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ECOLOGICAL CONSTRAINTS ON FRUIT INITIATION BY *CALYPTROGYNE GHIESBREGHTIANA* (ARECACEAE): FLORAL HERBIVORY, POLLEN AVAILABILITY, AND VISITATION BY POLLINATING BATS[1]

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Failure of a flower to initiate fruit can be attributed to an insufficiency of resources, genetic incompatibilities, or ecological constraints on pollination. Flower visitors can increase fruit initiation by pollinating flowers, or decrease fruit initiation by damaging them. If, however, resources limit fruit initiation, variation in visitation may be relatively unimportant. Visitors to *Calyptrogyne ghiesbreghtiana,* a rain forest understory palm, leave a record of their activity by feeding on floral tissue. I recorded variation in inflorescence visitation, floral display, and fruit initiation during 7 mo over two field seasons. On average, bats visited 50–60% of flowers; katydids and scarab beetles visited and damaged the remaining 40–50%. Four species of bat (Phyllostomidae) captured near inflorescences were found to be carrying *C. ghiesbreghtiana* pollen. Approximately 18% of flowers visited by bats and not damaged by insects initiated fruit, whereas insect-damaged flowers set a negligible number. Some variation in fruit initiation was explained by nightly variation in the proportion of inflorescences at each site that were potential pollen donors (male-phase inflorescences). Visitors responded to variation in floral display; katydids damaged more flowers on taller inflorescences, and in one season bats visited a greater proportion of flowers on inflorescences with many flowers. However, floral display only explained a small amount of variation in visitation. A similar amount of variation in flower visitation was explained by the degree to which inflorescences were obstructed by surrounding vegetation. I used path analysis to summarize the overall effect of floral display on visitation by both pollinators and florivores and the effect of visitation and site sex ratio on fruit initiation. Because almost all flowers were visited by bats or damaged by katydids, the amount of bat visitation was strongly negatively correlated with katydid damage. In spite of the low fruit set from bat-visited flowers, variation in bat visitation explained 27–37% of the variation in fruit initiation.

How is a plant's reproductive output determined? This fundamental question has aroused considerable interest in the last 15 yr (Stephenson, 1981; Lee and Bazzaz, 1982; Sutherland, 1986; Ayre and Whelan, 1989; Ehrlen, 1991). Much of this interest stems from the observation that many flowering plants produce considerably more flowers than fruits (Stephenson, 1981) and that fruit set can be highly variable in both time and space (Ågren, 1988; Copland and Whelan, 1989).

For many plants it has been suggested that fruit set is limited primarily by the amount of resources available to invest in fruits, rather than the availability of pollen (Stephenson, 1981; Willson and Burley, 1983), and thus variation in visitation will have little effect on fruit set. In contrast, variation in attendance by flower-visiting animals has been found to be important in determining the quantity of reproduction by some plants (e.g., Bierzychudek, 1981; Kwak and Jennersten, 1991). Where this variation is in response to floral display, it may lead to selection on floral characters (Galen, 1989).

Not all flower visitors are equal in their effect on fruit production (Montalvo and Ackerman, 1986; Ramsey, 1988; Dieringer, 1992). While some transfer pollen, others may reduce the amount of pollen transferred or even damage flowers. Destruction of flowers by floral herbivores has been implicated as an important cause of low fruit set (Schemske and Horvitz, 1988; Wallace and O'Dowd, 1989).

Assessing the role of flower visitors in determining reproductive output necessitates field observation of visitation by all flower visitors. Unfortunately, in most systems, recording this information for a large sample of plants is a difficult task. Visitors to the palm *Calyptrogyne ghiesbreghtiana,* however, leave an identifiable record of their activity by feeding on floral tissue, thus making it an ideal species for such studies. The purposes of this paper are to describe flowering and pollination of *C. ghiesbreghtiana,* quantify the variation in visitation of female-phase inflorescences by different animals, assess how visitation responds to variation in floral display, and by following all flowers through to fruit initiation, explicitly link the effect of visitors to reproductive output.

METHODS

Focal species—*Calyptrogyne ghiesbreghtiana* Linden ex. H. Wendl. is an understory palm (Arecaceae: Geonomeae) found in dense forests from Panama to Chiapas, Mexico (Wessels Boer, 1968). The population found in northern Costa Rica was described as a separate species, *C. sarapiquensis* H. Wendl. ex Burret (1930), but recently has been syn-

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onymized with *C. ghiesbreghtiana* (de Nevers, in press). Unlike some other geonomoid palms, *C. ghiesbreghtiana* is never cespitose and thus probably does not reproduce clonally. Its short stem rarely lifts the leaf bases more than 1 m above the ground.

Calyptrogyne ghiesbreghtiana has spicate monoecious inflorescences that progress through temporally separated male and female flowering phases. The flowers, which are made of fleshy, sweet tissue, emerge at night and are eaten by floral visitors. The stigmas and style of female flowers are entirely enclosed within a fleshy staminodial tube.

Study site—La Selva Biological Station is a 1,508-ha reserve operated by the Organization for Tropical Studies and located at the confluence of the Río Puerto Viejo and the Río Sarapiquí in the province of Heredia, Costa Rica (10°26′N, 84°00′E). The sites used in this research are ≈ 50 m above mean sea level. Mean annual rainfall is ≈ 3.9 m, with the months January to May typically the driest (Sanford et al., 1994). Research was conducted during these months in 1991 through 1994. Although there is some seasonality in rainfall, there is little variability in air temperature, relative humidity, and solar radiation throughout the year (Sanford et al., 1994), thus seasonal variation in climate is much less marked at La Selva than in most temperate or dry tropical habitats.

Although *C. ghiesbreghtiana* can be found in many different habitats at La Selva, it is most common in wet depressions and swamps. In 1992 I examined plants in three such sites ("Research," "Oriental," and "Saltito") and in 1993 I used only two sites (Oriental and Saltito). Sites were searched exhaustively for flowering individuals; the boundary of each site corresponded with a sharp decrease in density of *C. ghiesbreghtiana.* Data from all inflorescences were included except for the few instances in which palms flowered twice during observations, in which case data from the second inflorescence was excluded to maintain independence of data.

