Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae)

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Abstract

We studied the foraging behaviour and energetics of the nectar-feeding bat, *Leptonycteris curasoae* (= *L. sanborni*), in the Sonoran Desert near Bahia Kino, Sonora, Mexico, using radio-telemetry, light-tagging, and focal plant observations to answer three questions: (1) How far do these bats fly in a night and at what energetic cost? (2) How do they harvest nectar and pollen from columnar cacti that offer large but temporally variable nectar rewards? (3) What are the implications of their foraging behaviour for gene flow within populations of their food plants? *L. curasoae* visited flowers of three species of columnar cacti in April through June. Many bats roosted on Isla Tiburon 20 km from the Mexican mainland and commuted about 30 km to the mainland to feed. Bats flew for about 5 h each night for a total distance of about 100 km. Individuals foraged alone or in small groups in overlapping areas of 1–3 km^2 and visited the same feeding areas on successive nights. Within feeding areas, bats visited the flowers of many cactus plants, visited most flowers < 5 times, and removed about 0.1 mL of nectar per visit. Although bats flew nearly continuously early in the evening, they did most of their feeding between 24:00 and 02:00. When visiting flowers of *Pachycereus pringlei* (cardon), bats apparently waited until flowers had accumulated 0.8 mL of nectar before feeding, which suggests that rates of nectar secretion influence the timing of feeding in these bats. We estimate that the daily energy budget of *L. curasoae* is at least 40 kJ and that bats make about 80–100 visits to cactus flowers to acquire this energy. Foraging areas typically contain thousands of cactus flowers, and thus food does not appear to be a limited resource for these bats during the spring. The cost-efficient flight of this bat makes it an excellent pollen vector for self-incompatible, widely spaced desert cacti.

Key words: *Leptonycteris curasoae*, foraging behaviour, nectarivory, Sonoran Desert, energetics

INTRODUCTION

Numerous studies of vertebrate nectarivores have made important contributions to our understanding of foraging behaviour, energetics, and its potential consequences for the reproductive biology of plants (Feinsinger, 1987). Investigators have examined a wide array of topics, including behaviour in relation to optimal foraging theory (Pyke, 1978; Gass & Roberts, 1992), territoriality (Hixon, Carpenter, & Paton, 1983; Carpenter, Paton, & Hixon, 1983; Paton & Carpenter, 1984), energy budgets (Hainsworth, 1978; Tiebout, 1991), pollen dispersal (Price & Waser, 1982), digestive physiology and its relation to sugar preference (Martinez del Rio, 1990), adaptive morphology (Brown, Calder, &

Brown, 1978), and nectarivore community structure (Feinsinger & Colwell, 1978). Not surprisingly, the vast majority of these studies have focused on hummingbirds. Hummingbirds have been excellent candidates for the study of foraging behaviour and energetics because they are diurnal, easily observable, and, because of their high energy demand, exhibit rapid responses to energy manipulations (Hixon *et al.*, 1983).

Compared with hummingbirds, far less is known about the foraging behaviour of the principal nocturnal vertebrate flower visitors, bats. Nectar-feeding bats of the family Phyllostomidae (subfamily Glossophaginae) are known to pollinate the flowers of over 270 genera and 750 species of neotropical plants (Heithaus, 1982; Dobat, 1985). Recent work in arid and semi-arid regions of Mexico and South America indicates that certain species of columnar cacti depend heavily on pollination by one or more species of phyllostomid bats for maximum fruit set (Petit, 1995; Sahley, 1995;

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Fleming, Tuttle, & Horner, 1996; Valiente-Banuet *et al.*, 1996; Nassar, Ramirez, & Linares, 1997). Although a number of additional studies of bat-flower interactions exist (reviewed by Fleming, 1982; Heithaus, 1982; Dobat, 1985; Arita & Martinez del Rio, 1990; Helversen, 1993), foraging behaviour has rarely been examined. What little information exists indicates that some species (e.g. *Glossophaga soricina*) are solitary foragers whereas others (e.g. *Leptonycteris curasoae*, *Phyllostomus discolor*) sometimes forage in groups (Heithaus, Opler, & Baker, 1974; Sazima & Sazima, 1977; Howell, 1979; Lemke, 1984).

Glossophagine bats, which range in size from 8 to 30 g, are energetically expensive pollinators from the perspective of plants. Based on Nagy's (1987) equation for the field metabolic rate (FMR) of eutherian mammals (FMR in kJ/day $= 3.35\ m^{0.813}$ where m $=$ mass in g), these bats require at least 18–53 kJ of energy per day. To attract and feed these pollinators, bat-visited plants often produce large, robust flowers containing large amounts of nectar (0.07 to >10 ml/day) containing 13–34% sucrose equivalents of energy (Dobat, 1985; Scogin, 1985). They also produce relatively large amounts of pollen (up to 0.5 g per flower; Schmidt & Buchmann, 1986; Scogin, 1986; Fleming *et al.*, 1994) that are likely to supply a variety of amino acids which bats incorporate into proteins (Howell, 1974).

In this paper, we describe the foraging behaviour and energetics of the lesser long-nosed bat, *Leptonycteris curasoae* Martinez & Villa, while it visits flowers of three species of columnar cacti in the Sonoran Desert of north-western Mexico. In the spring, many individuals of this nectarivorous bat migrate to the Sonoran Desert from subtropical and tropical parts of Mexico (Cockrum, 1991; Wilkinson & Fleming, 1996; Ceballos *et al.*, 1997). In the northern part of its range, this bat feeds at flowers of the Cactaceae and Agavaceae and also eats the pulp of cactus fruit (Fleming, Nuñez & Sternberg, 1993). Distinguishing features of the bat-cactus mutualism at our study site include nocturnally opening flowers that produce large quantities of nectar representing a seemingly superabundant, but temporally variable resource. Weighing 23 g, *L. curasoae* is the second largest glossophagine bat. One important consequence of large body size is generally greater mobility via cost-efficient flight (Brown *et al.*, 1978). Also, unlike hummingbirds and most other nectar-feeding glossophagine bats, *L. curasoae* has an exceptionally gregarious roosting strategy, with colonies often containing several thousand to over 100 000 individuals (Cockrum & Petryszyn, 1991; Wilkinson & Fleming, 1996; Ceballos *et al.*, 1997). The habit of roosting in large colonies has important implications for commuter flight distances (Sahley, Horner, & Fleming, 1993) and influences the energetics and foraging behaviour of these bats.

