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ASYNCHRONOUS PHENOLOGIES OF A NEOTROPICAL ORCHID AND ITS EUGLOSSINE BEE POLLINATOR

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A variety of biotic and abiotic factors determines the timing of germination, flowering, and fruiting in plants (Rathcke and Lacey 1985). The "pollinator tracking" hypothesis suggests that flowering patterns are determined by trends in pollinator availability. For example, Waser (1979) found that ocotillo (*Fouquieria splendens*) flowers when migrating hummingbirds and local populations of carpenter bees are in greatest abundance. Similarly, color shifts in the flowers of scarlet gilia (*Ipomopsis aggregata*) match seasonal changes in the relative abundance of hummingbirds and sphinx moths (Paige and Whitham 1985). In both these studies the matching of flowering with pollinator availability was attributed to stabilizing selection on characteristics of plant flowering. Competition for pollinators among sympatric plant species (reviewed in Rathcke 1983, Waser 1983) has also received attention in this regard.

Correlations with other phenological events may exert control on flowering times, but this aspect of the evolution of flowering phenologies is poorly understood (Rathcke and Lacey 1985). Also, few empirical studies have considered potential constraints on the timing of flowering, but Kochmer and Handel (1986) concluded that phylogenetic and life-history constraints were important determinants of flowering phenologies for North Carolinian and Japanese floras.

Most orchids that are pollinated by male euglossine bees conform to predictions of the pollinator-tracking hypothesis. Ackerman (1983*a*) assessed seasonal changes in euglossine bee populations on Barro Colorado Island, Panama, using chemical baits, and compared bee seasonality to flowering records of orchids pollinated by the bees. In general, orchid flowering times coincided with a peak abundance of the bee species that pollinate them, which occurred between February and June in almost all bee species. However, the recorded flowering times for *Catasetum viridiflavum* and *C. bicolor* extended throughout the year, indicating that a significant amount of flowering takes place when pollinators are not abundant. We present 2.5 yr of direct observation of the flowering patterns in *Catasetum viridiflavum* Hook. and relate these observations to 6.5 yr of seasonal-abundance data for its pollinator, *Eulaema cingulata* (Fab.) (Ackerman 1983*b*, Roubik and Ackerman 1987). We show that the phenology of *C. viridiflavum* is asynchronous with that of its pollinator and suggest that this results from constraints on flowering that preclude pollinator tracking.

Materials and Methods

Catasetum viridiflavum is a dioecious, epiphytic orchid that occurs only in central Panama (Hills et al. 1972). Plants occasionally produce monoecious inflorescences (see Fig. 1). The flowers are large (3 cm) and sexually dimorphic, readily allowing visual censuses of the flowering and sex of plants in forest canopies. Plants that flower produce one to three inflorescences during a season. They are pollinated almost exclusively by *Eulaema cingulata* at our study sites (Ackerman 1983*a*, Roubik and Ackerman 1987). Bees are attracted to the plants by fragrant chemicals produced in the labella of flowers.

Vegetatively *C. viridiflavum* consists of a leafy shoot that bears a developing pseudobulb and a number of older leafless "back bulbs." The plants are drought-deciduous, dropping their leaves and becoming dormant at the onset of the dry season (December). Active growth resumes in the middle of the dry season (February), with the initiation of a new leaf-bearing shoot, and accelerates at the onset of the wet season (May). Inflorescences are only produced from the active leafy shoots. Fruit development occurs over a period of ≈2 mo but the capsules do not dehisce until the following dry season when the seeds are dispersed by the dry-season trade winds.

In February of 1985, 210 individuals of *C. viridiflavum* were located in the forest canopy of Barro Colorado Island (BCI), a lowland, moist, semi-deciduous forest preserve (see Croat 1978 and Leigh et al. 1982 for detailed descriptions) located in Gatun Lake, part of the Panama Canal, Panama. All plants grew from 1 to 25 m aboveground and were observed from trails or the shoreline. Between 15 June and 8 December 1985 each plant was censused for flowering, sex expression, and fruit-set every 2 wk to 1 mo. During 15 May–15 December 1986, 218 plants were censused in the same manner. This sample included 30 additional plants replacing 22 plants from the original survey that had died or could no longer be monitored because of changes in the forest canopy. Three final censuses were made on 31 March, 24 April, and 28 May 1987. These cen-

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suses included the routes used in previous years plus additional shoreline areas.

