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# Bat Morphology and Pollinator Specificity in a Neotropical Cloud Forest

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## ABSTRACT

This study explores the degree of specialization of nectarivorous bat species and the plants they visit by examining pollen loads. The bat species involved are *Anoura geoffroyi*, *Glossophaga commissarisi*, and *Hylonycteris underwoodi*, all of which feed on nectar and are found in the cloud forests of Monteverde. Five nights were spent mist-netting and pollen samples were taken from the head, fore-body and back of each individual caught. These were placed on slides that were observed under a microscope and pollen morphospecies were counted. Twenty-two pollen morphospecies were found and a few were identified. A 1-way ANOVA test was conducted to compare the mean pollen species richness for each bat species. No significant differences were found ( $F = 0.243$ ,  $P = 0.785$ ,  $DF = 2,33$ ). A cumulative catch curve determined that sampling was nearly exhaustive. A Sorenson index of similarity was conducted to compare the pollen species found on each bat species. Pollen morphospecies overlap was found to be similar between all bat species (*A. geoffroyi* vs. *G. commissarisi* = 0.615, *A. geoffroyi* vs. *H. underwoodi* = 0.583, *G. commissarisi* vs. *H. underwoodi* = 0.545). A few plant species were only visited by species with long snouts, suggesting specialization beyond the general syndromes of glossophagine bats and bat flowers in the Neotropics.

## RESUMEN

Este estudio explora el nivel de especialización de especies de murciélagos que toman néctar y las plantas que visitan al examinar las cantidades y clases de polen. Las especies que están involucradas son *Anoura geoffroyi*, *Glossophaga commissarisi*, y *Hylonycteris underwoodi*. Todas estas especies se alimentan de néctar y se pueden encontrar en los bosques nubosos de Monteverde. Durante cinco noches capturamos murciélagos y se colectaron muestras de polen de la cabeza, el pecho y la espalda de cada individuo que fue capturado. Las muestras de polen fueron puestas en portaobjetos de vidrio para observarlos en un microscopio compuesto para contar las especies de polen. Veinte y dos morfo especies de polen fueron encontrados y algunos de estos fueron identificados. Un ANOVA de una vía se llevo a cabo para comparar el promedio de la riqueza de especies de polen por especie de murciélago. No hubo ninguna diferencia significativa ( $F = 0.243$ ,  $P = 0.785$ ,  $DF = 2,33$ ). Una curva acumulativa de capturas determinó que los muestreos fueron tomados exhaustivamente. Un índice de Sorenson de Similaridad comparó las especies de polen en cada especie de murciélago (*A. geoffroyi* vs. *G. commissarisi* = 0.615, *A. geoffroyi* vs. *H. underwoodi* = 0.583, *G. commissarisi* vs. *H. underwoodi* = 0.545). Algunas de las especies de plantas solamente fueron visitados por especies de murciélagos con hocicos largos, así se sugiere una especialización más allá de los síndromes generales de murciélagos glossophagine y las flores de murciélagos en los Neotropicos.

## INTRODUCTION

Plant-pollinator mutualisms are often used as examples of coevolution: reciprocal adaptations between two or more species. Pollination interactions may tend toward specialization because pollen must be transferred from a flower's anthers to a conspecific's stigma to ensure pollination. Flowers have evolved morphologies and rewards to attract certain groups of pollinators, and the pollinators have responded by evolving reciprocal specialized morphology, physiology and behavior. These adaptations are referred to as "syndrome characters" (Helfersen 1993). Bat flowers, for example, open at night (often only for one night and some only for a few hours after dusk) are often bell- or brush-shaped, making them easily accessible, are white -or cream-colored and have a scent that is strong, fruity, sour or musty (Proctor 1996). Meanwhile, their bat visitors regularly have long snouts, reduced teeth; an extensile tongue with papillae for nectar and pollen collection, and many can hover like hummingbirds (Altringham 1996). A clear case of coevolution between a bat species and its flowers is that of *Dactylanthus taylorii* (Balanophoraceae), a plant endemic to New Zealand, which has only one pollinator, the bat *Mystacina tuberculata* (Mystacinidae), also endemic, which feeds on *P. taylorii* and arthropods (Altringham 1996, Nowak 1994).

