

Resource availability, diet and reproduction in *Glossophaga longirostris* (Mammalia: Chiroptera) in an arid zone of the Venezuelan Andes

MARICELA SOSA and PASCUAL J. SORIANO¹

Universidad de Los Andes, Facultad de Ciencias, Departamento de Biología, Mérida 5101, Venezuela

ABSTRACT. Seasonal variation in the consumption of cactus fruit by the bat *Glossophaga longirostris* was related to the availability of this resource in the arid pocket of Lagunillas in the Venezuelan Andes. When fruits were scarce, *G. longirostris* ate items not preferred in other seasons. The intra-specific flowering periods of the most common cactus species, *Stenocereus griseus* and *Subpilocereus repandus*, were synchronized but the number of flowers open per night was low. *S. griseus* and *S. repandus* had separate flowering and fruiting periods, possibly to reduce competition for dispersers and pollinators while providing food resources for bats throughout the year. *G. longirostris* is bimodally polyestrous with extended reproductive periods, probably as a response to the continual availability of cactus flowers and fruits. A strong interdependence between columnar cacti and *G. longirostris* was demonstrated. Sexual reproduction of the cacti would be greatly reduced without the bats, which in turn could not live in the arid study area without the food sources provided by these cacti.

KEY WORDS: arid zones, Cactaceae, Chiroptera, chiropterochory, diet, frugivory, *Glossophaga longirostris*, pollination, reproduction, Venezuela.

INTRODUCTION¹

Interactions between phyllostomid bats Subfamily Glossophaginae and Cactaceae have been poorly documented, and the literature only describes bat–flower interactions (Fleming 1989, Heithaus 1982). In an earlier study, we showed that in the arid zone of Lagunillas in the Cordillera de Mérida, Venezuela, *Glossophaga longirostris* (Chiroptera: Phyllostomidae) ate nectar, pollen and fruit of the columnar cacti *Stenocereus griseus*, *Subpilocereus repandus* and *Pilosocereus tillianus*, as well as fruit of *Chlorophora tinctoria* (Moraceae) (Soriano *et al.* 1991). Analysis of faecal samples showed important seasonal differences in the importance values of these items. We postulated that such variation was a consequence of the different resources offered by the plants as result of a phenological adjustment by the cacti which allowed them to use the same pollinator and seed disperser simultaneously without competing for its services.

¹ Corresponding author.

Current information on reproduction in *G. longirostris* is limited to that provided by Goodwin & Greenhall (1961) and Webster & Handley (1986). The latter authors indicated, from an examination of 383 females collected throughout its geographic range, that *G. longirostris* is bimodally polyestrous, with pregnancy peaks from December to April and June to October. The proposed pattern could be misleading, however, because the data came from localities differing in rainfall patterns and seasonal availability of food.

The reproductive peaks of frugivorous bats are determined by fruit availability, with reproductive activities synchronized so that the young are weaned at the beginning of or during the wet season (Bonaccorso 1979, Dinerstein 1986, Fleming *et al.* 1972, LaVal & Fitch 1977, Molinari 1984, Soriano 1983). No information is available on the reproductive biology of Glossophaginae bats specialized for nectar and pollen consumption, such as the genera *Lionycteris*, *Musonycteris*, *Platalina* and *Choeronycteris* (Graham 1987, Wilson 1979), although peaks of lactation are likely to coincide with the periods of greatest availability of flowers, which generally correspond to dry periods when plants flower synchronously with and between species (Croat 1975, Daubenmire 1972, Snow 1965).

Here we examine the hypothesis that by including pollen and fruit in its diet, *G. longirostris* has a different reproductive pattern in timing from that expected for nectarivorous species and from that already known for frugivorous species. Furthermore, since columnar cacti are the most important flowering plants in the arid region under study and since *G. longirostris* is an important agent in their pollination and seed dispersal, we sought to determine the relationship between the reproductive and feeding strategies of this bat and the resources provided by the columnar cacti.

STUDY AREA

This study was conducted in a region of thorn scrub located near the Laguna de Caparú (8° 29' 16" N and 71° 20' 10" W), 3 km south-east of San Juan de Lagunillas, Mérida State, Venezuela, at an altitude of 820 m. The vegetation of this region has been described by Marcuzzi (1956) and Blanco (1976), and is part of the ecological unit named 'arbustal espinoso' (Sarmiento *et al.* 1971) in which the main arboreal species are *Prosopis juliflora*, *Acacia tortuosa* and the columnar cacti *Stenocereus griseus*, *Subpilocereus repandus* and *Pilosocereus tillianus*.

The region shows a water deficit most of the year. Annual rainfall ranges from 450 to 550 mm with peaks in April–May and September–October, and a lengthy dry period from December to March (Soriano *et al.* 1991, Sosa 1991). Mean monthly temperature varies little throughout the year and averages 22.1°C.

METHODS

Diet and reproductive pattern

Bats were captured monthly from January to December 1990. On each occasion, we set up four to six mist nets between 0.5 and 3 m in height and 12 m

long on dark nights, from 1900 to 0100 h. The nets were checked every 20–30 min. The total capture effort was 192 net-nights or 895 net-hours.

