

❧ CHAPTER 12 ❧

The Role of Bats and Birds in the Reproduction of Columnar Cacti in the Northern Andes

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Introduction

The Andes of northern South America contain a set of dry valleys with climatic characteristics that result from orographic rainfall shadows (Sarmiento, 1975). These arid valleys constitute an archipelago of small arid enclaves separated from each other by wet vegetation formations. They occur from the Cordillera de Mérida, in western Venezuela, to Ecuador through the three Andean mountain chains of Colombia. During the Pleistocene, these enclaves were connected with the current arid region of the Caribbean coast (Sarmiento, 1975, 1976) and at present constitute refuges for the flora and fauna of the Andean dry ecosystems (Hernández et al., 1992). They therefore represent an important genetic reservoir where allopatric speciation may be occurring (Hernández et al., 1992).

Ecologically, these dry valleys can be classified into two types according to their climatic characteristics and altitude (Sarmiento, 1976). The first type includes enclaves found above 1,800 m, characterized by meso- and microthermic climates (annual mean temperatures below 20°C) and vegetation types with few features in common with those of the Caribbean coast. This lack of relationship is evidenced by the absence of columnar cacti, among other aspects. The second type comprises enclaves located below 1,800 m, which are characterized by warm climates (annual mean temperatures above 24°C) and which are similar in ecology, flora, and vegetation physiognomy to the Caribbean coast (Sarmiento, 1972, 1975). At least eleven units of the second type can be recognized in the northern Andes (Fig. 12.1). We will focus on these latter enclaves owing to the presence of columnar cacti, whose ecological relationships are the subject of the present chapter.

The plant communities of these medium- and low-altitude valleys show close floristic relationships to the vegetation of the Caribbean coast, although they contain

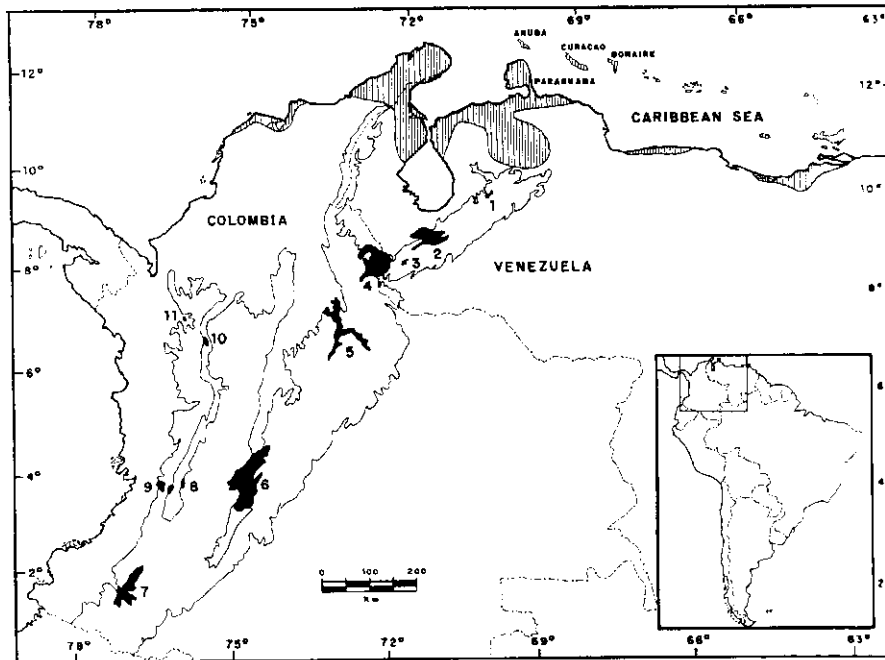


FIGURE 12.1. Arid zones in northwestern South America. Caribbean coastal dry zone (barred areas) and the eleven Andean enclaves (black areas). (1) La Puerta; (2) Lagunillas; (3) La Quinta; (4) Cucuta-Ureña; (5) Chicamocha; (6) La Tatacoa; (7) Patia; (8) Cauca River; (9) Dagua; (10) Santa Fé de Antioquia; (11) Sucio River. Modified from Sarmiento (1976) and Cavellier et al. (1996).

fewer plant species (Sarmiento, 1975). Columnar cacti are characteristic elements of these landscapes, where some individuals reach heights of 7–9 m and emerge above the tree canopy. Their flowers and fruits are located mainly at the tips of branches and provide access to bats and birds (Fig. 12.2). These vertebrates directly influence the reproductive biology of these Cactaceae, with which they have established different degrees of dependency in pollination (zoogamy) and seed dispersal (zoochory).

During the past decade, there has been an increase in the number of studies dealing with the interactions between birds, bats, and tropical columnar cacti. These studies have documented interactions between Cactaceae and phyllostomid bats of the subfamily Glossophaginae in certain arid enclaves of the Venezuelan and Colombian Andes and on some Caribbean islands, as well as the importance of birds in the process of seed dispersal (Bosque, 1984; Silva, 1988; Wendelken and Martin, 1988; Soriano et al., 1991; Sosa and Soriano, 1993, 1996; Petit, 1995; Silvius, 1995; Nassar et al., 1997; Rengifo, 1997; Ruiz et al., 1997; Naranjo 1998).

One of the most important species in these interactions is *Glossophaga longirostris* (Fig. 12.3a), a nectarivorous, pollinivorous, frugivorous bat (Goodwin and Greenhall, 1961; Pirlot, 1964; Alvarez and González, 1970; Gardner, 1977; Soriano et al.,



FIGURE 12.2. Panoramic view of the Lagunillas enclave at the middle Chama River basin. The branches of columnar cacti emerge from the open canopy of the woody plants. Photo by P. J. Soriano.

1991; Sosa and Soriano, 1996; Ruiz et al., 1997) that inhabits arid environments in northern South America (Webster and Handley, 1986). It is a nonmigratory species (Soriano et al., 1991; Sosa and Soriano, 1996; Ruiz et al., 1997). In contrast, another glossophagine species involved in these interactions is *Leptonycteris curasoae* (Fig. 12.3b), which is a migrant species in North America (Hayward and Cockrum, 1971; Cockrum, 1991; Fleming et al., 1993a) and whose presence in the Andean enclaves is restricted to certain periods of the year (Sosa and Soriano, 1993).

Our knowledge of the relationships between birds and columnar cacti is restricted to species lists of fruit consumers and indirect measures of fruit consumption, such as visitation rates (Ellner and Shmida, 1981; Bosque, 1984; Silva, 1988; Wendelken and Martin, 1988; Silvius, 1995). Comparisons between birds and bats with respect to their efficiency as potential seed dispersers and their role in germination have not been made, although Rengifo (1997) and Naranjo (1998) provide experimental evidence for the effect on germination of seeds passed through the gut of certain species of birds and the bat *Glossophaga longirostris*, respectively.

