

BAT ACTIVITY AND POLLINATION OF *BAUHINIA PAULETIA*: PLANT-POLLINATOR COEVOLUTION¹

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Abstract. The relationship between the pollination biology of a tropical plant, *Bauhinia pauletia*, and the foraging strategies of the nectarivorous bats visiting it was studied. At least two bat species are pollen vectors, *Phyllostomus discolor* and *Glossophaga soricina*. *Artibeus jamaicensis* and *Sturnira lilium* were also captured near *Bauhinia* flowers. Larger bats (*P. discolor*) drain flowers of nectar and forage in groups, while smaller bats (*G. soricina*) make brief visits and forage independently. These foraging strategies should optimize energetic gain for the bats and promote outcrossing for the plant. *Bauhinia pauletia* is self-compatible, but is found where conditions favor outcrossing. Andromonoecism (the presence of hermaphrodite and male flowers) in this species appears to be an adaptation to pollination by large pollinators that also promotes outcrossing.

Key words: *Andromonoecism, behavior, Bauhinia, Chiroptera, coevolution; energetics; pollination.*

INTRODUCTION

Bats are important pollinators in tropical communities, with at least 500 species of neotropical plants wholly or partly dependent on bats for pollination (Vogel 1969). Most of the literature on this subject has been devoted to describing instances of bat pollination and summarizing floral characteristics conducive to chiropterophily (Faegri and van der Pijl 1966). Some effort has gone into analysis of pollen feeding of glossophagine bats (Alvarez and Quintero 1969, Howell 1972).

The importance of bats as pollinators goes beyond the large number of species involved. Janzen (1970) has argued that the evolutionary plasticity afforded by outcrossing is extremely important in tropical communities, and Bawa (*in press*) found a high proportion of genetically self-incompatible tree species in one dry, lowland, tropical community. Others claim that wet tropical forest trees ought to be capable of inbreeding because of the large distances between trees (Baker 1955, Federov 1966), but such widely dispersed plants could be outcrossed if bats act as long-distance pollen vectors (Baker 1973).

The effectiveness of bats in outcrossing depends both on plant flowering strategies and the foraging patterns of bats. This paper studies one species of chiropterophilous plant and the foraging patterns of

the bats visiting it, in the Tropical Dry Forest life zone (Holdridge 1967) in Costa Rica.

Bauhinia pauletia Pers. (Caesalpiniaceae) is found from southern Mexico to Trinidad. In Costa Rica it is uncommon in the Pacific lowlands, occurring in distinct small patches in savanna or pasture habitats (Standley 1937), while elsewhere it occurs in sparse to moderate stands (Wunderline, *pers. comm.*).

METHODS

Floral biology

This study was conducted 1.5 km west of Cañas, Guanacaste Province, Costa Rica. A 100 by 15 m patch of *Bauhinia pauletia* containing more than 20 individuals was observed casually in December 1970 and intensively from October 11, 1971, to January 1, 1972.

Two types of flowers may be found on individual shrubs, hermaphroditic and functionally staminate with an aborted gynoecium (i.e., plants are andromonoecious). The flowers are borne on a woody inflorescence that retains floral scars after unfertilized flowers fall off.

Flowers were observed *in situ* to determine the time of opening and anthesis and the pattern of nectar production. The relative frequency of staminate and hermaphroditic flowers was determined for 10 nights, distributed from October 16 to December 12, by counting flowers along a transect. The reproductive success of 81 marked inflorescences was followed by comparing the number of floral scars to the

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number of fruits produced and multiplying by the percent of the flowers that set pods when hand-pollinated. These inflorescences were observed at 10- to 12-day intervals, October 15–December 12 to determine the rate of flower production and the reproductive success through time.

Breeding system studies of *Bauhinia pauletia* were conducted on November 20 and December 2. Buds were opened by hand at 1700 hr, anthers of hermaphroditic flowers were removed, and paper bags were placed over the flowers. Between 1900 and 2030 hr, the treated flowers were self-pollinated, cross-pollinated, or rebagged without further treatment. Twenty to 25 flowers distributed over several individuals were used for each treatment. Treated inflorescences were checked after 10 to 20 days to determine the extent of fruit set.