Direct observation of visitors—To determine which animals visited flowers during the night I watched inflorescences with a red-filtered flashlight in 1991, 1992, and 1994. In 1993 observations were made with the aid of an infrared night-vision scope and an infrared flashlight, and on two nights visitors were photographed. Observations were confined to fully flowering inflorescences, between 8:30 PM and dawn. All other observations of flower visitors were incidental, made during 12 mo of field work over 4 yr, which required examining inflorescences frequently by day and night.

Because bats were frequent visitors to *C. ghiesbreghtiana,* I collected pollen samples from bats caught near flowering inflorescences. Bats captured in mist nets were rubbed around the snout and forearms with a small lump of glycerol gelatin (Kearns and Inouye, 1993) containing Alexander's stain (Alexander, 1969). These gelatin samples were melted and mounted on glass slides, and examined with a light microscope for the presence of pollen. Pollen grains of *C. ghiesbreghtiana* could be distinguished by their size and shape from the other species of pollen sometimes found on bats. Bats were identified to species with the assistance of a key to the bats of La Selva Biological Station, developed by Robert M. Timm (unpublished data, University of Kansas).

Assessing the impact of flower visitors—Field observations established that different visitors treat the female flower in different ways. Bats remove the whole staminodial tube, revealing an undamaged style. Katydids chew on the staminodial tube, and chew off the style such that only a stump remains. Scarab beetles also chew on the staminodial tube, typically leaving mealy, chewed tissue behind and sometimes damaging styles. These three modes of feeding can be distinguished by examining the inflorescences in the morning. Bat-visited flowers are clearly distinguishable from insect-visited flowers, however katydid and scarab visits are less easy to separate. Because the reward tissue is removed by visitors and cannot be replenished, each female flower is probably visited only once. Subsequent visits to flowers elsewhere on the inflorescence may, however, contact already exposed stigmas. Indeed, bats appear to transfer pollen from their snout to exposed stigmas adjacent to the flower being fed on. Almost all female flowers on all inflorescences are visited by one of the three classes of visitor. By morning it is unusual to find flowers with expanded staminodial tubes that were not removed or chewed during the night.

To quantify the amount of visitation from these different sources I visited flowering palms every day, counted the number of female flowers that had emerged during the previous night, and noted what kind of visit they had received. Each floral pit was marked with ink, using a different color to denote which class of animal had visited each flower. Inflorescences were examined ≈ 4 wk later, when developing fruits were first apparent.

By constantly surveying each site I was able to determine the number of male- and female-phase inflorescences present on each night. The sex ratio is the proportion of inflorescences that were male in each site, on each night. To examine the effect of site sex ratio on fruit initiation I calculated the average sex ratio over the nights of female flowering for each focal plant. Some inflorescences were discovered after flowering (in the male phase) for an unknown number of previous nights. I assumed that these inflorescences had a phenology identical to the mean and so inferred their contribution to the sex ratio on the nights before I found them.

Measuring display parameters—For each inflorescence I measured the height from the ground to the apex (1992 only), the length of the rachilla, and the number of female flowers. Because bat visitation to inflorescences could be hindered by surrounding vegetation that made it difficult for bats to locate or access flowers, in 1992 I estimated the degree to which each inflorescence was obstructed by surrounding vegetation and gave each inflorescence an "index of obstruction" score that ranged from 0 to 4. I visualized a circle of 30 cm radius, in a horizontal plane, with its center on the tip of the inflorescence. If there were no intrusions into this imaginary circle I gave the inflorescence a score of 0. If one quarter or less of the circumference was interrupted by intruding vegetation, the inflorescence scored 1. If one-quarter to one-half of the circumference was interrupted by intruding vegetation, the inflorescence scored 2. If one-half to three-quarters of the circumference was interrupted by intruding vegetation, the inflorescence scored 3. If three-quarters or more of the circumference was interrupted by intruding vegetation, the inflorescence scored 4. I did not count narrow vertical intrusions, such as other reproductive spikes from the same plant or the narrow aerial roots of *Philodendron.*

Path analysis—To analyze the effect of the different display parameters on visitation by bats and by katydids and the effect of visitation on fruit initiation, I used path analysis (Li, 1975; Sokal and Rohlf, 1981; Schemske and Horvitz, 1988; Mitchell, 1993). Path coefficients are equivalent to the standardized coefficients of determination derived by multiple regression.

RESULTS

Inflorescence structure and phenology—*Calyptrogyne ghiesbreghtiana* bears spicate axillary inflorescences, each held erect by a tall peduncle. The average height of inflorescences (measured to the apex) is 198 ± 32 cm (SD, N = 131, 1992 data). The axis of the inflorescence, the rachilla (Uhl and Dransfield, 1987), bears parallel rows of floral pits. The average rachilla length is 22.4 ± 3.2 cm (SD, N = 131, 1992 data). Flowers are borne in triads, with one pistillate (hereafter "female") and two staminate (hereafter "male") flowers in each floral pit. The average number of floral pits per inflorescence is 238 ± 65 (SD, N = 131, 1992 data).

Both male and female flowers emerge at night, are

TABLE 1. Flowering phenology of *C. ghiesbreghtiana* inflorescences, during the period January–May, in 1992 and 1993.

Number of nights	1992			1993		
	Mean	SD	*N*	Mean	SD	*N*
With male flowers	4.73	1.22	92	4.83	1.35	52
Between flowering phases	3.37	2.05	101	3.51	1.16	69
With female flowers	2.05	0.50	132	2.03	0.54	92

white, and smell strongly of garlic. Male flowers have a fleshy filament tube, and female flowers have a fleshy staminodial tube. The fleshy tissue of both male and female flowers tastes sweet and is eaten by various floral visitors. Inflorescences are protandrous, with complete temporal separation of the male and female phases of flowering. The male phase of flowering typically lasts for four or five nights (Table 1). Male anthesis progresses from the apex of the rachilla downwards (basipetally). Male anthesis begins around dusk, and each flower lasts for only one night; flowers abscise by dawn if they are not eaten. After the male phase of flowering there is a period with no flowers, which typically lasts three or four nights (Table 1).

