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Movements of Cave Bats in Southeastern Brazil, with Emphasis on the Population Ecology of the Common Vampire Bat, *Desmodus rotundus* (Chiroptera)[1]

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ABSTRACT

A mark-recapture study of cave bats was carried out in the Alto Vale do rio Ribeira, SE Brazil. The size of the colonies varied monthly, indicating the occurrence of frequent movements among caves and a low degree of roost fidelity for the commonest species: *Desmodus rotundus, Carollia perspicillata, Anoura caudifer, Artibeus fimbriatus.* Phyllostomines (*Trachops cirrhosus, Chrotopterus auritus*) and *Peropteryx macrotis* seem more sedentary, as suggested by their higher recapture rates. *D. rotundus* uses multiple roosts, mostly within relatively small areas, with a 2–3 km radius. These vampires move preferentially along valleys, males moving more than females. Frequency of movements is probably related to the availability of roosts and climate. The climate of the Alto Ribeira is subtropical, with cool nights during the "dry" season, when part of the vampire population (and other species as well) would migrate to warmer regions. Recapture rates and the estimated individual ranges are similar to those observed for this species in other regions. The minimum population density of *D. rotundus* varied monthly from one to 3.5 individuals per km^2. *Diphylla ecaudata* moves more frequently and probably has larger individual ranges than *D. rotundus,* possibly due to its higher feeding specialization.

RESUMO

A ecologia de populações de morcegos cavernícolas do Alto Vale do Ribeira, Sudeste do Brasil, foi estudada através do método de marcação e recaptura. Em geral, o tamanho das colônias de morcegos variou mensalmente, o que indica a ocorrência de movimentos frequentes entre cavernas e um baixo grau de fidelidade ao abrigo, ao menos nas espécies mais comuns: *Desmodus rotundus, Carollia perspicillata, Anoura caudifer, Artibeus fimbriatus.* Taxas superiores de recaptura sugerem que os morcegos Phyllostominae (*Trachops cirrhosus, Chrotopterus auritus*), assim como *Peropteryx macrotis,* são mais sedentários. *D. rotundus* utiliza abrigos múltiplos, em geral situados em uma área relativamente pequena, com 2 a 3 km de raio. Esses vampiros deslocam-se preferencialmente ao longo de vales, sendo que os machos movimentam-se mais que as fêmeas. A frequência de deslocamentos está provavelmente relacionada à disponibilidade de abrigos e ao clima. O clima do Alto Ribeira é sub-tropical, com noites frias durante a estação "seca," quando parte das populações de morcegos migraria para regiões mais quentes. As taxas de recaptura e a área de vida estimada para os vampiros comuns são similares às observadas em outras regiões estudadas. A densidade populacional mínima variou mensalmente entre um e 3.5 indivíduos por km^2. *Diphylla ecaudata,* por sua vez, desloca-se mais frequentemente que *D. rotundus,* apresentando uma área de vida maior.

Key words: bat roosting behavior; caves; Desmodus rotundus; *local migration; Neotropical bats; population ecology.*

Bats are ecologically flexible, and most species have large geographic distributions through which their biology may vary considerably. This is the case with the common vampire bat, *Desmodus rotundus,* a species interesting because it has such specialized feeding and economic importance. Detailed studies on *D. rotundus* are in general restricted to a few areas in Mexico, Trinidad, Costa Rica, Argentina, and southern Brazil. The few studies which included foraging area, movements, population size and density, showed apparently discordant results (Wimsatt 1969; Lopez-Forment *et al.* 1971; Young 1971; Burns & Crespo 1974; Turner 1975; Schmidt *et al.* 1978, 1971; Wilkinson 1988; Delpietro & La Mata 1989; Delpietro *et al.* 1992).