The purpose of this chapter is to summarize available information on the ecological relationships between columnar cacti and their main pollinators and seed dispersers in the arid Andean enclaves of Colombia and Venezuela. We will describe the adaptive strategies that can be deduced from the floral and fruit features of the cacti that inhabit these enclaves. We will also compare the ecological role of birds and bats as seed dispersers of these columnar cacti. Additionally, we will discuss the different

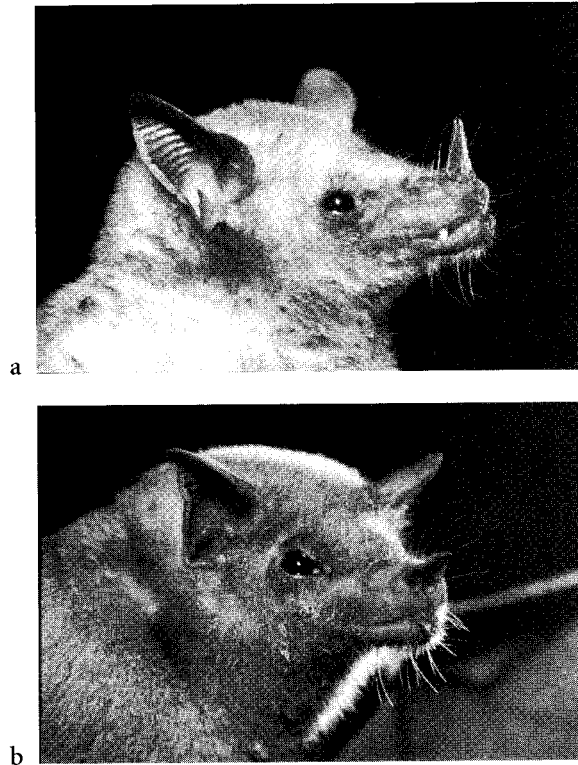


FIGURE 12.3. The main pollinator and seed disperser bats in the Andean enclaves. (a) *Glossophaga longirostris*, a resident species. (b) *Leptonycteris curasoae*, a migrant species. Photos by P. J. Soriano.

configurations of the bat-cactus system in the Andean enclaves (especially the occurrence of *Glossophaga longirostris* and *Leptonycteris curasoae*) and the ecological implications of the presence or absence of these bats. For this purpose, we will emphasize enclaves located in the Cordillera Oriental (Colombia) and the Cordillera de Mérida (Venezuela).

The Andean Arid Enclaves

We give special emphasis to seven of the 11 enclaves where columnar cacti occur in the Andes of Colombia and Venezuela (Fig. 12.1); four are located in the Cordillera de Mérida (Venezuela) and other three in the Cordillera Oriental and Cordillera Occidental (Colombia):

1. *La Puerta*. This enclave comprises a small swath restricted to the mountain hillsides of the middle Motatán river basin, between the towns of La Puerta (Trujillo

- State, Venezuela) and Timotes (Mérida State, Venezuela). Its approximate area is 27 km².
2. *Lagunillas*. The enclave extends from the town of Estanques, located in the middle Chama river basin, to the town of El Morro in the higher Nuestra Señora river basin in Mérida State, Venezuela. It occupies an area of 262 km² and represents the largest enclave in the Cordillera de Mérida.
 3. *La Quinta*. The enclave is located between the confluence of the La Grita and Del Valle rivers, to the west of La Grita (Táchira State, Venezuela). The approximate area is 29 km².
 4. *Cúcuta-Ureña*. The enclave is located at the Venezuelan and Colombian border in Táchira State (Venezuela) and Norte de Santander Department (Colombia). This enclave occupies an area of 1,472 km² with the driest zone occupying 13% of the total area.
 5. *Chicamocha*. This enclave is located between the middle Chicamocha river valley and the Suárez river valley, Santander Department (Colombia). It occupies an area of 1,400 km²; the driest portion represents 8% of the total area.
 6. *La Tatacoa*. This enclave is located in the high Magdalena river valley, between the towns of Honda (Tolima Department, Colombia) and Garzón (Huila Department, Colombia). It occupies an area of 11,185 km², and its driest zone represents 12% of the total area. This is the largest enclave in the northern Andes.
 7. *Patía*. It is located in the middle Patía river valley in the Cordillera Occidental of the Colombian Andes, Cauca and Nariño Departments. This enclave occupies about 1,127 km².

The large enclaves (*La Tatacoa*, *Patía*, *Lagunillas*, *Chicamocha*, and *Cúcuta-Ureña*) contain a moisture gradient; different community types occur along this gradient, from very arid to wetter zones (premontane thornshrub and tropical dry forest, respectively, sensu Holdridge; Espinal and Montenegro, 1963; Fwél et al., 1976). The driest zones containing the highest density of columnar cacti occupy very small areas relative to the total area of these enclaves. For most of these enclaves, dry forests have been replaced by cultivation and extensive grazing by cows and goats. Grazing has increased the processes of erosion and desertification.

These dry forests have a discontinuous canopy 4–8 m in height. Most of them share genera of woody plants, such as *Acacia*, *Bursera*, *Caesalpinia*, *Cercidium*, *Croton*, *Guazuma*, *Jatropha*, and *Prosopis*. They also share certain genera of columnar cacti, such as *Stenocereus*, *Subpilocereus*, *Pilosocereus*, and *Cereus* (Fig. 12.4a,d,g,j). Other Cactaceae present in these forests belong to the genera *Acanthocereus*, *Hylocereus*, *Mammillaria*, *Melocactus*, *Opuntia*, and *Rhipsalis*. Although the cactus composition of these forests is known (Ponce, 1989; Cavelier et al., 1996; chapter 16, this volume), we lack taxonomic studies to determine the extent of species shared between them.