The female phase of flowering follows this hiatus and proceeds from the base of the rachilla to the apex (acropetally), usually continuing for two nights (Table 1). Female flowers typically expand between 2000 hr and 2400 hr. The female flower has three ovaries, three stigmas and a single style. The stigmas and style are enclosed by the fleshy staminodial tube. If a female inflorescence is bagged to exclude visitors, the staminodial tubes remain intact and attached to the rachilla (despite suggestions to the contrary in Uhl and Dransfield [1987]) eventually growing moldy. Pollination cannot occur unless a floral visitor removes the staminodial tube and so exposes the stigma.

Calyptrogyne ghiesbreghtiana at La Selva produces flowers and fruits year-round (January–May, personal observation; June-December, Marco Tschapka, Universität Erlangen, unpublished data). Individual palms have only one inflorescence in flower at a time; the shortest observed interval between successive inflorescences was 24 nights between the last female flower of one inflorescence and the first male flower of the next. Because male and female flowers never occur simultaneously on a plant, this species is obligately outcrossed. Fruit development is first apparent ≈ 4 wk after flowering. I refer to this stage of development as fruit initiation. The mature fruits are single seeded.

Observations of visitors—Bats were frequently observed visiting inflorescences of *C. ghiesbreghtiana,* in all hours between dusk and dawn. In total, 27 hr of observation time were accumulated (8 hr with red light, 19 hr with night scope) over 17 nights in 4 yr, including both male- and female-phase inflorescences. Bats were observed to visit flowers on 13 of these nights. Photographs were taken of 70 flower visits by bats in the genus *Glossophaga* (possibly *G. commissarisi* Gardner [Glossophaginae] Marco Tschapka, Universität Erlangen, personal communication), including visits to both male- and female-phase inflorescences. A few photographs were taken of a bat that landed on a male-phase inflorescence (Fig. 1). On nights when bats were observed visiting, their visits were repeated and frequent. It was difficult to record the precise number of bat visits, because each was very short and they often occurred in a burst of activity (e.g., ≈ 30 visits in 20 min). Bat visits were also observed incidentally on numerous other occasions, as I walked past flowering plants during the night.

Bats of contrasting sizes visited inflorescences, and different bats exhibited different feeding behaviors. Some visitors to male flowers licked pollen but ate no flowers, whereas others ate whole flowers. Some bats hovered up and down, barely disturbing the inflorescence. Other bats flew into inflorescences in repeat attacks that set the inflorescence swaying back and forth. Other observers have seen bats land on inflorescences, then hang there for a few seconds (Mauricio Quesada, Palo Verde Field Station, Costa Rica, personal communication; Marco Tschapka, Universität Erlangen, personal communication). One bat that landed on an inflorescence was caught and identified as *Dermanura watsoni* Thomas or *D. phaeotis* Miller (Marco Tschapka, Universität Erlangen, personal communication). The diversity of appearance and behaviors observed suggested that bats of different subfamilies visited *C. ghiesbreghtiana* inflorescences.

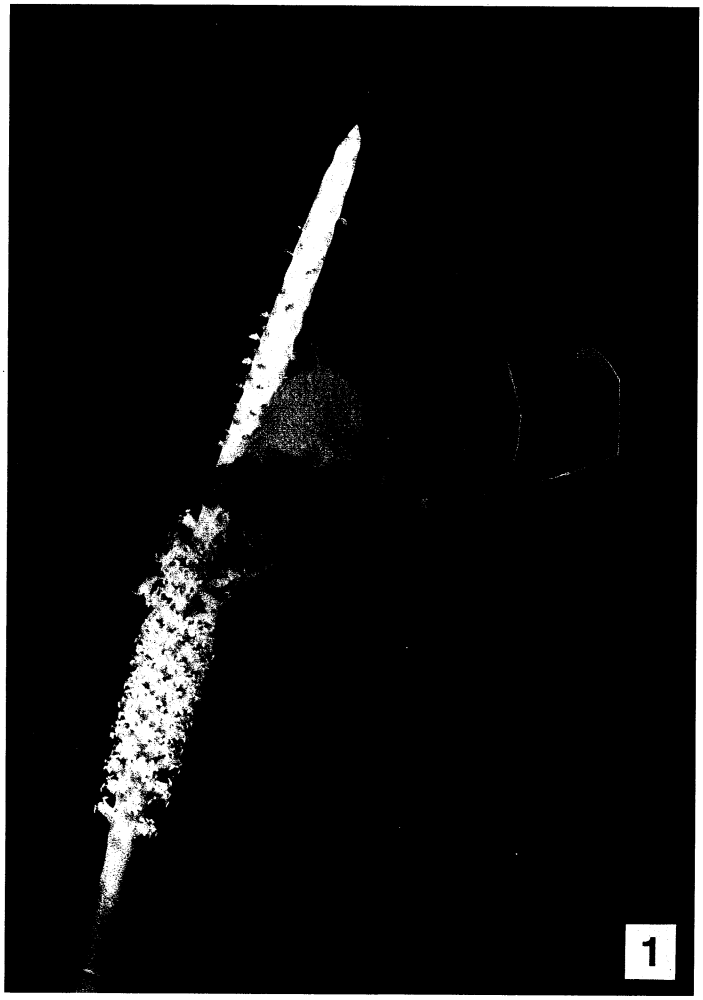
Bat-netting near flowering *C. ghiesbreghtiana* inflorescences yielded 69 captures of nine species of plant-visiting bats. Examining the gelatin samples, I found seven with fewer than five grains of *C. ghiesbreghtiana* pollen, and 17 with pollen counts ranging from five to >100 grains (Table 2). On this basis there is strong evidence for regular visitation of *C. ghiesbreghtiana* by *Carollia perspicillata* L. (Carollinae) and *Glossophaga commissarisi. Vampyressa nymphaea* Thomas (Stenoderminae) was caught six times only, but also appears to be a visitor. *Carollia brevicauda* Schinz and *C. castanea* H. Allen were caught frequently, but rarely carried pollen. Data for the remaining species are insufficient to draw conclusions.