Data on roosting habits and foraging territories are scarce for rain forest species (Wilson 1992), and especially for populations using caves as shelter in the Neotropical region. Studies in some regions of Mexico and Cuba led to the conclusion that bat caves (eutrophic caves harboring large, stable colonies of bats) are largely representative of the tropics (Ginet & Decu 1977, Sbordoni 1980, Decu 1986). However, data gathered throughout Brazil showed

[1] Received 28 March 1994; revision accepted 23 November 1994.

TABLE 1. *Number of monthly captures (including recaptures) of* Desmodus rotundus *specimens in caves from Upper Ribeira Valley, SE Brazil. Blanks = no visit made.* N = *number of specimens captured for the first time (and marked).*

Cave	Dec	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	*N*
Betari	24	29	25	22	27	24	10	9	7	3	4	145
Alambari	1			1	1	4	5		1	0	2	9
Água Quente	6	10	4	1	1	1	3	0	0	4	3	30
Córrego Seco	3					7	0	1	0		3	10
Santana	4	2	1		10	1	10	5	3	4	2	27
Couto	8	0	2	1	1	0			0	0	0	12
Água Suja	5	0	1	1	1	10	4	1	0	0	0	20
Areias I		9		7		8		6				24
Areias II					1		6		0			6
Total	51	50	33	33	41	55	38	22	11	11	14	

that bat caves are actually an exception, usually restricted to areas with low density of caves. This is the case with sandstone caves, such as those in Pará and São Paulo States (Trajano & Moreira 1991, Campanhã & Fowler 1993). Brazilian limestone caves rarely present very large, stable colonies. On the contrary, the number of individuals and species observed in each visit is variable, suggesting the occurrence of frequent movements between roosts in the area (local movements, *sensu* Cockrum 1956) and/or seasonal, long-distance movements (migrations, *sensu* Cockrum). Movements inside caves ("itinerant colonies") are also frequently observed.

The cave bat community of a subtropical karstic region in southeastern Brazil was studied for two years (Trajano 1985). This area has many suitable roosts where bats may distribute in the absence of pressures for thermoregulatory or defensive aggregations. This paper presents the results of the mark-recapture study of *Desmodus rotundus,* the most common bat species in this karstic area, contributing to the knowledge of its population ecology. I also captured and marked other bats, thus having the opportunity to compare the movements of other common species, such as *Carollia perspicillata, Artibeus fimbriatus, Anoura caudifer,* and some Phyllostomines. This was the first long-term study on Brazilian cave bats.

STUDY AREA

The Alto Vale do rio Ribeira (Upper Ribeira Valley), mainly in Iporanga District, is a karstic area with a high concentration of limestone caves ranging from small shelters to large caves up to 5 km long and 250 m deep, many crossed by headwater streams. Up to now, about 200 caves were recorded in the cadaster of the Sociedade Brasileira de Espeleologia. Bats were seen at least occasionally in nearly all caves, but large stable colonies (more than some dozens of individuals) are restricted to five percent of these.

The region is situated in the transition between the Tropical Atlantic and Araucaria Forest domains (Ab'Saber 1977). The climate is subtropical humid, without a typical dry season. However, the precipitation is lower between May and September, to which I will refer as "dry season." The mean annual temperature is between 18°C and 19°C which is the temperature inside caves. This area represents one of the remaining forested areas in São Paulo State, mostly covered by perennial subtropical humid forest (Hueck 1972). Most of this region is included in a State Park, the Parque Estadual Turístico do Alto Ribeira (PETAR).

The preservation of the area was due, at least in part, to the karstic landscape hampering mechanized agriculture and pasture. During the study period, many local inhabitants practiced subsistence agriculture. Their livestock consisted of poultry, pigs, and horses; a few bovines were also available as a food source for vampire bats.