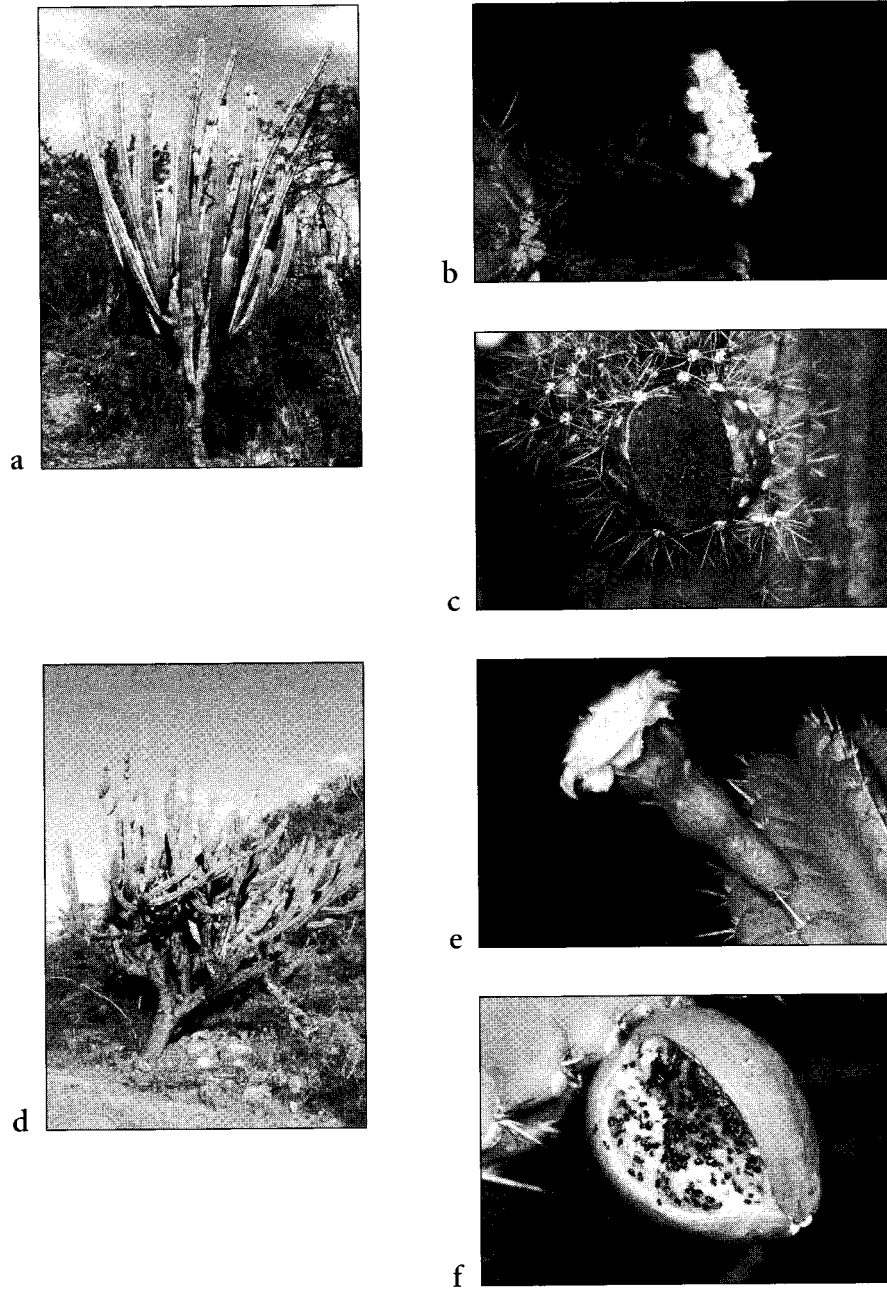


FIGURE 12.4. Representatives of the four genera of columnar cacti (individual, flower, and fruit) present in the Andean enclaves. (a, b, c) *Stenocereus griseus*; (d, e, f) *Subpilocereus repandus*; (g, h, i) *Pilosocereus tillianus*; and (j, k, l) *Cereus hexagonus*. Photos by P. J. Soriano.

Bats and Birds and the Reproduction of Columnar Cacti

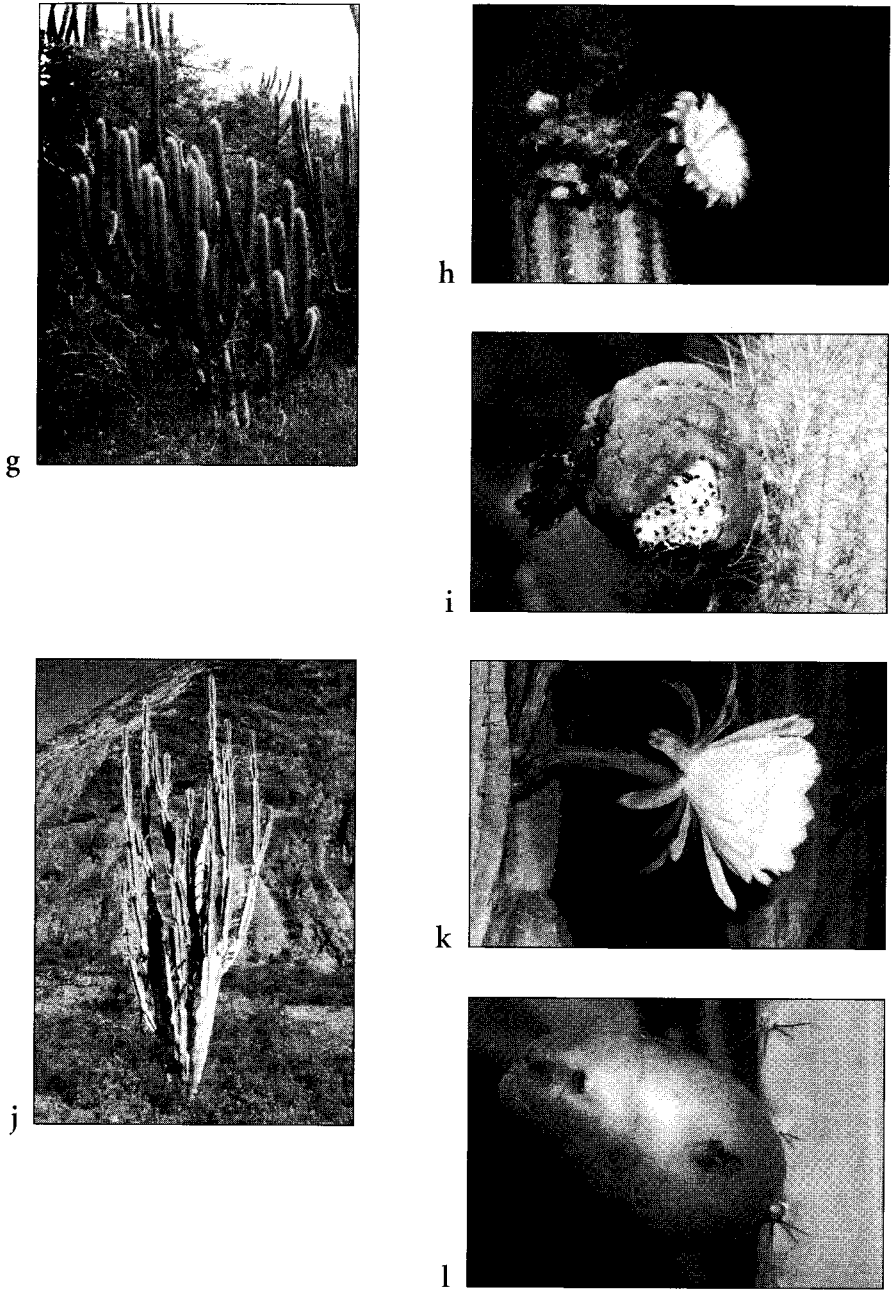


FIGURE 12.4. *Continued*

Reproductive Strategies of Columnar Cacti: Pollination and Seed Dispersal

MORPHOLOGICAL FEATURES OF FLOWERS AND FRUITS OF COLUMNAR CACTI

Flowers and fruits of the columnar cacti of the enclaves described in the previous section possess well-defined functional and anatomical features that favor chiropterogamy as a pollination mechanism (Valiente-Banuet et al., 1996, 1997; Nassar et al., 1997). Features of chiropterochory and ornithochory as strategies for seed dispersal can also be recognized in their fruits (Greenhall, 1957; Snow, 1981; van der Pijl, 1982; Soriano et al., 1991). Flowers of the genera *Pilosocereus*, *Stenocereus*, and *Subpilocereus* possess morphological and functional characteristics that clearly favor bat pollination (Fleming, 1989; Nassar et al., 1997). Major morphological features shared by these flowers are funnel-shaped corolla tubes with thick fleshy or leathery walls, greenish floral tubes, white to rose-colored petals, numerous stamens, and production of large quantities of pollen and nectar (Fig. 12.4b,e,h). Upon maturation, these flowers emit an odor reminiscent of decomposed vegetables.