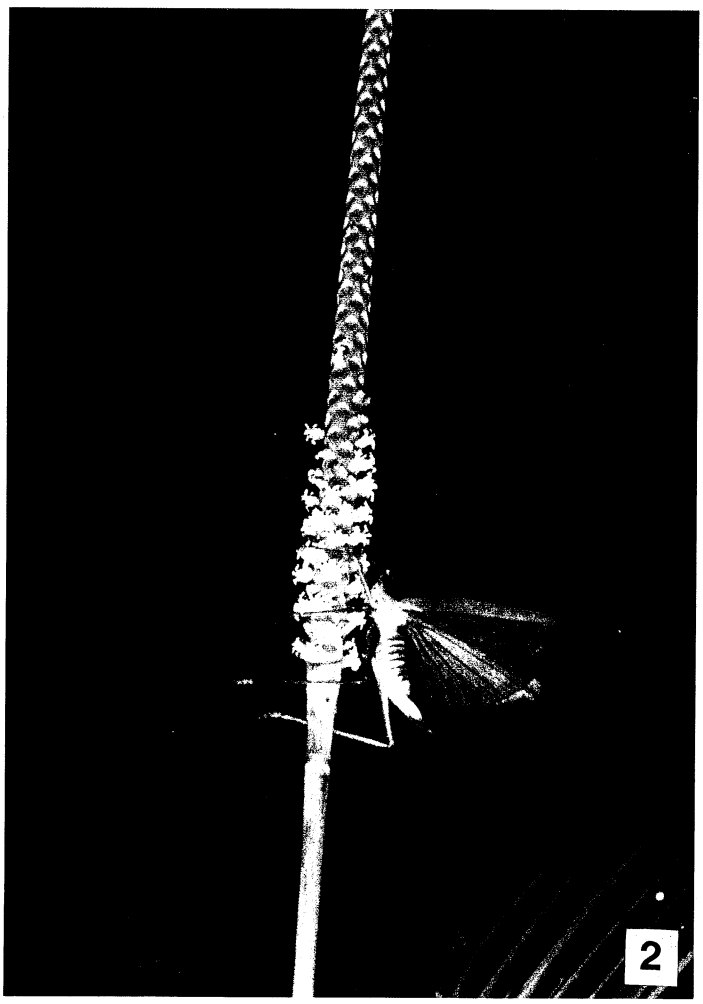
Katydids were seen on inflorescences frequently at night, actively chewing floral tissue of both male and female flowers (Fig. 2). When feeding on female flowers they removed the style and acted as floral predators. Monitoring activity through the night revealed that katydids sometimes stay on inflorescences for hours. Katydids eating *C. ghiesbreghtiana* flowers include *Copiphora rhinocerus* Pictet, *Copiphora* cf. *cultricornis* and *Acantheremus sp.* (Tettigoniidae: Copiphorinae), *Melanotus tico* Rentz and *Idiarthron sp.* (Tettigoniidae: Pseudophyllinae).

The scarab beetle *Lagochile collaris* Blanch. also was found feeding frequently on flowers, sometimes during the night, but more commonly in the morning. These beetles chewed the styles of female flowers, but did not always destroy them.

The only other visitors to inflorescences observed were weevils, ants, and occasionally stingless bees (*Trigona* spp.) However, because they were infrequent, diurnal, and caused little damage, they are unlikely to be important to *C. ghiesbreghtiana* reproduction.

Amount of visitation by different visitors—The staminodial tubes of almost all female flowers were eaten by





Figs. 1, 2. Visitors to the flowers of *C. ghiesbreghtiana* (rachilla of inflorescence ≈ 22cm). Photographs by Marco Tschapka. **1.** A bat, probably in the subfamily Stenoderminae, visiting a male-phase inflorescence. **2.** A katydid (Tettigoniidae: Pseudophyllinae) visiting a male-phase inflorescence.

floral visitors before dawn. Bats were the most frequent visitors to inflorescences, visiting on average 127 (1993) to 155 (1992) flowers per inflorescence (Fig. 3). Katydids were also frequent visitors, eating on average 72 (1992) to 103 (1993) flowers per inflorescence. Visitation by bats and katydids was, however, highly variable, ranging from 0 to 100% of flowers per inflorescence for both classes of visitor. The coefficients of variation for bat visitation were 0.63 (1992) and 0.73 (1993), and for katydid visitation 1.15 (1992) and 0.93 (1993). Scarab beetles were much less important, visiting on average 10–17 flowers per inflorescence, or 4–7% of the total (Fig. 3). The amount of flower predation by katydids was greater in the Saltito swamp than in the Oriental swamp, both in 1992 (Mann-Whitney $U = 233$, $P = 0.025$) and 1993 ($U = 644.5$, $P = 0.013$). Levels of flower predation were higher in 1993, but this difference was not statistically significant.

TABLE 2. The number of bats captured (1993 and 1994) and found to be carrying pollen of *C. ghiesbreghtiana*. Exclusively carnivorous or insectivorous bats are excluded. It was extremely difficult to separate *Dermanura watsoni* from *D. phaeotis* in the field, hence data from these bats were pooled.

Species	Captures	≥5 pollen grains	<5 pollen grains
Carollia perspicillata	19	7	1
Glossophaga commissarisi	14	6	2
Vampyressa nymphaea	6	3	1
Dermanura phaeotis or *watsoni*	4	1	1
Carollia castanea	15	0	1
Carollia brevicauda	8	0	1
Vampyrops helleri	1	0	0
Pyllostomus hastatus	1	0	0
Ectophylla alba	1	0	0

Fruit initiation attributable to different visitors—Fruit set from insect-visited flowers was very low (fruits/flowers <0.033; Fig. 4). Fruit set from bat-visited flowers was much higher, 0.16 (1992) to 0.21 (1993) (Fig. 4). Because katydids chewed so many flowers and these flowers had such low fruit set, katydids are best considered flower predators. In contrast, bats effected greater fruit set and visited more flowers, acting as effective pollinators. More