Plant voucher specimens were collected and deposited at the Missouri Botanical Garden, St. Louis, Missouri; Field Museum of Natural History, Chicago, Illinois; and Universidad de Costa Rica, San Jose, Costa Rica.

Pollinator activity

The behavior of flower visitors was studied by direct observation and photography. Bats were captured with nylon mist nets set near the shrubs on October 11 and 16, and November 16. Bats were tested for the presence of pollen, identified, banded with numbered aluminum bands, and released. Pollen loads were sampled by rubbing captured bats with a glycerin jelly preparation that was later mounted on glass slides as described by Beattie (1971). Pollen was identified by comparison with known types of pollen collected in Guanacaste.

Visual observations were made on November 4 and 5 between 1830 and 2130 hr to ascertain whether visitation rates varied with time, position of the flower, or type of bat. On November 4, three observers watched different sections of the patch containing several shrubs and 30–60 open flowers. Visitation times to the nearest 10 min and the size of the bat visitor ("large" vs. "small") were recorded. Observations were made by moonlight when possible or with the aid of dim flashlights.

Six observers repeated visual observations on November 5, from 1810 to 2125 hr. Each person recorded visits in a 17 m section of the patch containing roughly 40 to 70 flowers. The following information was recorded for each visit: size of the bat, relative flower position (top of canopy vs. low in canopy), and time of the visit to the nearest 5 min.

Since bat activity might be influenced by lunar cycles, stigmas were examined for pollen deposition

on two mornings, once after a full moon and once after a new moon (December 3 and 17). Twenty-six and 11 stigmas respectively were examined, and the number of pollen grains touching the receptive portion of each stigma was counted.

RESULTS

Bauhinia pauletia flowers opened nearly synchronously between 1815 and 1900 hr and were receptive for only one night. Individual flowers usually opened in less than 5 sec and some pollen was immediately available. Each inflorescence produced a pair of flowers every 2nd or 3rd day, with a mean interval between successive antheses of 2.7 days ($N = 489$, $SD = .576$).

Only five of the 10 stamens in a flower produced pollen. The remaining five stamens were atrophied and lacked productive anthers. Anther dehiscence began in the bud at 1800 hr, but pollen was not fully exposed until approximately 30 min after opening. Anthers were loosely attached to the stamens and often were detached during the night by pollinator activity or the wind. Little pollen was available by 0500 hr on the morning following opening.

Nectar flow began just before flower opening and continued at an approximate rate of 0.5 ml/hr for the first several hours. No measurements were made between 2330 and 0500 hr. Nectar accumulated in the calyx, and small amounts moved up the basal portion of the stamen filaments by capillary action.

All flowers began to droop and wilt the morning following anthesis, and those which had not been pollinated dropped after 1 to 3 days. Pollinated flowers remained and incipient pod formation could be noted a few days following pollination.

Flowers were either hermaphroditic or functionally staminate. Each night 25% to 60% of the flowers contained degenerate pistils that dropped from the flower at anthesis. On any particular night, a single plant produced predominantly one type; however, a pair of flowers on one inflorescence sometimes included both types. Individuals were not always consistent from night to night in the production of one or the other flower type. The rate of flower production and the percentage of hermaphroditic flowers on 10 nights covering a 2-mo period is shown in Fig. 1. The proportion of hermaphroditic flowers increased from October 16 to November 4, then decreased through the rest of the flowering period. The small increase seen on December 12 was not significant (proportionality test). The initial, highest, and lowest values, however, are significantly different from each other (proportionality test, $P > .95$). The mean percentage of hermaphroditic flowers for all nights was 42.0% ($N = 869$).

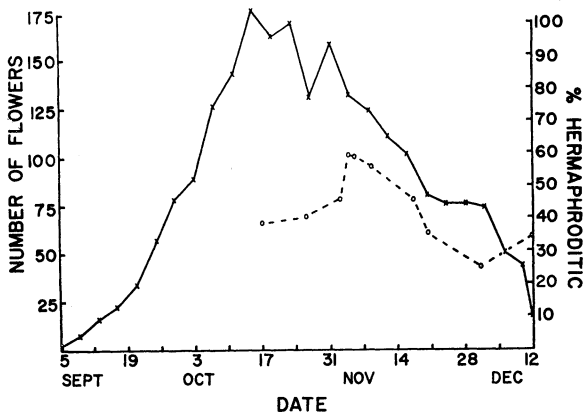


FIG. 1. The rate of flower production of 81 inflorescences and the proportion of hermaphroditic flowers produced in a patch of *Bauhinia pauletia* near Cañas, Costa Rica. Solid line = No. of flowers. Dashed line = % of hermaphroditic flowers.