Seasonal changes in the abundance of *E. cingulata* were determined from data sets compiled by Ackerman (1983*b*) on BCI and by Roubik and Ackerman (1987) at Pipeline Road (PR), in Parque Nacional Soberanía, 10 km from BCI. BCI and PR have similar forests, and Ackerman (1983*b*) demonstrated from a 1-yr census that the two sites display similar abundances and population dynamics of resident euglossine bees. Ackerman (1983*b*) censused bees on BCI at weekly intervals for 13 mo between February 1979 and February 1980. Bees were censused using 16 chemical baits placed on 7 × 7 cm pads of herbarium blotter. Bees at baits were counted every 15 min from 0830–1230. Roubik and Ackerman (1987) censused bee populations at PR monthly from October 1979 to September 1985. Bees were counted at three baits during the 1st wk of each month using the methods described above. In both studies almost all *E. cingulata* were attracted to skatole baits. Ackerman (1983*b*), Roubik and Ackerman (1987), and Roubik (1989) provide more detailed information on the sampling programs and assumptions used to census bee populations.

Results

C. viridiflavum produced flowers during nine months of the year (Fig. 1, Table 1). In the first 2 yr of the study, censuses began in May or June. At this time some plants possessed dried flowering stems on active shoots (Fig. 1) indicating that flowering had occurred at an earlier date. Observations extending to late May 1987 indicated that the onset of flowering took place in early April of that year (Table 1). In 1985 and 1986 few plants (generally 2–8 plants per census) flowered during the first half of the wet season (May to early August, Fig. 1). A greater abundance of flowering individuals was found in the late wet season in both these years, and peak flowering occurred in October (1985) or late August/early September (1986; Fig. 1).

In the years 1979–1985, peak abundance of the pollinator, *E. cingulata,* at PR occurred most often in April (Fig. 2). The raw numbers of bees censused during the 6-yr period showed a pronounced peak in April. Seasonal population peaks during individual years occurred most often in April, but also occurred in February and May (Fig. 2). Seasonal changes in bee abundance on BCI in 1979 and early 1980 exactly paralleled the pattern observed at PR (Fig. 2).

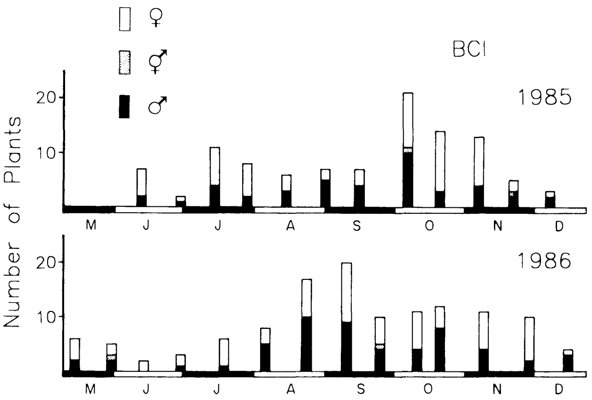

FIG. 1. The flowering phenology of *Catasetum viridiflavum* on Barro Colorado Island (BCI) for 1985 and 1986. Height of bars indicates the number of plants possessing flowers on a particular date plus plants known to have flowered since the previous census. The first bar for each year indicates the number of plants with flowers on that date, plus plants that had flowered prior to the first census. Plants that had flowered previously were indicated by dried flower stems (also sexually dimorphic) present on the current year's growth

Fruit-set in female *C. viridiflavum* in 1985 and 1986 exceeded 50% during the earliest portion of the flowering period, and was considerably lower (4–21%) later in the season (Table 1; *G* test, df = 1, $P < .001$ in both years). Hand pollinations of female *C. viridiflavum* on dead trees in Lake Gatun conducted during August 1984 almost always resulted in fruit formation (fruit-set = 95.8% of 71 flowers on 19 plants). To the degree that these data are representative of the general population, large changes in fruit-set should relate directly to changes in bee visits to orchid inflorescences. Thus seasonal changes in fruit-set (Table 1) on BCI during 1985–1986 were consistent with seasonal changes in

TABLE 1. Reproductive success of female *Catasetum viridiflavum* (on a per-inflorescence basis) on Barro Colorado Island, Panama, during different phenological periods.