METHODS

The mark-recapture study was carried out between December 1979 and October 1980. After a 1-yr faunistic survey in 38 limestone caves and 2 abandoned mines in the Alto Vale do Ribeira, southeastern Brazil (Trajano 1985), ten caves were selected: Serra region—Alambari de Baixo (24°36′S, 48°40′W; 900 m long); Areias da Água Quente (24°34′S, 48°40′W; 340 m); Córrego Seco (24°33′S, 48°41′W; 80 m; flooded during rainy periods); Santana (24°32′S, 48°42′W; 5180 m); Morro Preto (24°31′S, 48°42′W; 830 m); Couto (idem; 470

m); and Água Suja (24°31′S, 48°42′W; 1300 m); Lageado region—Areias I (24°35′S, 48°42′W; 3260 m) and Areias II (idem; 1760 m); Betari region—Betari (24°35′S, 48°38′W; 100 m). These caves were visited once each month for bat capture using one mist net at or near the cave entrances (usually small), from half an hour before to three hours after complete darkness. They were periodically inspected in order to locate the colonies.

Vampire bats caught from January on were marked with 4.0 mm alloy bands on the forearm, and were also punch-marked; other common species received only punch-marking (see Bonaccorso & Smythe 1972). Only one out of 64 vampire bats captured at least once (see below) had flesh grown around the band because it was applied too tightly. I have no evidence of differential mortality caused by banding. Thus, I regard this method adequate for the present study.

The following set of data was recorded for each bat specimen: collecting site, date, and time; direction of the movement at the entrance (indicated by the mist net side where the bat was captured); weight and forearm length; sex and reproductive condition (see Trajano 1985 for ecological, reproductive, and morphological data). Common vampire, *D. rotundus,* population sizes were estimated by the Fisher-Ford method (Begon 1979).

RESULTS

Population ecology of *Desmodus rotundus*.—The numbers of monthly captures (including recaptures) are shown in Table 1; a few specimens which escaped before marking were included. No vampire bats were collected in the Morro Preto Cave during the study period, although this species was recorded there in the preliminary survey (Trajano 1985).

The number of captures varied monthly and from cave to cave. Half the total number of captures were done in a single cave, Betari Cave, the smallest and relatively isolated from the others (Fig. 1). At that time, the Betari Cave harbored the largest colony, even by the end of the study period, when the number of captures decreased. This fluctuation in the number of captures seemed to occur in an irregular way. However, a general trend towards a progressive decreasing in the number of vampires collected is visible (Table 1).

For all caves, the progressive lowering in the number of bats caught in mist nets may be partially explained by learning—bats seen avoiding the nets were more and more frequent, and many individuals could have been using other entrances for emergence. The consequences of collection disturbance were made clear in February, when I visited Betari Cave twice: 25 vampire bats were captured on 21 February (Table 1), but only 6 were caught two days later, although the population apparently remained the same. Several bats were seen turning round the nets or passing through a small lateral opening.

Nevertheless, inspection of Betari cave showed an actual population decline after May, with no evidence of bat mortality inside it. Although a slight increase was observed in October, this population never returned to the initial levels.

An additional tendency is observed for the set of the six Serra region caves, among which most movements occurred (see below): the total number of bats collected in these caves decreased during the warmest months (January to March), increased by the end of the rainy to the beginning of the dry season (April to June), and decreased again from July on, the lowest number of captures being recorded in August. As in the case of Betari cave, the population seemed to start recovering in October.

Areias I was the only cave where the number of captures remained relatively stable (Table 1). Collections made in 1993 resulted in similar numbers for *D. rotundus,* all the other bat species previously recorded in this cave (Trajano 1985) being also sampled (H. F. Santos & M. Maso, pers. comm.). These, and movement data (see below) indicated that Areias I Cave, although not distant from the other caves in straight line, bore a stable bat community, relatively isolated from the other ones.

No colony observed inside the caves remained at the same place during all the study period. Inspection of the caves showed that most colonies occupied a particular site for a few months, then moved away, followed in many instances by returning after a period of weeks, months, or even years (no seasonality was apparent in this pattern). Even in the Betari Cave, bats kept moving from one place to another. Examination of the bat guano piles shows this is a common phenomenon in the Upper Ribeira. The same is true for other bat species. These "itinerant colonies" are also observed in other karstic areas, such as Bonito region, Mato Grosso do Sul State, and Itacarambi region, north of Minas Gerais State (pers. obs.).