Questions motivating this study included: (1) How far do these bats fly in a night and at what energetic cost? (2) How do they harvest nectar and pollen from columnar cacti that offer large, temporally variable nectar rewards? (3) What are the implications of their foraging behaviour for gene flow within populations of their food plants? Only by determining how *Leptonycteris* uses floral resources can we understand the interplay between the nectar supply of plants and the nectar demand of bats in this ostensibly co-evolved system.

STUDY AREA AND METHODS

Study area

Data on the foraging behaviour of *L. curasoae* were collected between 15 April–30 June 1989 and 1 April–30 June 1990 near Bahia Kino, Sonora, Mexico (29°N, 110°W). Located in the Central Gulf Coast region of the Sonoran desert (Shreve & Wiggins, 1964), this region is characterized by desert flatlands punctuated by hills rising from sea level to 400 m. The highest point in the 220 km² study area is Sierra Kino which contains a small cave used as a day roost by *L. curasoae*. Twenty kilometres offshore from Bahia Kino is Isla Tiburon, the largest island in the Gulf of California and the location of at least 2 maternity roosts used by this bat. Early spring temperatures at Bahia Kino range from 10 °C at night to 32 °C during the day. By early summer, daily temperatures reach 38 °C and hot evening winds change to humid breezes at night. Annual rainfall is about 200 mm, and most precipitation occurs in July through September.

Three species of columnar cacti, cardon (*Pachycereus pringlei* ((Engelm.) Britt. and Rose), saguaro (*Carnegia gigantea* ((Engelm.) Britt. and Rose), and organ pipe (*Stenocereus thurberi* ((Engelm.) Britt. and Rose), are common members of the plant community around Bahia Kino. Flowers of these cacti open at night, last less than 18 h, and are visited at night primarily by *L. curasoae*. They are also visited by birds and bees, beginning just before sunrise. The flowering seasons of these cacti are: cardon – early April to early June with peak flowering in mid-April to mid-May; saguaro – early April to late May with peak flowering in late April-early May; organ pipe – early April through July with peak flowering in mid-June to mid-July. Rank order of these species by number of open flowers per plant per night is cardon > saguaro >> organ pipe. Detailed information on flowering phenology, nectar secretion patterns, and the importance of nocturnal vs. diurnal pollinators for fruit and seed set in these cacti are presented in Fleming *et al*. (1996). Average densities of cardon, saguaro, and organ pipe, respectively, in 3 one-ha plots in our main study area were 7.7 (range 4–12), 7.3 (2–18), and 19.3 (13–31) adults/ha.

Using our data on flower phenology, nectar volume and composition, and cactus density (Fleming *et al.,* 1996), we estimated that the density of energy from flower nectar in our study area during the 1989–90 field seasons was highest (800–1200 kJ/ha) from mid-April to mid-May when cardon was in peak bloom (Fig. 1). A second, lower peak occurred in late June when organ pipe was in peak bloom.
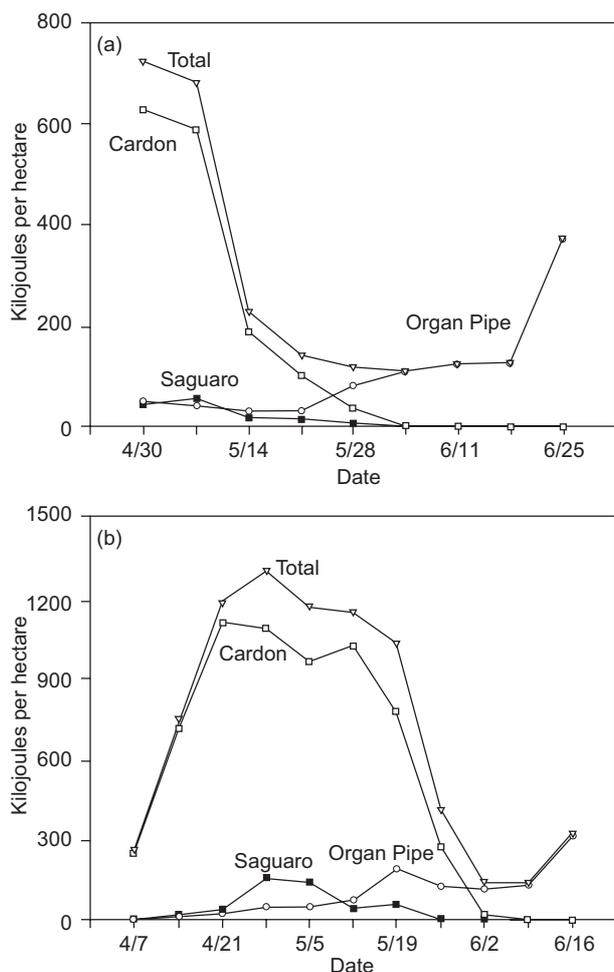
Fig. 1. Seasonal changes in the density of energy in the nectar produced by flowers of three species of columnar cacti in (a) 1989 and (b) 1990.

Data collection

To characterize the size and composition of the *Leptonycteris* population in our study area, we conducted evening exit censuses and netted bats at the Sierra Kino cave several times in 1989 and 1990. Numbers of bats leaving the cave were counted by an observer viewing the cave entrance through a Noctron IV night vision scope supplemented with infrared light. Counts were conducted every 2 weeks with each session beginning at sunset (19:30–20:00) and ending after the number of exiting bats decreased to less than 1/min.

We captured bats for radio-tracking and light-tagging using mist-nets set in front of 2 mine adits that bats used as night roosts and at the Sierra Kino cave. In 1990, we also captured bats at flowering cactus plants with pairs of elevated mist-nets and a harp trap (Tuttle, 1974). For all captured bats, we recorded sex, relative age, reproductive condition, and mass to the nearest 0.2 g. We attached either a radio transmitter weighing 0.9 g (Holohil Systems Ltd., Woodlawn, Ontario, Canada) or a chemiluminescent light tag (Buchler, 1976) weighing

< 0.5 g to the back of adult females using Silastic medical adhesive. Transmitters remained attached to bats for 10–14 d and provided information about long distance movements, locations of feeding areas, and time budgets; light tags lasted 4–6 h and provided continuous information about foraging movements.

Whenever possible, we radio-tracked bats from 2–3 sites located on hills, using the techniques of Fleming & Heithaus (1986). We focused on 1–3 bats each night, monitoring them from the time they emerged from their day roost until they returned to those roosts. We took telemetry readings synchronously on a different bat every 2 min. Locations of each bat were plotted on a topographic map (1:25 0000). We estimate the directional error in our telemetry data to be about 5% based on tests using transmitters whose locations were precisely known. Telemetry data allowed us to determine routes flown between day roosts and foraging areas (FAs) as well as the locations and sizes of FAs. We calculated the area of each bat's FAs using the convex polygon method (Hayne, 1949).

