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Flower Visitation by Bats in Cloud Forests of Western Ecuador[1]

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ABSTRACT

The importance of bat pollination has been demonstrated for many plant species. Yet this mutualism has rarely been studied on a community-wide level. In this paper we present results of a yearlong study of a bat–flower community in cloud forests on the western slopes of the Ecuadoran Andes. Of eight plant-visiting bat species caught, only *Anoura caudifera* and *A. geoffroyi* were carrying pollen. These species of *Anoura* supplement their diets with insects. Unlike glossophagines in other environments, however, which switch completely to a frugivorous or insectivorous diet during certain seasons, they are nectarivorous year-round and were never found with seeds or fruit pulp in their feces. Of the 13 morphotypes of pollen carried by the bats, 11 were identified to genus and 7 to species. Floral characteristics of all of these plants fit the traditional chiropterophilous syndrome well. Our study represents the first direct evidence of bat pollination for those plants identified to species, including four species of *Burmeistera* (Campanulaceae), as well as the first record of bat pollination for a plant of the genus *Meriania* (Melastomataceae). While overlap in the diets of the two *Anoura* was high, significant differences in visitation frequencies to particular plant species were detected. The larger bat species (*A. geoffroyi*) preferred large flowers, whereas the smaller species (*A. caudifera*) preferred small flowers.

RESUMEN

La importancia de los murciélagos en la polinización se ha demostrado para muchas especies de plantas; sin embargo, este mutualismo ha sido poco estudiado a nivel de comunidad. Presentamos los resultados provenientes de un estudio, de un año de duración, en una comunidad de murciélagos polinizadores y sus relaciones con las plantas en bosques nublados de las estribaciones occidentales de los Andes del Ecuador. De las ocho especies de murciélagos registradas, solo *Anoura caudifera* y *A. geoffroyi* transportaban polen. Estos *Anoura* complementan su dieta con insectos; no obstante, a diferencia de Glossophaginae en otros ambientes, que cambian su dieta exclusivamente a frutas o insectos estacionalmente, éstos se alimentan de polen a lo largo del año y nunca fueron encontrados con semillas o pulpa de fruta en sus heces. De los 13 morfotipos de polen transportado por los murciélagos, 11 fueron identificados hasta género y 7 hasta especie. Las características florales de todas estas plantas corresponden al síndrome quiropterolófilo. Nuestro estudio representa la primera evidencia directa de polinización por murciélagos para las plantas identificadas hasta especie, incluyendo cuatro especies de *Burmeistera* (Campanulaceae), así como el primer registro para el género *Meriania* (Melastomataceae). Aunque existía solapamiento en la dieta de los dos *Anoura*, se determinó diferencias significativas en las frecuencias de visita a especies particulares. La especie más grande (*A. geoffroyi*) mostraba preferencia por flores grandes, mientras que la pequeña (*A. caudifera*) prefería flores de menor tamaño.

Key words: *Andes;* Anoura caudifera; Anoura geoffroyi; *bat pollination; chiropterophily; cloud forest; Ecuador.*

KNOWLEDGE OF THE POLLINATORS that plants depend on is essential to conservation. Bats are important pollinators of several Neotropical plant species (Dobat & Peikert-Holle 1985, Helversen 1993). Chiropterophilous plants are often so dependent on bat pollinators that the plant would be severely threatened should their bat visitors disappear. For example, fruit set by four species of chiropterophilous Venezuelan cacti decreased from 46 to 76 percent to between 0 and 6 percent when bat visitors were excluded (Nassar *et al.* 1997). It is estimated that *ca* 590 species of plants in the New World are bat pollinated (Dobat & Peikert-Holle 1985).

