

An experimental analysis of feeding performance in *Syconycteris australis* (Megachiroptera, Pteropodidae)

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Summary. – The hypothesis that flower shape affects nectar-feeding performance was examined for the nectarivorous bat, *Syconycteris australis*. Experiments using feeders with artificial flowers of different diameters demonstrated that the narrow flower diameter had a negative effect on time spent feeding, amount of nectar taken, and rate of nectar extraction. These results suggest that flower morphology may influence both evolution of the masticatory system and resource partitioning by affecting feeding performance in flower-visiting bats.

Résumé. – L'hypothèse selon laquelle la forme de la fleur influencerait les performances d'absorption du nectar par la chauve-souris nectarivore, *Syconycteris australis*, a été examinée. Des expériences, utilisant un appareil d'alimentation composé de fleurs artificielles de diamètres différents, ont montré qu'un petit diamètre a un effet négatif sur le temps d'alimentation, la quantité de nectar collecté et la vitesse d'extraction du nectar. Ces résultats suggèrent que la morphologie de la fleur influence à la fois l'évolution du système masticateur et le partage des ressources en affectant les performances alimentaires des chauve-souris nectarivores.

KEY WORDS: *Syconycteris*, feeding, flower shape, nectar.

INTRODUCTION

Syconycteris australis (Pteropodidae: MacroglOSSinae) is an 18-20 gram blossom bat commonly found throughout Australia, New Guinea, and surrounding islands (Bonaccorso 1998; Lawrence 1991). The diet of *Syconycteris* consists of nectar, pollen, and soft fruits (Bonaccorso 1998; Flannery 1990; Law and Spencer 1995). Although *S. australis* is primarily nectarivorous in Australia, it is more omnivorous on New Guinea, where it includes a large proportion of soft fruits in the diet (Birt *et al.* 1997; Bonaccorso 1998; Law 1992). The tongue and skull of *S. australis* appear specialized for nectarivory (Birt *et al.* 1997; Freeman 1995; Law and Spencer 1995; Lawrence 1991), but this species is more flexible in diet, physiology, and foraging and

roosting behavior than other macroglossines (e.g., Bonaccorso and McNab 1997; Coburn and Geiser 1998; Law 1993, 1994; Law and Spencer 1995). At low altitudes on New Guinea, *S. australis* is sympatric with *Macroglossus minimus*, a somewhat more specialized macroglossine (Bonaccorso 1998; Lawrence 1991).

Although nectarivory probably has evolved several times independently within the Megachiroptera (Hood 1989; Kirsch *et al.* 1995; but see Springer *et al.* 1995), all nectar-feeding pteropodids share broad convergences in cranial morphology that appear to be associated with feeding on flowers. These morphological convergences include relatively longer snouts and jaws, reduced post-canine dentitions, reduction of the lower incisors, and gracile areas for attachment of masticatory muscles compared to bats that do not specialize on nectar (Dumont 1997; Freeman 1995; Storch 1968). The tongues of nectar-feeding bats are long, protrusible, and tipped with elongated papillae that act as a mop for extracting nectar from flowers (Anderson 1912; Birt *et al.* 1997; Koopman 1981).

The cranial morphology of nectar-feeding bats is generally considered to reflect an adaptation to feeding on flowers using the tongue, with decreased emphasis on mastication (Freeman 1995, 1998; Heithaus 1982; Mickleburgh *et al.* 1992). A long, narrow snout may also help a bat probe and penetrate flowers in which the corolla poses a barrier to reaching the nectar. *Mucuna macropoda* (Hopkins and Hopkins 1993) and banana flowers (*Musa* spp.) provide examples of flowers that nectarivorous pteropodids must penetrate with the snout while feeding. Insertion of the bat's head into a narrow corolla may enable a flower to place pollen more reliably on certain parts of a visitor, whereas a flower with a wider corolla might need to dust the entire bat with pollen to increase its chances of pollination.