The occurrence of movements between the nine studied caves (Morro Preto excluded) was demonstrated through the mark-recapture program. Between January and October 1980, a total of 234 specimens were banded. Of these, 64 were recaptured at least once (recapture rate = 27.4%). The

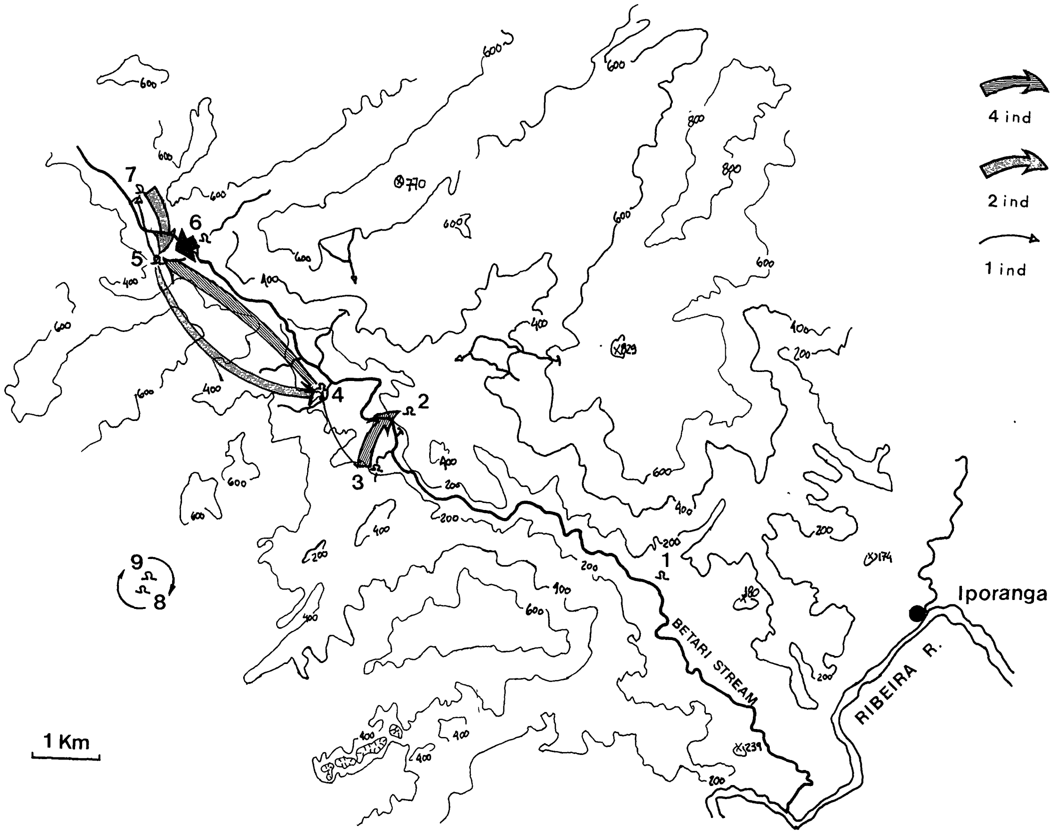

FIGURE 1. Location of the caves studied in the Upper Ribeira Valley, Southeastern Brazil, showing direction of *Desmodus rotundus* movements; arrow width indicates the number of individuals (IND) that moved between the caves. Caves: 1—Betari; 2—Alambari de Baixo; 3—Água Quente; 4—Córrego Seco; 5—Santana; 6—Couto; 7—Água Suja; 8—Areias I; 9—Areias II. "Long distance movements", to and from Betari Cave, were not represented.

total number of recaptures was 71, including 6 double and one triple recapture; thus, recapture rate per bat averaged 1.1. No band loss was recorded for individuals that received concomitant punch-marking.