Though it is clear that nectarivorous bats and the flowers they visit exhibit many traits that correspond to one another, it remains unknown how specialized groups of bats and plants have become within the general syndromes. For specialized nectarivory to occur, bat species would narrow their foraging choices as plants alter their morphology or reward to accommodate some subset of potential chiropteran visitors. Helfersen (1993), for example, suggests that several plant genera have adapted for pollination by the leaf-nosed bats, family Phyllostomidae, subfamily Glossophaginae, which are strictly Neotropical. The plant traits that Helfersen (1993) suggests are modified include flower shape, reward, pollen placement, color, scent, and accessibility.

Glossophagines are the only nectar- or pollen-feeding bats in the Neotropics, and bat-pollinated flowers are highly diversified in comparison to those of the Old World Tropics (Helfersen 1993). Helfersen (1993) estimates 800-1000 Neotropical bat-pollinated species, representing 0.5 - 1 % of Neotropical angiosperms. Many of these flowers have evolved bell-shaped flowers that tilt down, such as *Vriesea* (Bromeliaceae), or have flowers that hang upside down, such as *Mucuna* (Papilionaceae) and *Markea* (Solanaceae). An example of adaptations in response to flowers that hang upside down is demonstrated by *Lonchophylla lionycteris* and *L. platalina*, which lick up nectar and pump it through lateral grooves on their tongue (Helfersen 1993). Are there other coevolutionary changes on the genus and species level in the Neotropics? Snout and body sizes vary considerably in glossophagines, providing ample variation around which plants could evolve. For instance, they may show morphological adaptations including elongated snouts, reduced nose-leaf, reduced incisors and molars, and long tongues with papillae at the tip.

Presumably, both plants and glossophagines gain from specialization. The plant receives less foreign pollen, increases the likelihood of pollen transfer to conspecifics and also benefits from the long distances that bat pollinators travel before depositing their pollen, thus increasing the genetic diversity of offspring (Bawa 1990). This is especially important for plants that live in randomly spaced low-density populations (Altringham 1996). The bats profit from avoiding competition for nectar with non-glossophagines in the area.

How competition structures nectarivorous bat communities is largely unknown. Heithaus et al. (1975) found large niche overlap for 13 nectarivorous bat species in a dry forest community

in which one species was a nectar specialist. Others switched to fruit diets at times of nectar scarcity. This alone might preclude specialization; bats in less seasonal areas, such as wet or cloud forests that provide more continuous nectar resources, might show higher degrees of specialization. The cloud forests of Monteverde harbor seven of the twelve nectarivorous bat species of Costa Rica, comprising five genera. This study examines the possible specialization of nectarivorous bats and plants in Monteverde, by investigating species composition and richness of pollen loads.

## **METHODS**

This study was conducted in October and November 2001 at the Hummingbird Gallery near the Monteverde Cloud Forest Reserve, Puntarenas, Costa Rica. The area is in the Holdridge Life Zone of Lower Montane Wet Forest at an elevation of 1535 m (Haber 2000). At this site there are seven hummingbird feeders frequented by nectarivorous bats. Anticipated bat species were *Anoura geoffroyi*, *A. cultrata*, *Glossophaga soricina*, *G. commissarisi*, *Lonchophylla robusta*, *Choeroniscus godmani*, and *Hylonycteris underwoodi*.

### **Mist Netting**

Mist netting was conducted for five nights. Nets were opened at 6:00 pm, just after sunset, and closed at 7:00 pm when it became too misty to catch bats. Each individual was identified, sexed, weighed and their reproductive condition was noted. Pollen samples were taken from each individual's head, fore-body and back together with a piece of clear scotch tape and placed on glass slides.