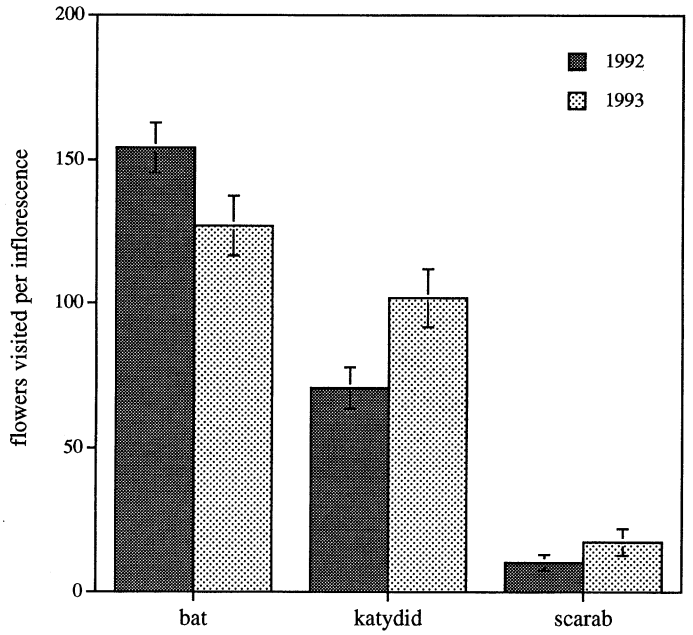


Fig. 3. Mean number of flowers visited per inflorescence, for each class of visitor, ±SE, in 1992 (N = 129, shaded bar) and 1993 (N = 89, stippled bar).

than 90% of the fruits initiated were directly attributable to bat visitation (Table 3).

Variation in bat visitation was positively correlated with variation in fruit initiation (1992 and 1993; Figs. 5, 6), whereas the amount of katydid floral herbivory was negatively correlated with the number of fruits initiated

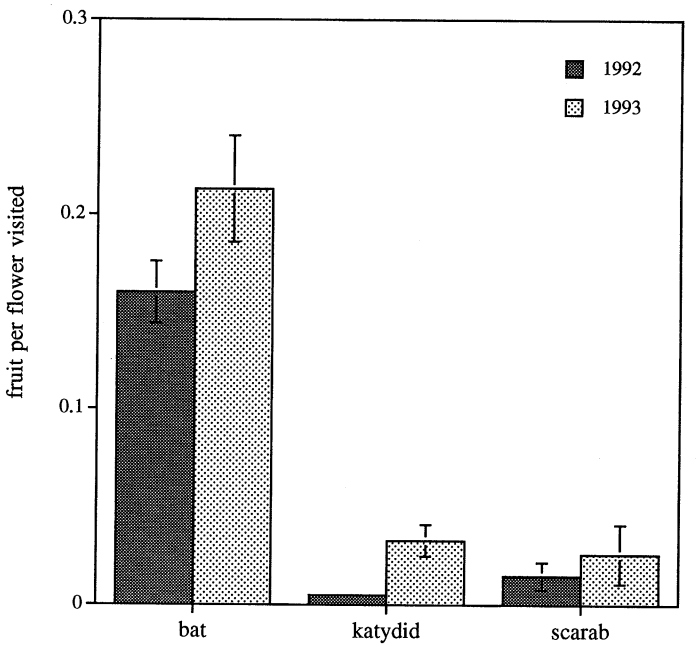
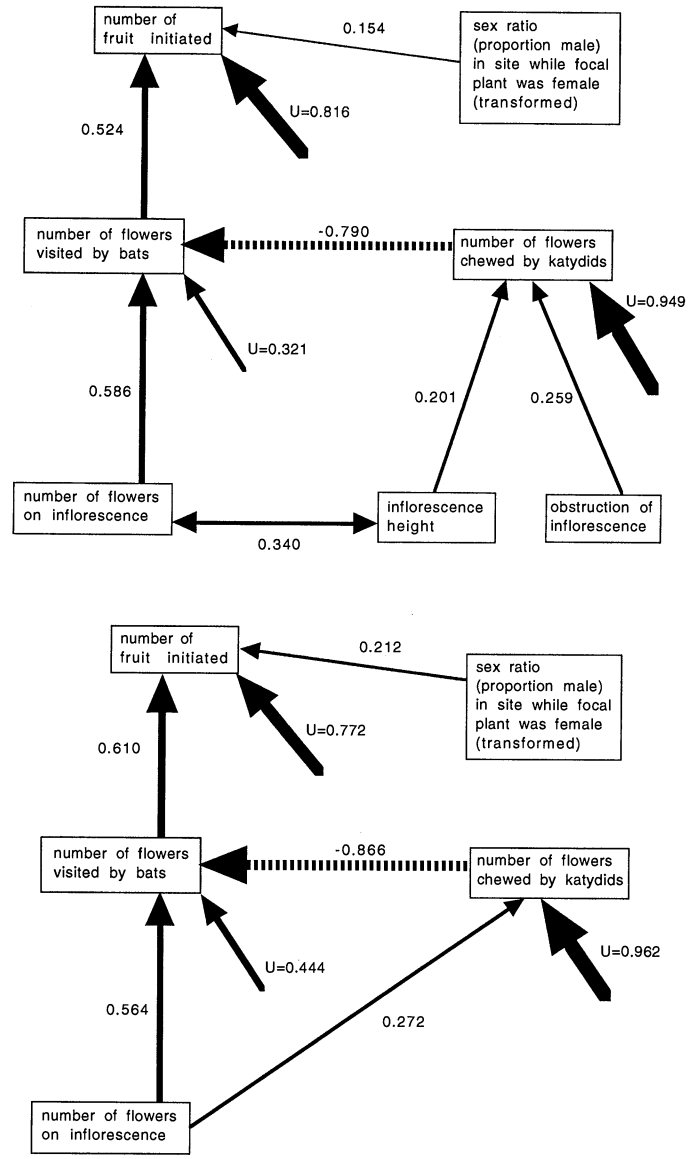


Fig. 4. Mean per-inflorescence fruit set attributed to each class of visitor (fruit initiated/flowers visited), ±SE, in 1992 (shaded) and 1993 (stippled). Not all visitors visited all inflorescences. For 1992: bat N = 122, katydid N = 114, scarab N = 44. For 1993: bat N = 82, katydid N = 78, scarab N = 24.

TABLE 3. Mean number of fruit per infructescence (±SD) attributable to each class of visitor in 1992 (N = 129) and 1993 (N = 89).

