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Survey of Columnar Cacti and Carrying Capacity for Nectar-Feeding Bats on Curaçao

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Abstract: We estimated the population sizes of the three species of columnar cacti that grow on the island of Curaçao using ground and aerial transects, and we examined the island's carrying capacity for two species of nectar-feeding bats that depend on nectar from the flowers of these cacti. We calculated carrying capacity based on the daily availability of mature flowers between January and December 1993 and the field energy requirements of bats as estimated from an equation for eutherian mammals (low estimate) and one for passerine birds (high estimate) based on body mass. Additional energy requirements of pregnancy and lactation were taken into account. We estimated that 461,172 columnar cacti were present on Curaçao (38% *Subpilocereus repandus*, 51% *Stenocereus griseus*, and 11% *Pilosocereus lanuginosus*). May through September are the critical months when bats rely most heavily on cactus for food. July 1993 was a bottleneck with the smallest number of mature flowers per day. July and August were months of greatest energy demand because females were lactating. We estimate that the carrying capacity for *Glossophaga longirostris* in July, when the bat (*Leptonycteris curasoae*) population was 900, was near 1200, an estimate that fits the observed population size of nectar-feeding bats on the island. We suggest that the extensive removal of native vegetation occurring on Curaçao be strictly regulated because further destruction of the cacti will result in a decrease and potential loss of the already low populations of nectar-feeding bats.

Estudio de los Cactus Columnares y la Capacidad de Carga de los Murciélagos Nectarívoros de Curaçao

Resumen: Estimamos el tamaño de la población de tres especies de cactáceas columnares que crecen en la isla de Curaçao, usando transectos de suelo y aéreos, también examinamos la capacidad de carga de la isla para dos especies de murciélagos nectarívoros que dependen del néctar de las flores de estas cactáceas. Calculamos la capacidad de carga basándonos en la disponibilidad diaria de las flores maduras entre enero y diciembre de 1993 y requerimientos de energía en el campo de los murciélagos, estimados con una ecuación para los mamíferos euterianos (estimación baja) y otra para los pájaros paserinos (estimación alta) basadas en la masa corporal. Requerimientos adicionales de energía atribuidos al embarazo y a la lactación fueron considerados. Estimamos que 461,172 cactáceas columnares estuvieron presentes en Curaçao (38% *Subpilocereus repandus*, 51% *Stenocereus griseus*, and 11% *Pilosocereus lanuginosus*). De mayo a septiembre son meses críticos durante los cuales los murciélagos dependen fuertemente de los recursos de las cactáceas como comida; julio 1993 representó un periodo de limitación con el número más pequeño de flores maduras por día. Julio y agosto fueron los meses de demanda de energía más grande a causa de la lactación de las hembras. Estimamos que la capacidad de carga de *Glossophaga longirostris* en julio, era de 2000, cuando la población de *Leptonycteris curasoae* era de 900 murciélagos, una estimación que corresponde al tamaño de la población de murciélagos nectarívoros observado en la isla. Sugerimos que la extensa eliminación de la vegetación nativa que existe actualmente en Curaçao sea controlada estrictamente, pues la destrucción adicional de las cactáceas resultará en una reducción y pérdida potencial de la ya escasa población de murciélagos nectarívoros.

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Introduction

Three species of columnar cacti occur on Curaçao, Netherlands Antilles: *Stenocereus griseus* (datu), *Subpilocereus repandus* (kadushi), and *Pilosocereus lanuginosus* (kadushi di pushi). These cacti are considered "fever-giving" weeds by some of the local people. In most development projects, consequently, the columnar cacti, as well as the other native vegetation, are systematically removed. During the dry season these cacti produce large numbers of flowers and fruits (Nassar 1991; Petit 1995a) that support several species of vertebrate nectar-feeders, frugivores, and omnivores. Most cactus fruits and seeds result from pollination by two nectar-feeding bats: *Leptonycteris curasoae curasoae* and *Glossophaga longirostris elongata* (Chiroptera: Phyllostomidae) (Petit 1995b). The mutualism between bats and cacti is strong on Curaçao because bats also depend on cacti (Petit 1996a). They feed on the nectar of flowers that open at night (one night per flower) and occasionally on fruits, dispersing their seeds. All bat species of Curaçao are threatened (Petit 1996b), and there is concern about the impact of further urban development on the island ecosystem, in particular the maintenance of a viable population of nectar-feeding bats and other animal species that depend on the cacti.

