchange genes with only half the population; opportunities for gene exchange were fairly limited outside of the peak flowering period. *Cupania guatemalensis* (Sapindaceae), which flowers less synchronously and has temporally separate sexual phases, can cross with less than one-quarter of other individuals within a typical sexual phase (data from Bawa 1977). Monoecious figs represent an even more extreme case due to the requirement for flowering asynchrony to extend year-round. We calculate that from 1977 to 1980, *F. natalensis* individuals could potentially have exchanged genes with at most 10% of all censused neighbors during each sexual phase (J. L. Bronstein and G. Michaloud, *personal observations*).

This low potential for gene exchange in fig populations is intensified by two other factors. First, the male and female sexual phases are relatively brief (Ramirez 1970, Newton and Lomo 1979, Wharton et al. 1980, Bronstein 1987). In contrast, many obligate outcrossers remain in each sexual phase for prolonged periods, increasing the likelihood of pollen transfer (Bawa 1983, Rathcke and Lacey 1985). Secondly, pollen sources are relatively few because monoecious fig trees can only act as males if they themselves were successful females (i.e., were pollinated). In contrast, for example, *Cupania guatemalensis* individuals sometimes begin with or flower only in the male phase in a given year, which

greatly increases the number of functionally male trees per functional female at each time period (Bawa 1977, see also Thomson et al. 1989).

Consequences of extreme asynchrony should therefore include (1) low mate diversity within successful reproductive episodes (a phenomenon not yet studied empirically or theoretically for figs) and (2) few successful episodes. In simulated *F. natalensis* populations of critical size, 35% of individuals failed to attract pollinators, and of those that did, 10% failed to successfully donate pollen. (Episodes that attracted any pollinators were simply recorded as "successful," although more realistically, the level of success should vary with such factors as the number of pollen-carriers departing per male-phase tree, the number of male-phase trees, and the number of female-phase trees competing for pollinators.) At present, little field data are available on fig pollination success and none on pollen-donation success, but each study to date has reported great variability in success among individuals and over time (Hill 1967, Michaloud et al. 1985, Kjellberg et al. 1987). Bronstein (1988) found that within a large Costa Rican fig population, pollination success ranged fully from 0 to 100%; in ≈15% of reproductive episodes, pollinator arrivals were rare enough that 10% or fewer of the syconia were entered.

Effects of varying phenological traits

Longer sexual phases greatly increased the chance of a "match" between female-phase trees and pollen-carrying wasps, thus reducing critical population sizes and elevating individual reproductive success (compare Tables 3 and 4). Yet most of the very few fig species whose phenologies have been studied to date attract and release pollen-carriers for relatively brief periods. It may be too early to assume that this phenological pattern is usual for figs, however. A few species have in fact been reported to initiate inflorescences asynchronously within trees, a phenomenon that prolongs both sexual phases (reviewed by Bronstein 1989). Individuals within these species sometimes flower so asynchronously that intervals between successive reproductive episodes effectively disappear (e.g., Baijnath and Ramcharun 1983, 1988). Such extreme within-tree asynchrony has been thought to be an adaptation of figs to reduce wasp mortality during harsh conditions, because it potentially can allow a pollinator population to persist for months by moving among inflorescences on a single tree (Ramirez 1970, Janzen 1979). The geographical and seasonal distributions of within-tree asynchrony are not, however, in accord with this hypothesis (Bronstein 1989): asynchrony is often most marked in the best season for wasp flight, not the worst, and species in seasonal environments do not show higher frequencies of within-tree asynchrony. We suggest that given the pollen-limited reproductive success and pollinator extinction inherent to this interaction, within-tree asynchrony may be more generally advantageous and more common than previously assumed. Much more precise phenological studies of figs are needed, however, to assess the frequency of this phenological pattern. Its possible benefits and costs must also be quantified. In particular, within-tree asynchrony would increase the probability of geitonogamy (within-individual pollen transfer), thereby reducing the primary benefit of temporal dioecy.

Results of our model suggest that the durations of reproductive episodes and the intervals between them also critically influence probabilities of reproductive success and pollinator persistence. For pollinators to persist within a simulated population, a minimum number of crops had to be receptive to pollinators each week. This number depends directly on population size/(duration + interval). Consequently, increasing either mean duration or mean interval led to a linear increase in CPS, which in effect is the population size necessary to maintain the same minimum number of crops receptive per week. The two apparent differences in the effects of changing mean duration (Fig. 6C) and mean interval (Fig. 6A) are largely artifactual. First, the more marked effect of altering interval was due simply to the wider absolute range over which we chose to manipulate it, given the greater intra- and interspecific variation in intervals (Table 1, Figs. 2 and 3). Secondly, the high CPS values obtained using very short durations were primarily caused by the very small variances scaled to those short durations in our simulations (compare Fig. 6C and 6D). When variance in duration is very low, adding another tree that attracts pollinators during the same week as an individual already present in the population is unlikely to allow an existing gap in the flowering sequence to be bridged, since that tree will most often release wasps at the same time as the other. Decreasing variance in interval will not have this effect (Fig. 6B), as long as there is some variance in duration.

