Coadapted Competitors: The Flowering Seasons of Hummingbird-Pollinated Plants in a Tropical Forest

Abstract. *A system of compensating phenological responses of different species to unusual rainfall conditions may play a major role in maintaining an orderly, staggered sequence of flowering peaks among the hummingbird-pollinated plants of a Costa Rican rain forest. Quantitative phenological studies over several years may be essential to understanding the temporal organization of many tropical communities.*

Plants sharing pollinators or dispersers tend to show staggered flowering or fruiting seasons (*1-3*), probably as a result of competition for animal vectors (*4*) or as a selection against hybridization (*3, 5*). The overall effect is to provide a temporally continuous resource for the vectors, stabilizing their presence in the community (*6*). Little is known about possible mechanisms that could permit these plant species to maintain an orderly flowering or fruiting sequence year after year, in the face of annual variations in environmental parameters. Precipitation patterns anywhere vary considerably from year to year (*7*), but at high latitudes pronounced and regular cycles of photoperiod and temperature can impose order upon phenological cycles. In the humid lowland tropics, these latter parameters cycle at very low amplitudes or irregularly, if at all, making the disruptive influence of abnormal periods of rainfall potentially greater. It should be noted that the direct proximate cues affecting flowering may be temperature or humidity changes (usually) associated with rainfall (*8*). These and other microclimatic factors may have to be considered in explaining the details of tropical phenological cycles, but the major patterns should still be at least indirectly related to rainfall patterns.

Theoretically, the plants sharing an animal vector might behave in one of two ways in order to preserve an orderly sequence of flowering or fruiting peaks after unusual (relative to long-term averages) rainfall. These are (i) a displacement of the entire sequence, or (ii) a pattern of opposite and compensating responses among the different species such that a staggered sequence could still result, while the order of the species within the sequence changed. This latter would imply a high level of coadaptation among competing plant species, also that the advantages of minimizing competition for animal vectors outweigh the disadvantages of physiologically expensive phenological responses in some species. This pattern would also require that periods of "unusual" rainfall recur often enough to constitute a strong selective force.

Data on these questions were obtained during a 4-year study of the flowering phenologies of hummingbird-pollinated plants at Finca La Selva, Costa Rica (*9, 10*). We can assume that the level of coadaptation in this community may be high since nearly all of these plants are exclusively pollinated by hummingbirds, which in turn depend on the nectar of these flowers for the energy supplies required for breeding and molt (*3, 11*). The overall results of the study have been described (*12*); of particular interest to this discussion are the data from ten species pollinated by hermit hummingbirds (subfamily Phaethorninae). Hermit hummingbirds are nonterritorial, traplining foragers of the forest understory and have long, curved bills. The correspondingly long, curved corollas of their preferred food plants tend to largely exclude hummingbirds with shorter, straighter bills (*3, 11*). Thus, among the ornithophilous plants of La Selva, the hermit-pollinated species form a morphologically and ecologically defined subgroup that is ideal for detecting phenological interactions.

Rainfall records (Fig. 1A) indicate that unusually wet or dry months (that is, months with rainfall differing by more than 1 standard deviation from long-term means) occurred throughout the study. The phenological data (Fig. 1B) show that a regular sequence of flowering peaks was nearly always maintained. At no time during the study were more than three species in full bloom, or five species in good bloom (*10*). Moreover, the periods of greatest overlap include two *Heliconia* species whose blooming seasons may have converged due to microhabitat factors (*3*). Conversely, only during late November to early December was no hermit food plant ever at peak bloom; this in fact seems to be a time of flower scarcity for hermits, and may play a major role in regulating their populations (*13*).