The rate of flower production was greatest during October, then gradually declined (Fig. 1).

The results of the breeding system experiments are summarized in Table 1. All treatments resulted in some fruit set, with cross-pollinated flowers having the same success as selfed flowers and with control flowers showing the least success. The difference between fruit set in the self-pollinated group and the cross-pollinated group was not significant ($\chi^2 = 0.824$, $df = 1$). The fruit set of control flowers was significantly lower than that of selfed flowers ($\chi^2 = 5.017$). These data are based on observations of pod development 10 days after treatment. Wind and animal damage to treated flowers precluded following development of pods to maturity. Pod development was initiated by 58.8% of the artificially pollinated flowers.

Mature pods were produced by 12.0% of the 2373

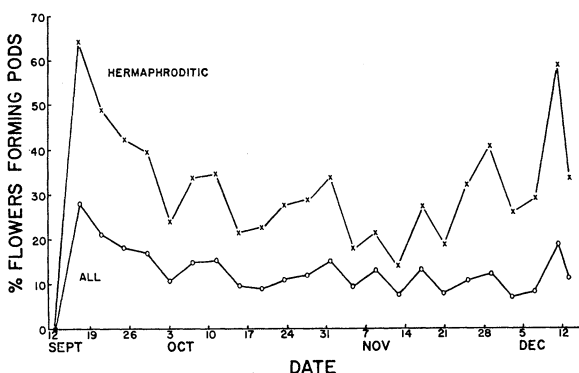


FIG. 2. The proportion of flowers producing pods through time. Solid line = % of all flowers forming pods. Dashed line = % of estimated No. of hermaphroditic flowers forming pods.

TABLE 1. Breeding system experiments

Treatment	N	Pods set	% Success
Cross	21	14	66.7
Self	30	16	53.4
Control	19	4	21.1

flowers that were observed but not treated. These flowers represent the output of 81 inflorescences over a 3½-mo period; however, single inflorescences produced flowers for several weeks only. Since only 43.3% of the flowers were estimated to be hermaphroditic and thus capable of producing fruits, pollination success can only be expressed by fruit set success for potentially reproductive flowers. Since 27.8% of the hermaphroditic flowers produced pods, the proportion of untreated flowers producing pods was roughly half the proportion (58.8%) of artificially pollinated flowers that showed incipient pod development. All observed ripe pods contained mature seeds, although these were often destroyed by insects (Bruchidae).

The temporal pattern of pod formation for all flowers on the monitored inflorescences is shown by Fig. 2. The estimated success of hermaphroditic flowers, based on the estimated proportion of hermaphroditic flowers and assuming a constant fertility rate of 58.8% is also shown. Fruiting success appears to be high initially, to decrease, then to increase somewhat at the end of the flowering period. Estimates of pollination success for the period prior to October 11 are based on extrapolation of known flowering rates. The pitfalls of extrapolation are acknowledged, but we feel it is justified by the consistent rates of flower production by individual inflorescences that we observed.

Many animals were attracted to *Bauhinia pauletia* flowers soon after anthesis, including small numbers of moths (Noctuidae, Pyralidae, and Sphingidae) and many leaf-nosed bats (Phyllostomatidae). Observations and photographs indicated that noctuids and pyralids withdrew nectar from the flowers while clinging to the calyx (Fig. 4A) and seldom contacted the stamens or pistil. Sphingids were potential pollinators but few were present. They contacted the floral reproductive parts, but we saw no more than one or two visits per night of observation. However, bats were commonly seen visiting flowers; some bees were observed collecting pollen early in the morning.