Nocturnal anthesis is another important feature of these Cactaceae, which helps restrict potential pollinators to nocturnal species. The anthesis is crepuscular and synchronous (between 1830 and 1930) in all columnar cacti in the northern Andean enclaves (Nassar et al., 1997; Ruiz et al., 2000). Their flowers remain open during the entire night and part of the next morning, with the exception of *Stenocereus griseus*, which closes before sunrise. These closing times are critical for excluding birds but do not exclude them completely. Petit (1995) and Nassar et al. (1997) have demonstrated that the bat species *Glossophaga longirostris* and *Leptonycteris curasoae* are the most effective pollinators of *Stenocereus griseus* and *Subpilocereus repandus* in Curaçao and northern Venezuela, respectively. Additionally, columnar cacti show a strong trend towards self-incompatibility, which increases their dependency on mobile pollinators, as has been established by Petit (1995) and Nassar et al. (1997) in *Stenocereus griseus*, *Subpilocereus horrispinus*, and *Subpilocereus repandus*, which are also present in the Andes. This set of chiropterogamic features and other evidence suggest that these Cactaceae depend mainly on glossophagine bats for fruit and seed set.

In contrast, the flowers of *Cereus hexagonus* (Fig. 12.4k) show features that favor pollination by moths of the family Sphingidae (P. Soriano, pers. obs.). Thus the floral tube is greenish in color and very long and narrow (about 20 cm in length); the perianth is 8–10 cm in diameter with white petals; and anthesis is nocturnal. Long floral tubes allow moths to reach the nectaries with their long proboscides but prevent access by bats.

Morphological features of fruits of the Cactaceae that favor chiropterochory and ornithochory as mechanisms of seed dispersal include size, shape, and pulp color. Fruits of *Stenocereus griseus* are spherical and 5 cm in diameter with a thin pericarp (1–2 mm) and numerous spiny areoles (Fig. 12.4c). When unripe, they are reddish

green, but when ripe, the areoles tend to be easily detached from the pericarp, and the endocarp becomes red (Soriano et al., 1991). This species also has a morph whose pericarp is greenish yellow with white pulp. The seeds are small (1.5×1 mm). The genus *Subpilocereus* has ellipsoid to oval fruits 4–8 cm in length and 1.5–3.5 cm wide without areoles (Fig. 12.4f). They are dehiscent with a thick pericarp (5–8 mm) of green color with purple stains. A white pulp with abundant small seeds (3×2 mm) is revealed upon opening the fruit. The fruits of *Pilosocereus* spp. are nearly spherical (5 cm long by 3–4 cm wide), without areoles, and bluish-green in color (Fig. 12.4i). They are dehiscent, with a thick pericarp (4–5 mm). The white pulp contains numerous small seeds (1×0.7 mm). Different species of this genus have populations that exhibit white pulp (*P. tillianus*, in Lagunillas), red pulp (*Pilosocereus* sp., La Tatacoa), or white and red morphs in the same population (*Pilosocereus* sp., La Quinta). *Cereus hexagonus* produces spineless oval fruits 10–13 cm long and 5–8 cm in diameter; upon maturation the pericarp changes from green to red (Fig. 12.4l). There are varieties with red or white pulp. The seeds are small (3×2 mm) and black. These characteristics attract birds and bats as potential dispersal agents (Greenhall, 1957; Silva, 1988).

SEED-DISPERSAL EFFICIENCY OF BIRDS AND BATS

Bird communities in Andean enclaves are as yet poorly studied; nevertheless, studies at Lagunillas (Soriano et al., 1999) show that the community of fruit-eating birds associated with two columnar cacti (*Stenocereus griseus* and *Subpilocereus repandus*) contains 19 species (Table 12.1). This species richness is equivalent to that of five other neotropical arid localities (Bosque, 1984; Silva, 1988; Santos, 1995; Silvius, 1995; Wendelken and Martin, 1988). Each of these areas shares taxonomic and functional similarities, including one species each in the families Columbidae, Mimidae, Parulidae, Picidae, Psittacidae, and Tyrannidae and at least two Emberizidae. Experiments and observations indicate that these species belong to three functional groups: seed dispersers, seed predators, and pulp consumers (Silvius 1995; Soriano et al., 1999). This appears to be the basic functional structure in cactus-rich arid communities.

In the Lagunillas community, birds remove twofold more seeds of *Stenocereus griseus* than *Subpilocereus repandus*, perhaps because of differences in their dispersal syndromes (Soriano et al., 1999). The main cactus-fruit eater is *Melanerpes rubricapillus* (Picidae), which transports 78% and 39% of seeds consumed by birds of *Subpilocereus repandus* and *Stenocereus griseus*, respectively (Table 12.1). Next in significance is the seed predator *Saltator albicollis* (responsible for 11% and 18% of the seed transport for the two species of cacti, respectively). Each cactus species or morph has a slightly different bird assemblage (Table 12.1). The bird assemblage associated with the red morph of *Stenocereus griseus* is richer (15 species) than that associated with the white morph (11 species) or with that of *Subpilocereus repandus* (ten species). The assemblages of *Subpilocereus repandus* and the white morph of *Stenocereus griseus* are the most similar (eight species in common). As a result, birds transport a greater num-

TABLE 12.1
 Avian Consumption of the Fruit of the Cacti *Subpilocereus repandus* and
Stenocereus griseus in the Lagunillas enclave, Mérida State, Venezuela^a

Family	Species	Function ^b	<i>S. griseus</i>			
			<i>S. repandus</i>	Red	White	Both
Phasianidae	<i>Colinus cristatus</i>	Pd		—	—	
Columbidae	<i>Leptotila verreauxi</i>	Pd		4.02	4.02	
Psittacidae	<i>Forpus passerinus</i>	Pd		1.79	1.79	
Trochilidae	<i>Phaethornis hispidus</i>	PE	0			
Picidae	<i>Melanerpes rubricapillus</i>	Di	78.75	26.55	13	39.55
Tyrannidae	<i>Pitangus sulphuratus</i>	Di			0.01	0.01
	<i>Tyrannus melancholicus</i>	Di(?)		0.01		0.01
Turdidae	<i>Turdus nudigenis</i>	Di		6.73		6.73
Mimidae	<i>Mimus gilvus</i>	Di		8.36	3.33	11.69
Emberizidae	<i>Saltator albicollis</i>	Pd	10.78	8.67	9.12	17.79
	<i>Tiaris bicolor</i>	Pd	0.03	0.69	0.39	1.08
	<i>Sicalis flaveola</i>	Pd		—		
	<i>Zonotrichia capensis</i>	Pd	0.03			
	<i>Euphonia lanirostris</i>	Di	0.93	0.67	2.16	2.83
	<i>Piranga rubra</i>	Di(?)		—		—
	<i>Tachyphonus rufus</i>	Di/Pd	6.86	0.52	0.65	1.17
	<i>Thraupis episcopus</i>	Di	2.59	2.96	2	4.96
Parulidae	<i>Coereba flaveola</i>	Cp	0	0	0	0
Fringillidae	<i>Carduelis psaltria</i>	PE	0.03	3.46	5	8.46
	TOTALS		100	64.45	35.68	100

^a Numerical data indicate the percentage of seeds transported or predated by bird species (determined by defecation analysis), based on the total number of seeds removed by the avian community observed during the fruiting periods of each cactus species ($n = 697$ obs.). Data are from Soriano et al. (1999).