More striking still is the way in which a regular sequence of flowering peaks was maintained; in no 2 years was the order of blooming precisely the same

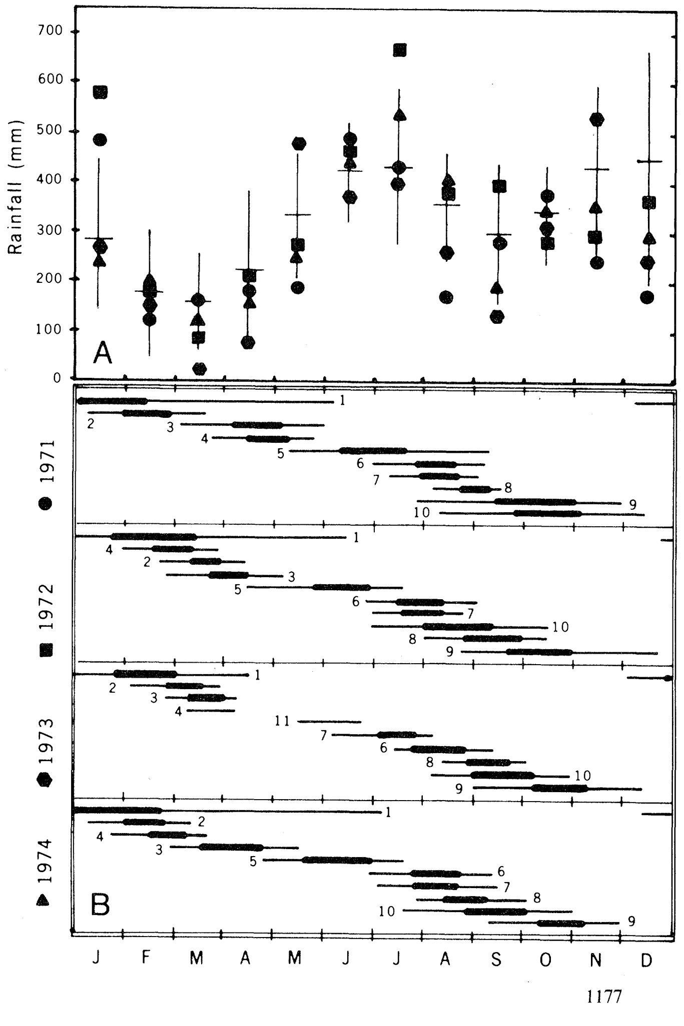

Fig. 1. (A) Monthly rainfall at Finca La Selva, Costa Rica, 1971 to 1974. Horizontal and vertical lines represent, respectively, mean monthly rainfall 1957 to 1975, plus or minus 1 standard deviation. Symbols for years are given along the left side of part B. (B) Blooming seasons of major hermit food plants 1971 to 1974. Heavy lines represent periods of peak bloom, thin lines periods of good bloom (*10*). Plant species are: 1, *Heliconia pogonatha*; 2, *Passiflora vitifolia*; 3, *Heliconia wagneriana*; 4, *Jacobinia aurea*; 5, *Costus ruber*; 6, *Heliconia* sp. 18; 7, *Heliconia* sp. 16; 8, *Aphelandra sinclairiana*; 9, *Costus malortieanus*; 10, *Heliconia* sp. 3; and 11, *Malvaviscus arborea*.

(Fig. 1B). Differing responses to particular periods of rainfall seem to be implicated. For instance, after a dry August in 1971, the flowering of *Heliconia* sp. 3 was retarded while that of *Costus malortieanus* was accelerated. The very wet period from December 1970 to January 1971 seemed to accelerate flowering of *Passiflora vitifolia* while retarding that of *Jacobinia aurea*, in comparison to other years. A severe drought between late February and April 1973 strongly affected the flowering of several species, producing a major flower shortage in May and June. This shortage was to some extent ameliorated by *Malvaviscus arborea*, which put on an unusually synchronized burst of flowering in June 1973; normally the species maintains a very low level of blooming year-round with little synchrony between individual plants, and is of only minor importance as a hermit food plant.