The behaviour of light-tagged bats was observed by 6 people located on hills around the study area with binoculars and night vision scopes. Descriptions of bat locations were continuously relayed to a base station using short-wave radios, and movements were continuously drawn on a scale map until each bat left the area or its light became too dim to see. Range of visual detection was 5 km.

To determine rates and patterns of visitation by *Leptonycteris* bats to cactus flowers, we observed groups of 1–8 flowers, usually on one plant but occasionally on adjacent plants, from 20:00 to 04:00 through night vision scopes or with unaided vision under bright moonlight. We observed a total of 27 plants. Most of our observations were made in our main study area located 7 km E of the Sierra Kino cave. To determine whether visitation rates were influenced by the number of open flowers on a plant and the number of open flowers in a plant's neighbourhood, we counted the number of open flowers and number of cactus plants and open flowers within a 30 m radius of 20 target plants. Flower visitation data included time of each visit (defined as a bat jamming its face into a flower) and whether each visit was by a solitary individual or by a bat flying in a group. Detailed data on the timing and number of *Leptonycteris* visits to individual flowers of the three species of columnar cacti were collected in 1989 and 1990 (Fleming *et al.,* 1996). In this study, we report additional data for cardon in April 1990 when visitation rates to this species were ≥ 2.3 times higher than visitation rates to the other 2 species.

To characterize levels of nectar depletion by bats, we measured the standing crop of nectar in cardon flowers in our main study area on 3 nights in April 1990. We measured the amount of nectar (in ml) present in 1 bagged (control) flower and 1 (10 April) or 2 (12 and 27 April) non-bagged (experimental) flowers on each of 6–10 plants spread over an area of several hectares at 21:00, 24:00, and 03:00. By 03:00, most bats had

returned to their day roosts. We determined the amount of nectar removed per visit to cardon flowers by *Leptonycteris* bats by allowing 4 captives to visit open cardon flowers in a 27 m³ screen flight cage. We added 0.19–0.37 ml of 26.5% sucrose equivalent nectar to 2 empty flowers and allowed bats to visit each flower 1–4 times before we measured the nectar remaining with a 3 ml syringe. Mean volume removed per visit did not vary with initial nectar volume (Kruskal–Wallis ANOVA, $\chi^2 = 5.05$, *d.f.* = 4, *P* = 0.28), so we pooled the data to calculate mean volume removed per visit. In our energetics calculations, we assume that *Leptonycteris* removes similar amounts of nectar from flowers of saguaro and organ pipe as it does from flowers of cardon.

In 1990, we used the point-quarter method (Cottam, Curtis & Hale, 1953) to estimate the density of adults of the 3 species of cacti and the density of open flowers, flowers that had opened in the last 3 days, and ripe fruit in the FAs of 4 radio-tagged bats. Two or three 100-m long transects were randomly located within each foraging area, and we sampled 10 random points per transect. Data were averaged for each FA. We also collected weekly phenological data for the 3 cacti at our main study site throughout the study (Fleming *et al.*, 1996).

We calculated the daily energy budget of *L. curasoae* by multiplying the average time a 23 g individual spent in 4 major activities – commuting between the day roost and FAs, flying within FAs, night roosting, and day roosting – using estimates of their energetic costs. We used the methods of Sahley *et al.* (1993) to estimate the mechanical power outputs of flight, converted these estimates to chemical power by dividing them by an assumed conversion efficiency of 0.23 (Pennycuick, 1989), and then converted power to kJ. To estimate the cost of day and night roosting, we multiplied McNab's (1989) value for the basal metabolic rate of *Leptonycteris* (2.0 ml O_2 g⁻¹ h⁻¹ = 0.268 W of chemical power) by 1.2 and 1.5, respectively, to account for the low intensity activity which occurs in these roosts (Fleming, Nelson, & Dalton, 1998) and then converted these values to kJ. We used methods described by Kearns & Inouye (1993) to estimate the energetic value of nectar produced by flowers of each cactus species based on data in Fleming *et al.* (1996).

RESULTS

The bat population

In 1990, about 2600 *L. curasoae* roosted in the Sierra Kino cave in early April. This number declined to nearly zero by the end of May as females moved to Isla Tiburon to give birth; the number of bats increased in mid-June as post-lactating females and their young returned to the mainland cave (Fig. 2). Although not so complete, the data for 1989 followed the same pattern. Most adult bats we captured in April and May were
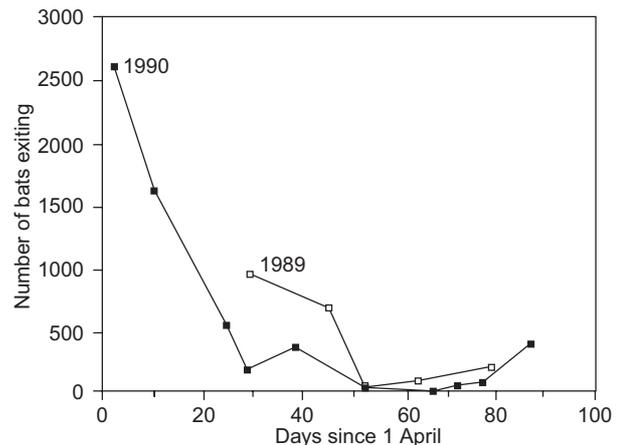

Fig. 2. Number of *Leptonycteris* departing from the Sierra Kino cave at sunset in 1989 and 1990.

females (94%, *n* = 64); most of the females in April (91%, *n* = 47) were pregnant and gave birth in mid-May. Mean mass of females in late pregnancy was 30.8 g (S.D. = 2.4 g, *n* = 41); mean mass of non-pregnant females was 23.4 g (S.D. = 2.2 g, *n* = 28).

In April and early May, the *Leptonycteris* population foraging in the study area probably contained both resident and transient females. Four of eight females fitted with radio-transmitters between 15 April and 9 May 1990 left the Sierra Kino cave or their FAs and flew east-north-east 1–7 nights after being tagged and were never detected again. No contact was made with the other four females after the initial night of release. Discounting radio failure, we suspect these females were captured while still in migration. Not until mid-May were we able to track radio-tagged females for more than seven consecutive nights. In 1989, seven of eight females that we tagged between 2–18 June roosted on Isla Tiburon and commuted to the mainland to feed; the other bat roosted in the Sierra Kino cave. In 1990, all nine bats tagged between 28 May and 16 June roosted on Isla Tiburon and fed on the mainland. By the end of June, radio-tagged bats again used the mainland cave as a day roost. Based on triangulation of radio-transmitter signals, we estimate that the Tiburon maternity cave(s) was about 29 km from the Sierra Kino cave.