	1992	1993
Total	27.00 ± 35.40	36.84 ± 48.31
Bats	25.25 ± 34.35	33.73 ± 46.77
Katydids	0.41 ± 1.30	2.70 ± 7.17
Scarabs	0.41 ± 4.05	0.27 ± 1.06



Figs. 5, 6. Path diagrams for the effects of floral presentation parameters on inflorescence visitation and the effect of visitation and site sex ratio on fruit initiation by *C. ghiesbreghtiana*. Postulated causal variables are connected to effect variables by a single-headed arrow. A double-headed arrow connects correlated variables postulated to be in a non-causal relationship. The thickness of the arrow corresponds with the size of the path coefficient, which is labeled on the arrow. All paths describe significant relationships (α = 0.05). All paths are positive, except that denoted by a dashed arrow. The letter U is used to denote the total effect of unexplained factors. **5.** 1992 data (N = 130 inflorescences). **6.** 1993 data (N = 89 inflorescences).

TABLE 4. Multiple regression of three floral display parameters on the proportion of flowers visited by bats (arcsine transformed) per inflorescence, 1992 (N = 126, r^2 = 0.133).

Independent variable	Standardized coefficient	P
Inflorescence height	−0.202	0.026
Number of flowers per inflorescence	0.247	0.007
Index of obstruction by surrounding vegetation	−0.270	0.002

(via an indirect path; Figs. 5, 6). Analyzing these relationships separately for each site in each year yielded very similar paths. There was still, however, much unexplained variation in the number of fruits initiated.

The mean number of fruits initiated per inflorescence was higher in 1993 than 1992, but the variance is great (Table 3). Because of the abundance of zeroes, these data are not normally distributed. A nonparametric comparison of the median number of fruit initiated finds no significant difference between the years (Mann-Whitney U = 5956, P = 0.840).

Effect of display parameters on visitation—The number of flowers on an inflorescence explained some of the variation in the level of bat visitation, as inflorescences with many flowers tended to have many flowers visited by bats (Figs. 5, 6). In 1993 there was also a weaker path from total flower number to the number chewed by katydids. Because the number of flowers on an inflorescence sets the upper limit to how many flowers could be visited, it is not surprising to find relationships between flower number and visitation. To determine whether inflorescences with more flowers were actually more attractive to pollinators, one must examine the effect of flower number on the proportion of flowers on each inflorescence that was visited by bats. Such an analyses reveals a significant effect of flower number on bat visitation in 1992 (Table 4), but the very low r^2 indicates that little variation was explained by display parameters. There was no significant effect of flower number on the proportion of flowers visited by bats or katydids in the 1993 data. It may have been more difficult to detect such an effect in the 1993 data, however, because sample size was smaller, and inflorescence height and degree of obstruction were not measured. Thus, inflorescences with more flowers can be more attractive to pollinators, but this effect is weak and may be temporally variable.

Almost every flower was visited by either a katydid or a bat, therefore there is a strong negative correlation between these two variables (Figs. 5, 6). Inflorescence height and the degree of obstruction by surrounding vegetation have weak but positive correlations with the amount of katydid visitation, but flower number had no direct effect (Fig. 5). Thus, taller inflorescences and inflorescences obstructed by vegetation have more of their flowers eaten by katydids. Variation in rachilla length was not included in the path diagram because it did not correlate with any visitation variables, except as a consequence of covariance with flower number and inflorescence height.

Analyzing the paths separately for each site, in each year, reveals that the path diagrams for visitation and display parameters are very similar between years and among sites, suggesting that the same processes were functioning in all sites during both field seasons. The only paths that substantially differ between sites were in the Oriental swamp in 1992 where there were only weak paths linking the number of flowers chewed by katydids to inflorescence height (path coefficient = 0.020) and obstruction (0.151), and in the Saltito swamp in 1993 where the path from flower number to katydid chewing was weak (0.085).

Effect of local sex ratio on fruit initiation—The three sites had different densities of flowering individuals (Table 5). Although each inflorescence produces both male and female flowers, the proportion of all inflorescences that are in male phase ("site sex ratio") on a given night tends to be >0.5, because the male phase has a greater duration. A similar pattern has been described for a population of another monoecious palm, *Orbignya spectablis* (Kuchmeister, Gottsberger, and Silberbauer-Gottsberger, 1993).

In both the 1992 and 1993 data there are significant, though weak, correlations between the number of fruits initiated and the site sex ratio (arcsine transformed to improve normality; Figs. 5, 6). The number of flowers visited by bats is considerably more important to variation in fruit initiation. If, however, the number of flowers visited by bats is kept constant (in a statistical sense), inflorescences initiate more fruits if they are in female phase on nights when many other inflorescences in the same swamp are in male phase. Analyzing this relationship separately for each site reveals that this effect was similar in both sites in 1993 (Oriental swamp, path coefficient = 0.247; Saltito swamp, 0.219), but in 1992 it was stronger in Oriental swamp (0.395) and weak in the Saltito swamp (0.036) and Research swamp (0.098).

TABLE 5. Number of inflorescences and sex ratio per site, per night [mean ± SD (N)]. To calculate the standard deviation for sex ratio, data were arcsine transformed, but the back-transformed values are reported here. Sample size for sex ratio is reduced in most instances because on some nights there were no inflorescences.

	Year	Saltito swamp (2,000 m²)	Oriental swamp (11,700 m²)	Research swamp (8,700 m²)
Inflorescences in male phase	1992	2.1 ± 1.7 (38)	2.5 ± 1.7 (47)	5.2 ± 3.2 (53)
	1993	2.7 ± 1.7 (57)	3.9 ± 2.6 (62)	—
Inflorescences in female phase	1992	1.3 ± 1.3 (38)	1.4 ± 1.3 (47)	3.0 ± 1.9 (53)
	1993	1.3 ± 1.0 (57)	1.9 ± 1.5 (62)	—
Sex ratio (proportion of inflorescences in male phase)	1992	0.613 ± 0.25 (36)	0.633 ± 0.16 (43)	0.603 ± 0.08 (52)
	1993	0.657 ± 0.17 (56)	0.632 ± 0.15 (62)	—

DISCUSSION

Bat pollination—*Calyptrogyne ghiesbreghtiana* is pollinated by bats and suffers severe floral herbivory by katydids. Bats were frequently observed visiting *C. ghiesbreghtiana* inflorescences and bats netted near flowering *C. ghiesbreghtiana* were often found to be carrying *C. ghiesbreghtiana* pollen (Table 2). More than 50% of all flowers were visited by bats (Fig. 3), and almost all the fruits initiated derived from flowers visited by bats and left unchewed by katydids or scarabs (Fig. 4; Table 3). The dependency of *C. ghiesbreghtiana* reproduction on flower-visiting bats is extreme, although the diversity of bat species is broad, including at least three species from three subfamilies of Phyllostomidae (Glossophaginae, Carollinae, and Stenoderminae).