### **Pollen**

In the lab a compound microscope at 100 x magnification was used to look for pollen on the slides. Pollen species richness was counted for each slide. Pollen was categorized into morphospecies and photographed or sketched (Appendix 1). A few morphospecies were then identified by comparing them to pollen samples of known bat-pollinated plant species collected near the study site and to photographs of pollen from Barro Colorado Island (Roubik and Moreno 1991). Pollen samples were also compared to samples taken from the hummingbird feeders and from photographs of pollen found on hummingbirds to make sure the bats had not picked up any pollen from the feeders rather than from flowers (Martin 1999).

The data were analyzed using a 1-way Analysis of Variance to compare pollen richness for each bat species. A cumulative catch curve was constructed to determine if sampling of slides had been done exhaustively. A Sorenson qualitative test of similarity was conducted to compare the overlap between pollen types carried on each bat species (Magurran 1988).

## RESULTS

### Mist Netting

A total of 82 individuals of three nectar-feeding bat species were captured: Twenty *Anoura geoffroyi*, 27 *Glossophaga commissarisi*, and 35 *Hylonycteris underwoodi*. *Anoura geoffroyi* is distinguishable by lacking a tail membrane, it has a forearm length of 39 - 47 mm. and a weight of 12 - 16 g. *Glossophaga commissarisi* has a shorter snout than the other species, has a forearm length of 32 - 36 mm. and a weight of 9 - 11 g. *Hylonycteris underwoodi* is a small dark bat with tiny teeth, a forearm length of 31 - 36 mm. and a weight of 8 - 10 g. (Nowak 1994; Timm and LaVal 1998). Pollen samples were collected from 74 individuals.

### Pollen

Due to time constraints, randomly selected sub-samples of 12 slides per bat species (a total of 36 slides) were checked for pollen. The cumulative catch curve shows that sampling was nearly done exhaustively (Figure 1). Several morphospecies of pollen were found on most individuals, varying from zero to six and averaging about two. A 1-way ANOVA test found no significant difference between the mean pollen species richness ( $\pm 1$  S.D.) carried by each bat species ( $F = 0.243$ ,  $P = 0.785$ ,  $DF = 2, 33$ ) (Figure 2).

In all, twenty-two morphospecies of pollen were found on the slides, none of which had been picked up from the feeders (Appendix 1). The degree of pollen morphospecies overlap found on each bat species was shown to be similar using the Sorenson test (Figure 3) (Magurran 1988). Thirteen plants were only visited by one bat species; two were visited by two bat species, and seven by all three bat species. Four pollen species were only found on *G. commissarisi*, five only on *A. geoffroyi*, and four only on *H. underwoodi*.

## DISCUSSION

There is variation in the size and snout length of Neotropical nectarivorous bats and the corollas of the flowers they visit to afford opportunities for specialization. Therefore it was expected that Monteverde nectarivorous bat species might differ in richness and composition of pollen loads. However, neither pollen species richness nor species composition differed significantly between bat species. The number of plant species visited per individual bat ranged from zero to six, with an average of about two. This suggests that individuals are general in their foraging habits and therefore are unlikely to be specialized for any particular plant species.

Although the three bat species carried similar species of pollen, there were some pollen species that were not found on all three bat species. That is, certain species of pollen were found exclusively on one or two bat species. Thirteen of 22 bat flower species (over half) were visited by a single bat species, two by two bat species, and seven (32%) by all three bat species. Four of the flowers were only visited by *H. undenwoodi*, and one was only visited by *H. underwoodi* and *A. geoffroyi*. These plants may have flowers with corolla lengths and widths that restrict visitation by the short-snouted *G. commissarisi*. With more information, pollen could be matched to plant species to test this directly.

These bats are considered to be nectar specialists and visit flowers with morphologies catering to chiropteran pollinators, with the exception of *G. commissarisi*, which is considered to

be opportunistic, feeding on nectar when available. Bat-pollinated plants are generally specialized in that bats are their primary pollinators and this is only done at night. New World bat flowers have further coevolved to attract a suite of glossophagine pollinators. Even within the Glossophaginae there is adequate morphological variation in bat species for specialization to occur. After examining pollen loads more closely in this study, the evidence for specialization is compelling enough to warrant further study.