^b — — consumption data not available; PE = pulp eater; Pd = predator; Di = disperser.

ber of seeds of the red morph than the white morph (Table 12.1). However, not all birds that eat fruits of these two species of cacti have a positive effect on their reproductive success because only seven of 19 birds appear to be legitimate seed dispersers.

Recent studies of some columnar cacti indicate that the phenotypic characteristics (e.g., color) exhibited by fruits influence the seed dispersal efficiency of birds and bats. The red color of pulp represents an adaptation to attract birds as dispersal agents, as these vertebrates select their food by color. In contrast, odor is more important for food choice in bats (van der Pijl, 1982; Debussche and Isenmann, 1989; Willson and Whelan, 1990; Willson et al., 1990). The red morph of *Stenocereus griseus* fruits should favor detection by birds. Rengifo (1997) provides experimental evidence demonstrating in the laboratory the preference for the red morph of *S. griseus* by the birds *Melanerpes rubricapillus*, *Mimus gilvus*, and *Thraupis episcopus*, whereas *Tachyphonus rufus* preferred the white morph. The general trend of field data shows that seed dispersers prefer the red morph and seed predators prefer the white morph (Table 12.1). Additional experimental evidence is needed to clarify this point.

Field experiments provide quantitative data about the role of bats and birds in the cactus-disperser system by using fruits of *Stenocereus griseus* and *Subpilocereus*

repandus and measuring the consumption index by each of these groups (Rengifo, 1997; Naranjo, 1998). (The consumption index is defined as the ratio of pulp removed to pulp offered; it ranges in value between 0 and 1, indicating no pulp consumption or complete depletion, respectively.) The consumption of *Subpilocereus repandus* fruits by bats was greater than consumption by birds (0.79 ± 0.05 and 0.48 ± 0.06 , $t = 2.0639$; $df = 24$; $p < 0.05$). However, for *Stenocereus griseus*, consumption by bats and birds was very similar (0.9 ± 0.03 and 0.8 ± 0.05 , $t = 2.2009$; $df = 11$; $p > 0.05$), because birds are attracted by the red fruit coloration, but bats do not discriminate by color and consume as many red as white fruits.

The high density of *Stenocereus griseus* at Lagunillas and La Tatacoa (Santos, 1995; Sosa and Soriano, 1996) in comparison with other species of cacti agrees with the prediction of Fleming et al. (1993b) that the fitness of plants whose fruit syndromes allow dispersal by two or more taxa is higher than those dispersed by a single agent. Silvius (1995) observed that the dehiscence of fruits of *S. griseus* shows similar day and night frequencies, which increases resource availability and reduces competition between both groups.

In addition to number of seeds transported by seed dispersers, the quality of the treatment produced by the passage of seeds through animal intestines is an important component of dispersal. Seeds can be affected in different ways: At one extreme, their germination probability is enhanced, and at the other, the seeds are destroyed in the process (Schupp, 1993). Seeds of Cactaceae contain substances that inhibit the germination process (Williams and Arias, 1978), which makes them dependent on the effective elimination of this substance by dispersers. Passage of seeds of *Stenocereus griseus* through the digestive tracts of birds and bats does not produce seed scarification. It does eliminate the seed coat and increases percentage of germination (Table 12.2; Rengifo, 1997; Naranjo, 1998). This passage reduces mean germination times (between three and five days) and increases percentage of germination compared with unwashed seeds in *Stenocereus griseus* and *Subpilocereus repandus* (Table 12.2).

In the case of *Pilosocereus tillianus*, we lack data for birds, but seed passage through the digestive tract of *Glossophaga longirostris* does not significantly affect mean germination time (Naranjo, 1998). This suggests that this bat is not needed to release the seed inhibitor. In addition, such factors as erratic flowering and fruiting (Sosa and Soriano, 1996) and reproduction mainly involving vegetative dispersal (Rico et al., 1996) probably hinder the establishment of a close dispersal association with a bat species.

Now that data are available for evaluating some dispersal components, such as seed removal and the effect of seed passage through the digestive tract of birds and bats, there is a need to study aspects of the quality of dispersal: movement patterns of dispersers (seed shadows), patterns of seed deposition, nutrients provided to the seeds by the feces of dispersers, and viability of seeds in the seed bank. Postdispersal effects, including seed predation, establishment, recruitment, and nurse-plant effects have been studied in Mexico but not in the Andean enclaves (Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 1991a; Valiente-Banuet et al., 1991b).

TABLE 12.2
Percent Germination of Two Species of Columnar Cactus Seeds Passed by the Digestive Tract of Bats and Birds and Two Controls (Unwashed and Washed Seeds)^a

Treatment	<i>Stenocereus griseus</i>		<i>Subpilocereus repandus</i>	
	Germination (%)	D_{max}^b	Germination (%)	D_{max}
Bats				
<i>Glossophaga longirostris</i> (n = 10)	88	0.28*	86	0.12*
Birds				
<i>Melanerpes rubricapillus</i> (n = 8)	72	0.23*	83	0.07 ^{NS}
<i>Mimus gilvus</i> (n = 4)	86	0.23*	—	—
<i>Thraupis episcopus</i> (n = 8)	76	0.25*	82	0.10*
<i>Tachyphonus rufus</i> (n = 2)	SD	SD	87	0.09*
Washed seeds	98		91	
Unwashed seeds	71		75	

^a n = 500 seeds per treatment. SD = Seeds damaged by the passage; significance: * p < 0.001; NS = not significant. Data are from Rengifo (1997) and Naranjo (1998).

^b D_{max} of the Kolmogorov-Smirnov two-sample test gives the efficiency of elimination of the inhibitor, measured as the maximum difference between animals and unwashed seeds treatment cumulative frequency distributions.