Although this research was conducted during the months January–May, the bat species that pollinate *C. ghiesbreghtiana* have been captured at La Selva in all months and *C. ghiesbreghtiana* pollen has been found on *Glossophaga commissarisi* throughout the year (Marco Tschapka, Universität Erlangen, personal communication). Therefore it is very probable that bat pollination of *C. ghiesbreghtiana* is a year-round phenomenon.

No other palms in the world are known to be bat pollinated (Henderson, 1986). The only other published information on *Calyptrogyne* pollination is an abstract (Beach, 1986) that suggests the palm is probably pollinated by bats. My data confirm these observations. Other species in the genus *Calyptrogyne,* and its sister genus *Calyptronoma* share the unusual floral morphology and may prove to be bat-pollinated.

There are reports of bats visiting the flowers of many other plant species (for a review see Dobat and Peikert-Holle, 1985) and a number of papers demonstrate that bats pollinate (Alcorn, McGregor, and Olin, 1961; Baker, 1973; Heithaus, Opler, and Baker, 1974; Heithaus, Fleming, and Opler, 1975; Gould, 1978; Lack, 1978; Sazima and Sazima, 1978; Howell, 1979; Lemke, 1984; Sazima, Vogel, and Sazima, 1989; Lord, 1991; Gribel and Hay, 1993). Bat pollination is thought to be important for many plant species in tropical forests (Faegri and van der Pijl, 1979), although community-wide surveys of pollination systems are rare (Schatz, 1990). It is estimated that 3% of the trees at La Selva are bat-pollinated, compared to 4.3% hummingbird-pollinated (Bawa et al., 1985).

The literature of pollination biology has been greatly influenced by the application of floral syndromes to infer likely pollinators (Wyatt, 1983). *Calyptrogyne ghiesbreghtiana* shares some of the traits associated with the traditional bat-pollination syndrome (see Faegri and van der Pijl, 1979) such as nocturnal anthesis, dull flower color, and strong odor. A garlic perfume, such as produced by *C. ghiesbreghtiana* flowers, has also been noted for flowers of at least two other bat-visited species, *Tetrastylis ovalis* (Passifloraceae) (Buzato and Franco, 1992) and *Vriesea gladioliflora* (Bromeliaceae) (Marco Tschapka, Universität Erlangen, personal communication). Morphologically, however, the flowers of *C. ghiesbreghtiana* are very distinct from the shaving-brush or cup-shaped flowers generally ascribed to the bat-pollination syndrome. Further, *C. ghiesbreghtiana* does not produce large quantities of liquid nectar, but rather a sweet tissue. Tissue rewards for flower visiting are not unique to *C. ghiesbreghtiana. Freycinetia* (Pandanaceae) provides a tissue reward and is pollinated by Megachiroptera (Lord, 1991). Tissue rewards to bats have also been suggested for *Pachira insignis* (Porsch, 1937), *Dumoria heckelii, Madhuca,* and *Bassia* (van der Pijl, 1956). By offering tissue rewards, plants risk attracting visitors with chewing mouthparts, such as the katydids that eat so many *C. ghiesbreghtiana* flowers.

Floral herbivory—Floral herbivory is extremely high in *C. ghiesbreghtiana.* Katydids destroyed on average 32% (1992) to 41% (1993) of flowers per inflorescence. Frequency histograms of the percentage of flowers eaten by katydids, per inflorescence, were extremely bimodal for both years, with modes at the lowest and highest levels of floral herbivory. Inflorescences with >80% of their flowers eaten by katydids constituted 18% in 1992 and 24% in 1993. It may be that bats avoided visiting inflorescences that were subject to intense katydid florivory, allowing katydids to destroy even more flowers. By morning, however, nearly all flowers were visited by either katydids or bats, indicating that bats did not abandon inflorescences with high levels of floral herbivory. The frequency of inflorescences with high levels of floral herbivory helps to explain why 42% (1992) to 43% (1993) of infructescences initiated five or less fruits, the modal category in both years.

The importance of floral predation in reducing levels of fruit production has been noted for a number of plant species (Breedlove and Ehrlich, 1968; Inouye, 1982; Zammit and Hood, 1986; Hendrix, 1987; Schemske and Horvitz, 1988; Evans, Smith, and Gendron, 1989; Wallace and O'Dowd, 1989; Allison, 1990a; Pettersson, 1991; Muenchow and Delesalle, 1992), and may contribute to low fruit production in many others. High ovary mortality, such as caused by floral herbivores on *C. ghiesbreghtiana,* is a condition for the evolution of low fruit-to-flower ratios according to Ehrlen's (1991) reserve ovary hypothesis. To date, however, there has been no review of the prevalence of floral predation among different species in different environments. Thus, the impact of floral herbivores on the evolution and ecology of plants in general is poorly studied, and little understood.

It has long been speculated that levels of herbivory in general are higher in tropical forests (Janzen, 1970), and there is some evidence to support this claim (Coley and Aide, 1991). It may also be that the depredations of floral herbivores are greatest in tropical forests, such as the habitat occupied by *C. ghiesbreghtiana.*

Display effects—The interaction between pollinators and flowers has been a popular model in the study of evolution (Willson, Miller, and Rathcke, 1979; Schemske, 1980; Waser and Price, 1981; Waser, 1983; Campbell, 1989; Galen, 1989; Eckhart, 1991). Specialist pollinators, such as the bats visiting *C. ghiesbreghtiana* may select for certain traits in the floral display of the plants they favor. In *C. ghiesbreghtiana* there is some evidence that inflorescences with more flowers attract relatively more pollinator visits (Table 4), although the overall amount of variation in visitation explained by floral display characters is very low. Florivores, however, can also respond

to variation in floral display. Katydids destroyed more flowers on taller inflorescences (height measured only in 1992, note the positive path between inflorescence height and amount of katydid chewing in Fig. 5); because flower number and katydid visitation are only weakly correlated, it is unlikely this is a function of taller inflorescences having more flowers. The attraction of katydids to taller inflorescences explains the negative coefficient for the effect of inflorescence height on the proportion of flowers visited by bats (Table 4), because as florivory increases, bat visitation must decrease. Given the impact of florivory in reducing fruit initiation in *C. ghiesbreghtiana,* the role of florivores in the selection of floral display traits is potentially as significant as the role of pollinators. Bats may select for increased flower number per inflorescence, and katydids may select for shorter inflorescences.