We rubbed the face of each bat captured with a gelatin cube prepared according to Thomas (1988), in order to detect the presence of pollen. We collected faecal samples from bats at the time of capture or after being held 1–2 h in cloth bags. We then marked them with a numbered aluminium ring on the forearm and recorded the following information for each bat: sex, reproductive condition, age group and weight. The reproductive condition of females was determined by palpating the volume and consistency of the abdomen; we established the categories of early, mid- or late pregnancy and non-pregnancy. The condition of the mammary glands was used to classify females as lactating or post-lactating by the presence or absence of expressed milk, respectively, after a gentle massaging of mammary glands, and hairless area around the nipples. We established relative age groups of juveniles, subadults and adults based on fur coloration and fusion of the metacarpal epiphyses (Kunz & Anthony 1982, Molinari 1984, Soriano 1983). Bats that were unable to fly were killed ($n = 14$) and preserved as reference material in the Colección de Vertebrados de la Universidad de Los Andes.

In the laboratory we separated each faecal sample with a dissection needle and identified seeds using a reference collection. The pollen in each sample was collected in a microscopic preparation according to Thomas's (1988) technique, and compared with a reference collection. The results were recorded as presence of each item per faecal sample without quantifying abundance. The relative importance of each item was then estimated as the percentage of each item in relation to the total number of items found. Our method did not permit us to detect the nectar intake of the animals; however, we used the presence of pollen in the faeces and on the fur of faces of the bats as an indicator of nectar consumption. Considering the great quantity of pollen produced by columnar cacti, it is probable that when the animal swallows nectar, its face is coated with pollen, which is ingested when the bat grooms with its tongue (Sosa 1991).

Our total sample size of *G. longirostris* was 496 bats (189 adult females). In addition to the bats captured in this study, we used 215 bats collected in previous years at the same site (Soriano *et al.* 1991) for the reproductive analysis.

Resource availability

We marked 94 randomly chosen reproductive individuals of three species of Cactaceae included in the diet of *G. longirostris* (32 *S. griseus*, 32 *S. repandus* and 30 *P. tillianus*), and on one day each month recorded the total number of flowers and fruits available. We determined the density of these plants in the study area by averaging the number of reproductive individuals present in six randomly chosen plots measuring 23 m \times 23 m (529 m²).

Each month we estimated the production of pulp biomass of each species per hectare, by multiplying the average number of fruits per plant by the average pulp weight of one fruit without seeds ($n = 15$ fruits per species) and then by the appropriate plant densities. To test whether fruit consumption by *G. longirostris* depended upon fruit supply or animal preference, we calculated the expected

frequency of the plant species in the diet of the bat on the basis of their annual fruit availability with the χ^2 test.

RESULTS

Diet

We obtained 236 faecal samples from 281 *G. longirostris* captured during this study and, in addition to the food items reported by Soriano *et al.* (1991), we recorded an unidentified seed type and insect remains. Seeds were the most common item (55%) in the faecal samples followed by pollen of Cactaceae (44%) and insects (1%). Of the five fruit species, *S. griseus* was most common (60%), followed by *S. repandus* (21%), *Chlorophora tinctoria* (9%), *P. tillianus* (7%) and the unidentified species (3%). Faecal samples of *G. longirostris* contained seeds belonging to only one type of fruit in 29% of the samples, two or more types of seeds in 4% and seeds mixed with pollen in 47%; pollen alone appeared in only 20% of the faecal samples.

Analysis of seasonal variation in the items eaten by *G. longirostris* revealed that pollen and seeds are very important in the diet throughout the year (Figure

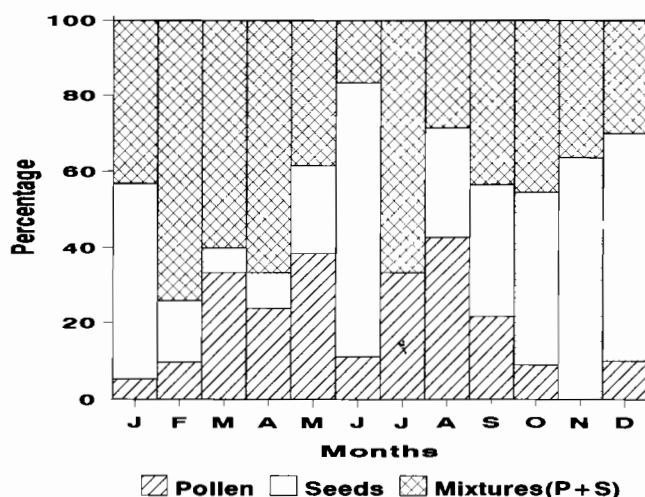


Figure 1. Seasonal variation in the items consumed by *G. longirostris*. Expressed as percentage of faecal samples.

1). However, in June the importance of pollen was low (10% pollen + 12% mixtures = 22%). The percentage of samples that contained only seeds was highest in June (72%) and again in the period September–January (64% in November). Pollen had two clear peaks, one between February and May and another between July and September.

