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ECOLOGY OF BAT GUANO ARTHROPOD COMMUNITIES IN A BRAZILIAN DRY CAVE

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Resumo. Várias características físicas, químicas e espaciais de depósitos de guano (distância da entrada, área dos depósitos, pH e porcentagem de matéria orgânica) foram analisadas com relação à riqueza e diversidade das comunidades de artrópodos associadas a estes depósitos na gruta da Lavoura, Matozinhos, Minas Gerais, Brasil. Foram coletados um total de 504 indivíduos de 51 morfoespécies pertencentes a 41 famílias das ordens Araneida, Pseudoscorpionida, Acarina, Isopoda, Collembola, Ensifera, Psocoptera, Thysanoptera, Heteroptera, Coleoptera, Lepidoptera, Diptera e Hymenoptera. A porcentagem de matéria orgânica e a área foram as variáveis que mais influenciaram as comunidades de guano nesta caverna, mesmo tal efeito tendo mostrado-se moderado. A competição parece não ser a principal força estruturadora destas comunidades, sendo a predação, aparentemente mais determinante para a estrutura destas comunidades.

Abstract. Several physical, chemical and spatial traits of guano deposits (distance from the cave entrance, area of the deposits, pH, and percentage of organic matter) were analyzed with respect to the richness and diversity of the arthropod communities associated with these deposits in Lavoura Cave, Matozinhos, Minas Gerais, Brazil. We collected 504 individuals in 51 morphospecies pertaining to 41 families of Araneida, Pseudoscorpionida, Acarina, Isopoda, Collembola, Ensifera, Psocoptera, Thysanoptera, Heteroptera, Coleoptera, Lepidoptera, Diptera and Hymenoptera. Organic content and deposits area were the most important variables found to influence guano communities in this cave, though their effects were moderate. Competition does not seem to be a structuring force for these detritivore-based guano communities, as food does not appear to be limiting, and predation is probably the most important factor. *Accepted 23 August 2000.*

Key words: Cave, invertebrates, guano, Neotropics, communities.

INTRODUCTION

The cave environment is characterized by high stability and the permanent lack of light (Poulson & White 1969, Culver 1982). In general, the physical environment within a cave varies considerably less than the epigean (external) environment. The temperature in caves is near the annual average of the external temperatures, and is commonly characterized by high humidity, often tending towards saturation (Gilbert *et al.* 1994). Primary producers are not present in caves, with the rare exception of a few chemoautotrophic bacteria that can use iron or sulphur as electron donors. So all the energy or food that enters a normal cave system is imported from the external environment. Cave communities are, in general, essentially based upon detritivorous species (Ferreira 1998).

The type of resource, as well as the form in which it enters the system, are important determinants of the faunal composition in a given cave environment. In some caves, guano of bats, birds, and crickets can form extensive deposits that are the main energy

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source (Poulson 1972, Gnaspini-Netto 1989, Herrera 1995).

Bat guano piles can be the main energy source in permanently dry caves, such as that examined in the present study. In relation to their alimentary quality and microclimate, guano deposits are heterogeneous, characterized by considerable variability in the microhabitats (pH, humidity, texture, percentage of organic substances, etc.) that shelter numerous distinct zoological communities, as well as different successional stages (Decu 1986). The physical and chemical features of guano patches vary in time. Fresh guano tends to be more alkaline and moist, becoming acid and drier when older (Bernarth & Kunz 1981, Gnaspini & Trajano in press, Ferreira & Martins 1999).

The distribution of cave organisms is influenced by several factors, especially potential food sources. Of course many organisms colonize caves via the entrance, so the distance from it can be an important factor in the distribution of some groups of limited mobility (Poulson & Culver 1969).

Cave organisms show different degrees of morphological, physiological and behavioral specializations (Holsinger & Culver 1988). Trogloxenes are those that can be found regularly in caves but that have to leave the cave to feed, so they are unable to complete their entire life cycle inside caves. Many of these organisms act as importers of energy from the external environment, often being primarily responsible for the energy input in permanently dry caves. Troglophiles can complete their life cycle in the external environment or in caves. Troglobites are the most specialized organisms, occurring only in caves. These animals can show morphological, physiological, and/or behavioral specializations, probably evolved either in response to the selective pressures found in caves or to the absence of normal external selective pressures.

Bat guano communities recycle guano and participate in other interactions related to the whole cave environment and beyond. Since many species associated with guano piles are troglophiles (Ferreira 1998), they can interact in other biotopes within the cave as well as outside.

In many respects, guano piles can be considered ephemeral resources, since after deposition by the bat colony ceases they tend to deplete with time, though this is so gradual that several detritivore generations may succeed each other on a given deposit. Guano communities, however, are distincly different from communities associated with other ephemeral resources, reflecting the peculiar aspects of resource availability and the level of existing trophic interactions.