General foraging behaviour

During May and June, resident bats spent nearly 7 h away from their day roost each night. They left their day roosts between 20:10 and 20:50, about 1 h after sunset (mean time after sunset = 60.8 min, S.D. = 11.6, *n* = 33 bat-days) and returned to their day roosts between 03:00 and 03:30, about 2 h before sunrise (mean time before sunrise = 136.0 min, S.D. = 9.4, *n* = 4 bats). Females from the mainland day roost spent about 6 h in their FAs, from 20:40 (range = 20:10–20:50) to 02:40 (range = 01:15–03:10) (*n* = 4 bats). Bats from the island maternity roost(s) spent about 4.5 h in their FAs
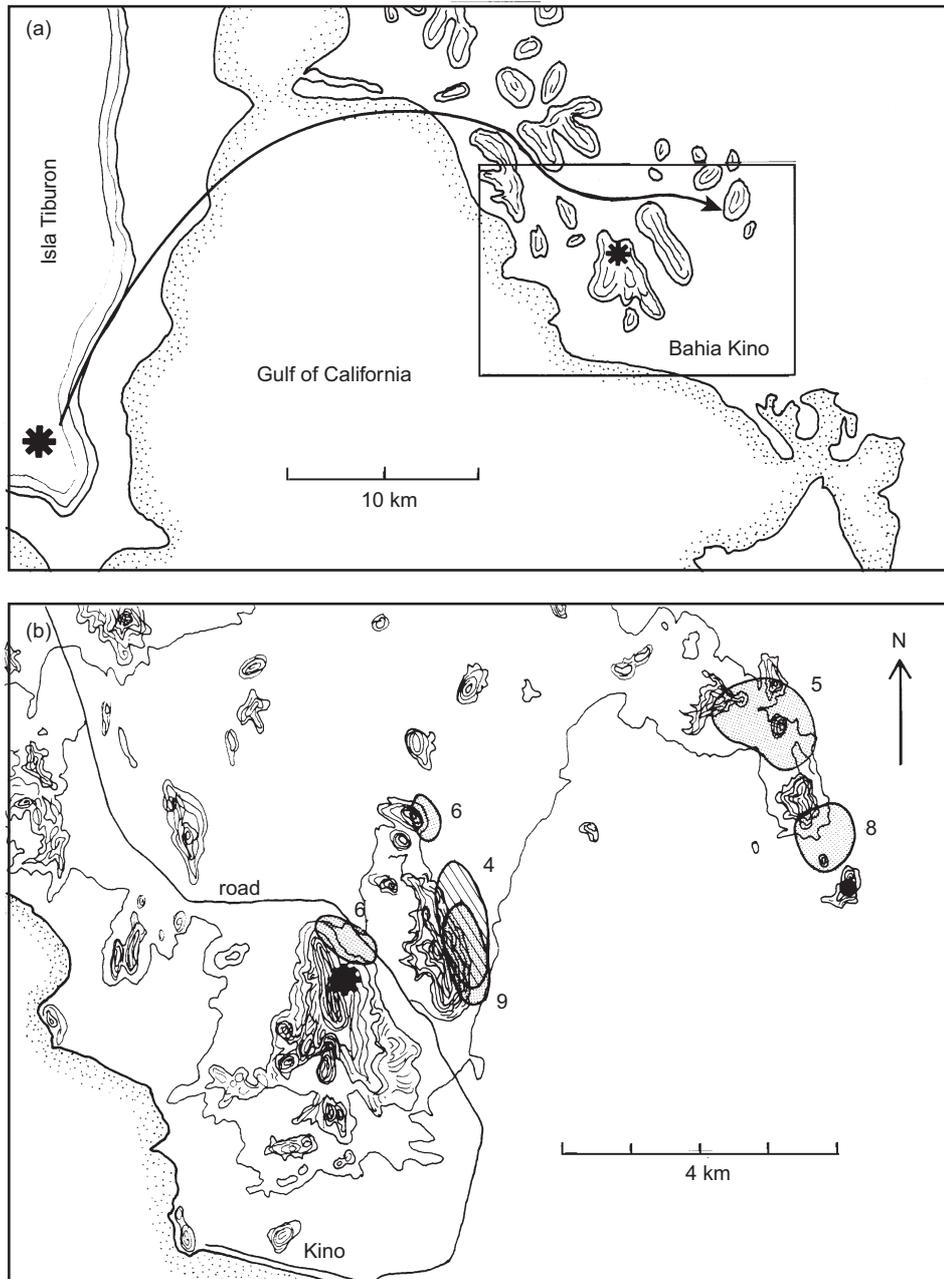
Fig. 3. Commuting routes (a) and composite foraging areas (b) of five radio-tagged individuals of *L. curasoae* in 1989. Locations of the Sierra Kino cave and one maternity roost on Isla Tiburon are indicated by asterisks. The rectangle in (a) is enlarged in (b). Major hills are indicated in both panels. The solid circle in (b) (near 8) indicates a mine that bats 4, 5, 8, and 9 occasionally used as a night roost; bats 4, 6, and 9 also used the Sierra Kino cave as a night roost. Only bat 6 roosted in the Sierra Kino cave during the day; the other bats roosted on Isla Tiburon.

(from 21:25 to 01:45) ($n = 6$ bats). They spent the remaining 1.5 h commuting between the island and their mainland FAs.