Reproductive pattern

G. longirostris had two reproductive peaks during the year (Figure 2a), a pattern similar to that indicated by Willig (1985) for *Glossophaga soricina*. Preg-

nant females were common from the end of the long dry season to the beginning of the first rainy season and at the end of the second rainy season. Lactation periods occurred in the dry season and in the transition between the second rainy season and the lengthy dry season.

When we studied in detail the dynamics of the first pregnancy period (Figure 2b), we observed a high proportion of females in early pregnancy in January and February (50% and 33%, respectively). Parturition probably occurred from March to May when we captured many females in late pregnancy (90%).

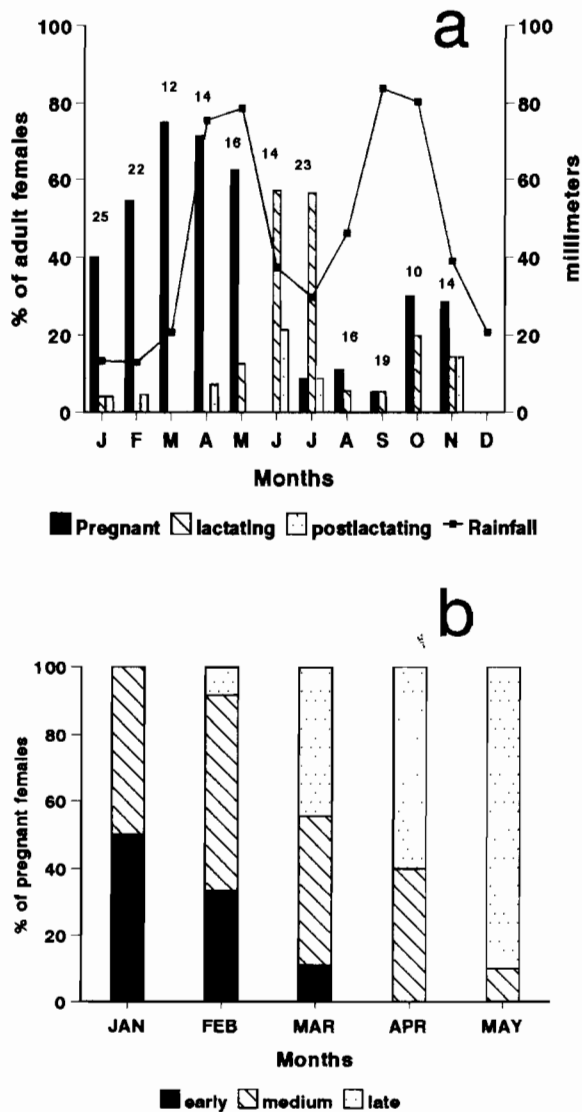


Figure 2. Reproductive pattern of *G. longirostris*. (a) The annual female reproductive cycle. Number of adult females captured is indicated for each month. (b) Detail of the first pregnancy period.

Despite insufficient data for December, the high proportion of females in mid-pregnancy in January (50%) supports the idea that the first reproductive period began in December.

We estimated that the gestation period lasted approximately three months, during which females could increase their average weight by more than 25%

Table 1. Average body weight of *Glossophaga longirostris* by age and sex.

Age group	n	Sex ¹	Weight (g) \pm SD	Range (g)
Juveniles	50	M, F	12.2 \pm 1.0	9.5–13.5
Subadults	41	M, F	13.5 \pm 1.0	12.0–16.0
Adults	95	M	14.2 \pm 1.0	12.0–17.0
	67	F a	14.5 \pm 1.1	12.5–17.5
	11	F b	15.0 \pm 0.9	13.0–16.0
	14	F c	15.8 \pm 0.7	14.5–17.0
	23	F d	17.8 \pm 1.4	16.0–20.5

¹ M = male, F = female.

a: Without reproductive signs; b: post-lactating; c: lactating; d: pregnant.

(Table 1). Unfortunately, we did not recapture enough females to confirm this. We have data for one female captured initially in mid-pregnancy (15.5 g) and recaptured a month later in late pregnancy (17.5 g). Data from animals which were killed indicated that fetuses weigh up to 4.5 g before term.

Population age structure reflected the protracted birth periods (Figure 3). Juveniles were present all through the year except in April, with a peak in June (43%) and October (27%). Subadults were most common in March (19%) and September (20%).

Resource availability

Of the three cacti species under study, the average density of reproductive individuals per hectare (and range in parentheses) were 603 (249–957) for *S. griseus*, 82 (13–255) for *S. repandus* and 134 (15–149) for *P. tillianus*. Of 94 marked cacti, only one of each species was non-reproductive.

The most important flower supply was provided by *S. griseus* and *S. repandus* which produced large quantities of flowers in the long dry season and the first rainy season. *S. griseus* had two flowering periods, one between January and April and another between July and November (Figure 4), whereas *S. repandus* had a single flowering period between January and July. Although *P. tillianus* produced some flowers throughout the year, it had two main flowering periods, the first between January and March and the second between June and October. There was a phase difference between the flowering peaks of *S. griseus* and *S. repandus* whose curves overlapped only in February. The main flowering peak of *P. tillianus* overlapped with *S. griseus* and *S. repandus* during the first months of the year. In other months in which it had flowers, there were always flowers of the other two cacti species available.