Whereas mean durations and intervals influence CPS in a qualitatively similar fashion, their effects on reproductive success of individuals within CPS populations differ. Altering intervals changes CPS, but not the number of crops receptive each week once at CPS, and therefore not the expected reproductive success of individuals within that population (Fig. 7A). Altering duration, however, has the effect of changing the number of "reserves" of wasps present within a CPS population. With very long durations, relatively few trees might be necessary to sustain a local wasp population, but searching wasps are rarely available so very few trees successfully attract them. With shorter durations, searching wasps are available many more weeks of the year, guaranteeing higher success for the average tree (Fig. 7C). Only if variance in duration is very small is expected reproductive success low (Fig. 7D), as flowering often becomes grouped on dates when no wasps are available (the same process that elevates CPS when variance in duration is very small).

Two biologically interesting points emerge. First, lengths of sexual phases and the durations of reproductive episode, which have rarely been measured precisely for figs, seem critical for determining the dynamics of these systems. In contrast, the high variability in the interval between flowering episodes, much more frequently remarked upon, has relatively little impact on either long-term pollinator persistence or short-term plant reproductive success. Variable interval length may be a simple consequence of different rates of resource accumulation over time (A. Herre, *personal communication*). If individuals were able to initiate reproductive episodes as soon as they accumulated sufficient resources, lifetime reproduction would be increased (Milton et al. 1982). Furthermore, as Bawa (1977, 1983) and Janzen (1979) have pointed out, variable interval length also acts to scramble the flowering order in the population, assuring that an individual will have different mates over time.

Secondly, it is evident from recent studies (Baijnath and Ramcharun 1983, 1988, Bronstein 1989, Windsor et al. 1989) and data summarized in Table 1 that there is great interspecific variation for the traits we found to strongly influence success for figs and pollinators. These observations suggest that life history strategies may differ among monoecious fig species. For example, given equivalent dispersal rates and ages at first reproduction, fig species with long sexual phases and short intervals between reproductive episodes may be the most successful colonizers of new habitats, since they can maintain a pollinator pool at the smallest population sizes.

Because the timing of flowering can strongly influence individual success, we expect the phenological traits examined here to be under strong selection. To study the consequences, an ecological model such as the one presented here is inappropriate; an evolutionary model, in which the performance of different flowering strategies within the same population can be compared, is necessary (e.g., Kjellberg and Maurice 1989). Possible trade-offs between flowering frequency and other life history traits, such as age at first reproduction and life-span, must also be examined before predictions can be made about the evolution of phenological traits.

Assumptions of the model

The particular values for critical population size and reproductive success derived by our model (although not the trends predicted by it) depend on several assumptions that we have made. Given the very high frequencies of reproductive failure that the model predicts, it is particularly important to assess the consequences of those assumptions.

First, we assumed fig wasps could survive 1 wk between trees. Note that the simulation in which the length of figs' male phase was doubled (Table 4) could equally well be interpreted to predict the consequences

of holding flowering phenology constant while doubling wasp life-span: longer survival increases the probability that wasps would reach a flowering tree, greatly lowering critical population size and raising success of individuals within those populations. However, laboratory results (e.g., Joseph 1958) and the only mark–recapture study to date (Kjellberg et al. 1988) indicate that 1 wk probably overestimates average life-span by several days. Thus, we expect that adding more realistic wasp behavior to our model would in fact further elevate CPS and lower expected success of individual trees.

Secondly, our model assumes that flowering frequency is regulated by an internal "clock," characterized by a mean and variance in flowering duration and a mean and variance in interval between successive flowerings. Therefore, such factors as previous flowering durations or intervals, previous reproductive success or failure, and the flowering status of neighbors were assumed not to influence flowering times of individual trees. If this assumption is incorrect, the predicted values of individual reproductive success would be inaccurate. For example, trees that could predictably pass through female phase at times of year when others were predictably in male phase would experience higher female-phase success than our model would predict (see Kjellberg and Maurice 1989). However, there is as yet no evidence from the very few detailed studies of fig flowering phenology (Hill 1967, Milton et al. 1982, Bronstein 1986, Michaloud 1988) that any of these factors influence flowering time. To date, the only variable found to be correlated with any phenological parameter has been tree size: Milton et al. (1982) found that trees with larger girths and crowns had shorter intervals between flowering episodes. They suggest that larger trees accumulate the reserves necessary for reproduction at a faster rate.

Thirdly, all times of year are equally favorable for flowering in our model. This assumption may be adequate for an equatorial species like *F. natalensis*; Michaloud (1988) has found no predictability of flowering with month or rainfall in this species (see *Methods*). In contrast, in seasonal sites, more fig individuals flower at certain times of year (Hill 1967, Wharton et al. 1980, Milton et al. 1982, Baijnath and Ramcharun 1983, 1988, Windsor et al. 1989), perhaps resulting from selection due to seasonal variation in conditions for flowering, seed dispersal, seed germination, and/or wasp survival (Bronstein 1989, Kjellberg and Maurice 1989, Windsor et al. 1989; cf. Marquis 1988). Strong seasonal variation that decreases the likelihood of flowering during certain periods will increase the probability of a gap occurring in the flowering sequence. Adding seasonality to our model does in fact lead to much higher critical population sizes and probabilities of reproductive failure (J. L. Bronstein, *personal observation*). Not surprisingly, biogeographical studies (e.g., Corner 1958) indicate that monoecious *Ficus*

species progressively drop out of the flora with increasingly seasonal conditions.

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