In addition to discussing general aspects of guano-based communities, the primary objectives of this study are to answer the questions:
(1) What effects do distance from the cave entrance, area, shape, pH, or percentage of organic content of guano piles have on the richness and diversity of their associated fauna?
(2) What is the similarity between the total cave fauna and the fauna associated with the guano deposits?
(3) Can conclusions be drawn about the structuring of the guano communities?

STUDY SITE

The study was carried out in Lavoura Cave (44°02'14.17"W, 19°31'26.74"S), in Matozinhos, Minas Gerais, Brazil. The cave entrance is situated at the base of a limestone outcropping with tumbled slabs of rock at its base. The outcropping and immediate vicinity have some scrubby vegetation, modified by man. On the top of the outcropping there is a cattle pen. The cave runs horizontaly for 290 meters and descends only 16 meters. Its entrance is at an altitude of 700 meters, and is a chamber of rock with a relatively low, flat ceiling. At the center of this, a skylight allows the entrance of sediments and organic material into the chamber from the cattle pen located above. This chamber is occasionally used by cattle and human inhabitants of the region. In the medial segment of the cave are dams of travertine (small rock dams), up to 40 cm deep. Such dams coincide with a large oblique fracture in the main gallery, where percolating water penetrates from the surface in the rainy season. Numerous haematophagous bat (*Desmodus rotundus*) guano deposits are distributed along the floor of the main gallery of the cave (ca. 140 meters). A few deposits are found in lateral galleries or on higher levels in the main gallery. For more detailed geological information concerning the cave system see Ferreira (1998).

METHODS

The deposits used in this study were those in the main gallery of the cave, mainly due to the difficulty of accessing the few deposits present in other places. The collections were made during eight visits to the cave in a period of one year. Collections were planned in a sequence aimed at minimizing the impact of each collecting event on the following one. For example, collection of the fauna associated with the guano deposits was made first, and collection of the general cave fauna later.

Distance from the cave entrance, area and shape. A total of 26 guano piles were marked with small aluminum tags. The distance from the cave entrance to the center of each pile was taken with a measuring tape. The area of each pile was calculated using Simpson's formula (Ferreira & Martins 1998), which integrates the lengths of parallel segments along the longitudinal axis of each pile. The shape of the deposits was quantified by DMI (Development of Margin Index; Barbour & Brown 1974, Kent & Wong 1982), a function of the area and perimeter of each deposit. Perimeter was measured with a marked string placed along the marginal contour of the pile.

Percentage of organic substances and pH. The percentage of organic substances was obtained from three samples of approximately 20 g from each of the 26 deposits which, after being weighed, were burned at 550°C for three hours. The organic content was equivalent to the percentage of mass lost after incineration. The determination of pH was made using three samples from each guano pile (2.5 g each) placed in bottles with 20 ml of distilled, deionized water. Such mixtures were homogenized for 1 minute and the pH of the solutions calculated with a pH meter.

Sampling arthropods. The arthropods associated with the 26 deposits were collected manually at standardized intervals (30 minutes per deposit, determined empirically in the first four deposits as being sufficient to collect all visible organisms), with the aid of forceps, brushes, and magnifying glasses, and fixed in 70% alcohol. The organisms in 10 deposits (numbers 7, 8, 11, 12, 14, 18, 21, 23, 24, 25) were also sampled with Berlese-Tullgren extractors (following Bernarth & Kunz 1981). The other piles were not sampled with Berlese funnels due to their solid or pasty consistency. Since this methodology was not applied to all deposits, the total richness and volumetric diversity (diversity per unit of volume of guano) were correlated only with the studied variables for this group of 10 deposits.

For Berlese samples, each guano pile was divided into sub-samples of 400 cm^2. Sub-samples were removed randomly from each guano pile until 10% of the total area had been sampled; the actual number of sub-samples used in the final analysis was thus related to the area of each guano pile. All organisms collected during this study were grouped in morphospecies and identified to the lowest possible taxonomic level.

Similarity between faunas. The cave was divided into 15 sectors of 10 meters, and a pitfall trap with formalin (2%) and a liver bait was placed in the middle of each sector for six days. After this period the captured organisms were fixed in 70% alcohol. The organisms captured with pitfalls were used to compare the composition of the total cave fauna to that associated with the guano deposits, in addition to material collected manually throughout the cave, but were not included in any of the other analyses of richness or diversity in this study. Comparison was made using the Renkonen similarity index between the general faunistic composition of the cave versus the deposits. The Renkonen index was used mainly because of the low number of individuals of each species collected, a situation for which this index is better suited than others (Wolda 1981).

Richness and diversity analyses. Only samples taken directly from guano deposits were used in these analyses. The calculations of richness and diversity used the Shannon-Wiener index (Zar 1996). Volumetric diversity was calculated using the relative abundance of each species in relation to the total volume of each deposit. The abundance of mites, for example, was estimated by comparing the number of individuals collected in a known volume (squares of 20 x 20 cm on the surface, to the depth of the pile) with the total volume of each deposit.