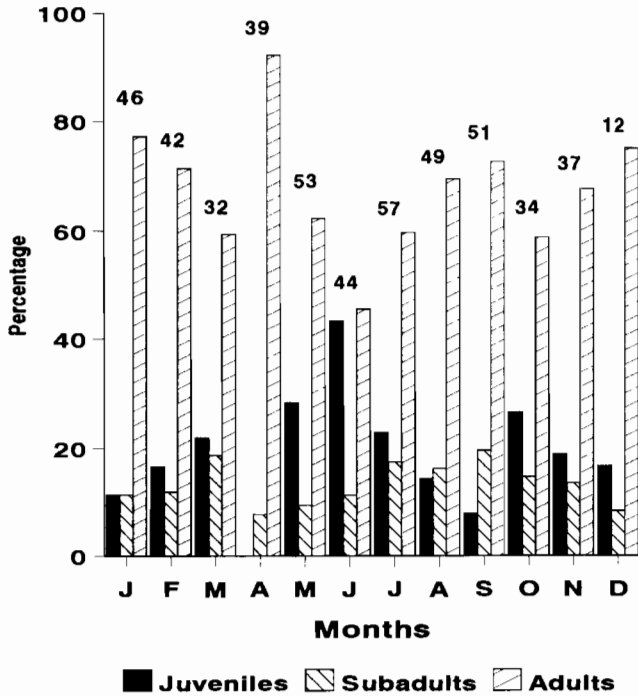


Figure 3. Monthly age structure of *G. longirostris*. Number of bats captured is indicated for each month.

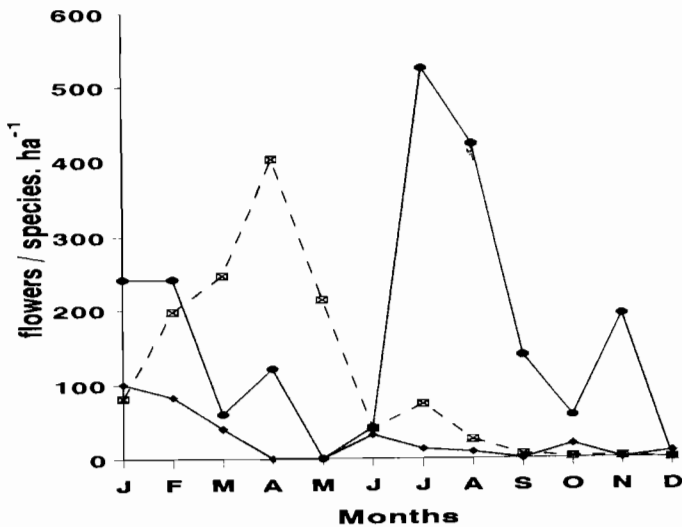


Figure 4. Monthly abundance of flowers of three columnar cactus species in Caparú, Lagunillas, Mérida: *Stenocereus griseus* —●—, *Subpilocereus repandus* —■— and *Pilosocereus tillianus* —▲—.

The fruit-ripening pattern of *S. griseus* had two peaks, January–March and August (Figure 5a). The single peak in *S. repandus* occurred between the two peaks of *S. griseus* (Figure 5b). These species showed very strong intraspecific synchronization in ripening periods and produced a large number of fruits per branch. During the ripening peaks, an individual of *S. griseus* produced up to 18 fruits per month and *S. repandus* up to 170. However, the mature fruit supply per individual per night was one and three fruits in *S. repandus* and one and two in *S. griseus* (M. Sosa, pers. obs.). *P. tillianus* had a well-defined ripening period between January and May and a longer one between July and November (Figure 5c). This cactus produced few fruits per branch (frequently 1 or 2; up to 10 in the largest individuals), and generally each individual had one open fruit per night (M. Sosa, pers. obs.).

These cacti produced approximately 1200 kg fruit ha⁻¹ in 1990 in the following specific contributions: 612 kg ha⁻¹ for *S. griseus*, 576 for *S. repandus* and 12 for *P. tillianus*. Of the 421 kg of fruit pulp ha⁻¹ produced by these species during the year, *S. griseus* contributed 363 kg ha⁻¹, *S. repandus* 57 and *P. tillianus* 1.

Temporal variation in the importance of the pulp of *S. griseus* in the diet of *G. longirostris* was a consequence of fruit flesh abundance as shown in Figure 5a (Pearson product–moment correlation $r = 0.60$, $P < 0.05$). However, despite the lower quantity of fruit available between September and November, its frequency in the diet remained high, with values ranging from 36% to 64%; this situation possibly demanded a greater energetic investment in food search, since bats would have had to increase their foraging area to satisfy their nutritional needs. With regard to *S. repandus*, Figure 5b shows a very close relationship between the quantity of pulp produced throughout the year and its frequency in the diet of this bat ($r = 0.85$, $P < 0.05$). Despite a similar trend in *P. tillianus* (Figure 5b) the correlation was not significant ($r = 0.07$, $P > 0.05$). Correlating fruit availability values against the corresponding frequency values of the next month showed coefficients with increased significance for all three cactus species (*S. griseus* = 0.70, *S. repandus* = 0.95 and *P. tillianus* = 0.67; all $P < 0.05$).