Adaptive Responses of *Glossophaga longirostris* and *Leptonycteris curasoae* to Environmental Conditions

INTERDEPENDENCE BETWEEN GLOSSOPHAGINES AND COLUMNAR CACTI

Studies conducted in some enclaves of the northern Andes show that the diet of *Glossophaga longirostris* varies geographically (Soriano et al., 1991; Sosa and Soriano, 1993, 1996; Ruiz et al., 1997, Cadena et al., 1998). In Lagunillas, *G. longirostris* is associated with three species of columnar cacti (*Pilosocereus tillianus*, *Stenocereus griseus*, and *Subpilocereus repandus*) and acts as their pollinator and seed disperser. The latter two species provide a food supply for the bats nearly all year-round. They have asynchronous flowering and fruiting peaks, which reduces interspecific competition for seed dispersers and pollinators. During the annual scarcity period, this bat eats fruits of *Chlorophora tinctoria* (Moraceae) (Soriano et al., 1991; Sosa and Soriano, 1993, 1996). At La Tatacoa, Ruiz et al. (1997) showed that *G. longirostris* eats mainly fruits and pollen of the cactus *Stenocereus griseus*, fruits of *Muntingia calabura* (Elaeocarpaceae), nectar and pollen of *Helicteris baruensis* (Sterculiaceae), and, in smaller amounts, pollen and fruits of the cactus *Pilosocereus* sp. Fruits of *M. calabura* constitute the principal food item in its diet during the annual scarcity period, in the same way as *Piper* spp. and *Solanum* spp. have been reported as eaten by other bat species in wet forests (Gilbert, 1980; Fleming, 1985; Marinho-Filho, 1991). At Chicamocha, in addition to columnar cacti, *G. longirostris* eats fruits of eight other plant species, mainly from the genera *Ambrosia*, *Cecropia*, and *Muntingia* (Cadena et al., 1998). In these enclaves, seasonal variations in diet are correlated mainly with the

availability of resources and they do not reflect food preference by *G. longirostris* (Soriano et al., 1991; Sosa and Soriano, 1996; Ruiz et al., 1997)

At Lagunillas, where *Leptonycteris curasoae* is found during part of the year, it consumes mainly nectar and pollen of the families Cactaceae and Agavaceae and in smaller amounts, fruits of *Stenocereus griseus* and *Subpilocereus repandus* (Sosa and Soriano, 1993). In contrast, at Chicamocha, this species was recorded eating pollen and fruit of *Stenocereus griseus* (Cadena et al., 1998). This information agrees with data obtained by Aranguren (1995) in the Peninsula of Paraguaná and that of other authors for arid zones of North America (Alcorn et al., 1961; Hayward and Cockrum, 1971; Gardner, 1977; Fleming, 1989), confirming that this species is a pollinator and seed disperser of Cactaceae. Although at Lagunillas, the diet of the two bats (*Glossophaga longirostris* and *L. curasoae*), as measured by similarity in fecal-sample content, overlaps 82% (quantitative index of Sørensen; Magurran, 1988), the diet of *G. longirostris* includes fruit of other cacti (e.g., *Pilosocereus tillianus*) and other non-cactus species not eaten by *L. curasoae* (Sosa and Soriano, 1993). High dietary overlap does not necessarily indicate interspecific competition, because *L. curasoae* is found only in the enclave during the period of high abundance of flowers and fruits of *Stenocereus griseus* and flowers of *Subpilocereus repandus* (December–April; Sosa, 1991; Sosa and Soriano, 1993). Availability of resources probably does not represent an environmental constraint during this period.

The reproductive pattern of *Glossophaga longirostris* is bimodal polyestry (Sosa and Soriano, 1996; Ruiz et al., 1997), which is synchronized with the production of flowers and fruits of columnar cacti. At Lagunillas, one of the annual birth peaks coincides with high availability of flowers and fruits of *Stenocereus griseus* and *Subpilocereus repandus*, but the second peak does not seem to correspond to a resource peak (Fig. 12.5a). At La Tatacoa, lactation peaks coincide with high levels of fruits of *Stenocereus griseus* (Fig. 12.5b). The differences found in diet and timing of reproductive periods between these two populations of *G. longirostris* appear to be adjustments to differences in the spatial and temporal distribution of food resources. In Curaçao, *G. longirostris* has a monoestrous pattern, which coincides with the strong overlap in the flowering periods of *Stenocereus griseus* and *Subpilocereus repandus* (Petit, 1997).

In contrast, the reproductive pattern of *Leptonycteris curasoae* is seasonal monoestry (Smith and Genoways, 1974). On Peninsula de Paraguaná, as in most of its geographic distribution, *L. curasoae* exhibits a single peak of parturition and lactation in the period May–July, which can extend until August (Hayward and Cockrum, 1971; Martino et al., 1998; but see chapter 14, this volume). During this period, *L. curasoae* is absent from Lagunillas (Sosa and Soriano, 1993), and preliminary surveys seem to indicate that this species abandons the Andes then (Ruiz and Soriano, 1998; Sánchez and Cadena, 1999; Soriano et al., 2000a). The single reproductive peak is possibly the consequence of the high energetic cost involved in migration and will be discussed below.

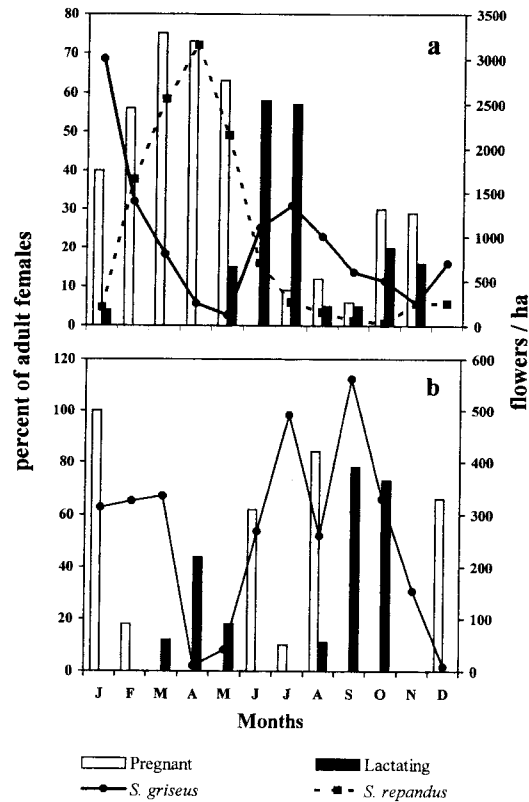


FIGURE 12.5. Reproductive pattern of *Glossophaga longirostris* versus the main floral resources in (a) Lagunillas and (b) La Tatacoa. Data are from Sosa and Soriano (1996) and Ruiz et al. (1997).

CONFIGURATION OF THE BAT-CACTUS SYSTEM IN THE ANDEAN ENCLAVES

The seven enclaves considered here show differences in size, species richness, and abundance of columnar cacti, as well as in the presence or absence of resident and/or migrant bat species (Table 12.3). Recent preliminary data have confirmed the presence of *Glossophaga longirostris* in Chicamocha as well as the presence of *Leptonycteris curasoae* in Chicamocha, La Quinta and La Puerta (Ruiz and Soriano, 1998; Sánchez and Cadena, 1999; Soriano et al., 2000a). These data show that the configuration of the bat-cactus system in a given enclave depends on particular combinations of variables, which include different species of Cactaceae, other plants, and other bat species. At least four different configurations are known.