Fifty-one vampire bats captured in December 1979 (when bands were not available) were punch-marked; some of them were recaptured in January, then received a band. These 51 captures were included in the study of movements, but not in the estimation of population size because such mark remains visible for 3–4 mo at maximum.

Monthly population sizes, estimated by the Fisher-Ford method, are shown in Table 2. Collection days in Betari cave were used for the calculations.

A day-to-day survival rate close to 1.0 was obtained, as expected for a long-lived, K-selected species. The unusually large population size estimated for February (Day 36) may be in part an artifact, as a result of absence of recaptures, possibly due to the small number of previously marked (and released) individuals; inspection of the caves did not indicate any sharp increase in the number of observed vampire bats in relation to the other months. Thus, estimates of minimum population size varied from 350+ individuals to 100 individuals (by the end of the study). It must be noted that half of this population concentrated in the Betari cave. The studied area has about 100 km^2, so the minimum vampire bat density varied seasonally from one to 3.5 individuals per km^2.

The numbers of recaptures of bats marked in the same and in other caves are shown in Table 3. At first view, three kinds of movements may be distinguished: "short-distance" movements between the Serra caves (Fig. 1); from Areias I to the neighbor Areias II and vice-versa (Fig. 1); and "long-

TABLE 2. Desmodus rotundus *population sizes in the Upper Ribeira Valley, Southeastern Brazil, estimated by the Fisher-Ford method.*

			Recaptured marks (day)									
Day	Capt	Rel	36	63	89	123	152	173	208	234	271	Population
1	50	49										
36	39	37	0									1435
63	33	31	6	1								243
89	41	41	2	7	4							210
123	55	55	3	3	4	2						353
152	38	37	2	1	2	3	5					295
173	22	22	2	0	4	2	4	2				182
208	11	10	0	0	0	2	3	2	0			154
234	11	10	0	0	0	0	1	2	2	0		179
271	14	14	0	0	0	4	1	1	1	0	2	107

Day-to-day survival rate = 0.99113.

distance" movements between Betari and Serra caves. No seasonality was observed in the frequency, direction, and distance of the displacements that were recorded during the study period.

Movements in the Serra area occurred preferentially between caves situated near each other, and along stream valleys (Fig. 1) that represent the easiest pathway in this hilly region. Infrequent movements across hills explain the semi-isolation of Areias I vampire bat population, because Lageado and Serra regions are in different watersheds separated by 600 m high mountains (see altitude of the cave entrances).

The present data suggest a relatively small range for *D. rotundus* in the Alto Ribeira, with a 2–3 km radius, where bats preferentially move. Although not exhibiting fidelity to individual roosting sites, these bats are relatively sedentary, and may shelter in the same area for a long time (see below).

Twenty-one marked vampire bats (32.8% of the total recaptured) were caught in more than one cave. Of these, 17 were males and 4 were females. Most males (13 individuals) had fully developed scrotal testes, being potentially reproductive; these itinerant males were recaptured in all seasons. The four females were pregnant and/or lactating both at the capture and the recapture times.

Individuals banded for this study have since been observed in the caves of Alto Ribeira. The last observation was in June 1991: an individual marked in 10 June 1980 in Água Quente cave and recaptured two days later in Alambari de Baixo cave was collected again in Água Quente after a decade. At the time it was banded, this vampire bat was a fully grown male no less than one year old; hence, it was at least 12 years old when recaptured. This is not a record for the species (Lord *et al.* 1976), but confirms its high longevity in subtropical SE Brazil. These data demonstrate that vampire bats may remain in the same area and use the same roosts for several years (see Delpietro *et al.* 1992).