Morphologies exhibited in bat-plant interactions are not as pronounced as in other groups (like hummingbirds and hawkmoths, for example; Futuyma and Slatkin, 1983) and, therefore, do not suggest a high likelihood of obligate mutualism. On the contrary, they do not preclude more diffuse specialization. Beyond the general bat pollination syndrome of nectarivorous bat pollinators and their bat flowers, genera or species of bats and bat flowers may have interacted through a process of more specific coevolution. However, results of this and other studies uphold that the degree of mutual dependence between any two or more species is low.

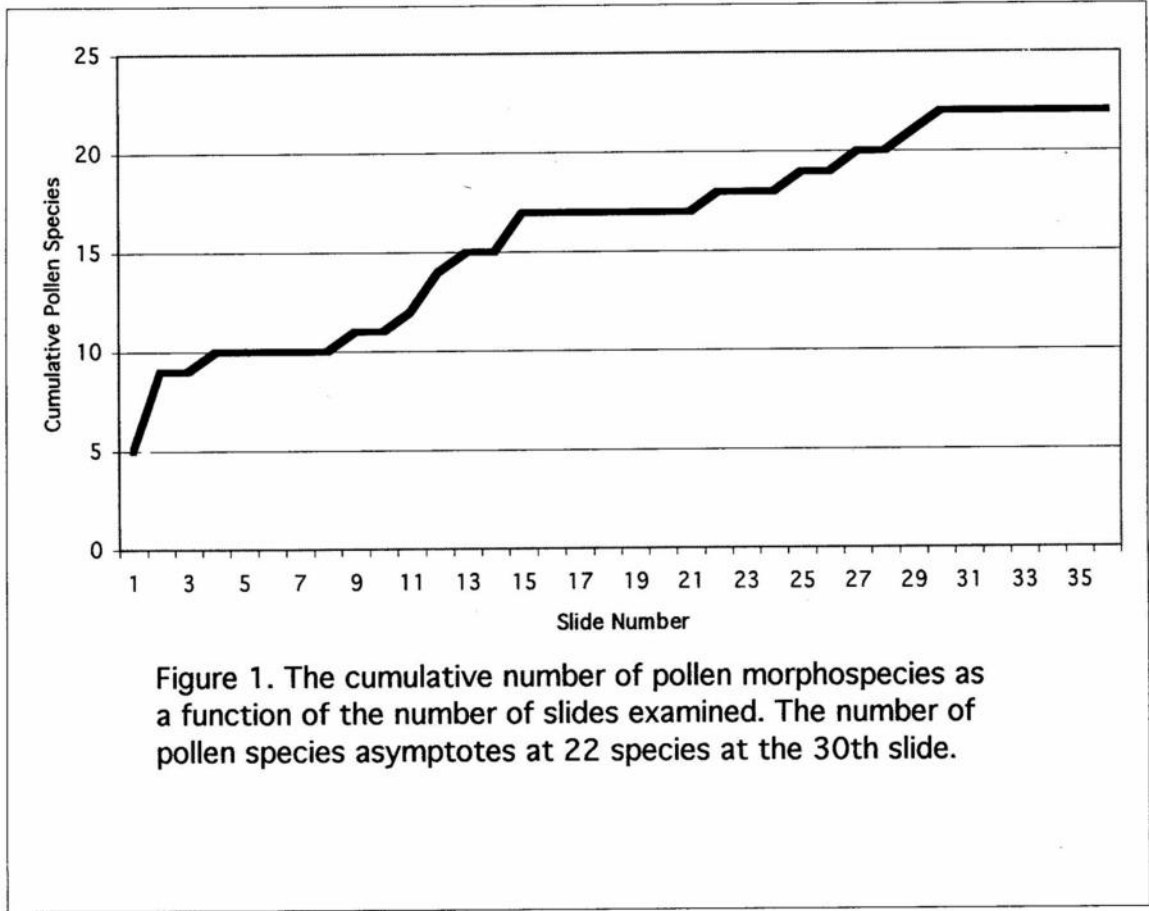
These results reflect the complex interactions of tropical ecosystems and the biodiversity and species richness they hold. Conservation of these ecosystems is essential for sustaining the high level of diversity and richness that must be maintained for the reproductive success of the plants and the survival of the bats involved in these bat-plant relationships. The degree to which each species has influenced the other's evolution deserves more exploration. Further research on the morphologies of bat flowers and of the various bat species would be valuable to expanding our knowledge of bat-plant interactions in the Neotropics. Also, a more extensive study of bat-flowers, including taking pollen samples of all possible bat-pollinated flowers, would be necessary in order to identify all the plant species visited by *Anoura*, *Glossophaga* and *Hylonycteris*.