The objective of this study was to examine a bat–plant community in the cloud forests of Ecuador. We sampled the bat community with mist nets, recorded which bat species were carrying pollen, and identified the angiosperm species to which

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this pollen corresponded. Only rarely has chiropterophily been studied on a community-wide level—the vast majority of research has detailed the reproductive biology of individual chiropterophilous plant species (Heithaus *et al.* 1974, Sazima & Sazima 1978, Voss *et al.* 1980, Buzato & Franco 1992, Cunningham 1995, Machado *et al.* 1998, Tschapka & von Helversen 1999; but see Heithaus *et al.* 1975, Fleming *et al.* 2001). A potential problem with this approach to the study of bat pollination is that it may tend to bias research in favor of those plants that already correspond closely to the traditional chiropterophilous syndrome. Recent studies have questioned the strength of the correlation between floral syndromes and pollinator assemblages, suggesting that both pollinators and plants are more generalized than previously thought (Herrera 1996, Ollerton 1996, Waser *et al.* 1996, Johnson & Steiner 2000). By identifying all pollen found on the bats, we can examine the extent to which these potentially bat-pollinated plants possess typical chiropterophilous traits without being biased by the traditional syndrome concept.

Two nectarivorous bats, *Anoura geoffroyi* and *A. caudifera* (Phyllostomidae: Glossophaginae), are known to occur in these cloud forests (Jarrín-V. 2000). Species of several primarily frugivorous phyllostomid genera, including *Sturnira*, *Platyrrhinus*, and *Artibeus*, have also been documented to visit flowers in other environments (Heithaus *et al.* 1975, Dobat & Peikert-Holle 1985, Pedro & Taddei 1997); however, nothing is known about which cloud forest plants these bats may be visiting. No direct evidence in the form of pollen presence on bats or visual confirmation of bat visitation currently exists for any cloud forest species.

The primary goal of this research was to document the participants in this cloud forest bat–plant mutualism. We also addressed the following questions: To what extent do the flower-visiting bats supplement their diets with fruit and insects? What is the degree of "fidelity" of these bats to particular angiosperm species? To what extent do the diets of these bats overlap? and How well do the bat-visited plants correspond to the traditional chiropterophilous syndrome?

MATERIALS AND METHODS

Research was conducted in two cloud forest reserves on the western slopes of the Andes of Ecuador: the Bosque Integral Otonga (Otonga) and the Reserva Florística Ecológica Río Guajalito (Guajalito). Otonga (00°25′S, 79°00′W) is located in Cotopaxi Province between 1300 and 2300 m elevation. Following Valencia *et al.* (1999), part of this site is classified as evergreen montane forest and part as montane cloud forest. Otonga consists of *ca* 1000 ha of primary forest, secondary forest, recovering pastures, and plantations of native trees. It has an average annual relative humidity of 90 percent, 2500 mm annual rainfall, and an average yearly temperature of 16°C. A rainy season lasts from December to June and a dry season occurs from July to November. The immediate borders of Otonga are covered with sugarcane fields and pastures. Otonga, however, is near a large expanse of forests protected by the "Reserva Forestal del Río Lelia" and "Reserva Ecológica Los Ilinizas," which allows it to maintain high diversity (Suárez 1998).

Guajalito (0°13′S, 78°48′W) consists of *ca* 150 ha of primary and secondary forest. It is located in the Chiriboga sector of Pichincha Province between 1800 and 2000 m elevation and is classified as montane cloud forest (Valencia *et al.* 1999). Average daily temperatures range from 14 to 22°C and annual rainfall is 2000—2800 mm. Guajalito and the surrounding areas, which include the "Reserva Ecológica La Favorita," make up 400 ha of cloud forest (*ca* 320 ha of primary forest, 35 ha of secondary forest, and 45 ha of pastures).

Bats were captured in nylon mist nets set along paths in primary forests and borders of disturbed habitats. Netting was conducted on nine occasions between September 1999 and July 2000 for a total of 64 days. We typically opened two to four 12 × 3 m nets and two to four 7 × 3 m nets between 1800 and 2400 h each night. Pollen samples were collected from the bats' fur with gelatin cubes containing fuchsin dye and immediately mounted on slides (Beattie 1971). Feces were collected in epindorf tubes. All bats were sacrificed and deposited in the Zoology Museum of the Pontificia Universidad Catolica del Ecuador (QCAZ) for other ongoing research on morphology and reproduction. Nectarivorous species were dissected to extract gut contents. Feces and gut samples were examined with a dissecting microscope for the presence of seeds, and slides were prepared with gelatin to view pollen. All other alcohol-preserved *Anoura* in the QCAZ museum collections ($N = 12$) were also dissected to examine gut contents. Guts of these individuals were dissolved in KOH before mounting on slides as above.