MOVEMENTS OF *DIPHYLLA ECAUDATA*.—*D. ecaudata* is a much less abundant vampire bat than *D. rotundus*, and the number of specimens captured did not allow an extensive population study. Never-

TABLE 3. *Number of recaptures of* Desmodus rotundus *specimens according to the sites of marking and recapture.*

	Recapture site								
Marking site	Betari	Alambari	Água Quente	Cór. Seco	Santana	Couto	Água Suja	Areias I	Areias II
Betari	38	2	1	1			1		
Alambari		1		1					
Água Quente		4	2	1					
Córrego Seco	1				4				
Santana	1			2	8		1		
Couto					2				
Água Suja					2				
Areias I								5	1
Areias II								1	

TABLE 4. *Number of monthly captures (including recaptures) of* Carollia perspicillata *specimens in caves from Upper Ribeira Valley, SE Brazil.*

Cave	Dec	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct
Betari	0	0	2	1	0	1	0	0	1	0	1
Alambari	0	x	x	1	0	1	1	x	1	0	0
Água Quente	0	0	0	0	0	1	2	0	0	0	0
Córrego Seco	0	x	x	x	x	3	1	1	1	x	0
Santana	0	0	1	x	0	1	1	0	0	0	2
Couto	1	0	1	8	0	1	x	x	1	0	0
Água Suja	1	0	3	3	1	3	0	0	0	0	0
Areias I	x	0	x	1	x	1	x	1	x	x	x
Areias II	x	x	x	x	1	x	0	x	0	x	x
Total	2	0	7	14	12	5	2	4	0	3	14

theless, some data are presented here for comparison with *D. rotundus.*

Thirteen *D. ecaudata* specimens were banded, of which seven were recaptured at least once, multiple recaptures being frequent (in parentheses, time interval between captures): Betari–Água Quente (3 mo); Água Quente–Água Quente (1 mo)–Água Quente (1 mo); Couto–Santana (4.5 mo)–Água Quente (2 mo)–Água Quente (1 mo); Betari–Betari (1 mo)–Areias I (3.5 mo); Areias II–Areias I (2.5 mo); Santana–Córrego Seco (1 mo); Santana–Santana (2 mo). The high recapture rate, when compared to that of *D. rotundus,* may be due to a very small population size and/or to a greater susceptibility to catching.

In the Alto Ribeira, *D. ecaudata* moves more frequently than *D. rotundus,* and seems to have a larger range. A possible explanation for this difference lies in the feeding habits of this species. *D. rotundus* is more generalist and efficient, attacking a larger variety of mammals and birds (Greenhall 1988). *D. ecaudata* is specialized on birds and frequently kills its prey (Uieda 1994), probably requiring a larger area to feed.

Movements of non-Desmodontinae bats.—The numbers of monthly captures in each cave for the other bat species also varied in time and space, and *Carollia perspicillata* was selected to illustrate this trend (Table 4). Relatively stable colonies were rare: *Artibeus fimbriatus* in Alambari de Baixo Cave, *Lonchorhina aurita* in Água Suja Cave. It must be noted that all the *Artibeus* specimens were previously identified as *A. lituratus* (Trajano 1985). However, most are actually *A. fimbriatus. A. lituratus* seems to be an occasional bat in the Alto Ribeira caves, occurring in small caves, such as Betari and Córrego Seco.

Recapture data are available for the following bat species (in decreasing order of relative abundance in the Alto Ribeira—Trajano 1985): *C. perspicillata, A. fimbriatus, Peropteryx macrotis, Chrotopterus auritus, Trachops cirrhosus,* and *L. aurita.*

Punch-marking used in these bats was visible for no longer than 3–4 mo. Since the study covered 10 mo, marks were lost, and the observed recapture rates correspond to minimum rates: *T. cirrhosus* 23.08 percent; *C. auritus* 14.29 percent; *P. macrotis* 12.50 percent; *L. aurita* 9.52 percent; *A. fimbriatus* 7.94 percent; *C. perspicillata* 6.12 percent.

All these recaptures were done in the same cave where the bats were marked, except for one *L. aurita* specimen, captured in Água Suja Cave and recaptured three months later in Couto Cave.

Based on the comparison of recapture rates, stability of colonies (measured by the monthly number of captures), and observation of the position of the colonies inside the caves, these species may be ordered according to their degree of sedentariness. High recapture rates associated with the regular presence in certain caves indicate sedentariness.