All the physical and chemical parameters were tested in a Principal Component Analysis (PCA; Manly 1986). Richness, total richness, diversity and volumetric diversity were tested by linear regression on the first factor (most significant) extracted from the PCA. All variables not showing normal distribution were transformed to logarithms (ln). In the case of linear regression, significant values of R, calculated for each variable, would show whether the independent variable (Factor 1) is correlated with the dependent variable, positively or negatively, as well as the magnitude of this influence.

All physical and chemical variables were related to the dependent variables (richness, total richness, diversity and volumetric diversity) in graphs to make their effects more visible.

RESULTS

The 26 guano piles varied in distance from the cave entrance, area, DMI, pH, and percentage of organic substances, as well as in richness and diversity (Tabs. 1, 3).

The basis of the guano food web in Lavoura cave are detritivorous organisms that directly consume guano, and microorganisms that live in the deposits. These include mites, the most common organisms on guano, springtails (Entomobryidae), booklice (Psyllipsocidae), beetles (Leiodidae, Tenebrionidae), moths (Tineidae) and flies (Phoridae, Milichiidae). Facultative detritivores also occurred, such as woodlice (Platyarthridae) and crickets (Phalangopsidae: *Endecous* sp.). Detrivores were in turn consumed by predators like pseudoscorpions (Chernetidae), spiders (*Loxosceles similis*), and heteropterans (Reduviidae: *Zelurus* sp.).

Of the total of 38 species found in the guano piles, only 3 (7.89%) were troglomorphic species (2 springtails and 1 woodlouse). Their actual evolutive status (troglobites or troglophiles) remains, however, unknown. These 3 species were the only troglomorphic individuals found in the cave.

The tree axis extracted from the PCA analysis explained almost 77.5% of the total variance (Fig. 1, Table 2). The first factor extracted was explained more by organic content and area of the guano piles (Tab. 2) and accounted for almost 30.1% of the total variance found. The second factor extracted was explained more by distance from the cave entrance and pH, being responsible for 26.3% of the total variance.

Factor 1 was positively correlated with richness ($F_{1,24}$ = 9,45; R = 0,532; P < 0,005 – Fig. 2A), diversity ($F_{1,24}$ = 8,01; R = 0,500; P < 0,009 – Fig. 2B), total richness ($F_{1,24}$ = 16,57; R = 0,639; P < 0,0004 – Fig. 2C), and volumetric diversity ($F_{1,24}$ = 8,75; R = 0,517; P < 0,007 – Fig. 2D).

The distance from the cave entrance, even if not showing a linear effect, appeared to be important in

TABLE 1. Measured variables for each guano pile.

Pile	Distance from entrance (m)	Area (cm²)	DMI	pH	% organic content	Richness (visual)	Total richness	Diversity	Volumetric diversity
1	43.58	1744.00	2.01	5.28	48.38	5	*	1.38	*
2	43.58	2798.00	0.73	6.19	31.54	2	*	0.69	*
3	48.18	15190.00	1.55	8.14	66.71	3	*	1.05	*
4	46.61	5380.00	2.20	6.46	35.46	1	*	0.00	*
5	49.34	1786.00	1.67	7.27	22.64	2	*	0.69	*
6	49.34	2077.74	1.42	6.85	48.25	2	*	0.60	*
7	68.99	1444.48	0.83	6.39	45.40	1	2	0.00	0.01
8	69.94	2833.05	0.86	7.29	62.60	1	2	0.00	0.02
9	71.54	3206.79	1.21	6.49	37.50	2	*	0.69	*
10	71.87	3739.50	0.86	7.50	64.36	0	*	0.00	*
11	70.83	5803.56	1.36	7.37	66.54	0	2	0.00	0.45
12	78.73	4654.77	1.46	7.21	67.72	2	5	0.56	1.11
13	78.26	2435.14	0.87	7.11	34.32	4	*	0.94	*
14	81.00	3945.60	2.23	6.73	63.40	9	10	1.99	0.01
15	99.69	22790.43	1.47	5.60	69.00	8	*	2.03	*
16	100.37	5870.00	1.27	4.56	63.11	2	*	0.69	*
17	127.41	1069.60	2.02	7.72	50.72	0	*	0.00	*
18	128.00	5911.70	1.69	5.71	72.45	1	4	0.00	1.24
19	140.50	2537.50	2.19	7.45	64.35	4	*	1.10	*
20	141.05	6602.40	3.13	7.70	57.99	4	*	1.11	*
21	141.79	4584.37	0.72	5.04	78.53	4	6	0.99	0.58
22	145.48	743.60	1.71	7.72	71.80	2	*	0.69	*
23	150.42	1423.50	0.81	6.75	49.86	0	4	0.00	1.13
24	151.64	2642.50	1.16	7.61	54.95	0	2	0.00	0.64
25	157.25	2166.30	1.58	7.23	33.05	0	2	0.00	0.56
26	159.81	1007.40	1.01	7.42	39.80	0	*	0.00	*