Pollen was identified using a reference collection compiled during the course of this study. The reference collection was supplemented by pollen

TABLE 1. *Diet of plant-visiting phyllostomid bats based on presence of seeds in gut or in feces and pollen on fur, in gut, or in feces. Average forearm (FA) length in mm is included to allow comparison of relative size.*

Subfamily	Species	*N*	FA ($\bar{x}$ ± SE)	Frequency of occurrence (%)	
				Fruit	Pollen
Glossophaginae	*Anoura geoffroyi*	11	43.2 (0.74)	0	82
Glossophaginae	*A. caudifera*	23	35.9 (0.39)	0	91
Stenodermatinae	*Sturnira bidens*	17	38.5 (0.31)	76	0
Stenodermatinae	*S. erythromys*	20	39.5 (0.28)	70	0
Stenodermatinae	*S. ludovici*	11	44.7 (0.59)	55	0
Stenodermatinae	*Artibeus phaeotis*	4	39.8 (0.61)	25	0
Stenodermatinae	*Platyrrhinus dorsalis*	11	46.6 (0.17)	18	0
Stenodermatinae	*P. vittatus*	5	58.9 (0.72)	20	0

salvaged from herbarium specimens (Herbario Internacional of PUCE) known to occur in the cloud forests. Specimens of those plants identified as bat-visited were deposited in the herbarium.

Because the number of pollen grains found on a bat cannot be correlated reliably with the number of flowers that bat visited, pollen was scored as present or absent for each bat regardless of the quantity or where it was found (fur, gut, or feces). We used chi-square statistics to test the null hypothesis that there were no differences in floral diet among bat species.

RESULTS

We caught 102 plant-visiting bats of eight species (Table 1). Of these, only *A. geoffroyi* and *A. caudifera* visited flowers. Individuals of the other six species (*Artibeus phaeotis*, *Platyrrhinus dorsalis*, *P. vittatus*, *Sturnira bidens*, *S. erythromys*, and *S. ludovici*) were never found with pollen. These species consumed fruit, as evidenced by the seeds in their feces. Eighteen (82%) of the 22 *Anoura* individuals we caught were carrying pollen on their fur. The guts of 13 of these were examined, along with the guts of 12 QCAZ museum specimens. Twenty-three (90%) of these 25 guts contained pollen. Overall, of the 34 *Anoura* examined, 30 (88%) were positive for pollen.

The two species of *Anoura* did not eat fruit; seeds were never found in their feces or gut samples. The *Anoura*, however, did supplement their diets with insects; 40 percent of gut samples were found to contain insect parts (*e.g.*, wings and legs.). Further study is needed to determine whether these insects were actively hunted or were found in flowers and ingested incidentally during flower visits.

The *Anoura* were often carrying several types of pollen at time of capture. Ninety-six percent of the gut samples positive for pollen were mixed loads. Average load for stomachs was 3.6 (SD = 1.4, *N* = 23) morphotypes. Of fur samples, 74 percent were mixed loads with an average load of 2.4 (SD = 1.1, *N* = 19) morphotypes per bat. Up to 7 different morphotypes of pollen were found on a single bat.