Sixty-seven bats were captured in mist nets near *B. pauletia*, 66 of them in 24 net-hours during October. Three subfamilies of Phyllostomatidae were represented: Phyllostomatinae: *Phyllostomus discolor* Wagner, $N = 40$; Glossophaginae: *Glossophaga soricina* Pallas, $N = 13$; and Stenoderminae: *Artibeus*

TABLE 2. Pollen load type

Bat	Pollen load type				
	<i>Bauhinia</i>	<i>Crescentia</i>	<i>Bauhinia</i>	Unknown 23	Zero
			<i>Crescentia</i>	<i>Bauhinia</i>	
<i>Phyllostomus discolor</i>	10	1	7	0	0
<i>Glossophaga soricina</i>	0	3	7	1	1
<i>Artibeus jamaicensis</i>	2	0	0	0	4
<i>Sturnira lilium</i>	1	0	0	0	0
<i>Uroderma bilobatum</i>	0	0	0	0	1

jamaicensis Leach, $N = 8$; *Sturnira lilium* E. Geoffroy, $N = 5$; and *Uroderma bilobatum* Peters, $N = 1$. We banded 41 bats on October 11, and 26 on October 16. Only one of these, a male *P. discolor*, was recaptured near *B. pauletia* (five nights after banding).

The distribution of pollen among the bat species is summarized in Table 2. On 32 of 48 bats tested (84.2%) large amounts of pollen ("pollen loads") adhered to the wings, head, and body. *Phyllostomus discolor* and *G. soricina* carried pollen most frequently (91% of 32 pollen loads were carried by these species). Pollen grains from both *B. pauletia* and *Crescentia* spp. (Bignoniaceae) were abundant, while one unidentified type was also present. Both *Crescentia alata* HBK and *Crescentia cujete* L. were in flower nearby, but their pollen was indistinguishable. Mixed *Bauhinia* and *Crescentia* pollen loads were common, especially on *G. soricina*. *Phyllostomus discolor* carried *Crescentia* pollen only in mixed species pollen loads, and even then *Crescentia* was uncommon relative to *Bauhinia* pollen. In contrast, *G. soricina* often carried *Crescentia* and *Bauhinia* pollen in equal amounts, so this species appeared to visit *Crescentia* flowers more often than *P. discolor*.

The capture and pollen load data indicate that *P. discolor* and *G. soricina* were the principal bat visitors to *B. pauletia*. This is supported by photographs of bats approaching or feeding at flowers. It was possible to identify bats on the basis of size, shape of the head, form of the flight membranes, and color in 30 photographs. *Phyllostomus discolor* (Fig. 5B and 5C) was identified in 13 pictures and *G. soricina* (Fig. 5D) in 17. No other species could be identified.

On November 4 and 5 during 27 man-hours of observation 1147 visits to flowers by bats were recorded. It was possible to distinguish bats of two sizes, large and small. The four common bat species netted near the flowers were also clearly large or small. Their forearm lengths are an index of differences in total sizes: *P. discolor* = 59.2–63.2 mm; *A. jamaicensis* = 54.9–60.6 mm; *G. soricina* = 33.1–39.1 mm; and *S. lilium* = 40.5–43.6 mm (Goodwin and Greenhall 1961).

Most visits were made by large bats on both nights (Table 3). The ratio of 4:1 (large:small) in observed visits is close to the ratio obtained from netting results for *P. discolor* and *G. soricina* (3.1:1.0).

We noted a number of other differences between large and small bats in addition to frequency of visits. These included variations in the floral visitation behavior, movement patterns within the plant vicinity, and height of flowers visited. Large bats (924 observations, 9 photographs) invariably grasped a section of branch beneath an open flower with their feet, then bent their heads into the calyx. The wings were usually spread and not used for support. The bat's weight bent the thin branches so that nectar was drained from the inverted flowers. Visits lasted 1–3 seconds (Fig. 4C and 4D).

Small bats, on the other hand, generally hovered in front of a flower and appeared to lap the nectar (Fig. 4D). Such visits lasted less than 1 sec. Small bats sometimes clung to flowers with their thumbs and feet, but flowers were not inverted by their weight. The duration of this clinging visit was also very short, less than 1 sec. The hovering visit was much more common, in a ratio of 12:1 based on 13 photographs.