The most important threat to the bat-cactus mutualism seems to be unregulated land development and concurrent removal of all native vegetation (the Blawbaai resort project, housing projects of Tera Corá, etc.). The destruction of cacti is becoming alarming, and the carrying capacity for animals dependent on their flowers and fruits may be decreasing to a nonreversible level. Unfortunately, there are no records of cactus population sizes for Curaçao. We present the first survey of the columnar cacti of Curaçao and provide an estimate of their monthly carrying capacity for nectar-feeding bats. We used ground transects to determine the relative abundance of each cactus species, and we used an aerial survey to estimate the total number of cacti on the island. Estimates of carrying capacity depend on various assumptions (mentioned below) that, we hope, will be replaced by data as new research increases our knowledge of cactus resource availability and the daily energy requirements of nectar-feeding bats. To our knowledge, this is the first study of carrying capacity for nectar-feeding bats.

Methods

Study Site and Ground and Aerial Surveys

Curaçao is a semiarid island (average annual rainfall is 560 mm; Meteorological Center of Mahuma, personal communication) 70 km off the northern coast of Vene-

zuela with a surface area of 44,400 ha. The economy of Curaçao is based on an oil refinery and tourism.

In August 1993, 18 transect locations were chosen randomly on the map of Curaçao. Each transect was 100 m long and 10 m wide, for a total area of 18,000 m². All columnar cacti greater than 1.2 m tall and with at least two branches were identified and counted within the transects. We determined the proportion of each species for all transects and assumed that these data represented species' distributions for the entire island.

Ten sets of four aerial photographs were taken manually and systematically. A constant altitude (300 m) was maintained throughout the flight after take-off and before landing. Each of the 10 sets of photographs covered land areas ranging from 370,000 to 600,000 m² (calculated from the average of two ground measurements between known points; 1 cm² of picture of land = 469.53 m² of actual land) for a total area of 467.13 ha, or 1.05% of the surface of the island. It is possible that topographic features and photographic distortion introduce some error into the calculations. Cacti are conspicuous elements of the vegetation of Curaçao and thus were clearly visible in most photographs. The cacti appearing in one of the 10 areas photographed were recounted by walking through the area, and the same number of trees was found. We estimated the number of columnar cacti (all species combined) present on the entire island from our aerial census.

Carrying Capacity of Columnar Cacti for Bats

The energy required for maintenance and flight by the two bat species (field metabolic rate, FMR) was calculated following Nagy's (1987) equations for eutherian mammals (kJ needed per individual per day = $3.35 \times \text{effective mass}^{0.813}$) as the lower estimate, and for passerine birds (kJ = $8.88 \times \text{effective mass}^{0.749}$) as the higher estimate. These two "bracket" values represent the limits between which the bats' energetic requirements are likely to fit because bats tend to have higher FMRs than terrestrial mammals and the FMR values may approach those of passerine birds (von Helversen & Reyer 1984; F. Bonaccorso, personal communication; T. Kunz, personal communication). For males of each species we defined "effective mass" as mean mass and for females as mean mass plus mass due to maternal investment during months of pregnancy and lactation (Petit 1995a). Females carry a fetus and spend increased amounts of energy in the last stages of pregnancy and when lactating (Kurta et al. 1990). During most of pregnancy the mass of a bat is reasonably accurately related to its energy requirement (T. Kunz, personal communication). We calculated the average mass of a pregnant female from the mean mass of nonpregnant females (26.0 g for *L. curasoae* and 12.7 g for *G. longirostris*; Petit 1995a) plus the maximum mass of a captured pregnant bat (40.5 g for *L.*

curasoe and 18.3 g for *G. longirostris*; personal observation), divided by two. This gave an average pregnant mass of 33.3 g for *L. curasoe* and 15.5 g for *G. longirostris*. If 80% of the females were pregnant in a given month (Petit 1995a) and 20% were nonreproductive, we calculated daily energy requirement for a representative individual of a population of that species for that month based on the mass of 40% pregnant females, 10% non-reproductive females, and 50% males (male:female ratio was assumed to be 1:1). During the months of lactation females were assumed to require 50% more energy than nonpregnant, nonlactating bats. Lactation may require up to twice as much energy as pregnancy in two species of insectivorous bats (Kurta et al. 1989; Kurta et al. 1990); our estimate is probably conservative. The daily energy requirement for a representative individual of a population where, for example, 75% of females were pregnant and 25% were lactating was thus calculated as 37.5% of a pregnant bat's requirement, 12.5% of a lactating bat's requirement, and 50% of a male's requirement. Few bats were captured each month (Petit 1995a), and the accuracy of the proportion of reproductive females could be improved with larger sample sizes.