Two further conclusions are suggested by Fig. 1: first, unseasonably wet or dry periods affect flowering most strongly if they occur just before anthesis, perhaps interfering with differentiation of the flower bud itself (*14*). Second, the phenology of dry season flowerers may be more sensitive to unusually wet periods, while rainy season flowerers may be more affected by unusually dry periods and less by very wet ones. However, a sufficiently severe drought can retard or abolish flowering of even dry season bloomers. Only in such severe droughts will the advantages of flowering in sequence be overcome by physiological stress to the plant.

These data suggest that compensatory phenological reactions to periods of unusual rainfall exist among the hummingbird-pollinated plants of La Selva, and that these reactions may play a fundamental role in the year-to-year organization of the bird-flower community. Corresponding data from a California bird-flower community (*15*) and tropical bee-flower community with strong differentiation between wet and dry seasons (*2, 16*) suggest that in more seasonal climates displacement of the entire flowering sequence is the major mechanism for preserving staggered blooming sequences. Quantitative phenological studies of several years' duration, combined with ecologically based experimentation on physiological control mechanisms may prove essential to an understanding of the temporal organization of tropical plant communities.

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Fenfluramine and Fluoxetine Spare Protein Consumption While Suppressing Caloric Intake by Rats

Abstract. *The effects of fenfluramine and other anorectic drugs on the consumption of both protein and total calories by rats given simultaneous access to two isocaloric diets containing 5 or 45 percent casein were examined. Anorectic doses of fenfluramine failed to decrease protein intake but increased the proportion of total dietary calories represented by protein. In contrast, anorectic doses of* d-*amphetamine decreased protein and calorie consumption proportionately. Subanorectic doses of fenfluramine also increased the proportion of caloric intake represented by protein among animals given prior treatment with the serotonin precursor tryptophan. Fluoxetine, a drug that blocks reuptake of serotonin, similarly spared protein consumption while reducing caloric intake. These observations indicate that two distinct brain mechanisms, sensitive to different drugs, underlie the elective consumption of protein and calories.*

The effects of anorectic drugs on food consumption have traditionally been studied by giving a rat access to a single diet, usually rat chow, and then measuring its total food intake. This procedure allows the investigator to detect changes in the total number of calories that the animal consumes. It does not, however, allow detection of any changes that the drug might cause in food preference: the test animal has no way of displaying its choice.

We now describe an experimental procedure that allows the investigator to distinguish the effects of a drug on the intake of calories, per se, from its effects on the consumption of a particular nutrient—in this case, protein. We treat animals with a drug and then allow them to select among two or more isocaloric

Table 1. Effects of fluoxetine on food intake and protein consumption. Groups of 8 rats (34- to 41-day-old males), which were trained to consume their daily food intake during an 8-hour dark period, received fluoxetine or saline intraperitoneally and were given access to two isocaloric diets (5 and 45 percent protein). C, control; F, fluoxetine.

Time (hours)	Dose (mg/kg)	Food consumed (g)		Protein as percent of total calories consumed*	
		C	F	C	F
1	5	11.6 ± 0.8	6.5 ± 1.0*	22 ± 2	28 ± 2
1 to 3	5	4.0 ± 0.4	4.7 ± 0.7	26 ± 2	34 ± 2†
3 to 5	5	5.6 ± 0.9	4.7 ± 1.1	25 ± 4	25 ± 4
5 to 8	5	5.3 ± 0.5	5.6 ± 1.1	23 ± 4	24 ± 5
1	10	11.7 ± 0.9	4.4 ± 0.9‡	17 ± 2	26 ± 3§
1 to 3	10	3.6 ± 0.7	4.6 ± 0.7	14 ± 4	28 ± 4*
3 to 5	10	3.2 ± 0.5	4.5 ± 0.8	24 ± 5	21 ± 5
5 to 8	10	5.5 ± 0.6	7.0 ± 1.0	30 ± 4	19 ± 5

*$P < .005$. †$P < .025$. ‡$P < .001$. §$P < .05$. All as compared to the control.