Because a flower corolla poses a physical barrier to reaching the nectar, it should be more difficult for a bat to extract nectar from flowers with narrow corollas than those with broad, open corollas. Nectar within narrow flowers is not easily accessible to bats that cannot or will not penetrate the flower with the snout (bats would have to tear the flower open or eat the entire flower to get the nectar). Because some bats may simply lack the morphology necessary to feed efficiently from flowers in which the corolla acts as a barrier to the nectar, flower shape likely plays a role in both resource partitioning and pollen transfer. Flower shape may deter visitation by animals that are not frequent or reliable flower visitors, including many frugivorous bats. Requiring a bat to insert its head into a flower to reach the nectar may also enable a plant may to more accurately place pollen on the bat.

An experiment was designed to test the hypothesis that flower shape affects feeding performance in *Syconycteris australis*. Bats were introduced to two feeders that varied only in the diameter of an artificial "corolla" that guarded a nectar reservoir. Feeding performance was expected to be reduced at the feeder with the narrower corolla, which posed a greater physical barrier to reaching the-nectar.

METHODS

Five adult individuals of *Syconycteris australis* were captured in mist-nets at the Kau Wildlife Refuge (Madang, Papua New Guinea) and brought to the Christensen Research Institute. Bats were housed there in 5 × 5 m flight cages for 2 to 3 days for feeding experiments. No more than two individuals were housed together in a flight

cage (and thus included together in a feeding experiment) at any one time. On the single occasion when two individuals were housed together, a fluorescent glow-light was affixed to the back of one to ensure that the two individuals would not be confused. During a feeding experiment, one of two feeders ("wide" or "narrow") was randomly selected to be placed in the cage, and the bat was observed while feeding ad libitum for two hours. During this time, the feeder provided the only food available to the bats. After two hours, and the feeder was changed to the other diameter for another two-hour observation period. Bats were released at their capture sites at the conclusion of each experiment.

The feeders used in the experiments differed only in the diameter of the clear plastic, cone-shaped "corolla" attached to the nectar supply (Fig. 1). Both feeder "corollas" were 25 mm in length, but differed in diameter of the external opening (27 mm in the wide feeder, 15 mm in the narrow feeder). The narrow feeder roughly approximates the size and shape of a banana flower, an important food source for *Syconycteris* on New Guinea (F. Bonaccorso, pers. comm.), and so is within the range of flower shapes commonly visited by *Syconycteris*. The feeder corollas guarded the nectar reservoir, a 25-ml pipette graduated to 0.1 ml and filled with a 15% honey-water solution. The feeders were oriented vertically, so that the artificial corolla opened directly downwards. A platform below the feeder and a sponge on the feeder provided perches from which the bat could feed. The duration of each visit to the feeders was recorded by stopwatch from the time the bat landed on the feeder until it flew away. The amount of nectar taken was read from the level in the graduated nectar reservoir following each visit. The rate of nectar extraction (ml/s) was calculated for each visit.

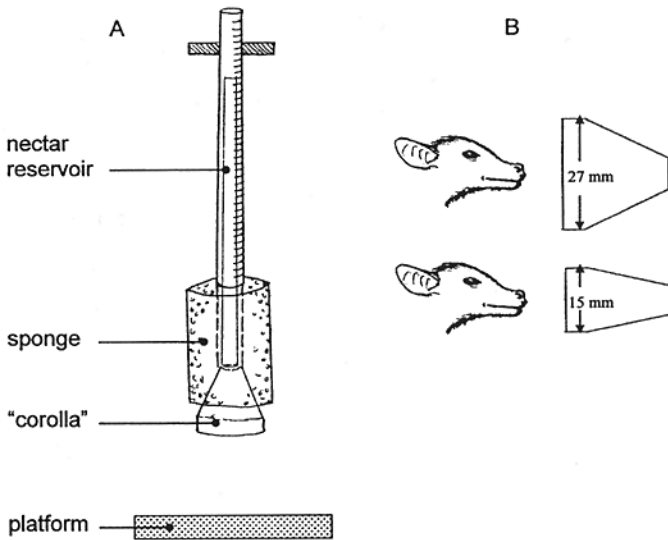


Fig. 1. — Feeder design. A) Schematic of feeder design; B) corolla diameters used shown relative to head of *Syconycteris australis*.