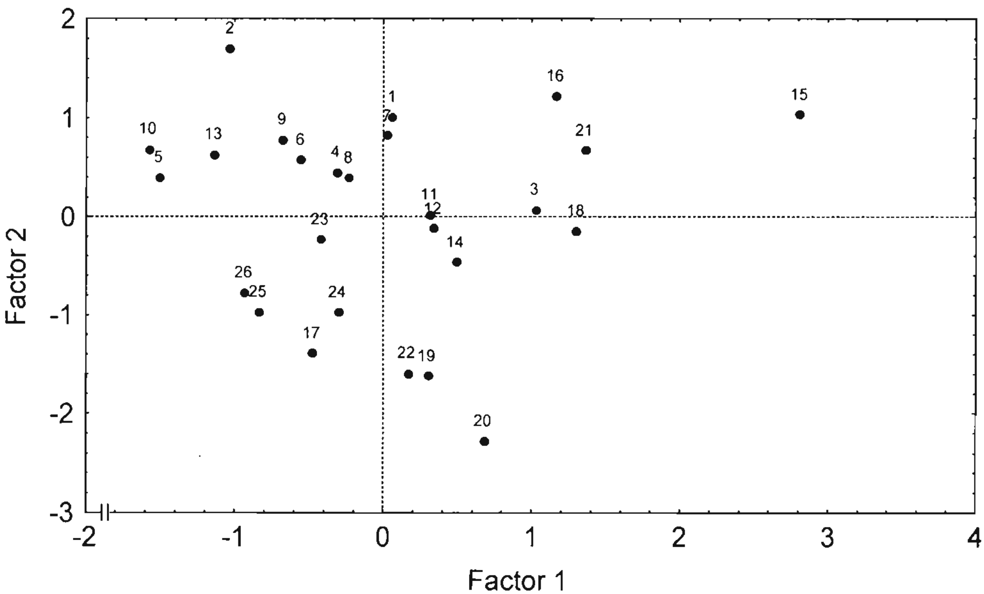

FIG. 1. Factor 1 versus Factor 2 extracted from the PCA.

the patterns of richness and diversity of guano communities, as will be discussed below (Fig. 3 A,B).

While there was no simple linear effect evident, guano pH had a clear influence on the communities. Regardless of sampling method, the richest communities occurred in deposits with moderate pH, tending to acid. Communities in both very acid or basic deposits were less rich and less diverse, so there appears to be an optimum intermediate pH value (Fig. 4 A,B).

In guano and other substrata (mainly soil) in the cave, a total of 504 individuals in 51 morphospecies belonging to 41 families of Araneida, Pseudoscorpionida, Acarina, Isopoda, Collembola, Ensifera, Psocoptera, Thysanoptera, Heteroptera, Coleoptera, Lepidoptera, Diptera and Hymenoptera were collected (Tab. 3). Acarina was the richest taxon, with 13 morphospecies associated with the guano piles (25.5% of the morpho-species found in the deposits). Mites were also most abundant in guano (31% of the total abundance of morphospecies), followed by spiders (15%) and booklice (13.45%). The abundance of predators (mainly *Loxosceles* spp.) correlated positively with prey abundance in the different sectors of the cave ($F_{1,24}$ = 9,41; R = 0.531, $P < 0.005$).

Manual collection in each sector of the main gallery resulted in 161 individuals of Araneida, Ensifera, Heteroptera, Coleoptera, Lepidoptera, and Diptera. Manual collection allowed the capture of many predators (especially spiders) that were not collected by pitfalls or funnels. The total fauna collected by pitfalls was 124 individuals of Pseudoscorpionida, Ensi-

TABLE 3. Factors extracted from the physical and chemical variables of the guano piles (Marking loadings are > 0.6500).

	Factor 1	Factor 2	Factor 3
Distance	0.172199	–0.695495	0.603099
Area	0.729358	0.205538	–0.410574
DMI	0.239741	–0.586301	–0.600309
pH	–0.443684	–0.634447	–0.317188
Organic content	0.830066	–0.206105	0.239487
Eigenvalues	1.504955	1.314710	1.050632
% variance	30,1	26,3	21,0

(Marked loadings are > 0.6500)

TABLE 2. Richness and abundance of the groups found in Lavoura Cave.