Radio-tagged bats flying from Isla Tiburon seldom flew the shortest possible distance from their roost to their mainland FAs. Instead, they usually flew north along the island coastline and crossed over to the mainland near the point where the land masses were closest, then flew south to their FAs (Fig. 3a). This distance was approximately 30–35 km, whereas the most direct dis-tance was about 25 km. In contrast, these bats usually flew straight back toward their island roost early in the morning. By determining the approximate location and time of departure from the Tiburon maternity roost, the route taken, and location and time of arrival on the mainland, we were able to estimate the speed of com-muting flights. Minimum flight speeds over water averaged 7.8 m/s (S.D. = 1.9, $n = 6$ bats); over land flight speed decreased significantly to 4.3 m/s (S.D. = 0.9, $n = 7$ bats; Mann–Whitney U, $z = 2.29$, $P = 0.02$).
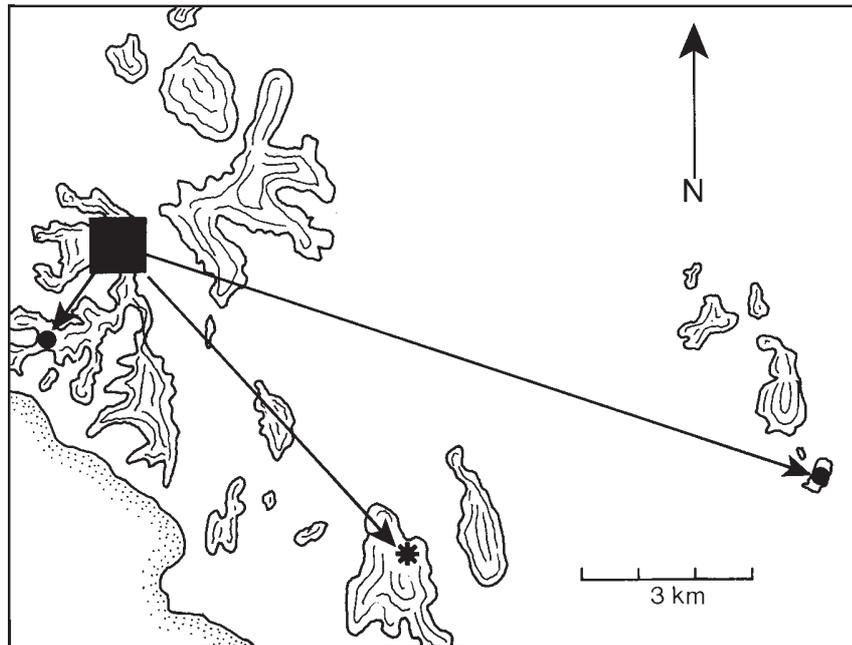
Fig. 4. Location of the composite foraging area and three night roosts of one radio-tagged female bat in May 1990. One night roost was the Sierra Kino cave (asterisk). This bat roosted on Isla Tiburon during the day.

We used data from three radio-tagged bats (which roosted on Isla Tiburon) whose locations were constantly known on a total of four nights to estimate time budgets. These bats spent an average of 17.5% (range = 13–21%) of their time resting in night roosts and an average of 82.5% (range = 79–87%) of their time in flight. By systematically plotting their locations every few minutes, we identified two types of flight patterns: (1) direct flights between day and/or night roosts and FAs, and (2) erratic, zig-zag flights within FAs. Percentage time spent in erratic flight was 53% (range = 48–64%) whereas direct flight represented 29% (range = 23–36%) of total time. Most of the time spent in direct flight was between the day roost and FAs rather than between night roosts and FAs.

On a total of five nights, four radio-tagged bats were monitored such that all FAs used throughout the night could be detected and measured. Two of these bats foraged continuously in a single long bout lasting about 250 min in areas of 0.98–2.43 km². On the other three nights, bats foraged for shorter periods in smaller areas and night-roosted between foraging bouts. Two bats had three foraging bouts each and one bat had two foraging bouts for an average duration of 63 min (S.D. = 27, range = 26–112 min) and average area of 0.43 km² (S.D. = 0.14, range = 0.29–0.69 km²). On all occasions, these bats returned to the same foraging location after a period of night-roosting. These and other bats were monitored on other nights, and although the data are not as complete (due to loss of contact during a part of the night), they suggest that foraging in relatively small areas for relatively short periods separated by bouts of night-roosting was more common than continuous foraging throughout the

night. Bats returned to the same general location to forage over several nights, although the exact location of FAs often changed 200–400 m from night to night. When the locations of these FAs were combined over a period of 2–5 nights, their areas ranged from 1.3 to 3.2 km² (*n* = 4 bats; see Table 2).

Although bats usually night-roosted in or near their FAs, they sometimes flew considerable distances to night roost in caves or mine adits. For example, one bat used four sites located up to 12.8 km from its FA as night roosts in 8 d (Fig. 4). On 24 June 1989, two bats with broadly overlapping FAs (bats 4 and 9 in Fig. 3b) separately flew at least 10 km to the south-east for about 1 h before returning to their regular FAs. These long flights substantially increased total distances flown by bats on some nights.

We light-tagged a total of 12 bats on two nights in April 1990 to obtain a general picture of foraging patterns used by *Leptonycteris* when visiting cardon cactus flowers (Fig. 5). Instead of depleting the nectar from flowers on one cactus and then proceeding to another plant to deplete all of its nectar, these bats visited flowers on several plants in rapid succession. They flew erratically, zig-zagging among plants, and made quick approaches and visits to 1–2 flowers on one plant before switching to another plant, only to return to the first plant a few minutes later. They foraged at a group of plants for several minutes, then either left those plants permanently or returned to them later in the evening. Three of the light-tagged bats were continuously observed for four foraging bouts, defined as bats constantly flying and visiting flowers, so that the size of their FAs could be measured. Mean foraging duration was 56 min (S.D. = 11.5, range = 50–73 min),

Fig. 5. Foraging path of one female bat light-tagged on 19 April 1990. This female was tagged and released at a mine that she used as a night roost (star). The bat was in nearly continuous view for one hour (24:00–01:00). The shaded figures are hills

Table 1. Proportion of time *Leptonycteris* bats were observed visiting open flowers of cardon (*Pachycereus pringlei*) and proportion of time they were observed foraging in groups of 2–4 individuals

Time period (MST*)	Proportion of flower visits		Proportion of time in a group in 1990
	1989 (n = 147)	1990 (n = 749)	
20:00–20:59	0.0	0.12	0.05
21:00–21:59	0.0	0.06	0.15
22:00–22:59	0.03	0.09	0.15
23:00–23:59	0.16	0.09	0.25
24:00–24:59	0.27	0.28	0.30
01:00–01:59	0.36	0.20	0.20
02:00–02:59	0.14	0.13	0.10
03:00–03:59	0.04	0.03	0.0

* MST = Mountain standard time

and mean FA area was 0.24 km^2 (S.D. = 0.08, range = 0.13–0.32 km^2). These means are similar to values that we obtained with the less precise method of radio-telemetry.

Flower visitation rates and patterns

Bat visits to cardon flowers were clumped in space and time. Of the 27 cardon plants we observed, 23% were not visited by bats, 35% received ≤10 total visits, and 42% received >10 total visits (range = 16–320 visits per plant). Mean number of visits to cardon flowers that were visited at least once was 6.6 (S.D. = 7.1, n = 31 flowers on 7 plants); 57% of these flowers received < 5 visits. Because the FAs of different bats overlap (e.g. Fig. 3b) and bats sometimes forage in groups (see below), these visits could have been made by more than one individual. In captivity, bats removed an average of 0.096 ml (S.D. = 0.02, n = 5 trials) of nectar per visit to a cardon flower.