A. caudifer, C. perspicillata, and *A. fimbriatus,* in this order, are the most nomadic, frequently moving between roosts. *A. caudifer* individuals, for instance, although more common than those of *P. macrotis* and the Phyllostomines, were not recaptured, a fact indicating a great degree of nomadism. *A. fimbriatus* is the least nomadic among these three species, especially considering its large size (large-sized species tend to be more nomadic than small ones, according to Fleming *et al.* 1972), and the regular occupation of Alambari Cave. These three species move more frequently than *D. rotundus,* probably presenting a larger range. Movements inside caves ("itinerant colonies") were also observed, as in *D. rotundus.*

On the other hand, *T. cirrhosus, C. auritus,* and *P. macrotis* are more sedentary, tending to philopatry. The former inhabits few caves and forms large, stable colonies. *C. auritus* and *P. macrotis* are more evenly distributed and form small colonies. Isolated or small groups of individuals (not in contact) of *P. macrotis* were regularly seen in crevices at the entrance zone of certain caves as Morro Preto and Alambari. Groups of 2–6 *C. auritus* individuals were frequently observed closely packed hanging from the ceiling (see Sazima 1978), usually not far from the entrances of caves such as Betari and Água Quente.

DISCUSSION

Twenty-five bat species were recorded between 1978 and 1980 in Alto Ribeira caves, showing a diversity comparable to that of other Neotropical communities (Trajano 1985). From that time on, only one species was added: *Vampyressa pusilla,* collected in the Água Quente Cave. Twenty species were recorded in a recent long-term study of the bat community from 20 caves in Brasília region, Central Brazil (Bredt *et al.* 1994); of these, 17 were also found in the Upper Ribeira, including *D. rotundus, D. ecaudata, C. perspicillata, A. caudifer, M. nigricans, P. macrotis, F. horrens,* and several Phyllostomines.

The following ecological scenario is envisaged for the Upper Ribeira Valley. Due to the great number of suitable roosts represented by large caves with a relatively stable and humid topoclimate, bats tend to distribute throughout them, in general forming small to medium-sized colonies. The individuals would use a certain number of caves within their residence area, establishing more or less stable associations. The number of caves used most frequently depends on the species: one in highly philopatric species (as seems to be *T. cirrhosus*) to several (as probably in *A. caudifer* and *C. perspicillata*), *D. rotundus* being intermediate in this aspect. A given species will use some roosts on a more or less regular basis and use others sporadically. Hence, the composition of the bat assemblage in each cave is not fixed: different species may appear in different seasons, in addition to those inhabiting such caves during most of the year.

Seasonal decreases in the total number of bats captured in the studied caves may be due to dispersal through the available roosts within the area, including other caves and vegetation (local movements), or to migration to other regions. In the case of *D. rotundus,* the observed pattern may be interpreted in relation to climate. Dispersion within the studied area may occur during the warmest months (January to March), when the number of favorable roosts is relatively greater because it includes small roosts (small caves, crevices, hollow trees), whose climate is not buffered. As it becomes cooler (April to June), the bats concentrate in larger caves, with a more stable topoclimate. However, the epigean temperature at night, when these animals are foraging, may drop to a few degrees above 0°C during the coolest months (June to August) and, due to energetic constraints (McNab 1973), many vampire bats would migrate to warmer regions, probably near the coast. It is possible that, as observed by Turner (1975) in Costa Rica, vampire access to prey diminishes in the cooler nights, when these prey group closely for sleeping. Thus, in addition to nightly temperatures, a lowered food availability during the winter may compel vampire bats to migrate from the Alto Ribeira.

Local migrations in glossophagines such as *Lonchophylla* spp., with seasonal occupation of some cave roosts, were interpreted as responses to local food availability (fluctuations in flower abundance) in these relatively specialized bats (Sazima *et al.* 1989). The same may be true for *Anoura caudifer* and other glossophagines from the Upper Ribeira.