The bats were carrying 13 different morphotypes of pollen. Eleven were identified to the level of genus, and seven to species (Table 2). These belonged to a wide range of taxa representing eight different families. While several of these genera had been known or surmised to contain other bat-pol-

TABLE 2. *Number of* Anoura geoffroyi *and* A. caudifera *carrying each type of pollen at time of capture. For each individual, pollen was scored as present if found on fur, in feces, or in the gut. Abbreviations:* Bombacopsis squamigera *(Bomb);* Pitcairnia brogniartiana *(P bro);* Burmeistera sodiroana *(B sod);* B. succulenta *(B suc);* B. truncata *(B tru);* Burmeistera *sp. 1 (B sp.);* Clusia *sp. (Clus);* Marcgravia coriaceae *(M cor);* Meriania pichinchensis *(M pic);* Passiflora *sp. (Pass);* Markea *sp. (Mark); unknown pollen no. 1 (Unk 1); and unknown pollen no. 2 (Unk 2).*

	N	Bomb	P bro	B sod	B suc	B tru	B sp.	Clus	M cor	M pic	Pass	Mark	Unk 1	Unk 2	Total
A. geoffroyi	11	1	4	1	0	2	0	2	4	4	1	3	1	0	23
A. caudifera	23	0	4	9	15	8	2	0	11	8	1	3	9	1	71
Total	34	1	8	10	15	10	2	2	15	12	2	6	10	1	94

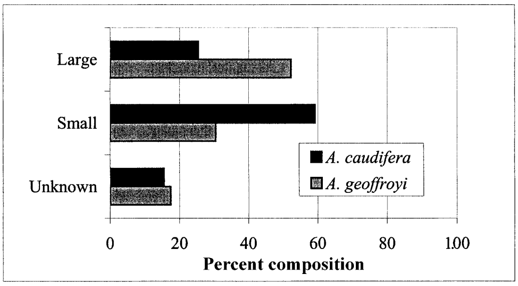

FIGURE 1. Percent composition of large and small flowers in the floral diet of *Anoura caudifera* ($N = 23$) and *A. geoffroyi* ($N = 11$). Size was measured as distance from anthers to nectar source. *Markea* sp. (10.8 cm), *Pitcairnia brogniartiana* (11.0 cm), and *Marcgravia coriacea* (5.6 cm) are classified as large while *Meriania pichinchensis* (2.6 cm), *Burmeistera sodiroana* (2.8 cm), *B. succulenta* (2.3 cm), *B. truncata* (2.8 cm), and *Burmeistera* sp. (3.1 cm) are classified as small. Lack of access to fresh flowers precluded measurement of *Passiflora*, *Clusia*, and *Bombacopsis*; these along with the two unidentified pollen morphotypes comprise the 'unknown' category.

linated species based on floral morphology (Dobat & Peikert-Holle 1985), this study represents the first concrete evidence of bat visitation for each of these species. It also represents the first record for the genus *Meriania*.

Comparison of flower use by the two *Anoura* species indicated a high degree of overlap in diet. They visited virtually the same set of flowers; of the 13 species utilized by the bats, *A. caudifera* used 11 and *A. geoffroyi* used 10 (Table 2). Yet, although flower usage did not vary qualitatively, frequency of visits to each flower species differed.

This difference in floral visitation correlated with size of the flowers (Fig. 1). Flower size was approximated by measuring the distance from the anthers to the nectar source. Those flowers with an anther–nectar distance greater than 5 cm were classified as "large," and those less than 5 cm were classified as "small." For those species classified as "unknown," lack of access to fresh flowers precluded measurement. A chi-square analysis of these data revealed a significant difference ($\chi^2 = 6.74$, df = 1, $P < 0.01$). *Anoura caudifera*'s diet contained 59 percent small flowers and 25 percent large flowers, while *A. geoffroyi*'s diet contained 52 percent large and 30 percent small.

Previous studies have identified a set of morphological/phenological characters shared by plants using bats as pollinators (Baker 1961, Dobat & Peikert-Holle 1985, Helversen 1993). The bat-visited plants identified in this study all fit this chiropterophilous syndrome well (Table 3), with the exception that none emit a noticeable odor. A separate discussion of each of the plants follows. Figure 2 presents illustrations of floral morphology for each plant. *Passiflora* sp., *Clusia* sp., and *Bombacopsis squamigera* are not discussed because their flowers were not observed in the field; pollen was identified with herbarium material. For a detailed discussion of chiropterophily in a rain forest species of *Passiflora*, see Sazima and Sazima (1978).