Using flower availability and nectar output in each cactus species, we computed carrying capacity for each month for adult bats only. Twice every month we counted mature flowers in one plot of 50 *Stenocereus griseus*, one plot of 50 *Subpilocereus repandus*, and in an area with 33 *Pilosocereus lanuginosus* trees (see Petit 1995a for site description). Numbers obtained for *Pilosocereus lanuginosus* were converted to an estimate for 50 plants. Using cactus ratios obtained from the terrestrial census, we calculated the total number of flowers open per night in each species for each month.

Each flower opens for only one night, and when nectar is collected every two hours the median quantity of nectar produced per flower per night in *Stenocereus griseus* is 0.503 mL and that of *Subpilocereus repandus* is 0.560 mL (Petit & Freeman 1996). Continuous removal

is known to increase nectar availability in *Stenocereus griseus* (Petit 1995a), however, and we chose the higher value (0.560 mL) as the typical volume of nectar produced per flower of each species (nectar production by *Pilosocereus lanuginosus* flowers is unknown). Nassar (1991) found greater volumes of nectar produced by the same cactus species in Venezuela than what S. Petit and C. E. Freeman (1996) found on Curaçao; production may thus vary with season or location. Carrying capacity may need to be revised when more information on nectar secretion rates and energy contents becomes available for all species. The mean energy output from nectar per flower of *Subpilocereus repandus* per night is 2.78 kJ (Petit 1995a). This value was multiplied by the total estimated number of flowers open per night on the island to derive the total energy available per night from columnar cactus flowers.

Finally, the "minimum" (from data on passerine birds) and "maximum" (from data on eutherian mammals) daily carrying capacities of the columnar cactus flowers were computed for each month, using total available energy on the island per day and the daily energy requirement of a "representative" individual in that month:

$$E_{\text{cacti}} = N_{\text{Lepto}} \times E_{\text{Lepto}} + N_{\text{Glosso}} \times E_{\text{Glosso}},$$

where E_{cacti} is the total energy from cactus nectar on the island (assuming all of it can be used by bats), E_{Lepto} and E_{Glosso} are the corrected values for mean FMR of the species, and N_{Lepto} and N_{Glosso} are the numbers of bats of each species that can be supported (Lepto = *L. curasoe* and Glosso = *G. longirostris*).

Because the size of the *L. curasoe* population is known (800–1000; Petit 1996b) with more accuracy than the size of the *G. longirostris* population, we calculated the carrying capacity of *G. longirostris* when the population size of *L. curasoe* is 900. We also calculated the number of bats of each species that can be supported when the other species is absent. Most of the bats' diet is composed of columnar cactus pollen and nectar, espe-

Table 1. Daily energy requirements of *L. curasoe* based on Nagy's (1987) equations for eutherian mammals and passerine birds.

Month	Lower (eutherian) estimates			Higher (passerine) estimates		
	kJ/d, ♂	kJ/d, ♀	(♂ + ♀)/2	kJ/d, ♂	kJ/d, ♀	(♂ + ♀)/2
January	51.4	47.3	49.3	109.8	101.8	105.8
February	51.4	47.3	49.3	109.8	101.8	105.8
March	51.4	57.8	54.6	109.8	122.5	116.2
April	51.4	57.8	54.6	109.8	122.5	116.2
May	51.4	57.8	54.6	109.8	122.5	116.2
June	51.4	61.1	56.2	109.8	130.1	119.9
July	51.4	71.0	61.2	109.8	152.7	131.3
August	51.4	59.1	55.3	109.8	127.3	118.6
September	51.4	47.3	49.3	109.8	101.8	105.8
October	51.4	47.3	49.3	109.8	101.8	105.8
November	51.4	47.3	49.3	109.8	101.8	105.8
December	51.4	47.3	49.3	109.8	101.8	105.8

Table 2. Daily energy requirements of *G. longirostris* based on Nagy's (1987) equations for eutherian mammals and passerine birds.