Another factor involved in bat movements is the number of available caves at a given area (cave density). The Betari Cave, although one of the smallest among the studied sites, had by far the largest and most stable *D. rotundus* colony. It is a relatively isolated cave, situated outside the areas where caves concentrate in the Alto Ribeira (Fig. 1). Livestock, including cattle, is more abundant near the town of Iporanga, where Betari is located. Probably, as there are more prey nearby, the vampires tend to remain in the area and concentrate in the few available roosts.

This opportunistic behavior may be an explanation for the fact that Brazilian sandstone caves in general harbor large bat colonies (Trajano 1985, 1987). For a given area, sandstone caves are usually much less abundant than the limestone ones. Moreover, the less irregular landscape in sandstone regions is more favorable to extensive cattle raising and agriculture. In this situation, vampire bats seem to show a high degree of roost fidelity.

In conclusion, in a karstic area with high density of favorable roosts, *D. rotundus* does not show fidelity to a particular cave. However, vampire bats seem to move preferentially between a set of caves situated in a relatively small area, which function as a unit to which the bats show a certain degree of fidelity.

Several other authors mention the use of multiple roosts by *D. rotundus* (*e.g.*, Wilkinson 1985, 1988; Turner 1975; Wimsatt 1969). Wimsatt (*op. cit.*), for instance, found a high degree of turnover in colonies inhabiting certain roosting sites in Mexico, which the individuals shifted in a daily and perhaps opportunistic basis; these colonies would be "temporarily associated members of a larger, mobile population." This seems to be in disagreement with Wilkinson (1985), who showed that females may form stable associations, although Wimsatt had not analyzed the sexes separately.

Wilkinson (1985) recorded that many vampire bats visited more than one roost every night, and that females visited more roosts per night than males. In the present study, however, there were more males (63%) entering the caves than females, suggesting that every night they visit more or at least the same number of roosts as females. As well, in the Alto Ribeira male vampire bats moved more frequently between diurnal roosts than the female ones, contrary to that observed by Wilkinson (*op. cit.*) in Costa Rica.

According to Wilkinson (1985, 1988), radiotracking data did not support the hypothesis of movements among roosts to minimize the distance between roost and prey, as proposed by Turner (1975) and others. Based on his observations of significant associations between adult females (but not between males), Wilkinson suggested that females may fly extra distances to roost with other particular females in order to facilitate food sharing. However, the reason why some females change their roosts, being followed by their associates, remains obscure. I think it is possible that these females were saving energy, returning to the roost nearest to the previous night's foraging center.

The hypothesis of minimization of foraging distances is not implausible for part of *D. rotundus* movements in the Alto Ribeira. It might explain, for instance, the four female movements recorded. These females, being pregnant and/or lactating, could be in a critical energetic situation. However, it does not explain why males move more than females. A possible complementary hypothesis is the occurrence of male movements to warrant access to a higher number of females, as suggested by Wilkinson (1988).

Economy of flight energy also explains the relatively small foraging area observed for this species in different studied regions (Fleming *et al.* 1972, Schmidt *et al.* 1971, Burns & Crespo 1974). Turner (1975) hypothesized a range consisting of a band about 2 km on either side of and along the rivers. Preferential movements of vampire bats along river valleys was cited by Taddei *et al.* (1991) for the State of São Paulo and corroborated in the present study.

When large and roughly comparable samples of vampire bats (a few hundred specimens) have been banded, recapture rates observed in different regions were similar: 24.7 percent in Mexico (Schmidt *et al.* 1971); 20.2 percent in Costa Rica and Panamá (Fleming *et al.* 1972); 28.3 percent in Costa Rica (Turner 1975); 22.4 percent in southeastern Brazil (Campanhã & Fowler 1993); 27.4 percent in the present study. Recapture rates seem to be related to the individual range (LaVal 1970, Fleming *et al.* 1972). Thus, such close values support the idea that different populations of *D. rotundus* consistently have small ranges. This may be due to the same energetic constraints throughout the distributional area of this species.

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