BURMEISTERA.—Five species of *Burmeistera* (Campanulaceae) were found at the study sites: *B. truncata*, *B. sodiroana*, *B. succulenta*, *Burmeistera* sp., and *B. crassifolia*. Of these, the flowers of the first four were visited by bats while *B. crassifolia* was not. While they all have very similar floral morphology, the few differences in *B. crassifolia* flowers nicely illustrate the validity of the traditional chiropterophilous syndrome. *Burmeistera crassifolia* flowers have a mottled white and bright red col-

TABLE 3. *Chiropterophilous characters in bat-visited flowers. Traits are recorded as present (X), absent (−), or unknown(?). The genus* Burmeistera *here includes* B. sodiroana, B. succulenta, B. truncata, *and* Burmeistera *sp.*

Chiropterophilous character	*Burmeistera* (4 spp.)	*Pitcairnia brogniartiana*	*Markea* sp.	*Meriania pichichensis*	*Marcgravia coriaceae*
Pale coloration	X	X	X	−	X
Campanulate morphology	X	−	X	X	−
Penicillate morphology	−	−	−	−	X
"Head-mask" morphology	X	−	−	X	−
Robust	X	X	X	X	X
Well exposed	X	X	X	X	X
Pendulous	−		X	−	−
High pollen supply	X	X	X	−	X
Smooth and waxy surface	−	−	−	X	−
Long flowering duration	X	X	X	?	X
Nocturnal anthesis	X	X	X	?	?
Nocturnal nectar production	X	?	X	?	?