1. *Configuration with a migrant species.* The exclusive presence of a migrant species in an enclave indicates that the availability of food is not sufficient to support bats for at least part of the year. In such a situation, only one species is able to use the

Bats and Birds and the Reproduction of Columnar Cacti

TABLE 12.3
Columnar Cacti and Glossophagine Bats in the Andean Enclaves^a

Enclave	Area (km ²)	Columnar Cacti ^b				Glossophagine Bats				
		S. g.	S. r.	S. h.	P. spp.	G. l.	L. c.	G. s.	A. g.	C. g.
La Puerta	27				++		X		X	
La Quinta	29	+			++		X	X	X	
Cúcuta-Ureña	191	+			++		X	X		
La Tatacoa	1342	+++			+	X		X	X	
Lagunillas	262	+++	++		++	X	X			
Chicamocha	112	+++		+	++	X	X		X	
Patia	1127				++				X	X

^a Data are from Cadena et al. (1998); Ruiz and Soriano (1998); and Soriano et al. (2000a). Among the bats, *Leptonycteris curasoae* is a migratory species.

^b S. g., *Stenocereus griseus*; S. r., *Subpilocereus repandus*; S. h., *Subpilocereus* cf. *horrispinus*; P. spp., *Pilosocereus* spp.; G. l., *Glossophaga longirostris*; L. c., *Leptonycteris curasoae*; G. s., *Glossophaga soricina*; A. g., *Anoura geoffroyi*; C. g., *Choeronycteris godmani*; X, present; +, rare; ++, abundant; +++, very abundant.

seasonal resources of the enclave and abandons it in the unfavorable period. To do this, the bat must be highly mobile, as has been reported for *L. curasoae* (Sahley et al., 1993). This seems to be the case at La Puerta, La Quinta, and Cúcuta-Ureña, where, due to scarcity of columnar cacti (Table 12.3) and/or noncomplementary phenological patterns, high resource levels do not occur year-round and therefore the presence of a resident species is not possible. In these enclaves, *L. curasoae* is present only seasonally. The small size of the two first enclaves is an additional factor that contributes to the absence of a resident species. Although the Cúcuta-Ureña enclave is relatively large (Table 12.3), its low species richness and paucity of columnar cacti discourages the presence of resident species.

2. *Configuration with a resident species.* This situation is typified by La Tatacoa (Table 12.3), which has a large area, in which phenological patterns of cacti species guarantee an adequate supply of resources all year to support a resident population of bats, in contrast with Cúcuta-Ureña and La Quinta (Ruiz et al., 1997, 2000). Large area and a significant population of one of the cacti seem to be the main advantages of La Tatacoa. The absence of a migrant species seems to be a consequence of the isolation of the enclave. In fact, whereas the distance separating most enclaves is about 60–100 km (Fig. 12.1), La Tatacoa is at least 220 km from the nearest enclave (Chicamocha). Fleming (1997) suggested that *L. curasoae* can migrate up to 480 km on its fat reserves before it must replenish them. This means that its maximum flight distance in one night is around 160 km. Therefore, an isolation distance 220 km must constitute, for La Tatacoa, a barrier to *L. curasoae*.
3. *Configuration with a resident and a migrant species.* This configuration includes the same conditions as the last configuration to maintain the resident species as well as proximity to other enclaves that allows the arrive of migrant species. The situation is exemplified by the enclaves of Lagunillas and Chicamocha (Table

12.3). This table shows that those enclaves in which *Stenocereus griseus* is absent or scarce are those in which a resident bat is absent. *S. griseus* provides resources during a significant portion of the year because of its bimodal phenological pattern and abundant flower and fruit production. Thus the presence of *S. griseus* in high densities seems to be especially important for the presence of resident species.

4. *Configuration with exclusively opportunistic species.* This type is characterized by the absence of bat species strongly linked to columnar cacti, and the only glosophagine species are those representatives from wetter, bordering ecologic units. Marginal presence of these “alien” species occurs in all types described before. For instance, *Glossophaga soricina* acts marginally in Cúcuta-Ureña as an opportunistic species, and in a similar way, *Anoura geoffroyi* can contribute to cactus pollination in the enclaves of La Puerta and La Quinta (Table 12.3). However, this configuration type occurs as the only possibility in those enclaves where, simultaneously, the resource supply is not guaranteed all year-round and isolation from neighbor enclaves prevents visitation by migrant species. Such is the case at the Patia enclave in the Cordillera Occidental of Colombia, where *A. geoffroyi*, *Choeroniscus godmani*, and *Phyllostomus discolor* were recorded eating pollen of Cactaceae (Cadena et al., 2000). Although these bat species do not belong to this arid ecosystem, they occasionally use the resources offered by its columnar cacti.

MOVEMENTS OF *LEPTONYCTERIS CURASOAE*

In North America, seasonal movements of *Leptonycteris curasoae* follow the flowering patterns of the plants that it consumes (Cockrum, 1991; Fleming et al., 1993a; Fleming, 1995). The same pattern emerges along that region of the Caribbean coast where its populations might travel back and forth to the Andean enclaves. Thus, on the Península de Paraguaná, populations of *L. curasoae* decrease in the period September–April (Martino et al., 1998), when the floral supply declines in the coastal region (Petit, 1997). At Lagunillas, this species’ highest abundance coincides with the greater availability of columnar cacti flowers (Fig. 12.6); when this resource declines in May–July, *L. curasoae* disappears (Sosa and Soriano, 1993, 1996). Likewise, at Chicamocha this species is in highest abundance when columnar cacti exhibit their peaks of flower and fruit production; it disappears from the enclave in April–July (Cadena et al., 1998; Sánchez and Cadena, 1999). Although data are not available for resource supplies in the other enclaves under consideration, we speculate that the trough in flower production observed at Lagunillas might be a synchronous and general pattern over all Andean enclaves, as these enclaves display lower cacti richness and reduced population (Table 12.3).

Although the cactus nectar consumed by *Leptonycteris curasoae* has high caloric content (Helvesen and Reyer, 1984; Petit and Freeman, 1996), when a reduction in flower supply occurs, the energy obtained could be lower than the investment in flying long distances from roosting to foraging sites. The amount of nectar that a single

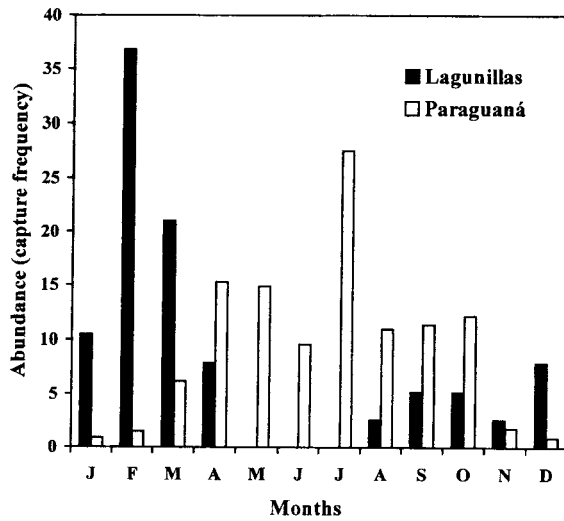


FIGURE 12.6. Monthly relative frequency of captures of *Leptonycteris curasoae* in Lagunillas and Paraguaná. Data are from Sosa and Soriano (1996) and Martino et al. (1998). Although the Paraguaná data come from one cave and are not directly comparable with Lagunillas data, banded individuals in Paraguaná have been found on the mainland (A. Martino, pers. com.).