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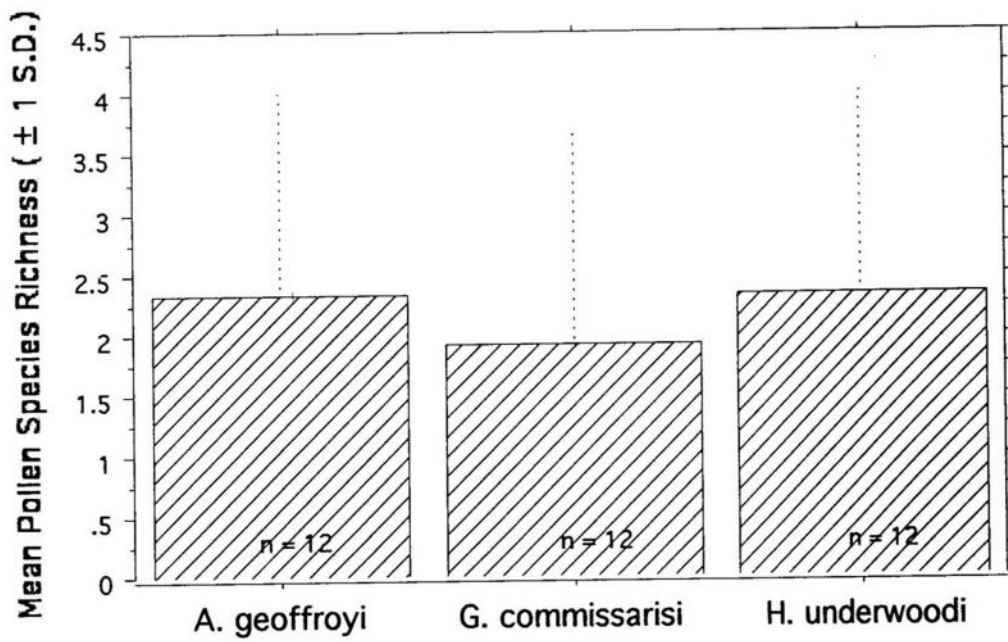


Figure 2. Mean pollen species richness carried by each bat species in the cloud forests of Monteverde. One-way ANOVA shows no significant difference  $F = 0.243$ ,  $P = 0.785$ ,  $DF = 2, 33$ .

Bat species:      *A. geoffroyi*      *H. underwoodi*

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*G. commissarisi*      0.615      0.545

*H. underwoodi*      0.583

Figure 3. Similarity values for pollen morphospecies carried by each bat species calculated from a Sorenson test of similarity (Magurran 1988).

Appendix 1. Pollen morphospecies found on slides taken from *G. commissarisi*, *H. underwoodi* and *A. geoffroyi*: A. Unknown B. *Vriesea* sp. Bromeliaceae C. Unknown D. Unknown E. Unknown F. Unknown G. Unknown H. Unknown I. Unknown J. Unknown K. Unknown polyad L. *Inga* sp. Papilionaceae M. Possibly *Chamaedora* sp. Arecaceae N. Unknown polyad O. Unknown P. Unknown Q. Unknown R. Unknown T. Unknown U. Unknown V. Unknown