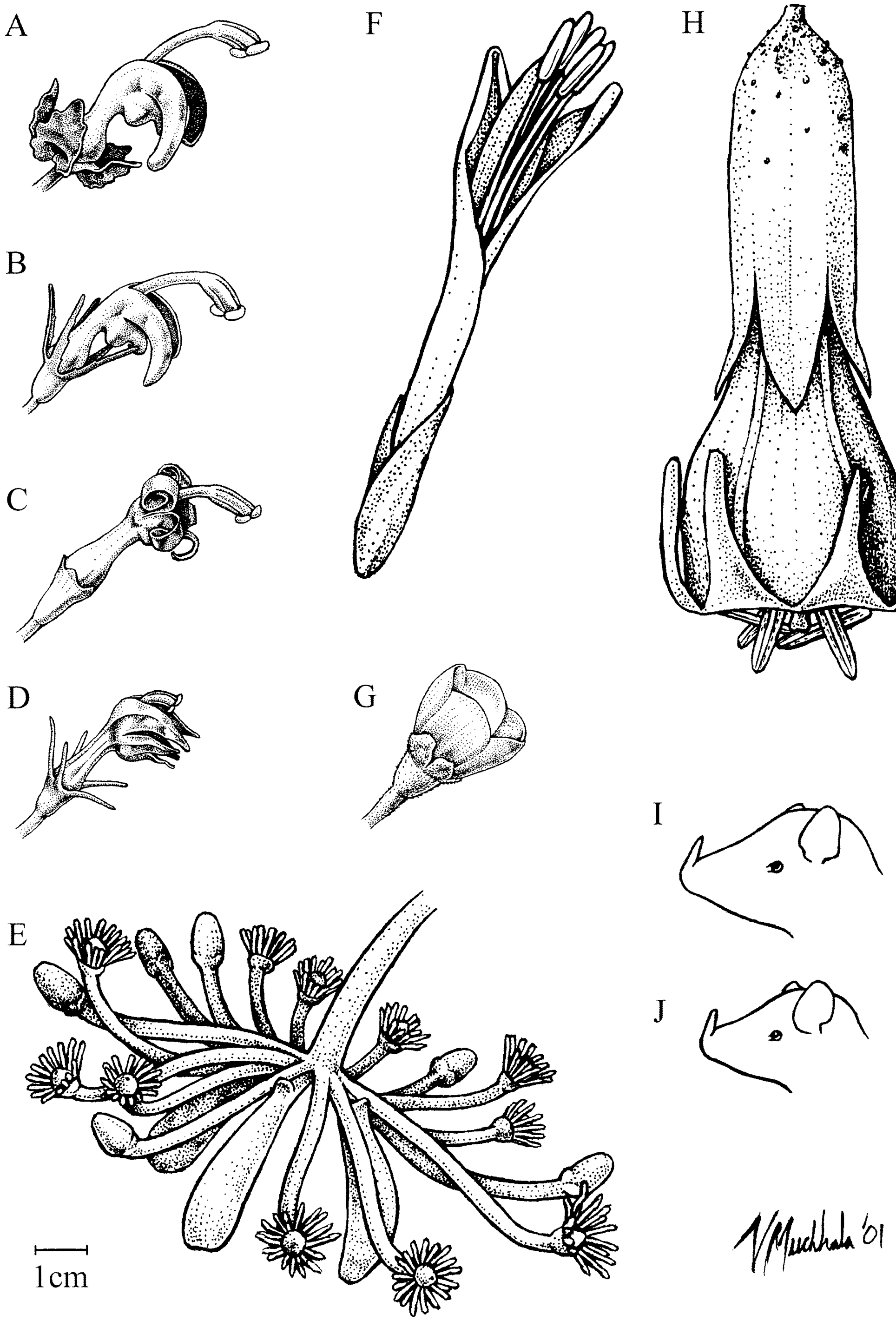

FIGURE 2. Floral morphology of seven bat-visited cloud forest species. (A) *Burmeistera* sp., (B) *B. truncata*, (C) *B. sodiroana*, (D) *B. succulenta*, (E) *Marcgravia coriacea*, (F) *Pitcairnia brogniartiana*, (G) *Meriania pichichensis*, and (H) *Markea* sp. (I) *Anoura geoffroyi* and (J) *A. caudifera* heads are shown for scale.

oration, are thin and tubular, and have short stems that barely place the flower past the leaves of the plant. In contrast, the other four *Burmeistera* species have green flowers with occasional purple blotches, have a more "campanulate" morphology (the "head-mask" morphology described by Dobat and Peikert-Holle 1985), and are thrust out well beyond the plant's foliage.

The flowering phenology of *Burmeistera* sp. and *B. sodiroana* was examined in closer detail. The flowers are protandrous and last about six days. One to two buds open daily per plant, between 1715 and 1800 h. The morphology of the petals protects nectar from dilution by rain (Fig. 2). The flower is held at a 45° angle; in *Burmeistera* sp., it is thrust above the foliage, while in *B. sodiroana*, the stem drops below the branch before angling up. Nectar production began around 1800 h and continued until midnight. Copious amounts of pollen were available the first two nights. By the third night, the pollen supply was exhausted and the stigma was exposed. After approximately three more days, nectar production stopped and the stem lowered until the flower was hanging below the branch. The corolla eventually dropped off and an inflated berry developed—*ca* 4 cm in diameter and green for *Burmeistera* sp. and 1 cm and bright pink for *B. sodiroana*. As we studied floral morphology during 4–7 June, bats were observed visiting both species. A hummingbird was also observed visiting *Burmeistera* sp. at dusk (1800 h). During the visit, the head of the hummingbird was several centimeters below the stigma, suggesting that this species was not an effective pollinator; however, the stigma of the bat-visited *B. succulenta* does not extend as far outside of the flower as that of *Burmeistera* sp. Perhaps *B. succulenta*, like *Syphocampylus sulfureus* (Sazima *et al.* 1994), exploits the pollination services of both hummingbirds and bats. Examination of the timing of nectar production would help to confirm this.

An individual *Burmeistera* plant stays in flower for several months, and *Burmeistera* pollen was found on bats year-round. This steady-state flowering schedule suggests that *Burmeistera* promotes traplining behavior in *Anoura* bats.