Flowers visited once by small bats were very likely to be visited several more times. For example, one flower was visited 14 times in 30 min. Since the bat that was visiting this flower approached from the same direction and angle each time, the impression created was that the same bat was making repeated visits.

Observations revealed that large bats are most prone to visit flowers classed as "high" in the canopy. Of 924 visits, 87.6% were to high flowers and the

TABLE 3. Ratio of large and small bat visits

	Nov. 4		Nov. 5	
	%	N	%	N
Large	80.1	219	80.5	705
Small	19.9	52	19.5	171

TABLE 4. Patterns of visitation for large bats

	Mean	Range	SD	N
No. of visits per peak*	14.63	2–61	13.57	49
Duration of peaks (min)	10.9	5–25	5.83	49
Interval between peaks (min)	21.6	10–55	10.78	43
No. of peaks per section	8.2	7–9	.7528	6

* Peak = any concentration of visits of which at least three occur within one 5-min interval.

remainder to “low” flowers. Small bats visited 59.7% high flowers and 40.3% low flowers in 223 visits. Both types of bat visited higher flowers more often (χ^2 , $P > .99$), but large bats visited the high flowers almost to the exclusion of low flowers. It appeared that the large bats visited inflorescences that would not drop into foliage during their visits.

Social behavior during foraging also differed for large and small bats. Large bats appeared to arrive in groups to feed. Groups of two to six bats were often seen flying in a linear formation over the flowers. Vocalizations were commonly heard as these groups flew by. While it was impossible to count all bats feeding in an area at any given time, we estimated that groups consisted of from two to 12 individuals. In contrast, small bats appeared to forage alone.

The pattern of visitation to flowers in restricted sectors of the *Bauhinia* patch supports the hypothesis that large bats feed in groups. The pulsed nature of visits was striking (Fig. 3). After a period of active flower visitation in one section, very few or no visits were likely for up to 55 min (average interval between peak visitation periods = 21.6 min, $N = 43$). The average period of active visitation was 10.9 min ($N = 49$), consisting of an average of 14.4 visits. An average of 8.2 periods (range = 7–9) of active visitation were observed in each of the six sections observed for 3 hr on November 5. These patterns are summarized in Table 4. The distribution of

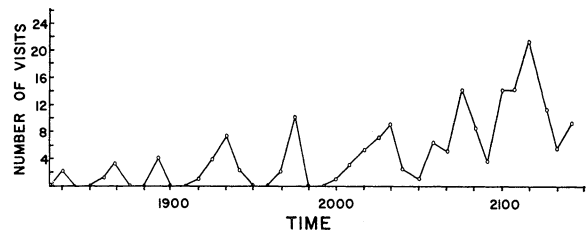


FIG. 3. The distribution of visits by large bats to 40–70 *B. pauletia* flowers, November 5.

flower visits by large bats through the evening is exemplified by Fig. 3 (from Observer 2, November 5). Note that activity reached a peak late in the evening, but that the visits were pulsed throughout the observation period.

Observations on November 4 gave similar results, but the data were not lumped with those of November 5 because a different time interval was used. The pulsed visitation pattern was generally the same, and there were five to seven visitation periods observed.

No such patterns were discerned for small bats. Repeated visits in particular sectors were usually to the same flower and seemed to be by the same bat. No groups of small bats were ever seen flying over the flowers.

Finally, analyses of pollen loads suggested another difference in visitation patterns. *Glossophaga soricina* (a small bat) carried *Bauhinia pauletia* pollen only in mixed pollen loads with *Crescentia* pollen. Small bats carried either pure or mixed *Crescentia* pollen. *Phyllostomus discolor* (a large bat) had pure *B. pauletia* pollen loads on 55% (10) of the bats tested, and on only 41% (7) were very small amounts (< 5% of all pollen) of *Crescentia* pollen found.

The differences in the flower-visiting behavior between large and small bats are summarized in Table 5.