Month	Lower (eutherian) estimates			Higher (passerine) estimates		
	kJ/d, ♂	kJ/d, ♀	(♂ + ♀)/2	kJ/d, ♂	kJ/d, ♀	(♂ + ♀)/2
January	26.2	26.4	26.3	59.0	59.4	59.2
February	26.2	26.4	26.3	59.0	59.4	59.2
March	26.2	26.4	26.3	59.0	59.4	59.2
April	26.2	26.4	26.3	59.0	59.4	59.2
May	26.2	30.1	28.1	59.0	67.1	63.1
June	26.2	31.0	28.6	59.0	69.0	64.0
July	26.2	37.4	31.8	59.0	84.1	71.6
August	26.2	39.6	32.9	59.0	89.2	74.1
September	26.2	33.0	29.6	59.0	74.3	66.7
October	26.2	26.4	26.3	59.0	59.4	59.2
November	26.2	26.4	26.3	59.0	59.4	59.2
December	26.2	26.4	26.3	59.0	59.4	59.2

cially from May through September, when few other plants are flowering on Curaçao (Petit 1995a). These months, for which carrying capacity was calculated, are thus referred to as critical months. Based on the carrying capacity estimated for critical months, we were also able to determine how many cactus trees were required to support each individual of *L. curasoeae*. Fruits do not compose a major part of a bat's diet (Petit 1996a), probably because of competition from birds. Most fruit samples in the feces of bats captured in 1993 were found after September (S. Petit, personal observation). Nectar from columnar cacti is thus the energetic reward most accurately associated with the carrying capacity of nectar-feeding bats.

Results

A total of 43 *Subpilocereus repandus*, 58 *Stenocereus griseus*, and 12 *Pilosocereus lanuginosus* was counted in ground transects. These yield proportions of 38.1% *S. repandus*, 51.3% *S. griseus*, and 10.6% *P. lanuginosus*, which are assumed to represent the relative abundances of these columnar cacti on Curaçao.

In the aerial survey 4852 columnar cacti were counted in 467.13 ha, for an average of 10.4 cacti per ha. We estimated the total number of columnar cacti present on the island to be 461,172, assuming that the aerial survey was representative of the overall cactus density.

The energy requirements of the bats (Tables 1 and 2)

Table 3. Average number of mature flowers per day of each month for 50 trees of each cactus species.*

Flowers/species/day												
Months												
Species	January	February	March	April	May	June	July	August	September	October	November	December
SR	0	0	1.0	4.0	11.5	7.0	11.5	14.0	18.0	6.0	7.5	5.0
SG	0	2.0	14.0	14.0	26.5	13.0	7.0	6.5	13.0	2.5	7.0	0
PL	0	0	0	0	0	0	0	0	6.1	2.3	14.4	0.8
Weighted flowers/day												
Months												
Species	January	February	March	April	May	June	July	August	September	October	November	December
SR	0	0	0.4	1.5	4.4	2.7	4.4	5.3	6.8	2.3	2.9	1.9
SG	0	1.0	7.2	7.2	13.6	6.7	3.6	3.3	6.7	1.3	3.6	0
PL	0	0	0	0	0	0	0	0	0.6	0.2	1.5	0.1
Total	0	1.0	7.6	8.7	18.0	9.4	8.0	8.6	14.1	3.8	8.0	2.0
Total flowers												
Months												
	January	February	March	April	May	June	July	August	September	October	November	December
	0	9472	69,794	80,318	165,819	86,119	73,502	79,903	130,659	35,114	73,566	18,290

*Numbers weighted based on 38.1% *S. repandus* (SR), 51.3% *S. griseus* (SG), and 10.6% *P. lanuginosus* (PL), and estimation of total number of mature flowers present on one day of each month on Curaçao.

Table 4. Daily energy available from columnar cactus nectar on Curaçao and carrying capacity for each bat species (in the absence of the other) based on energetic requirements from Nagy's (1987) equations.