Taxon	Evolutive status	Total richness	Guano richness	Richness in other substrata	Total cave abundance	Guano abundance	Abundance in other substrata
– Arthropoda		51	38	13	504	223	281
– Arachnida		21	17	4	213	110	103
– Araneida		6	2	4	136	33	103
Sicariidae (*Loxosceles* sp.)	Troglophile	1	1	0	121	33	88
Ctenidae	Troglophile	2	1	1	3	1	2
Pholcidae (*Blechroscelis* sp.)	Troglophile	1	0	1	11	0	11
Theraphosidae	Troglophile	1	0	1	1	0	1
Oxyopidae (*Peucetia flava*)	Accidental	1	0	1	1	0	1
– Pseudoscorpionida		2	2	0	4	4	0
Chernetidae	Troglophile	2	2	0	4	4	0
– Acarina		13	13	0	69	69	0
Ameroseiidae (*Ameroseius* sp.)	Troglophile	1	1	0	12	12	0
Phytoseiidae	Troglophile	1	1	0	2	2	0
Laelapidae (*Hypoaspis miles*)	Troglophile	1	1	0	19	19	0
Macronyssidae (*Cryptonyssus* n sp.)	Troglophile	1	1	0	4	4	0
Stigmaeidae (*Stigmaeus* sp.)	Troglophile	1	1	0	7	7	0
Histiostomatidae (*Histiostoma* sp.)	Troglophile	1	1	0	1	1	0
Bdellidae	Troglophile	1	1	0	1	1	0
Acaridae (*Tyrophagus putrescentiae*)	Troglophile	1	1	0	13	13	0
Microzetidae	Troglophile	1	1	0	1	1	0
Rhagidiidae	Troglophile	1	1	0	1	1	0
Tydeidae	Troglophile	1	1	0	1	1	0
Aphelacaridae (*Aphelacarus acarinus*)	Troglophile	1	1	0	3	3	0
Sphaerochthoniidae (*Sphaerochthonius phyllophorus*)	Troglophile	1	1	0	4	4	0
– Crustacea		1	1	0	10	10	0
– Isopoda		1	1	0	10	10	0
Platyarthridae	Troglomorphic	1	1	0	10	10	0
– Insecta		29	20	9	281	103	178
– Collembola		3	3	0	17	17	0
Entomobryidae	Troglomorphic	3	3	0	17	17	0
– Ensifera		2	1	1	95	12	83
Phalangopsidae	Troglophile	2	1	1	95	12	83
– Psocoptera		3	3	0	41	30	11
Psyllipsocidae	Troglophile	3	3	0	41	30	11
– Thysanoptera	Troglophile	1	1	0	1	1	0
– Heteroptera		1	1	0	30	10	20
Reduviidae (*Zelurus variegatus*)	Troglophile	1	1	0	30	10	20
– Coleoptera		8	4	4	16	5	11
Tenebrionidae	Troglophile	2	2	0	8	2	6
Aderidae	Troglophile	1	1	0	1	1	0
Melyridae	Accidental?	1	0	1	2	0	2
Cantharidae	Accidental?	1	0	1	1	0	1
Coccinellidae	Accidental?	1	0	1	1	0	1
Leiodidae	Troglophile	1	1	0	2	2	0
Dermestidae	Troglophile	1	0	1	1	0	1
– Lepidoptera		3	2	1	70	21	49
Tineidae	Troglophile	1	1	0	34	15	19
Pyralidae	Troglophile	1	1	0	6	6	0
Noctuidae	Troglophile	1	0	1	30	0	30
– Diptera		7	4	3	10	6	4
Psychodidae	Troglophile	2	0	2	2	0	2
Phoridae	Troglophile	1	1	0	3	3	0
Milichiidae	Troglophile	1	1	0	2	1	1
Cecidomyiidae	Troglophile	1	0	1	1	0	1
Diptera (not identified)	?	2	2	0	2	2	0
– Hymenoptera		1	1	0	1	1	0
Signiphoridae	Accidental	1	1	0	1	1	0

fera, Psocoptera, Heteroptera, Coleoptera, Lepidoptera, and Diptera.

Only 13 species of the total cave fauna were collected exclusively in substrata other than guano (soil or vegetable debris). So almost 75% of the species found in the cave were directly or indirectly associated with guano deposits. The guano pile fauna and the fauna from other cave substrata (from the pitfall traps and manual collection) showed a similarity of 85% using the Renkonen index.

DISCUSSION

Ecological studies of invertebrates associated with guano piles in caves are scarce, the majority of them describing food webs and species composition (Decou & Decou 1964, Negrea & Negrea 1971, Poulson 1972, Decou *et al.* 1974, Decu & Tufescu 1976, Martin 1976, Bernarth & Kunz 1981, Strinati 1982, Gnaspini-Netto 1989). The great diversity of groups found in guano in Lavoura cave (almost 75% of the species total) demonstrates the importance of this resource for the structure of the communities of this cave.

General patterns in richness and diversity. The term "patterns" is used here with caution, bearing in mind that collections were made in the brief period of only one year.

The communities from deposits collected only manually were clearly underestimated in relation to those obtained by Berlese funnels, making direct comparisons between samples obtained by the two different methods impractical.