The bat activity level around *B. pauletia* varied considerably on different nights. This is reflected by the low netting success of November 16 com-

TABLE 5. Patterns of visitation to *Bauhinia pauletia* by large and small bats

Large	Small
(Probably <i>Phyllostomus discolor</i>)	(Probably <i>Glossophaga soricina</i>)
Visits high flowers	Visits high and low flowers
Grasps branch beneath flower, pulling it down	Hovers
Drains nectar well	Laps small amounts of nectar
Visits in groups in pulses	Visits singly, flies independently
Visits same flower infrequently	Returns to same flower at short intervals
Carries 55% pure <i>Bauhinia</i> pollen loads; 45% mixed pollen loads (all mixed loads > 90% <i>Bauhinia</i>)	Carries no pure <i>Bauhinia</i> pollen loads; 100% <i>Crescentia</i> or mixed loads

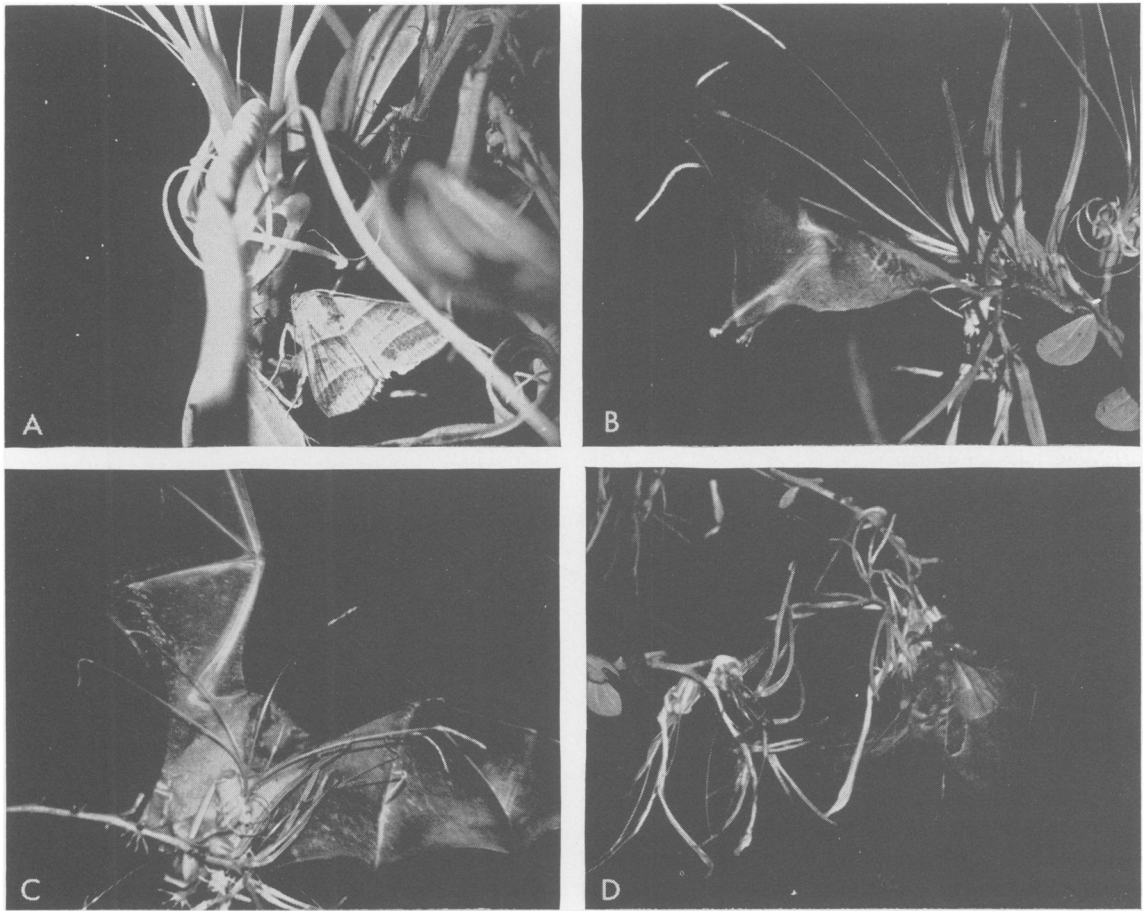


FIG. 4. *Bauhinia pauletia* flower visitors. (A) Noctuid moth approaching base of flower. (B) *Glossophaga soricina* hovering while feeding. (C) *Phyllostomus discolor* reaching for branch below a flower. (D) *Phyllostomus discolor* hanging while feeding.