Bats did not seem to concentrate their foraging activity on flower-rich plants or in flower-rich neighbourhoods. Correlation analysis revealed that total number of flower visits per cardon plant was independent of: (1) the number of open flowers on the target plant; (2) the total number of open flowers within 30 m of that plant; and (3) the number of columnar cacti bearing open flowers within 30 m of that plant (Pearson product-moment correlations ≤0.38, d.f.s = 18, Ps ≥0.10).

Bats frequently flew past open flowers early in the evening, perhaps to ascertain good feeding sites, but seldom fed at them until later. In both years, peak flower visitation occurred between 24:00 and 02:00 (Table 1); the cumulative visitation curves, however, differed significantly between years (Kolmogorov-Smirnov two-sample test, P < 0.01). A similar pattern occurred at organ pipe cacti (Fleming *et al.,* 1996). In 1990, the time between visits to a cardon flower averaged 13.5 min (S.D. = 14.8, n = 130 visits to 19 flowers on seven plants). Modal time between visits, however, was < 5 min and the distribution was strongly right-skewed (g$_1$ = 1.44, t = 6.86, d.f. = ∞, P < 0.001). These observations corroborate our observations of light-tagged bats, which indicate that individuals repeatedly visit flowers on one or more neighbouring plants before moving off to a new set of plants.

Most flower visits were by solitary bats, but small groups, usually containing 2–4 bats, were also seen, most often between 23:00–01:59 (Table 1). We may have underestimated the proportion of time that bats spent foraging in groups because more bats could often be heard flying in the vicinity of a plant than could be seen simultaneously by an observer. Observations of bats foraging in groups plus our radio-tracking data (e.g. Fig. 3b) indicate that the FAs of different bats overlapped. We never observed a bat defending flowers on one or more plants against other bats.

Once bats began visiting cardon flowers, beginning around 23:00, the amount of nectar in open flowers decreased relative to that in bagged flowers on the same plant (Fig. 6a). By 03:00, the average amount of nectar left in open flowers was about 61% of control levels and coincided with the amount of nectar present in flowers when heavy flower visitation began (about 0.8 ml; Fig. 6b). Thus, bats did not empty most flowers they visited but instead left about eight visits worth of nectar in them.
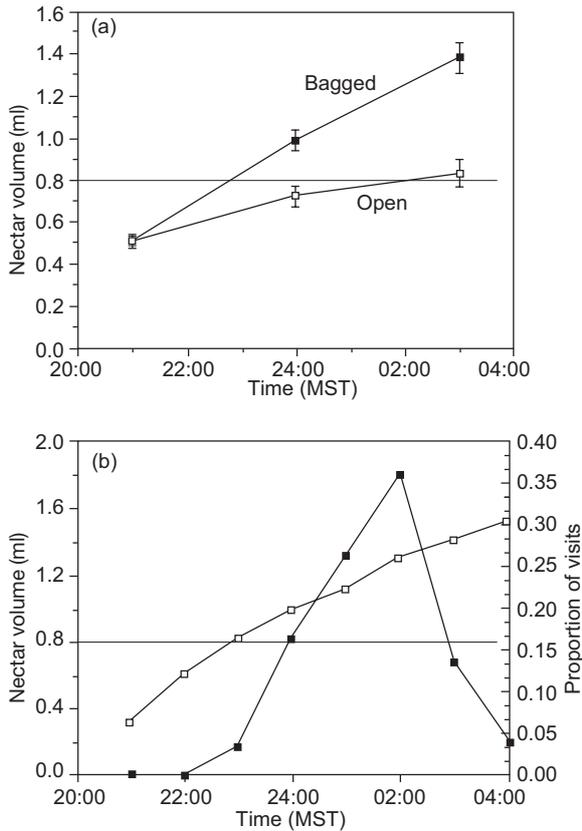
Fig. 6. (a) Mean (S.E.) volume of nectar present in bagged and unbagged cardon flowers in April 1990 (data from three nights are combined). (b) The accumulation of nectar in bagged cardon flowers and the temporal pattern of bat visits to cardon flowers in April 1989. The horizontal line in both panels represents an apparent threshold volume of nectar that must accumulate in a cardon flower before bats begin to visit them heavily. MST = Mountain standard time.

Cactus flower densities in foraging areas

We surveyed the FAs of four radio-tagged bats in 1990 to determine the density and phenological status of the three species of columnar cacti. The size of the areas used by these individuals over 2–5 nights (i.e. their composite FAs) was 1.3–3.2 km² (Table 2). The total number of adult cacti per composite FA was 3 030–10 660, and the total number of open cactus flowers per night per composite FA was 4 655–15 900. The size of composite FAs in this small sample was independent of cactus density and total number of open flowers. Cardon flowers were the most common resource in one FA, but organ pipe flowers were the most common resource in the other three FAs.

Daily energetics

Our estimates of the daily energy budget of a 23 g

Leptonycteris are summarized in Table 3. Our radio-tracking data indicate that each bat spends about 4.9 h in flight each night during which it flies about 98 km; half of this distance is reached during the long commutes between Isla Tiburon and the mainland. Total time in flight represents only about 21% of the bat's time budget but about 44% of its total energy budget. In contrast, day roosting represents about 75% of its time budget but only 50% of its energy budget. We estimate that the (minimum) daily energy budget of this bat is about 40.2 kJ.

How many flower visits must the bat make to acquire at least 40 kJ of energy? Based on our data on the energetic value of nectar (Fleming *et al.*, 1996), we estimate that *Leptonycteris* obtains 0.52, 0.43, and 0.41 kJ of energy from flowers of cardon, saguaro, and organ pipe, respectively. In making these estimates, we assumed that bats remove 0.1 ml of nectar at each flower visit. To pay for the flights to and from Isla Tiburon (i.e. 6.6 kJ), a bat needs to make 13–16 flower visits, depending on whether it is visiting flowers of cardon or organ pipe. To meet its daily energy requirement of 40.2 kJ, a bat must make a minimum of either 77, 94, or 98 visits to flowers of cardon, saguaro, and organ pipe, respectively, per night. If it completely drained each flower that it visited, *Leptonycteris* would need to visit only 5.1, 15.5, or 6.1 flowers of cardon, saguaro, or organ pipe. By visiting each flower 3–4 times, as suggested by our observations, however, an individual should visit 19–26, 23–31, or 25–33 flowers of cardon, saguaro, and organ pipe, respectively, to acquire 40.2 kJ of energy.