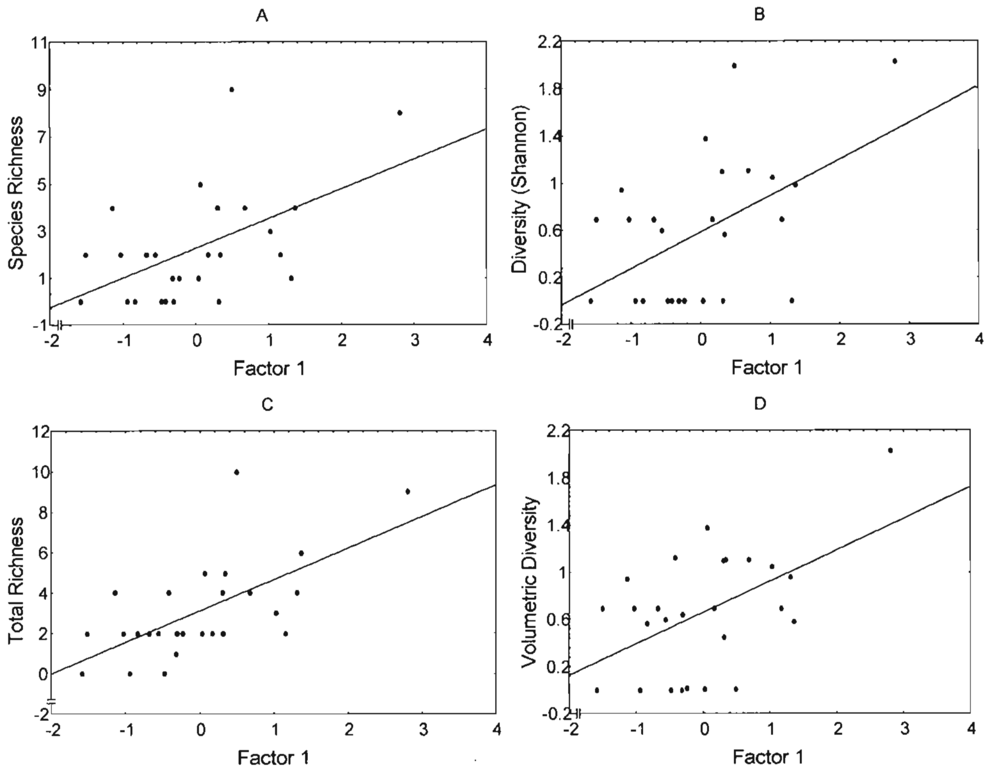

FIG. 2. (A) Correlation between richness (visual collection) and Factor 1 (PCA); (B) Correlation between diversity (Shannon – visual collection) and Factor 1 (PCA); (C) Correlation between total richness (visual collection + Berlese samples) and Factor 1 (PCA); (D) Correlation between volumetric diversity and Factor 1 (PCA).

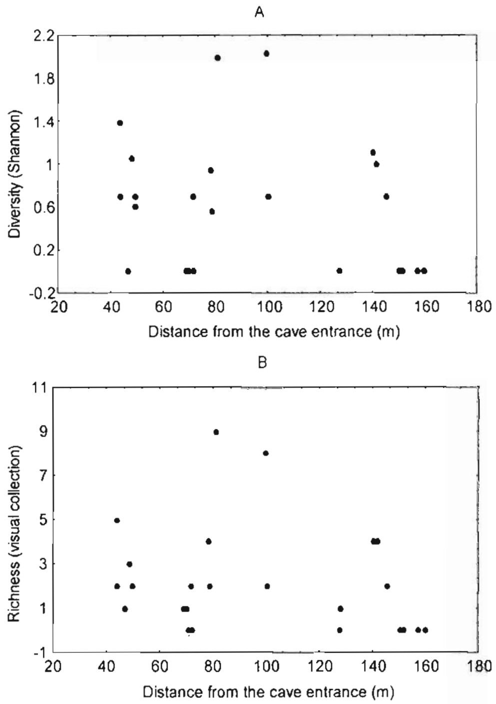

FIG. 3. Correlation between diversity (visual collection – (A), richness (B), and distance from the cave entrance.

The patterns of variation in richness and diversity of the guano communities in relation to the distance from the cave entrance do not follow those found by Ferreira & Pompeu (1997), who found a clear and consistent reduction in richness and diversity with increasing distance in Taboa cave (Sete Lagoas, Minas Gerais state).

The high richness in deposits near the cave entrance is likely to reflect the ease of colonization compared to deposits deeper inside. Also, the great amount of organic material that accumulates in the cave entrance (e.g., carcasses of cows thrown from the pen above the cave) supplies an additional resource focus, and probably has an influence on richness.

The slight peak in richness and diversity found at approximately 80 m from the cave entrance is probably due to the existence of water percolation in this area during the rainy seasons. Some piles, situated between travertines, become moistened by water that percolates through a crack in the ceiling and the wall of the galery. This rain water crosses the cattle pen located above, dissolving and carrying organic substances. Although not quantified, the additional organic substances in the water during the rainy season, as well as the moisture itself (though cyclic), may explain the higher relative richness and diversity of arthropods in this region of the cave. This is reinforced by the presence of some morphospecies (of isopods, springtails, and booklice) found only in this region of the cave.