pared to October 11 and 16. Differences in moonlight may have influenced activity (Crespo et al. 1972). For example, bat activity was nearly absent during 20 min of observation on December 2 (full moon), but was estimated to be light to moderate on December 16 (new moon). Apparent differences in bat activity during these nights were reflected in the amounts of pollen deposited on stigmas. The mean number of grains adhering to the stigmatic surfaces of pistils collected on December 3 was 23.2 ($N = 26$, $SD = 42.22$), while on December 17 the average number of grains per stigma was 294 ($N = 11$, $SD = 152.4$). This difference was highly significant (χ^2 , $P > .99$).

DISCUSSION AND CONCLUSIONS

This study reveals that coevolution between plants and pollinators can be more complex than the exchange of food for pollinator services. Bats not only effect pollination, they also promote outcrossing in *B. pauletia* as discussed later. Furthermore, two dis-

tinct floral resource utilization strategies are seen in bats, and these strategies may be related to their evolution of social behavior.

Breeding systems which promote outcrossing allow for greater evolutionary plasticity than inbreeding systems (Stebbins 1970). It has been suggested that genetic variability is important to plants subjected to changing selective pressures such as herbivores or seed predators that are also evolving (Janzen 1970). Plant breeding systems in the tropical dry forest region are typified by the prevalence of self-incompatibility systems among trees (Bawa *in press*), a large number of dioecious species (Bawa and Opler *pers. comm.*), and the frequent occurrence of other strategies that promote outcrossing (e.g., heterostyly, protandry). This supports the hypothesis that maintenance of plasticity is generally important there. *Bauhinia pauletia* is not a likely exception to this generality. As extensive insect damage to seeds was observed, *B. pauletia* appears to be subjected to the type of changing selection discussed by Janzen

(1970). Also, the sympatric bat-pollinated *B. unguolata* ensures outcrossing through genetic self-incompatibility (Bawa pers. comm.).

Although *B. pauletia* is genetically self-compatible, self-pollination (autogamy) of flowers is improbable. The apparent correlation between pollen deposition on stigmata and bat activity (on two nights in December) suggests that pollen movement depends greatly on animal transport. The strategy of andromonoecism seems also to be associated with dependence on animal transport of pollen. Self-pollination of flowers during a bat visit is improbable, since bats tend to push the stamens and pistil apart (Fig. 4B–4D) so anthers are unlikely to contact the stigma. Although small bats tended to visit particular flowers repeatedly, mixed pollen loads on *G. soricina* suggest that these small bats fly from flower to flower in a "trapline." Probably these bats visit a series of flowers repeatedly, and their visits decrease the probability of autogamy. The movement of groups of large bats from one area to another clearly promotes outcrossing. Pollen transfer among flowers of the same plant (geitonogamy) is not precluded by bat behavior, but it is clear that bats cause much if not most crossing.

The simultaneous production of male and hermaphrodite flowers on the same individual (andromonoecism) is rare, and its significance has not been investigated adequately. Carr et al. (1971) report andromonoecism in *Eucalyptus* spp. of the series *Corymbosae* but make no attempt to relate the phenomenon to pollination systems. It clearly reduces inbreeding, since functionally male flowers cannot be self-pollinated. We feel andromonoecism has additional adaptive value because it increases the ratio between pollen and ovules (or pollen and stigmatic surface). Large quantities of pollen may be necessary to ensure deposition of sufficient pollen to fertilize up to 30 ovules per stigma, especially since pollen is scattered over the entire ventral surface of bats. The stigmatic surface area is .008 cm², while the ventral surface area of just the wings of an average glossophagine bat is 144 cm² (Findley et al. 1972). This means the ratio of wing area (of an average small bat) to stigma surface area is 18,000:1. The need for large amounts of pollen in this system are obvious. Andromonoecism, therefore, may be associated with specialization for pollination by pollen vectors that are very large relative to stigma size.