	Fruit set		Fruit loss before dehiscence		% Fruiting suc-
Period	% set	No. flowers	% lost	No. fruits	cess*
		A. 1985			
Before June 15	80.0†	10	9.1	11	72.7
June 16–Sept 1	21.3	47	0	10	21.3
Sept 2–Dec 8	5.7	88	0	5	5.7
		B. 1986			
Before May 15	52.9†	17	77.8	9	11.7
May 16–Aug 24	4.3	46	0	2	4.3
Aug 25–Dec 15	4.8	125	0	6	4.8
		C. 1987‡			
Mar 31–Apr 24	55.6	9	...		...
Apr 25–May 28	17.9	28	...		...

* Percentage of flowers with fruits remaining until the dry season, when dehiscence occurs.

† Values of fruit-set in the earliest time period were determined from the number of flower scars on clearly visible infructescences.

‡ Difference in fruit-set between census periods was significant (Fisher exact test, $P = .041$).

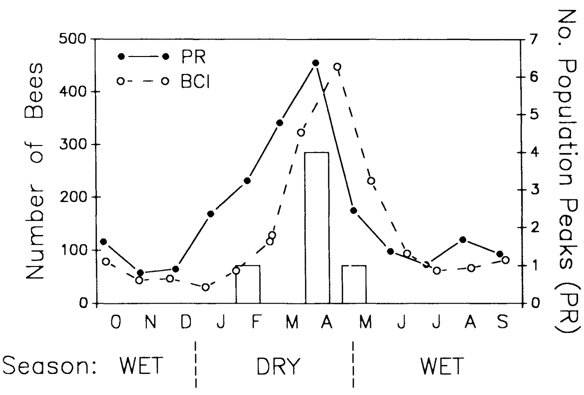

FIG. 2. Changes in seasonal abundance of male *Eulaema cingulata* at Pipeline Road (PR) and Barro Colorado Island (BCI). Data from PR represent the period October 1979–September 1985 (Roubik and Ackerman 1987). ●——● depicts sums of the number of bees attracted each month to chemical baits at PR; bars indicate the number of times peak annual abundance was observed in a particular month. ○– – –○ depicts abundance of *E. cingulata* on BCI between February 1979 and February 1980 (Ackerman 1983*a*, *b*). Values represent sums of four weekly censuses plotted against median sampling date.

bee abundance observed at PR and BCI (Fig. 2). Data collected in April and May 1987 (Table 1) indicated that fruit-set declined significantly by May. This trend coincides with the observed decline in bee abundance between April and May in most years that bees were censused (Fig. 2).

Female plants that flower early must retain fruits up to 9 mo before dehiscence occurs in the dry season. Many such fruits were lost during the wet season. These fruits evidently rotted and fell from the plants; dehiscence did not occur as observed in the dry season. Fruit loss only occurred from inflorescences produced in the early portion of the flowering season in 1985 and 1986 (Table 1). The percentage of fruits lost varied greatly among years, but the fruiting success (percentage of surviving fruits) of inflorescences produced early in the season was consistently greater than that when plants flowered later (Table 1; Fisher exact test: 1985, $P = .064$; 1986, $P < .001$).

Discussion

The factors that determine the phenologies of euglossine bees are likely related to the general availability of food plants. At lowland sites in central Panama the food plants of euglossine bees flower in greatest abundance in the late dry season and early wet season, closely matching observed patterns of seasonal bee abundance (Ackerman 1985). *Eulaema cingulata*, the pollinator of *C. viridiflavum*, is distributed throughout the Neotropics (Ackerman 1983*a*) and, in central Panama, pollinates at least six different species of orchid (Roubik and Ackerman 1987). Thus its phenology would not be expected to be closely tied to that of a single orchid species having a relatively small geographic range. In contrast, *C. viridiflavum* relies almost exclusively on *E. cingulata* for pollination and might be expected to flower when pollinators are most active at orchid inflorescences.