PITCAIRNIA BRONGNIARTIANA.—*Pitcairnia brongniartiana* (Bromeliaceae) has a long flowering stalk arising from the center of the plant. This allows the flowers to be well exposed. Anthesis was nocturnal and only one flower was open per stalk per night. Like *Burmeistera*, this suggests that *P. brongniartiana* is designed to exploit traplining behavior. The flower consists of white petals around several long stigmas (11 cm). Anthers produced copious amounts of yellow pollen.

MARKEA.—The *Markea* sp. (Solanaceae) in the study sites also closely matches the chiropterophilous syndrome. The flowers of this epiphytic plant are pendulous and hang far below the rest of the foliage. They are campanulate and very long (10.8 cm). Flowers began opening at 1800 h and were fully open by 1900 h. The four stamens were sturdy, protruded outside of the flower, and contained large amounts of pollen. Nectar was produced at night and prevented from dripping out of the flower by hairs around the base of the stigma.

Markea sp. also appears adapted to promote traplining behavior. Only one or two flowers were open per plant per night despite the presence of many buds. One individual flowering in late December was found to still be in flower in early July.

The large size of these flowers is intriguing. In the New World, campanulate bat-pollinated flowers usually form small "head-masks" that allow bats to continue hovering while extracting nectar (Helversen 1993). The morphology of *Markea* sp. is such that the bat will not be able to touch the nectar with its nose while hovering. Do bats dive into the flower or hover outside during the visit and use their long tongues to reach the nectar? Unfortunately, bat visitation of *Markea* sp. was not observed.

MERIANIA PICHICHENSIS.—While it was possible to anticipate bat pollination in many of the flowers before finding pollen on bats, it was a surprise to find *Anoura* visiting flowers of *Meriania pichichensis* (Melastomataceae). Orange flowers are never referred to as a chiropterophilous character. On closer inspection, the flowers of this species can be seen to diverge from its bee-pollinated relatives (Renner 1989) found in cloud forests. First, the flowers never completely opened but retained a campanulate shape, while petals in other Melastomataceae lay flat. Second, the petals of *M. pichinchensis* are much sturdier and have a shiny, reflective surface which, as suggested by Helversen and Helversen (1999), may aid in sonar detection. Also, flowers of other cloud forest Melastomataceae are a brilliant pink; in comparison, the orange flowers of *M. pichinchensis* are rather dull.

MARCGRAVIA CORIACEAE.—The morphology of *Marcgravia* flowers (Marcgraviaceae) is quite different from other cloud forest bat flowers: 10–12 flowers are arranged around 2–4 large nectaries. While bats visit these nectaries, pollen is placed on the underside of the bat's body. The inflorescence is well exposed, placed on the end of branches beyond the plant's foliage.

DISCUSSION

The plant-visiting bats we caught in these cloud forests specialized on either fruits or nectar (Table 1). Frugivorous bats were never encountered with pollen, and seeds were never present in the feces or guts of nectarivores. This dietary constancy is interesting because previous studies have shown that it is often difficult to place bats in strict guilds based on diet. For example, a number of "frugivorous" species in the genera *Sturnira*, *Platyrrhinus*, and *Artibeus* have been documented to visit flowers (Heithaus *et al.* 1975, Dobat & Peikert-Holle 1985, Pedro & Taddei 1997). In many environments, glossophagines are nectarivorous for only part of the year and rely on fruit or insects for the rest (Alvarez & Gonzalez Quintero 1970, Fleming *et al.* 1972, Howell 1974). In a review of phyllostomid feeding habits, Gardner (1977) reported that *Anoura* consume both nectar and fruit. The *Anoura* we caught in these cloud forests did not eat fruit and visited flowers consistently throughout the year.

In addition to the high dietary constancy of its frugivores and nectarivores, this cloud forest bat community is interesting in that it apparently lacks omnivores. Of the guilds Kalko *et al.* (1996) listed for rain forest bat communities, the guild "omnivores of the subcanopy" is conspicuously missing (Jarrín-V. 2000). This guild is represented by such generalists as *Phyllostomus hastatus* and *Micronycteris brachyotis*, which consume nectar, pollen, fruits, insects, and vertebrates. The greater apparent specialization of the bat community in these cloud forests may reflect the lack of seasonal climatic extremes. Although there is a rainy season, flowers and fruit are available throughout the year. In contrast, no flowers are available for bats from mid-March to early December on Barro Colorado Island (Bonaccorso 1979) and only one is available from late June to early September in the lowlands of northwestern Costa Rica (Heithaus *et al.* 1975). The main advantage of a more general diet is the ability to switch food sources as the environment changes; a constant environment may favor specialists.