The problem of utilization of large pollen vectors has been solved by other bat-pollinated plants in three basic ways. For example, *Pseudobombax barbigon* (Bignoniaceae) also maintains a high ratio of pollen to stigma area, but by producing hundreds of stamens per flower. Pollen may also be placed on a

bat selectively as in *Bauhinia unguolata*, which deposits pollen primarily on a bat's abdomen. Finally, larger stigmata, such as found in *Ochroma pyramidale* (Con. ex Lam.) Urban (Bombaceae), can greatly reduce the relative difference between pollinator and stigma-surface areas.

This explanation of andromonoecism can be extended to other pollination systems. *Aesculus californica* (Spach) Nutt. (Hippocastanaceae) is pollinated by butterflies, but it has a minute stigmatic surface (Benseler 1968). The stigmas of eucalypts are also very small, especially relative to the large number of ovules per flower.

Bauhinia pauletia nectar is used by at least two species of bats that have evolved different resource utilization strategies. Circumstantial evidence suggests that the great majority of the large bats were *Phyllostomus discolor*, while small bats were *Glossophaga soricina*. *Artibeus jamaicensis* and *Sturnira lilium*, characterized by reduced uropatagia easily distinguished in most photographs, were not seen. In addition, fewer than one-third of the captured *A. jamaicensis* carried pollen. Since we found that *A. jamaicensis* and *S. lilium* visited other flowers in the study region, we cannot assume that they never visited *B. pauletia*; however, they are certainly less important to *B. pauletia* pollination than *P. discolor* and *G. soricina*.

Resource utilization patterns appear to be related to aspects of the social behavior of these bats. Visitation by *P. discolor* is clearly coordinated, as indicated by the pulsed pattern illustrated in Fig. 4. This pattern and the formation of bats flying over the plants suggests a social organization that includes feeding groups. If so, more than one group was involved on November 4 and 5, as observers at opposite ends of the *B. pauletia* patch simultaneously watched peaks of visitation on 14 occasions. Therefore, it is impossible to speculate on the cohesiveness of these assemblages. Group foraging by *Phyllostomus hastatus* (Goodwin and Greenhall 1961) and *Myotis adversus* (Dwyer 1970) has been observed. As *Artibeus jamaicensis* and *Carollia perspicillata* may also forage in groups, this strategy may be more widespread than previously thought. In contrast, *G. soricina* forages singly around *Bauhinia pauletia*.

Energetic considerations are of extreme importance in plant-pollinator relationships (Heinrich and Raven 1972, Wolf et al. 1972) and may account for these bat foraging differences. Since the large bat *P. discolor* always drains nectar from *B. pauletia* flowers, the reward in nectar in successive visits is correlated with the time between visits. Short times between repeated visits to the same flower will net the visitor little nectar. By visiting flowers in groups *P. discolor* may decrease the probability of quick successive

visits to the same flower. Furthermore, bats might learn to allow the optimal time between visits to the same group of flowers for sufficient replenishment of nectar and to return before competing groups discover the new resource.

In contrast, individuals of the smaller bats spend a very short time at each flower, probably lapping small amounts of nectar at each visit. With the slow depletion of nectar, repeated visits to the same flower are not energetically disadvantageous. In fact, there may be some advantage to learning the position of particular flowers and then repeatedly utilizing these sources, because search time would decrease relative to feeding time. Independent foraging appears to be favored when nectar is not drained with each visit.

These bat-foraging strategies may parallel finch-foraging strategies in deserts. Cody (1971) found that the formation of foraging flocks of mixed finch species was related to food abundance, the birds forming flocks as food became less abundant. He hypothesized that renewable resources temporarily depleted are most efficiently utilized by flocks that can learn to vary the time between returns to the same feeding points. *Phyllostomus discolor* foraging may fit this pattern. Independent foraging of finches was observed when resources were abundant. This may be analogous to the independent foraging of *G. soricina*, which does not immediately deplete the floral nectar supply and thereby has an abundant resource.

In summary, *Bauhinia pauletia* is a genetically self-compatible plant living in conditions where maintenance of genetic variability is an asset. Bats pollinate its flowers and promote outcrossing. Andromonoecism increases the probability of pollen transfer from these large pollinators to relatively small stigmata and also decreases the probability of autogamy. Two kinds of bat have evolved different nectar-resource-utilization strategies, but both behaviors tend to result in cross-pollination of *B. pauletia* flowers.

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