Month	Total kJ/d	No. of <i>L. curasoae</i> *		No. of <i>G. longirostris</i> *	
		Passerine FMR	Eutherian FMR	Passerine FMR	Eutherian FMR
January	0	0	0	0	0
February	26333.5	247.9	533.7	443.0	1002.3
March	194026.6	1670.3	3553.7	3276.4	7385.0
April	223283.1	1922.2	4089.6	3770.5	8498.6
May	460976.6	3968.4	8443.1	7310.4	16385.0
June	239411.4	1996.0	4256.9	3739.7	8371.3
July	204334.3	1556.5	3337.1	2855.2	6425.4
August	222129.3	1873.7	4020.0	2998.5	6758.0
September	363232.5	3432.4	7361.7	5449.9	12283.4
October	97615.9	922.4	1978.4	1648.4	3715.4
November	204513.8	1932.6	4144.9	3453.5	7784.2
December	50846.4	480.5	1030.5	858.6	1935.3

*FMR = field metabolic rate.

are obviously higher in *L. curasoae* than in *G. longirostris* because of the greater mass of *L. curasoae*. "Eutherian" monthly estimates ranged from 49.3 to 61.2 kJ per day in *L. curasoae* and from 26.3 to 32.9 kJ per day in *G. longirostris*. When the equation for passerine birds (Nagy 1987) is used, the estimate derived from the eutherian mammals equation is approximately doubled (e.g., *L. curasoae* FMR for a female in January increases from 49.3 kJ per day to 105.8 kJ per day). Monthly estimates ranged from 105.8 to 131.3 kJ per day for *L. curasoae* and 59.2 to 74.1 kJ per day in *G. longirostris*.

The contribution of each cactus species to the energy pool available from mature flowers in uneven (Table 3); flower production in *P. lanuginosus* was low compared to the other two species. Consumption of cactus flower nectar was near zero in January and greatest from April through September, a period that corresponds to peak reproductive activity in female bats (Petit 1995a). We calculated total energy available from cactus nectar using a value of 2.78 kJ per flower and were able to determine the carrying capacity for each bat species based on the information in Tables 1 and 2 (Table 4). During the critical months when few flowers other than those of cacti are available to bats (May through September), carrying

capacity ranged from 1556–3337 in July to 3968–8443 in May for *L. curasoae* and 2855–6425 in July to 7310–16,385 in May for *G. longirostris*. We calculated the number of *G. longirostris* that can be supported with the daily energy required for one individual *L. curasoae* for each month and found a ratio of about 1 *L. curasoae* to 1.8–1.9 *G. longirostris*. The carrying capacity for *G. longirostris* when the population of *L. curasoae* is 900 ranged from 1204–4692 to 5652–14,642 during the five critical months (Table 5). Within this critical period, July was the bottleneck; a population of only 1200 to 4700 *G. longirostris* could be supported. In July one individual of *L. curasoae* needed between 139 and 297 columnar cactus trees per day to satisfy its daily energetic requirement with nectar (Table 6).

Discussion

On Curaçao, columnar cacti are not as abundant as one might expect from their conspicuousness. Fewer than 500,000 of these cacti occur, with the population size for *Subpilocereus repandus* (about 175,000) being equivalent to the human population on the island. De-

Table 5. Carrying capacity of cactus nectar for *G. longirostris* when the population size of *L. curasoae* is 900 for each "critical" month, based on energy requirements calculated with the equation for passerine birds and for eutherian mammals.

Month	Passerine	Eutherian
May	5652	14,642
June	2054	6603
July	1204	4692
August	1568	5245
September	4022	10,785

Table 6. Number of cactus trees needed to support one *L. curasoae* individual each day, from May through July, based on energy requirements calculated with the equations for passerine birds and eutherian mammals.

Month	Eutherian	Passerine
May	55	117
June	109	232
July	139	297
August	115	247
September	63	135

veloped areas are generally free of cacti, and we note that gardens often contained exotic plants that require watering, despite the high price of water on Curaçao. Because of the relatively low density of cacti on the island, we recommend the initiation of an educational program on the value of the native flora and fauna, the establishment of regular cactus census, and the elaboration of laws designed to prevent excessive removal of native flora and fauna.