RESULTS

A total of 33 successful feeding visits were observed. Bats most commonly landed on the platform to feed, but also fed while hanging from the sponge attached to the feeder. Unsuccessful visits, where the bat landed on the feeder or platform but did not take an observable amount of nectar, were more common than successful visits. Unsuccessful visits were usually very brief (< 5 seconds) and are not included in the following analysis of feeding behavior.

The first successful visit of each bat to each feeder was exceptionally long, lasting from one to seven minutes. During the first visit to a feeder, the bats licked and sniffed the platform and feeder, searching until the source of nectar was located. Subsequent visits were much shorter in duration (typically between 20-30 seconds) and the bats appeared to locate the nectar source quickly. The extensive duration of the first visit probably reflected inexperience with the feeder, rather than the bat being exceptionally hungry. Since the first successful visit of each bat to each feeder appeared to be a different type of episode than later feeding visits, data from the first visit are not included in the following analysis, which is based on a total of 25 subsequent visits to feeders (15 to wide feeders and 10 to narrow feeders).

Means and standard deviations for time spent feeding, amount of nectar taken, and rate of nectar extraction are presented in Table 1. All bats exhibited reduced performance at the narrow feeder. The narrow feeder was associated with an increased mean duration of each visit and a decrease in the mean amount of nectar taken, resulting in a marked decrease in the mean rate of nectar of extraction for all bats in the study. Two bats did not feed successfully at the narrow feeder.

TABLE 1. — Feeding performance in five individuals of *Syconycteris australis*. The first visit to each feeder is not included.

| BAT | FEEDER | N | TIME (s) | AMOUNT (ml) | RATE (ml/s) |
|------------------|--------|---|-------------------|---------------|-----------------|
| A | wide | 4 | 22.5 (± 6.5 s.d.) | 1.78 (± 0.59) | 0.086 (± 0.051) |
| | narrow | 2 | 36.5 (± 20.5) | 1.15 (± 0.21) | 0.035 (± 0.014) |
| B | wide | 4 | 37.8 (± 23.0) | 2.78 (± 1.36) | 0.082 (± 0.038) |
| | narrow | 4 | 61.0 (± 34.7) | 2.58 (± 1.36) | 0.043 (± 0.009) |
| C | wide | 4 | 12.3 (± 5.4) | 1.53 (± 0.94) | 0.113 (± 0.059) |
| | narrow | 4 | 14.3 (± 16.8) | 0.88 (± 1.04) | 0.060 (± 0.013) |
| D | wide | 1 | 22.0 | 1.30 | 0.059 |
| | narrow | 0 | — | — | — |
| E | wide | 2 | 30.5 (± 3.5) | 1.95 (± 0.35) | 0.064 (± 0.004) |
| | narrow | 0 | — | — | — |
| \bar{x} wide | | | 25.0 | 1.87 | 0.081 |
| \bar{x} narrow | | | 37.3 | 1.52 | 0.046 |

Figure 2 demonstrates the impact of feeder diameter on feeding rate for the three individuals that fed successfully at both feeders. Although the small sample sizes do not confer much statistical power to the comparisons, Mann-Whitney U-Tests indicate

that for each individual, feeding rate decreased at the narrow feeder at the 90 % level of confidence ($U = 0.0$, $p = 0.064$; $U = 2.0$, $p = 0.083$; $U = 1.5$, $p = 0.061$).

Kruskal-Wallis comparisons among these three individuals indicate that rate of nectar extraction does not seem to differ significantly between individuals at either feeder diameter (wide feeder: $H = 2$, $p = 0.724$; narrow feeder: $H = 4$, $p = 1.000$). The facts that feeding rate is not highly variable between individuals and that all individuals appear to be equally affected by feeder shape support the assertion that feeder shape is a primary factor affecting feeding performance in this experiment.