Flowering time in *C. viridiflavum* appears to be maintained by factors that preclude pollinator tracking; bee population and flowering peaks are frequently out of phase by as much as 6-mo. Patterns of fruit loss indicate the potential for counter-selection against plants that flower early, near the time of peak pollinator abundance. However, fruit loss did not completely negate the higher fruit-set of early flowering plants during our study (Table 1). The failure of *C. viridiflavum* to flower when pollinators are abundant might also result from constraints imposed, in part, by the abiotic environment. At the time of highest bee activity, *C. viridiflavum* is initiating new growth after the dormant period that occurs in the early dry season. The general increase in flowering towards the latter part of the growing season (Fig. 1) suggests that plants maximize growth following dormancy as a precondition for reproduction later in the growing season. Other orchid species may overcome this constraint by separating periods of growth from periods of flower and fruit production. In central Panama orchids in the genus *Mormodes*, closely related and vegetatively identical to *Catasetum* (Williams and Allen 1980), flowering in the dry season when their pollinators are most abundant (Ackerman 1983*a*). *Mormodes* does not possess leaves when in flower (e.g., see Williams and Allen 1980:358), suggesting that *C. viridiflavum* might also flower at this time. In *Mormodes*, however, inflorescences arise from pseudobulbs produced in the previous year, while in *Catasetum* they are produced from the current years' growth. Thus patterns of growth and flowering are different in the two genera, suggesting that flowering time in *Catasetum* may be constrained by factors related to growth form.

Our results indicate that constraints have markedly affected the evolution of flowering time in *C. viridiflavum*. Flowering time is not simply a function of pollinator abundance, and plants have not responded to selection as predicted by the hypothesis of optimal pollination (Kochmer and Handel 1986). It appears that constraints on growth and flowering imposed by drought-induced dormancy best explain the observed phenology in *C. viridiflavum*, although the possibility of a negative correlation between early fruit-set and ultimate fruiting success has not been eliminated by our observations. These effects are not mutually exclusive and deserve further study.

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Literature Cited

Ackerman, J. D. 1983*a*. Specificity and mutual dependency of the orchid–euglossine bee interaction. Biological Journal of the Linnean Society **20**:301–314.

———. 1983*b*. Diversity and seasonality of male euglossine bees (Hymenoptera: Apidae) in central Panama. Ecology **64**:274–283.

———. 1985. Euglossine bees and their nectar hosts. Pages 225–233 *in* W. G. D'Arcy and M. D. Correa A., editors. The botany and natural history of Panama. Missouri Botanical Garden, Saint Louis, Missouri, USA.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA.

Hills, H. G., N. H. Williams, and C. H. Dodson. 1972. Floral fragrances and isolating mechanisms in the genus *Catasetum* (Orchidaceae). Biotropica **4**:61–76.

Kochmer, J. P., and S. N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. Ecological Monographs **56**:303–325.

Leigh, Jr., E. G., A. S. Rand, and D. M. Windsor, editors. 1982. The ecology of a tropical forest, seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C., USA.

Paige, K. N., and T. G. Whitham. 1985. Individual and population shifts in flower color by scarlet gilia: a mechanism for pollinator tracking. Science **227**:315–317.

Rathcke, B. J. 1983. Competition and facilitation among plants for pollination. Pages 305–329 *in* L. Real, editor. Pollination biology. Academic Press, New York, New York, USA.

Rathcke, B. J., and E. P. Lacey. 1985. Phenological patterns in terrestrial plants. Annual Review of Ecology and Systematics **16**:179–214.

Roubik, D. W. 1989. Ecology and natural history of tropical bees. Cambridge University Press, New York, New York, USA.

Roubik, D. W., and J. D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. Oecologia (Berlin) **73**:321–333.

Waser, N. M. 1979. Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). Oecologia (Berlin) **39**:107–121.

———. 1983. Competition for pollination and floral characters differences among sympatric plant species: a review of evidence. Pages 277–293 *in* D. E. Jones and R. J. Little, editors. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, New York, USA.

Williams, L. O., and P. H. Allen. 1980. The orchids of Panama. Missouri Botanical Gardens, Saint Louis, Missouri, USA.

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