The relative frequency of pollen in the diet of *G. longirostris* also reflected the supply of flowers in the environment (Figure 6).

DISCUSSION

The diet results were similar to those of Soriano *et al.* (1991) except that in this study *Stenocereus griseus* had a higher value and pollen appeared in greater quantity. These differences were due to a larger sample size and to the inclusion of a technique for detecting pollen on bat faces in this study. The mixed diet of *Glossophaga longirostris* that included fruit, nectar and pollen was probably a response to the simultaneous availability of these food sources and to the energy demands of the bat, rather than to the scarcity of any of these food items. However, although the number of cactus flowers in December was low (Figure

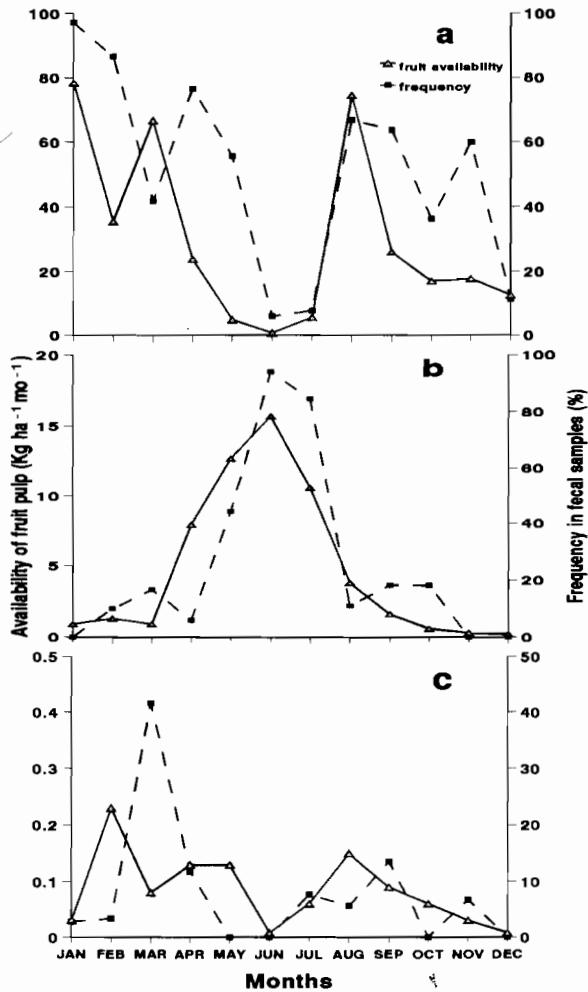


Figure 5. Relationship between fruit pulp abundance of three cactus species and their occurrence in the diet of *G. longirostris*. (a) *Stenocereus griseus*; (b) *Subpilocereus repandus*; (c) *Pilosocereus tillianus*.

6), the frequency of pollen was 30% which indicated that this bat actively sought this resource to satisfy its nutritional needs in a period of food scarcity. Fruits and nectar could be the main carbohydrate sources, while the high protein content of pollen (43.7%, reported by Howell (1974)) probably supplied the nitrogen needed by the bat. We speculate that the nectar supplied by the flowers of these columnar cacti could not satisfy, by itself, the energetic needs for the search for more flowers. Therefore, the fruits of the Cactaceae could constitute the additional energetic source needed for that search. It is likely that the phase difference observed in the peaks of fruit occurrence in the diet of *G. longirostris* also occurred with the different pollen types, since there was a well-marked asynchrony in flowering peaks. Unfortunately, this asynchrony

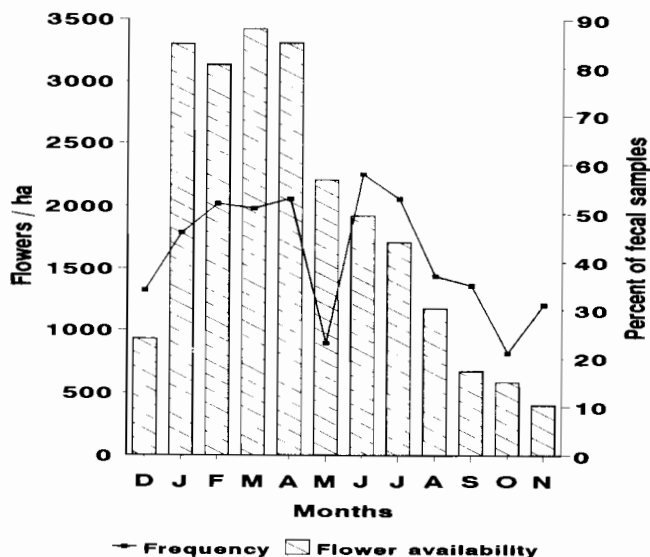


Figure 6. Relationship between floral abundance of the three columnar cacti and the presence of pollen in the diet of *G. longirostris*.

was impossible to demonstrate because we could not differentiate between the types of pollen.