While *A. geoffroyi* and *A. caudifera* do specialize on nectar and pollen, they do not show high constancy to particular angiosperm species. This is evidenced both by the large total number of flowers they visit (11 species for *A. caudifera* and 10 for *A. geoffroyi*) and the large number of pollen species they carry on their fur each night. In this study, 74 percent of the *Anoura* were carrying mixed pollen loads on their fur at the time of capture. These loads contained on average 2.4 species. The diverse nightly visitation patterns of these bats likely have negative implications for the pollination of the plants. Presumed costs of such low "pollinator fidelity" include stigma blockage, pollen loss to heterospecific stigmas, and production of sterile or inviable hybrids (Rathcke 1983).

Overlap in the diet of *A. geoffroyi* and *A. caudifera* is high—of the 13 bat-visited flowers, *A. geoffroyi* was carrying the pollen of 10 and *A. caudifera* was carrying the pollen of 11. Thus, in addition to the bats visiting more than one flower, the flowers are visited by more than one bat. This provides further support for the "diffuse" nature (*cf.* Janzen 1980) of bat–flower coevolution as suggested by Heithaus (1982). Without exclusive species-specific interactions between bats and flowers, species-specific coevolution cannot occur; the congruence between bats and the flowers they pollinate (Helversen 1993) is instead a result of each guild responding to the other as a group.

Although there is high overlap in the kinds of flowers visited by *A. geoffroyi* and *A. caudifera*, there are differences in frequencies of exploitation of particular species. Our results showed that *A. geoffroyi* preferentially visits larger flowers while *A. caudifera* prefers small flowers. *A. geoffroyi* is *ca* 20 percent larger than *A. caudifera*, with an average forearm length of 43.2 mm versus 35.9 (Table 1). Nicolay and Dumont (2000) demonstrated that nectar-feeding performance of the blossom bat *Syconycteris australis* (Pteropodidae) is affected by the size of simulated flower corollas. Rate of nectar extraction was significantly lower from feeders with narrow "corollas." We suggest that *A. geoffroyi* may exhibit similar difficulties feeding from small *Burmeistera* flowers, while *A. caudifera* may have difficulty accessing the nectar of large *Markea* and *Pitcairnia* flowers.

Anoura geoffroyi and *A. caudifera* occur sympatrically over most of their contemporary ranges. Both are widespread to *ca* 25°S latitude, yet avoid most of the Amazon basin (Koopman 1981). Specialization to some extent on the appropriately sized flower may reduce competition between these two species of *Anoura*, allowing them to coexist over their large ranges.

What can this study tell us about the "validity" of the chiropterophilous floral syndrome? Waser *et al.* (1996) argued that contrary to predictions based on the floral syndrome concept, floral phenotypes do not correspond well to pollinators because (1) plants do not exclusively rely on the "correct" pollinator for their syndrome and (2) pollinators do not exclusively pollinate plants in their syndrome. We cannot comment on the former assertion because we do not know whether or not the bat-pollinated plants identified in this study also use the pollination services of other taxa. This study, however, does provide evidence against the latter. In these cloud forests, bats carry pollen only from plants that correspond closely to the bat pollination syndrome. Furthermore, we did not find any plant species with chiropterophilous traits that were not visited by bats; *i.e.,* in creating the reference collection for this study, we took pollen from 76 species found in flower in the reserves, and for every one of these with traditional chiropterophilous characteristics, we found its pollen on the bats at least once. Thus, our study lends support to the utility of the chiropterophilous floral syndrome in predicting bat pollination and to the importance of these characteristics in the mutualism between bats and flowers.

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