The number of individuals of species that use feces deposits tends to be proportional to their general availability (Doube 1986). However, in the case of guano, the larger the deposit the more is accumulated without being consumed, since the organisms remain mostly on the surface, and thus some deposit area effect is expected, in addition to a greater potential microhabitat variability over a larger surface. Fluctuations in the size of the populations in guano are more related to the "quality" than the quantity of this resource (Decu 1986). So larger deposits with a wider diversity of microhabitats have a greater number of associated species, as suggested by the present work.

There is some evidence that larger deposits may act as sources of colonization for smaller ones (one of three large deposits examined had a negative correlation between distance to nearby small deposits and similarity to those deposits; unpublished results), but dynamics of between-deposit movement remain largely unknown and merit further research.

Shape effects. The low significance of the Development of Margin Index (DMI) of the deposits in the first axis extracted from the PCA suggests that many species must locate the deposits by chemotaxy. If colonization occurred exclusively by random movements, we might expect to find a stronger explanation of this parameter in the first factor, since more ramified deposits would be more easily encountered and colonized than deposits of similar area but with rounded forms.

Chemistry effects. Physical-chemical composition is an important determinant of the richness and abundance of pioneer communities on organic deposits (Cornaby 1974; Denno & Cothran 1976; Kuusela & Hanski 1982; Kneidel 1984 a, b). The reduction of guano pH over time is well known (Herrera 1995; Gnaspini & Trajano, in press; Ferreira & Martins 1999); fresh guano is alkaline, later acidifying because of ammoniac fermentation (Hutchinson 1950).

Guano piles are not, however, completely closed systems, and are thus affected by general processes such as chemical (water percolation, floods, etc.) and physical (landslides, sedimentation, etc.) processes inherent to the cave environment. For these reasons, pH is not necessarily a reliable indicator of the time of guano deposition in any situation. In some cases, pH of old deposits can become alkaline due to biodegradation, which results in the mixing of the guano with adjacent alkaline soil. Old piles placed in speleothems (mineral deposits) can also be continuously or randomly in contact with carbonate-rich percolating waters, raising their pH.

The relationship between guano pH and its arthropod communities can be explained in two ways, not mutually exclusive. First, there may simply be an optimum and intermediate value for pH, with values at either extreme reducing the numbers and kinds of associated organisms. Second, if pH really indicates age (a situation which seems unlikely in this cave), fresh deposits (very basic) may not have had time to be colonized, while old ones (very acid) may have become exhausted as an alimentary resource (due to consumption or mineralization of the organic matter).

As with pH, the percentage of organic matter seems to decrease in old guano piles. However, also this variable does not necessarily indicate time of deposition, since old deposits can remain at relatively homogeneous levels, or even increase their percentage of organic substance if there is deposition of exuvia or bat corpses on them.

Organic content, however, was the most important variable in the first factor, indicating its importance for the creation of richer and more diverse communities in guano piles. This effect is expected, since in guano deposits with higher levels of organic content there are probably more varied conditions of the resource, reflecting the higher habitat heterogeneity, which can support richer and more diverse communities.

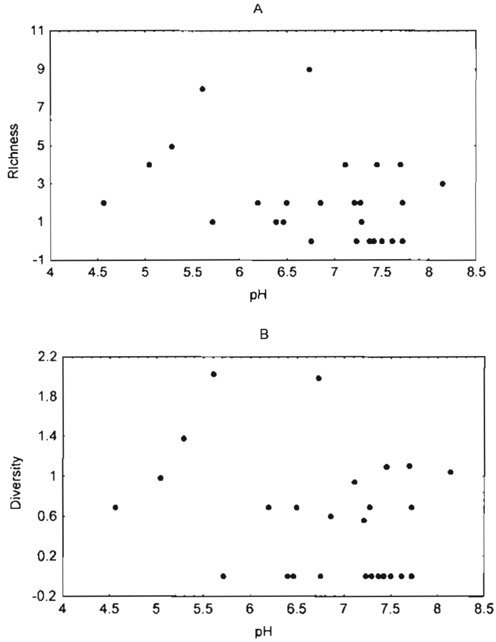

FIG. 4. Correlation between richness (A), diversity (B), and pH of the guano piles.

General conclusions. Communities associated with ephemeral resources tend to show similar structures and dynamics, with food as the main limiting resource (Diamond & Case 1986, Doube 1986). Guano can, in a general sense, be considered an ephemeral resource, since it becomes less and less available over time once deposition ceases. However, this loss of quality is very slow, and seems to be more related to the mineralization of organic composites with the aging of the deposit than to consumption *per se*, therefore the amount of guano would not seem to be a limiting factor for the communities that use it.