We think that the presence of insects in the diet of *G. longirostris* was accidental, since they were present in such low frequency (1%) and were always mixed with pollen or seeds. Similarly, in the stomach contents of *Leptonycteris sanborni*, Howell (1974) found fragments of insects associated with flowers visited by this bat. Probably *G. longirostris* does not actively seek insects for its nourishment but ingests them when it eats fruit pulp, nectar and pollen.

Stenocereus griseus, *Subpilocereus repandus* and *Pilosocereus tillianus* had flowering periods that lasted several months and offered few open flowers and ripe fruits per night. This forced visitors to move from plant to plant and favoured cross-pollination, an indispensable requirement for the formation of fruit with viable seeds (Léon de la Luz & Dominguez 1991). Nassar (1991) has shown that the flowers of *S. griseus* and *S. repandus* are totally self-sterile while *P. moritzianus*, a species closely related to *P. tillianus* (B. Trujillo, pers. comm.), is partially self-compatible. The asynchronous flowering of *S. griseus* and *S. repandus* and their fruit-ripening patterns possibly evolved as a strategy to avoid competition for pollinators and seed dispersal agents, providing at the same time an almost round-the-year food supply.

This type of spatio-temporal arrangement of resources would imply a solitary food search strategy, already suggested to occur in *G. soricina* by Heithaus *et al.* (1974, 1975). This is because a low quantity of resources per plant per night would not be sufficient to nourish a large number of animals. Nassar (1991)

has indicated that *G. longirostris* and *L. curasoae* usually search for flowers alone or in small groups and that the brevity and periodicity of visits to particular flowers could indicate the use of a 'trap line strategy'.

The pollination of *S. griseus*, *S. repandus* and *P. tillianus* depends mainly on *G. longirostris*, which is the most abundant bat in the area. Although *Leptonycteris curasoae* and *Phyllostomus discolor* also visit these plants, the low number of individuals of these species captured in the study area suggests that their role as pollinators was not important. Moths of the Sphingidae family also visit columnar cactus flowers at night (Nassar 1991; M. Ponce, pers. comm.). We doubt, however, whether they are effective pollinators owing to the anatomical incompatibility between the mouth parts of the insect and these flowers.

In general, seasonal variation in the occurrence of fruit in the diet of *G. longirostris* reflects seasonal variation in fruit availability. When there is a scarcity of its usual diet, *G. longirostris* apparently switches to other food sources such as the fruit of *Chlorophora tinctoria* and an unidentified plant which were not eaten during other periods of the year, even when they were available. Our unpublished data on faecal samples of *Artibeus jamaicensis* and *A. lituratus* reveal that these fruits are present at other times of the year but were not consumed by *G. longirostris*. On the other hand, *G. longirostris* possibly extended its foraging area to seek food, or changed its roosting localities in response to a limitation of resources, which would have been reflected in the low capture rate in November and December of 1989 and 1990 (Sosa 1991).

The relationship between the availability of cactus fruit and the diet of *G. longirostris* (Table 2) seems to support the adaptive syndromes of seed dispersal

Table 2. Relationship between fruit availability of three cactus species and their frequency in the diet of *G. longirostris*. Expected frequencies were calculated on the basis of annual fruit availability.

Species	Frequency	
	Expected	Observed
<i>Stenocereus griseus</i>	160.5	126
<i>Subpilocereus repandus</i>	25.0	45
<i>Pilosocereus tillianus</i>	0.4	15

$\chi^2 = 59.9$; $df = 2$; $P < 0.001$.

proposed by Soriano *et al.* (1991). The fruit of *S. griseus* has characteristics that suggests ornithochory (e.g. red print colour), and it occurred in a lower proportion than expected in the diet of *G. longirostris*. In contrast, fruits of *S. repandus* and *P. tillianus* have morphological features that make them particularly adapted to chiropterochory (e.g. they are green when ripe) (Pijl 1972) and they were eaten in higher proportions. Nevertheless, as *P. tillianus* is associated with calcareous soils on steep slopes (Ponce 1989; M. Fariñas, pers. comm.) it is probable that the density values we report would be lower than the true values

because land around Laguna de Caparú has gentle slopes. Consequently, fruit abundance per hectare for this species could be slightly greater for the arid and hilly region of Lagunillas.

The phase differences between the curves of fruit availability of the three cactus species and their importance in the diet of *G. longirostris* (Figure 5) was due to a bias in our evaluation of ripe fruit availability. We had difficulty in determining the ripeness of the fruit of *S. repandus* and *P. tillianus*, and because of the short residence time of mature *S. griseus* fruits on plants, we used apparently mature fruit to quantify resources when in fact they were not ripe. In reality, these fruits were not available for bats which have been shown to be very selective and to eat only mature fruit (Stashko & Dinerstein 1988). These problems could be overcome by reducing the time interval between each phenological census and by using fruit traps (Stashko & Dinerstein 1988) to more accurately assess the abundance of this resource.

The same anatomical type of fruit offered by the three cactus species, an extended period of ripening and few open fruits per night, allows an optimum use of the 'fruit' resource by seed dispersers, since an excess in fruit production could be an unfavourable investment for the plant: excess seeds could be eaten by animals (e.g. mouse opossums or rodents) that might not be good dispersers or be seed predators.