The accuracy of our estimation of carrying capacity could be improved by increasing the frequency of censuses or the number of areas surveyed. Also, the caloric content of pollen is unknown for our cacti, but pollen could contribute significantly to the energy needs of bats. Twenty entomophilous plant species in a Greek Mediterranean ecosystem contained an average of 24 kJ per gram of pollen (Petanidou & Vokou 1990; see also Colin & Jones 1980). Law (1992a) suggests, however, that energy from nectar and fruits is the limiting resource for the Australian blossom bat *Synconycteris australis* and that pollen is primarily a source of nitrogen, nonlimiting when the bat forages on nectar and later licks the pollen off its fur.

Pollen is likely to be critical in providing essential amino acids to bats (Howell 1974) on Curaçao, because of its high digestibility and high protein content (Law 1992b). Pollen may be an important energetic reward, but two aspects of our model may compensate for its omission: a conservative energy requirement was used for lactating bats, and resource scarcity due to unavailability or competition may also cause an increase in daily energy requirements that is not accounted for in the model. In July one individual of *L. curasoae* needs between 130 and 300 cacti to satisfy its daily energetic requirement and may have to cover extensive terrain (at least 12.5 ha at 10.4 cacti per ha) to consume enough nectar and pollen. The scarcer the resources, the more energy is needed to forage; we expect this function to have a strong impact on carrying capacity.

The limiting carrying capacity that we found for July 1993 (900 *L. curasoae* and 1200–4700 *G. longirostris*) fits the observed bat populations. Recent work by Y. Winter and O. von Helversen (Personal communication) shows that all nectar-feeding bat species ($n = 6$) for which they calculated FMR are energetically similar to passerine birds. The expected population size of *G. longirostris*, difficult to estimate from direct counts because the species' roosting behavior, should thus be closer to 1200 than to 4700. Petit (1996b) counted between 800 and 1000 individuals of *L. curasoae* in two censuses in 1992–1993, and 1350 to 1600 *G. longirostris*. The number of individuals of the latter species, however, was thought to be an underestimate. Individuals of *G. longirostris* may have been overlooked because they live in small colonies in cracks, open caves, and buildings.

It is possible that a limiting carrying capacity occurs at

other times of the year. For example, nectarivorous bats feed heavily on *Ceiba pentandra* flowers at the beginning of the dry season, but this tree flowers only once every 2 years on the island, and it did flower in 1993 (Petit 1995a). Once every 2 years, the glossophagine bat population may thus be limited by lack of food resources in January and February. Nevertheless, bats depend on cacti for their reproductive success. It may be also that other nutrients besides carbohydrates and proteins (e.g., calcium; Porter 1978) limit bat reproduction.

If we consider that one individual of *L. curasoae* requires 200 cactus trees per day for meeting its energy needs and that approximately 200 cactus trees occur on 1 ha of "cactus land" (from *S. repandus* plot in Petit 1995a), we may infer that 1 ha supports one *L. curasoae*. A housing or commercial development project involving the clearing of 800 ha of cactus land would thus be sufficient to destroy the resources needed to maintain the *L. curasoae* population of the island.

In effect, a severe decrease in bat population size may be expected from a reduction in the cactus population. In addition, a negative feedback from a decreasing population of *L. curasoae* is likely to occur because this species depends on the large size of its colonies to maintain a positive energy budget (Arends et al. 1995). *L. curasoae* is found in warm, poorly-ventilated caves, where large numbers of individuals congregate tightly to keep warm to avoid spending energy on the maintenance of body temperature (Arends et al. 1995). Only two such chambers are populated by *L. curasoae* on Curaçao (Petit 1995a), and it is possible that 800 individuals may be close to the minimum physiological effective population size for this species on this island. *G. longirostris*, found in open, cooler caves than *L. curasoae*, may spend proportionately more energy than *L. curasoae* to maintain its body temperature.

It appears that the bat populations are at carrying capacity, or zero population growth, in July and August, when the females are lactating. This implies that females will be less successful in raising offspring than in a growing population because of the scarcity of energy resources and other nutrients during lactation (Freeland & Choquenot 1990). In addition, the two bat species may compete for nutritional resources at that time. Intraspecific competition is also likely. To maintain the nectarivorous bat populations, cacti must therefore be preserved. Columnar cacti are slow-growing plants, and recovery after removal may occur too late for the bat pollinators—and, consequently, for other animals that rely on the fruits from these trees during the dry season.

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