More specifically, bat guano invertebrate communities, even though structured on an "ephemeral" resource, show only a few similarities to, and some basic differences from, communities associated with typical ephemeral resources. Perhaps the main similarity is in composition; guano communities tend to present a diversified guild of detritivores that are consumed by numerous species of predators, similar to other ephemeral resources. The orders most commonly found in guano are the same as found in carcasses, deposits of feces, or other similar resources (Coleoptera, Diptera, Acarina, Collembola; Doube 1986). Another aspect of such detritivore-based communities is that the activities of the species in question have no effect on the future production of the resource, such as occurs in plant-herbivore systems for example. This makes these communities, in general, less complex than those associated with non-ephemeral resources (Doube 1986).

However, guano communities are different from other ephemeral communities in relation to the limitation of resources and trophic relations. The amount of guano is not the main limiting factor, and fluctuations in guano populations seem to be more related to the quality than the quantity of the resource (Decu 1986). Since the resource does not seem to be limiting, exploitative resource competition, prevalent in other ephemeral resources, becomes largely irrelevant for the guano communities. In contrast, the large number of predator species found in the present study, and the significant correlation with the abundance of detritivores, as found elsewhere (Ferreira & Martins 1998), suggests that predation may be of primary importance in the structure of guano invertebrate communities.

The correlation of richness and diversity of the guano communities with the area of the deposits may suggest, initially, that guano is limiting as a resource. However, as discussed above, guano tends to accumulate, clearly not limiting the growth of most or many of the associated populations, except possibly in terms of surface area. Bigger piles certainly possess a higher small-scale structural diversity than smaller piles, and a high number of distinct microhabitats should support more diverse communities, with species using different components or conditions of this resource.

Communities associated with the guano of bats are, accordingly, influenced fairly clearly by the area and organic content of the deposits. The many physical and chemical factors appear to vary with respect to their influences on these communities. Predation, in contrast to competition, seems likely to be the most important structuring factor of the guano commu-

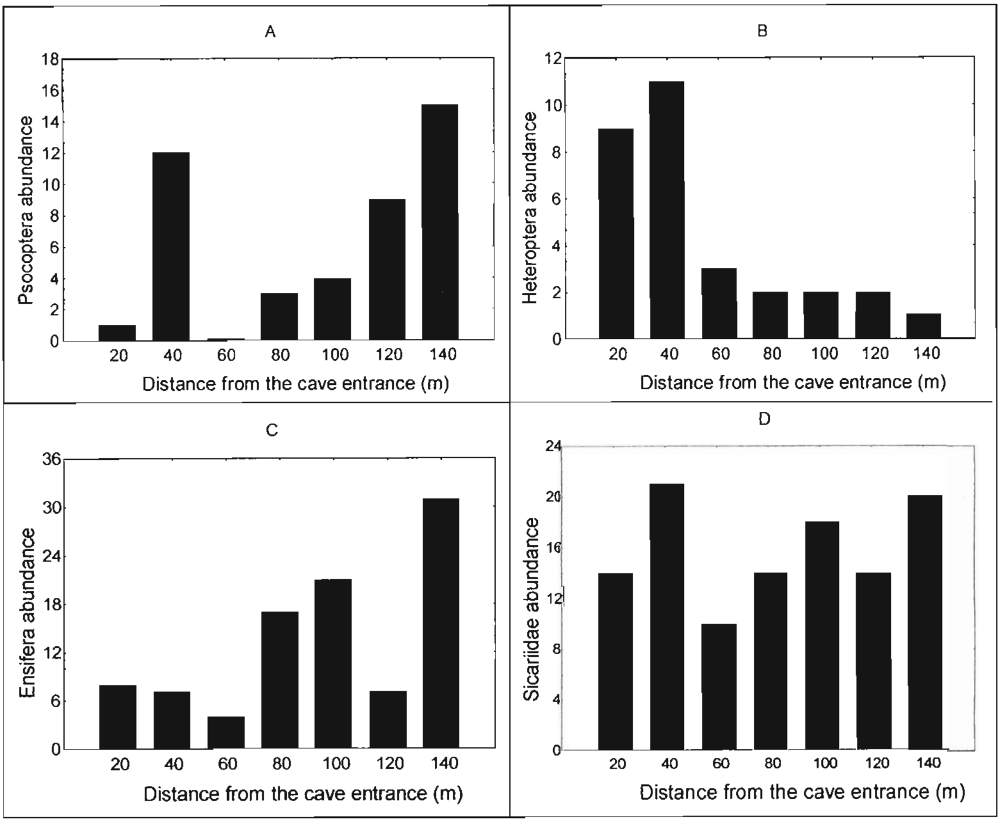

FIG. 5. Distribution of some taxa in relation to the distance from the cave entrance; Psocoptera (A), Heteroptera (B), Ensifera (C), and Sicariidae (D).

nities. Some of these conclusions are based not only on the present study but also on several aspects that were suggested by other authors (e.g. Decou & Decou 1964, Negrea & Negrea 1971, Decou *et al.* 1974, Decu & Tufescu 1976, Decu 1986). Nevertheless, these aspects were, for the first time, empirically tested in this work.

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