G. longirostris was the main seed dispersal agent of *S. repandus* and *P. tillianus*, since fruits of these species were consumed in large quantities by this bat. Dispersal of *S. griseus* depends, in addition to *G. longirostris*, on the bat *L. curasoae* and possibly on such frugivorous birds as *Mimus gilvus* (Mimidae), *Coereba flaveola* (Parulidae) and *Euphonia lanirostris* (Thraupidae) (Soriano *et al.* 1991, Sosa 1991) and Robinson's mouse opossum *Marmosa robinsoni* (P. J. Soriano, pers. obs.).

G. longirostris is bimodally polyestrous (Wilson 1979) and females can give birth to two offspring per year, although the reproductive periods do not coincide with those indicated by Webster & Handley (1986). As we supposed in our hypothesis, the reproductive peaks of *G. longirostris* are broader than those in frugivorous bats which depend on a seasonal supply of food resources (Bonaccorso 1979, Dinerstein 1986, Fleming *et al.* 1972, LaVal & Fitch 1977, Molinari 1984, Soriano 1983, Willig 1985). The first reproductive peak of *G. longirostris* was larger than the second, probably because of the large quantity of fruits and flowers provided by *S. griseus* and *S. repandus*. The second peak did not seem to coincide with abundance of food in the environment, but may have been the result of the endogenous rhythm in this species (Sosa 1991), selected by inter-annual variation in food supply. Possibly not all of the females reproduced in the second reproductive period because the energy cost that lactation entails (Kurta *et al.* 1989, Racey & Speakman 1987, Speakman & Racey 1987) is very high and the survival probabilities of the young can be affected by food scarcity at the beginning of the long dry season.

With regard to food availability and the reproductive cycle of *G. longirostris*, fruits of *S. griseus* were the most important food resource during the first half of the main pregnancy period. This was not the case, however, during the second pregnancy period (Figures 2a, 5a). A relationship between lactation periods and abundance of these food items is not evident. *S. repandus* provided an abundant fruit supply during the second half of the first pregnancy period and during the following lactation period. Flowers of *S. griseus* and *S. repandus* were also important food sources during pregnancy and lactation periods, which could have benefited the young bats because the pollen of some chiropterophilous plants is known to provide tyrosine that serves as a growth stimulant. This amino acid is found in abundance in the milk of small mammals (Howell 1974).

Thus, there is clear evidence of an interdependent relationship between columnar cacti and *G. longirostris*. The sexual reproduction of these plants would be seriously affected by the absence of these pollinators and seed dispersers and, at the same time, these bats could not subsist in this arid region of Venezuela without the food sources provided by these plants.

ACKNOWLEDGEMENTS

We acknowledge the help of S. Segnini and T. Schwarkopf with the statistical analysis of the data, and J. Delfin Diaz, P. Ramoni, J. Jiménez, I. Casart, M. Muñoz and A. De Ascensão helped us in the field work. We also thank Ted Fleming and an anonymous reviewer whose suggestions made important improvements to this paper. The work received financial support from the Asociación Educativa para la Conservación de la Naturaleza, EcoNatura, assigned to the first author, and the generous donation of a vehicle by the Fundación Polar.

LITERATURE CITED

- BLANCO, C. A. 1976. *Flórula de la zona xerófila Ejido-Estanques del Estado Mérida. Primera parte*. Trabajo de Ascenso disert., Universidad de Los Andes, Facultad de Ciencias Forestales. 91 pp.
- BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences* 24:359-408.
- CROAT, T. B. 1975. Phenological behavior of habits and habitat classes on Barro Colorado Island (Panama Canal Zone). *Biotropica* 7:270-277.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in northwestern Costa Rica. *Journal of Ecology* 60:147-170.
- DINERSTEIN, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica* 18:307-318.
- FLEMING, T. H. 1989. Climb every cactus - BCI's Sonoran Desert Bat-Cactus Project concludes its first field season in Mexico. *Bats* 7:3-6.
- FLEMING, T. H., HOOPER, E. T. & WILSON, D. E. 1972. Three Central American bat communities: structure, reproductive cycles, and movements. *Ecology* 53:555-569.
- GOODWIN, G. G. & GREENHALL, A. M. 1961. A review of the bats of Trinidad and Tobago. Descriptions, rabies infection, and ecology. *Bulletin of the American Museum of Natural History* 122:187-302.
- GRAHAM, G. L. 1987. Seasonality of reproduction in Peruvian bats. *Fieldiana Zoology, New Series* 39:173-186.
- HEITHAUS, E. R. 1982. Coevolution between bats and plants. Pp. 327-367 in Kunz, T. H. (ed.). *Ecology of bats*. Plenum Press, New York.