In the rain forest understory there is great potential for interference in the effect of floral display by the abundance of vegetation and fallen material from the canopy. I quantified this parameter crudely with an estimate of the "index of obstruction" and found a significant relationship between obstruction and the amount of floral predation. Katydids were more likely to eat flowers on inflorescences caught in a jumble of obstructing vegetation. This effect was of similar magnitude to the effect of flower number or height on visitation; although because it is undoubtedly not a heritable character of the plant, it serves only to illustrate the considerable noise in the system of visitor-mediated selection on floral traits. Selection on floral phenotype may be insignificant if other ecological factors not linked to floral phenotype (such as obstruction of the display) are more important determinants of fitness differences (Herrera, 1993).

The mate density effect—Among obligately outcrossing plants it might be expected that fruit set would be greater for those plants near many possible pollen donors. A density effect such as this could contribute to an "Allee effect" for plant populations (Kunin, 1992), where there is a positive relationship between reproduction and plant density. This density effect may also arise through a quite different phenomenon, the increased attractiveness to pollinators of a dense patch of flowers (Sih and Baltus, 1987). Some studies have described a positive relationship between plant density and fruit or seed set (Platt, Hill, and Clark, 1974; Silander, 1978; Heithaus, Stashko, and Anderson, 1982; Allison, 1990b; Widen and Widen, 1990; House, 1992; Kunin, 1992), but such a pattern could also arise if plant establishment and reproductive success are limited by the same patchy resource. Other studies have documented a positive relationship between local mate density and pollination, under natural levels of variation in density (Feinsinger et al., 1986; House, 1993), and under controlled conditions (Feinsinger, Tiebout, and Young, 1991) without demonstrating an impact on fruit set. Kunin (1993) controlled plant density and found effects on both visitation and seed set, suggesting that the efficiency of pollen transfer increased with density of conspecifics.

The effect of site sex ratio on fruit initiation by *C. ghiesbreghtiana* provides field evidence for a positive mate-density effect on fruit initiation. Because the availability of pollen is expressed as a proportion of male-phase inflorescences (which varies in time), rather than a density of plants (which varies in space), it is unlikely that the effect observed in *C. ghiesbreghtiana* is attributable to a resource other than pollen. Further, there is no temporal trend in site sex ratio that could cause spurious correlations between fruit initiation and unmeasured variables with seasonal trends. Data do not support a patch attraction effect, because visitation was not affected by the total number of inflorescences in the site (multiple regression analysis of author's unpublished data). Path analyses similar to those reported, but considering the effect of number of possible pollen donors (i.e., not including other competing female-phase inflorescences), find weak nonsignificant paths from the number of pollen donors to fruit initiation. This result suggested that actual competition among female-phase inflorescences for the pollen from male-phase inflorescences is more biologically significant than simply the number of possible mates.

The field sites chosen in this study were favored because they offered a high density of the study organism, a bias that is probably typical in most field studies. That a weak Allee effect can be detected even in these sites suggests that the same phenomenon may be important in less densely populated patches. It is theoretically possible that this effect sets a lower limit for the density of a viable population of plants (Kunin, 1992). The search for more evidence of an Allee effect in natural plant populations should continue in such low-density patches.

Causes of low fruit set—Low mean fruit set by *C. ghiesbreghtiana* can be attributed in part to the activity of flower-eating katydids. The impact of floral herbivory does not, however, explain the relatively low fruit set by flowers that were visited by bats but not katydids. Low fruit set by bat-visited flowers could be attributed to poor pollen transfer, or the abortion of fertilized ovules because of genetic incompatibilities or an insufficiency of maternal resources. The significant influence of local mate density on fruit set by *C. ghiesbreghtiana* suggests sensitivity to pollen supply, and therefore effectiveness of pollen transfer was probably important. Further studies could examine the causes of low fruit set by assessing the stigmatic pollen loads of bat-visited flowers, and by exploring the effect on fruit set of variation in the resource environment of maternal plants.

The effectiveness of pollen transfer by a flower visitor depends on the foraging behavior of that animal (e.g., Montalvo and Ackerman, 1986). Observations of bats at inflorescences revealed different flower-visiting behaviors that could influence the amount of pollen transferred. The smaller species in the subfamily Glossophaginae, such as the *Glossophaga commissarisi* that visited *C. ghiesbreghtiana,* almost always hover while visiting flowers (Helversen, 1993). In contrast, bats in the subfamily Stenoderminae do not hover (Helversen, 1993), and consequently will sometimes land on the inflorescence to feed, as did the *Dermanura* sp. that was captured on a *C. ghiesbreghtiana* inflorescence. Bats that landed on the inflorescence had a greater opportunity to transfer pollen because they contacted many more flowers than would a hovering bat. It may be that fruit set by some flowers was

relatively low because they were visited by bats that make little contact with the inflorescence and consequently did not transfer pollen effectively.

Conclusions—Inflorescences of *C. ghiesbreghtiana* attract pollinating bats and flower-eating katydids. The number of flowers pollinated by bats is greatly constrained by the number of flowers destroyed by katydids. In spite of the low fruit set from bat-visited flowers, variation in bat visitation explained 27–37% of the variation in fruit initiation. Katydids were attracted to taller inflorescences, and in one field season inflorescences with more flowers attracted more bat visits. Floral predation by katydids was greater for inflorescences that were obstructed by surrounding vegetation. Fruit initiation was greater for inflorescences that flowered when the sex ratio in the site was more male biased. The importance of both pollinator visitation and the positive effect of nearby pollen donors indicates that variation in pollen supply determines much of the variation in fruit initiation.

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