These energetic calculations are for reproductively inactive bats. Seven out of the 15 resident bats we radio-tracked were lactating and hence should have significantly higher daily energy requirements than non-reproductive bats. Based on studies summarized by Kunz & Nagy (1988), the energy budgets of lactating bats are 50–100% higher than those of non-reproductive bats. If this is true for *Leptonycteris*, then the daily energy requirements of lactating bats will be 60–80 kJ; the number of visits to cardon flowers a lactating bat needs to make to obtain this much energy will range from 116 to 154.

DISCUSSION

The foraging behaviour of *L. curasoae* is characterized by relatively long commuting flights, consistent short-term use of a foraging area of about 1 km², occasional long forays to night roosts or other areas, and visits to many flowers scattered over many plants. Bats spend the early part of the evening visiting plants without feeding, apparently to gather information on the locations of open flowers, and then do most of their feeding between 24:00 and 02:00 after flowers have accumulated substantial amounts of nectar.

Table 2. Size of the nightly and composite foraging areas of four radio-tagged *Leptonycteris* bats and the mean number of columnar cacti per hectare in these areas

Bat	Dates in 1990	No. of nights tracked[1]	Foraging area (km²) Nightly[2]	Composite[3]	Plants per ha Cardon	Organ Pipe	Saguaro	Total
3.1	21–27 May	5	0.54	1.33	63.5	28.3	14.2	106.6
4.3	30 May–3 June	3	2.00	3.18	4.3	25.5	0.5	30.3
5.1	8–10 June	2	0.58	1.72	6.0	48.2	3.1	57.4
2.2	9–16 June	3	0.64	1.52	2.1	27.0	5.1	34.2

[1] Number of nights tracked may not be consecutive.
[2] Average area for each foraging bout.
[3] Total area over all tracking nights.

Table 3. Summary of the estimated daily energy budget of a 23 g *Leptonycteris curasoae*

Activity	Time (min)	Cost Watts	Kilojoules
Commute	110	1.05	6.60
Forage	190	0.97	11.13
Night roost	60	0.40	1.52
Day roost	1080	0.32	20.90
			Total = 40.15

Foraging behaviour

Long commuting flights are a particularly striking aspect of the foraging behaviour of *L. curasoae*. Commuting distances of 25–35 km probably are not unique to bats living in the Bahia Kino region. Fleming has visited two other *Leptonycteris* roosts in Mexico (caves in Pinacate Biosphere Reserve, Sonora, and Chamela Bay, Jalisco) and one in south-eastern Arizona where many bats must fly tens of kilometres to their feeding grounds every night. A similar situation occurs at a maternity roost in Chiapas, Mexico (R. Medellin, pers. comm.). Thus, in addition to relatively long seasonal migrations (Wilkinson & Fleming, 1996), long nightly commuting flights appear to a basic feature of the foraging ecology of this bat.

Long commuting flights are a consequence of the gregarious roosting behaviour of *L. curasoae*. Unlike most nectar-feeding phyllostomids of the subfamily Glossophaginae, which live in small colonies, this species lives in a few widely scattered colonies containing tens of thousands to over 100 000 individuals (Cockrum & Petryszyn, 1991; Arita, 1993; Wilkinson & Fleming, 1996). Roosting in large colonies in warm caves or mines during the maternity season provides two metabolic benefits: pups have high rates of growth and development, and the daytime maintenance costs of females are low (Arends, Bonaccorso & Genoud, 1995). Long commuting flights are the "cost" individuals pay for this gregarious roosting behaviour. As discussed in detail by Sahley *et al.* (1993), a relatively large body size (for its phyllostomid subfamily) and high wing-loading are two morphological features that allow *Leptonycteris* to fly long distances in an energetically efficient fashion.

A second unusual feature of the foraging behaviour of *Leptonycteris* is that it leaves its day roost shortly after sunset, flies continuously during the early evening with little feeding, and concentrates most of its feeding into a 2-h period between 24:00 and 02:00. Why does it not remain in its day roost, saving energy and avoiding exposure to predators, until later in the evening when flowers have accumulated enough nectar to make foraging worthwhile?

Our explanation for this behaviour is that bats probably need to spend time early in the evening determining the availability and locations of open flowers in their current FAs before deciding to stay there or to move to another FA. Optimal foraging theory predicts that, in the absence of complete information regarding the availability and variability of a food resource, a forager should exhibit sampling behaviour, especially if patch types change in quality (Stephens & Krebs, 1986). Other plant-visiting phyllostomid bats spend time and energy scouting for food resources (Heithaus & Fleming, 1978; Morrison, 1978), so similar behaviour in *Leptonycteris* is not surprising. But, whereas fruit-eating bats such as *Artibeus jamaicensis* and *Carollia perspicillata* devote relatively little time and energy each night looking for new food resources, *L. curasoae* apparently assesses its potential food supply for several hours each night. Given the high levels of floral resources relative to the demand for them by bats in the Bahia Kino region (see below), such behaviour seems puzzling unless the locations of good feeding sites change substantially from night to night. Such spatiotemporal variability appears to be common in certain habitats occupied by hummingbirds (e.g. Gass & Sutherland, 1985). Our data for energy production in the three species of columnar cacti visited by *Leptonycteris* indicate that resource availability changes substantially over a period of weeks (Fig. 1). Night-to-night variability in flower production within plants, however, is currently unstudied. High night-to-night consistency in the use of the same general feeding locations by *L. curasoae* suggests that this variability is likely to be low. But slight shifts in exact feeding locations from one night to another also suggest that the locations of good feeding areas vary somewhat through time.

A third noteworthy feature of the foraging behaviour of *Leptonycteris* is that it does most of its feeding between 24:00 and 02:00. Results summarized in Fig. 6 indicate that these bats do not begin to visit cardon flowers heavily until they have accumulated about 0.8 ml of nectar and that once nectar harvesting begins, bats crop nectar levels in flowers down to an average level of about 0.8 ml. These results suggest that 0.8 ml of nectar may represent a 'threshold' below which bats have difficulty in removing nectar profitably. In contrast, our preliminary observations indicate that captive bats will feed at cardon flowers containing 0.19–0.37 ml of nectar. Further work is needed to resolve this contradiction between field and laboratory observations.