- HEITHAUS, E. R., FLEMING, T. H. & OPLER, P. A. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56:841–854.
- HEITHAUS, E. R., OPLER, P. A. & BAKER, H. G. 1974. Bat activity and pollination of *Bauhinia pauletia*: plant–pollinator coevolution. *Ecology* 55:412–419.
- HOWELL, D. J. 1974. Bats and pollen: physiological aspects of the syndrome of chiropterophily. *Comparative Biochemistry and Physiology* 48:263–276.
- KUNZ, T. H. & ANTHONY, E. L. P. 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. *Journal of Mammalogy* 63:23–32.
- KURTA, A., BELL, G. P., NAGY, K. A. & KUNZ, T. H. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62:804–818.
- LAVAL, R. K. & FITCH, H. S. 1977. Structure, movements and reproduction in three Costa Rican bat communities. *Occasional Papers, Museum of Natural History, University of Kansas* 69:1–28.
- LEÓN, de la LUZ, J. L. & DOMINGUEZ, R. 1991. Evaluación de la reproducción por semillas de la pitaya agria (*Stenocereus gummosus*) en Baja California Sur, México. *Acta Botanica Mexicana* 14:75–87.
- MARCUZZI, G. 1956. Contribución al estudio de la ecología del medio xerófilo venezolano. Región de Lagunillas en el Estado Mérida. *Boletín de la Facultad de Ingeniería Forestal* 3:8–42.
- MOLINARI, J. 1984. *Dinámica reproductiva y ecología trófica de Carollia brevicauda y otros murciélagos frugívoros*. Lic. Biol. dissert., Universidad de Los Andes, Mérida, Venezuela. 136 pp.
- NASSAR, J. 1991. *Biología reproductiva de cuatro cactáceas quiropterófilas venezolanas (Cereae: Stenocereus griseus, Pilosocereus moritzianus, Subpilocereus repandus y S. horrispinus) y las estrategias de visitas de los murciélagos asociados a éstas*. Tesis de licenciatura dissert., Universidad Central de Venezuela, Facultad de Ciencias, Caracas, Venezuela. 136 pp.
- PIJL, L. VAN DER. 1972. *Principles of dispersal in higher plants* (2nd edition). Springer-Verlag, Berlin. 161 pp.
- PONCE, M. 1989. *Distribución de cactáceas en Venezuela y su ámbito mundial*. Trabajo de Ascenso, Universidad Central de Venezuela, Facultad de Agronomía, Maracay, Venezuela. 215 pp.
- RACEY, P. A. & SPEAKMAN, J. R. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Pp. 107–126 in Loudon, A. & Racey, P. A. (eds). *Mammalian reproductive energetics. Symposium of the Zoological Society of London* 57.
- SARMIENTO, G., MONASTERIO, M., AZOCAR, A., CASTELLANO, E. & SILVA, J. 1971. *Estudio integral de las cuencas de los ríos Chama y Capazón*. Oficina de Publicaciones Geográficas, Instituto de Geografía y Conservación de recursos Naturales, Escuela de Geografía, Universidad de Los Andes, Mérida, Venezuela. 63 pp.
- SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* 15:274–281.
- SORIANO, P. J. 1983. *La comunidad de quirópteros de las selvas nubladas en los Andes de Mérida. Patrón reproductivo de los frugívoros y las estrategias fenológicas de las plantas*. MSc Dissertation, Universidad de Los Andes, Mérida, Venezuela. 113 pp.
- SORIANO, P. J., SOSA, M. & ROSSELL, O. 1991. Hábitos alimentarios de *Glossophaga longirostris* Miller (Chiroptera: Phyllostomidae) en una zona árida de los Andes venezolanos. *Revista de Biología Tropical* 39:267–272.
- SOSA, M. 1991. *Relaciones ecológicas entre el murciélago Glossophaga longirostris y las cactáceas columnares en el bolsón árido de Lagunillas, Mérida, Venezuela*. Lic. Biol. dissert., Universidad de Los Andes, Mérida, Venezuela. 106 pp.
- SPEAKMAN, J. R. & RACEY, P. A. 1987. The energetics of pregnancy and lactation in the brown long eared bat *Plecotus auritus*. Pp. 367–393 in Fenton, M. B., Racey, P. A. & Rayner, J. M. V. (eds). *Recent advances in the study of bats*. Cambridge University Press, Cambridge, UK.
- STASHKO, E. R. & DINERSTEIN, E. 1988. Methods of estimating fruit availability to frugivorous bats. Pp. 221–231 in Kunz, T. H. (ed.). *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C., London. 533 pp.
- THOMAS, D. W. 1988. Analysis of diets of plant-visiting bats. Pp. 211–220 in Kunz, T. H. (ed.). *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C., London. 533 pp.
- WEBSTER, W. D. & HANDLEY, C. O., Jr. 1986. Systematics of Miller's long-tongued bat, *Glossophaga longirostris*, with description of two new subspecies. *Occasional Papers, The Museum, Texas Technical University* 100:1–22.
- WILLIG, M. R. 1985. Reproductive patterns of bats from Caatingas and Cerrado biomes in Northeast Brazil. *Journal of Mammalogy* 66:668–681.
- WILSON, D. E. 1979. Reproductive patterns. Pp. 279–386 in Baker, R. J., Jones, J. K. & Carter, D. C. (eds). *Biology of bats of the New World family Phyllostomidae. Part III*. Special Publications of the Museum, Texas Technical University, No. 16. Lubbock, Texas. 441 pp.