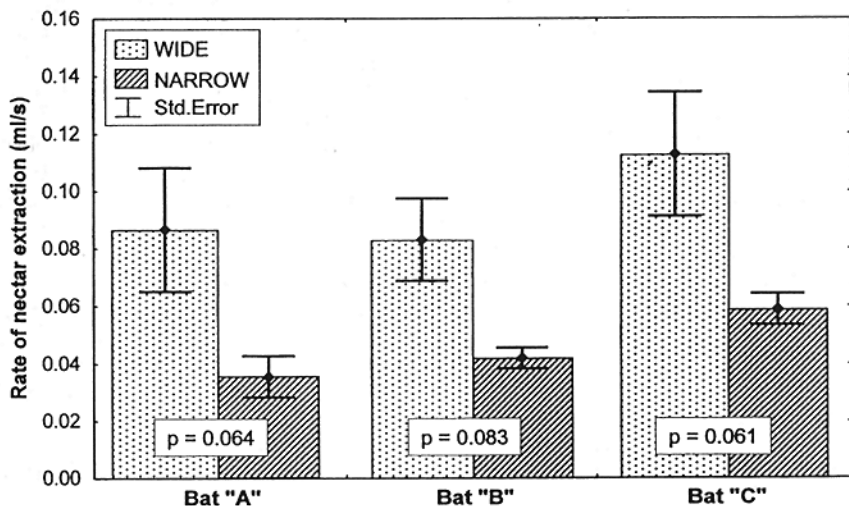


Fig. 2. Mean rate of nectar extraction for three bats that fed successfully from both feeders. P-values are from Mann-Whitney U-tests between feeder diameters for each individual.

DISCUSSION

The results of this study suggest that nectar-feeding performance of *Syconycteris australis* is affected by corolla shape. Feeding rate is one measure of nectar feeding performance, and may be associated with both the net rate of energy intake during foraging and the risk of predation at a flower (Heinreich 1975). Other factors, such as the ability to extract small amounts of nectar and to use alternate foods (i.e., fruits in *Syconycteris*) are probably also important components of overall feeding performance and may contribute to the evolution and functional morphology of nectarivorous bats. The narrower corolla diameter made it more difficult for *S. australis* to access and extract nectar from our feeders. Because our feeders used inflexible plastic corollas, these results are probably exaggerated relative to those that would be obtained using more flexible natural flowers of similar dimensions. However, these experiments suggest that bat-pollinated flowers with narrow corollas may have a negative impact on feeding performance compared to flowers with large, open corollas.

It is not surprising that feeding rate is greater at wide flowers than at narrow flowers. The narrow feeder approximates the size of a banana flower, but lacks olfactory

and visual signals that may serve as nectar guides on actual flowers. Although banana flowers are important food resources for *Syconycteris*, and many wild bananas rely on macroglossines for their pollination (Dobat and Peikert-Holle 1985), their shape is not necessarily designed to maximize feeding rate in these bats. Rather, the narrow corollas of banana flowers may enable more accurate transfer of pollen between the bat and the flower while discouraging visitation by less dedicated flower visitors that serve as less reliable pollination vectors. The bats that can feed from narrow flowers may benefit from access to a resource unavailable to less specialized species.

Nectarivores, like *Syconycteris*, are probably less affected by flower shape than occasional flower-visiting frugivores. Other frugivorous pteropodids often visit flowers but are larger and lack the specialized skulls and highly protrusible tongues that help nectarivorous bats feed from small, narrow flowers. Highly dedicated nectarivores, such as *Macroglossus*, may be even less affected by flower shape than *Syconycteris*, which by comparison is a morphological and dietary generalist.

The negative relationship between corolla diameter and feeding performance illustrated in these experiments also suggests that flower shape may play a role in the evolution of cranial shape in nectarivorous bats. Because flower shape can affect feeding performance, bats with longer snouts and tongues may be able to use flowers of certain shapes more efficiently than those with lesser development of this morphology. Morphologically specialized nectar-feeding bats likely can more easily use a wider range of flowers, including flowers with long and narrow corollas, than can less specialized bats. Nectar-feeding performance seems to be affected by physical characteristics of flowers, such as corolla diameter, but the impact of flower shape on performance may be mediated through morphological specializations of flower visitors. Through these interactions, variation in performance likely has contributed to both the evolution of skull morphology and patterns of resource utilization in flower-visiting bats.

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