flower can produce is about 0.6–1.1 mL/night, of which less than 0.1 mL is harvested in a single visit (Arends et al., 1995; Nassar et al., 1997). This low volume of nectar in relation to the energetic demand of the bat promotes visits to many plants with open flowers in the same night, which implies a great investment in flight time (Arends et al., 1995; Nassar et al., 1997). The energy available in the nectar of Cactaceae averages 2.78 kJ/flower, and this glossophagine needs 49–61 kJ/day, which is equivalent to 200 cactus flower visits per night; the caloric requirement may double for lactating females (Petit and Pors, 1995). Increasing the investment in foraging for resources also increases the cost:benefit ratio, which can be energetically unfavorable for the animal. Thus *L. curasoae* may migrate to other localities where resources are more abundant to reduce the energetic expense involved in food search.

The high energetic expenditure that migratory movements demand of *L. curasoae* in northern South America restricts its reproduction to a single annual event, which takes place outside of the Andean enclaves (Hayward and Cockrum, 1971, Bradbury, 1977; Cockrum, 1991; Sosa and Soriano, 1993; Martino et al., 1998). However, gregarious behavior in large maternity colonies (which can surpass 20,000 individuals in hot caves) is very important for economizing energy and increasing the growth rate of the juveniles and thus reducing the lactation period for females (Tuttle and Stevenson, 1982; Arends et al., 1995). The Andean enclaves do not seem to possess adequate refuges that permit the establishment of successful maternity colonies.

Conservation of the Andean Arid Zones

The dry zones of Colombia and Venezuela include relatively large areas ecologically connected with the plains of the Caribbean (coastal regions of northern Colombia and Venezuela) and with the Andean arid enclaves. However, these zones have been little studied (Hernández et al., 1992) when compared with the tropical wet forests in the lowlands. They have also received little attention in conservation plans. With the exception of a few hectares on the margins of Macuira National Park (on the Peninsula de la Guajira in Colombia) and the Médanos de Coro National Monument (in Venezuela), no dry areas are under protection in the national park systems of either country. It is important to conduct studies to provide the necessary information to prepare management and conservation plans for these areas. These plans should take the following into account:

1. The inter-Andean dry valleys represent an important reservoir of plant and animal species adapted to xeric conditions. Given the current isolation of these dry enclaves, they may represent important areas of speciation and endemism. For instance, the area of Villavieja in La Tatacoa is the type locality of the subspecies of bat *Glossophaga longirostris reclusa* (Webster and Handley, 1986). Likewise, the population of this bat in Lagunillas constitutes another endemic subspecies (*Glossophaga longirostris maricelae*; Soriano et al., 2000b). Similarly, the columnar cactus *Pilosocereus tillianus* is endemic to Lagunillas, and it is very probable that each enclave contains populations undergoing the speciation process. Some of the columnar cacti could represent currently unrecognized endemics, as is the case in a new, undescribed species of Cactaceae, *Pilosocereus* sp., located in La Tatacoa.
2. The Andean enclaves constitute a refuge for some populations of *Leptonycteris curasoae*, allowing it to maintain its population levels during the annual period of resource shortage along the Caribbean coast. This bat is a key element in the pollination of columnar cacti in the enclaves, where resident species are absent. The geographical arrangement of the enclaves, aligned throughout the Cordillera de Mérida and the Cordillera Oriental similar to the steps of a staircase, allows the passage of *L. curasoae* from the Caribbean coast to Chicamocha. This arrangement renders the enclave cacti vulnerable, because the disappearance or severe disturbance of intermediate enclaves would sever the passage and prevent *L. curasoae* from pollinating the Cactaceae in farther enclaves. This effect would be particularly pernicious in those enclaves lacking resident species. The persistence of the Andean enclaves can only be guaranteed through implementation of conservation policies in both countries.

Summary

Most of the Andean enclaves in Colombia and Venezuela contain species of columnar cacti from the genera *Pilosocereus*, *Stenocereus*, and *Subpilocereus*. All of these enclave

species possess flowers that exhibit syndromes of chiropterogamy, and bats play the main role in their pollination. The fruits of these cacti show certain morphological features that favor both chiropterochory and the ornitochory. In these environments, the presence of two species of Glossophaginae bats has been detected: *Glossophaga longirostris* and *Leptonycteris curasoae*. These bats fulfill the double roles of pollinator and seed dispersers. The first species forms resident populations in some of these environments, whereas the second seems to be a seasonal visitor, if present at all. In addition, at least two functional groups of fruit-consuming birds exist in the community: seed dispersers and seed predators. Using the available information on these environments, we make a comparison of the roles of both groups in the reproduction process of these cacti. The dispersion of seeds is a function that seems to be shared between birds and bats. We use the arid enclave of Lagunillas, Venezuela, as a study case for the comparison of the communities of birds associated with two species of columnar cacti that bear fruits of different color. We also describe and compare four possible configurations of the bat-cactus system from some Andean arid enclaves.

Resumen

En la mayoría de los enclaves andinos de Colombia y Venezuela se observa la presencia de especies de cactáceas columnares pertenecientes a los géneros *Pilosocereus*, *Stenocereus*, y *Subpilocereus*. Todas estas especies poseen flores que presentan síndromes de quiropterogamia y los murciélagos juegan un papel muy importante en su polinización. Los frutos de estas cactáceas muestran ciertos atributos morfológicos que favorecen la quiropterocoria y la ornitocoria. En estos ambientes, se ha detectado la presencia de dos especies de murciélagos glosófaginos (*Glossophaga longirostris* y *Leptonycteris curasoae*). Estos juegan el doble papel de polinizadores y dispersores de semillas de estas cactáceas. La primera especie tiene poblaciones residentes en algunos de estos ambientes. La segunda parece ser un visitante estacional de los mismos aunque en ocasiones está ausente. En relación a las aves asociadas al consumo de frutos de cactáceas se sabe que existen al menos dos grupos funcionales en la comunidad: los dispersores y los depredadores de semillas. Con base en la información disponible para uno de estos ambientes, se realizó una comparación de los papeles de ambos grupos en los procesos reproductivos de las cactáceas. Con respecto a la dispersión de las semillas, este papel parece estar compartido por las aves y los murciélagos. Usamos el enclave de Lagunillas (Venezuela) como estudio de caso para comparar las comunidades de aves asociadas a dos especies de cactáceas columnares que presentan frutos con diferente color. Así mismo, se describen y comparan cuatro posibles configuraciones del sistema murciélago-cactáceas en distintas enclaves áridos andinos.

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