If it turns out that *Leptonycteris* is sensitive to threshold levels of nectar in cactus flowers, then it is likely that cactus plants can influence flower visitation behaviour of bats by their rates of nectar secretion. One reason why bats feed infrequently early in the evening may be that they are waiting for enough nectar to accumulate in flowers to make them profitable to visit. If flowers on some plants secreted nectar at a faster rate, then *Leptonycteris* should begin to feed at them earlier in the evening. One way to test this prediction is to inject a full night's volume of nectar into flowers as soon as they open. T. H. Fleming conducted a preliminary experiment to test this prediction at Bahia Kino in April 1994. Compared with control flowers on the same cardon plant on the previous evening, flowers supplemented with 1.5 ml of 31.5% sucrose equivalents of nectar when they opened were visited 3 h earlier (20:00 vs. 23:00) and received over three times as many total visits (14.4 visits per supplemented flower ($n = 4$) vs. 4.4 visits per control flower ($n = 7$)). From these preliminary results, we tentatively conclude that nectar secretion rates do influence the timing of flower visits by this bat.

A fourth unusual aspect of the foraging behaviour of *Leptonycteris* is the size of its foraging area and the relatively high number of flowers it visits each night. To meet its energetic needs, we calculate that *Leptonycteris* only has to consume the nectar produced by 5–15 flowers, depending on which cactus species it visits. At peak blooming times, this would require visiting only 1–2 plants in an area of <1 ha each night. Instead, most individuals visit many flowers spread over many plants in an area of 25–50 ha; some individuals spread their flower visits over 100–250 ha in one night. Thousands of open cactus flowers occur in the FAs of *Leptonycteris*, whereas individual bats visit fewer than 100 flowers to meet their daily energy needs. This mismatch between the area that the bats need to meet their energy and nutrient needs and the area in which they actually forage contrasts strongly with the behaviour of certain species of hummingbirds whose territory size is adjusted on a daily basis so that plant resource levels match their energetic needs (Carpenter *et al.*, 1983).

If *Leptonycteris* does not experience a shortage of nectar and pollen at Bahia Kino, then we would not necessarily expect individuals to be selective regarding which plants they visit and how many times they visit

each flower; nor should they defend floral resources. In line with these expectations, we found no correlation between visitation rates to plants and the number of open flowers they bore or the number of open flowers in a plant's neighbourhood. Nor did bats spread their flower visits evenly among the flowers they visited. Instead, their flower visits were clumped among plants and flowers; many flowers received no or very few visits, whereas a few received many visits. Bats did not appear to defend particular plants against visits by other *Leptonycteris*.

Given the large supply of flowers in each bat's FA relative to its energetic needs, we conclude that the *Leptonycteris* population at our study site is not food-limited during peak flowering times. Thus, it is not surprising that these bats do not exhibit territorial defence as does the bat *Glossophaga soricina* when feeding on flowers produced by *Agave desmettiana* (Lemke, 1984). Studies of territoriality in nectar-feeding birds suggest that when resources are superabundant, as they are during certain times of the year at Bahia Kino, an individual does not profit from defending resources (Carpenter & Macmillen, 1976; Carpenter, 1987) and territorial behaviour should not occur. Moreover, given the large size and low flight costs of *L. curasoae* (Sahley *et al.*, 1993), there is a low energetic cost associated with having a large foraging area and a potential benefit to obtaining information about spatial patchiness or variability in flower availability on a given night by searching large areas.

Energetics

Based on time budgets and estimates of the energetic costs of different activities, we estimated that the daily energy requirements of a non-reproductive *Leptonycteris* should be about 40 kJ. While this value agrees with Howell's (1979) estimate (40.4 kJ) and with the prediction of 42.9 kJ from Nagy's (1987) equation for eutherian mammals, it is likely that we have somewhat underestimated the actual daily cost of living in this bat because of our rudimentary knowledge about many aspects of its behaviour and their actual energetic costs. A more direct estimate of daily existence energy (DEE) using doubly-labelled water would be desirable (Kunz & Nagy, 1988), but recapturing labelled individuals living in large colonies or in remote roosts will be very difficult.

How does our estimate of the DEE of *Leptonycteris* compare with other species of nectar-feeding phyllostomid bats? Only two other species have been studied (Table 4). Comparisons show interesting similarities and differences. All three species of bats fly for 4–5 h per night. *L. curasoae* apparently flies much faster and therefore flies 36–100% farther per night than the two smaller species. For its size, *L. curasoae* apparently has a lower flight cost and a relatively lower DEE, but because these two measures were calculated by very different methods for each species, no firm conclusions

Table 4. Estimates of the foraging energetics of three species of nectar-feeding phyllostomid bats

Species	Mass (g)	Type of study	Hours in flight	Distance flown (km)	Cost of daily flight (kJ)	Individual daily existence energy (kJ)	Source
Glossophaga soricina	10.9	Lab	4.2	45	21.3	41.0	1
Anoura caudifer	11.5	Field	5.0	72	31.3	51.9	2
Leptonycteris curasoae	23.0	Field	4.9	98	17.7	40.2	This study

1 = Winter *et al*. (1993), 2 = Helversen & Reyer (1984)

regarding species differences are yet possible. Despite differences in methodology, these results provide preliminary estimates of the DEE of phyllostomid nectar-feeding bats. These estimates indicate that these bats will need to visit dozens (<100 for *L. curasoae*) to hundreds (an estimated 860 for *A. caudifer*; Helversen & Reyer (1984)) of flowers per night, depending on flower size and amount of nectar extracted per visit, to remain in energy balance.

Foraging consequences for plant reproductive biology

Because it involves visiting each flower a few times and many flowers spread over many plants, the foraging behaviour of *L. curasoae* has important consequences for the reproductive biology of columnar cacti. Most columnar cacti, including saguaro and organ pipe but not cardon (Fleming *et al*., 1994), are self-incompatible hermaphrodites and need to be outcrossed to set fruit (Petit, 1995; Sahley, 1995; Fleming *et al*., 1996; Valiente-Banuet *et al*., 1996; Nassar *et al*., 1997). Given their tendency to visit flowers of neighbouring plants before moving on to another part of their relatively large FA, *Leptonycteris* likely produces a mixture of short (i.e. <100 m) and long (i.e. > 500 m) distance pollen movements. Indeed, in April, migratory individuals have the potential of moving pollen substantial distances between populations. Therefore, we predict that this bat will produce substantial levels of gene flow within and between populations of columnar cacti. Experimental studies to test this prediction are currently underway. A few of the many questions that remain to be answered regarding the foraging behaviour of *L. curasoae* include: What is the effect of nectar secretion schedules on flower visits and plant fitness? Why does *Leptonycteris* spend so much time flying around before feeding each night? Does *L. curasoae* forage in a similar fashion in other parts of its range where columnar cacti do not play an important role in its diet (see Ceballos *et al*., 1997)? Future studies of *L. curasoae* and other nectarivorous bats should provide important new insights into the evolutionary ecology of vertebrate nectarivore-plant pollination mutualisms.

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