Structure of bat guano communities in a dry Brazilian cave

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Physical, chemical and spatial variables of bat guano deposits (pH, percentage of organic matter, distance from the cave entrance, area and shape of the deposits) were analyzed with regard to the richness and abundance of arthropod communities in Morrinho Cave, Bahia State, Brazil. In total, 12,356 individuals were sampled, belonging to 85 morphospecies in at least 26 families of Acarina, Araneida, Pseudoscorpionida, Isopoda, Coleoptera, Collembola, Diptera, Ensifera, Heteroptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Psocoptera, Siphonaptera, Thysanoptera, and Zygentoma. Richness and diversity of invertebrates were correlated with the area and distance from the cave entrance, pH, organic content and moisture content of the guano piles. Communities associated with bat guano are apparently more dependent on the guano microenvironment itself than on the overall cave environment.

KEY WORDS: cave, invertebrates, diversity, guano, communities, habitat selection, Neotropics, Brazil.

INTRODUCTION

Caves are usually stable environments compared with epigean habitats (Poulson & White 1969, Culver 1982). Besides permanent darkness, the inner temperature in caves is close to the mean annual surface temperatures and the air tends towards saturation (Gilbert et al. 1994). In the absence of photoautotrophic organisms, consumers need to find other allochthonus food resources, which are normally scarce. They mainly comprise organic matter imported into caves by water or gravity and animal excreta or carcasses. In some dry caves, the main resource is guano of bats, birds or crickets, sometimes in large piles (Poulson 1972, Gnaspini-Netto 1989, Herrera 1995, Ferreira 1998, Ferreira & Martins 1998, Ferreira et al. 2000). Therefore, the diversity of most cave communities is essentially dependent upon detritivorous species (Trajano 1987, 1992; Ferreira & Martins 1999a, 1999b).

The diversity of feeding habits of bats in tropical regions is remarkable (Fleming et al. 1972, Wilson 1973, Herzig-Straschil & Robinson 1978). Depending on the feeding habits of cave-dwelling bats, the guano can be: frugivorous, with small undigested seeds, sometimes with pulp still attached to the feces; haematophagous, with a pasty consistency and a reddish colour when fresh, becoming black and often powdery with age (Gnaspini-Netto 1989); insectivorous, usually containing chitinous pieces of insects or other arthropods. The variability in feeding habitats of bats allows comparisons of the community composition and diversity of invertebrates that live on different types of bat guano.

Bat guano piles may be the main energy source in permanently dry caves, like that in the present study. Guano deposits are heterogeneous in relation to their nutritive quality and microclimate; in fact, they present by considerable variability of microhabitats (determined by pH, humidity, texture, organic content, etc.), which host several distinct communities and successional stages (Decu 1986). The physical and chemical features of guano patches vary in time. Fresh guano tends to be more alkaline and moist, but becomes more acidic and drier when older (Bernath & Kunz 1981, Ferreira & Martins 1999a). However, this pattern is not found in all cave systems (Ferreira et al. 2000).

Several factors influence the distribution of cave organisms, especially the availability of potential food sources. Many organisms colonize caves through their entrances, so the distance within a cave from the entrance should be an important variable affecting the dispersion and distribution of some animal groups of limited mobility (Poulson & Culver 1969, Ferreira & Pompeu 1997).

Cave organisms are variable with respect to morphological, physiological and behavioral specializations (Holsinger & Culver 1988; based on Schiner-Racovitza's system). The trogloxenes can be regularly found in caves, but always leave the cave to feed. Many trogloxenes import energy from the external environment by eating outside and defecating inside caves, often being primarily responsible by energy input in permanently dry caves. Troglophiles can complete their life cycle both outside and inside caves. Outside of caves, trogloxenes and troglophiles (especially arthropods) generally occur in humid and/or shaded environments. Troglobites are the most specialized organisms, and occur exclusively inside caves. They have morphological, physiological and/or behavioral specializations, probably evolved in response to the environment they experience inside caves.

In many respects, guano piles can be considered ephemeral resources, since after deposition ceases, they tend to become depleted over time. This process is suf-

ficiently gradual to support multiple generations of detritivores in a given guano pile. Bat guano communities are often considered isolated but a high number of cave invertebrate groups associate and interact with them (FERREIRA & MARTINS 1999a).

The main objective of this study was to describe general aspects of a guano-based community, while other question dealt with:

(1) Are there effects of distance from the cave entrance, area, shape, pH or percentage of organic matter in guano piles on the diversity of their invertebrate fauna?

(2) Is there any pattern in the distribution of different taxa using guano deposits?

(3) Are there differences in invertebrate communities between frugivorous and haematophagous guano piles?

(4) What conclusions can be drawn about the structure of the arthropod communities in guano piles?

METHODOLOGY

Study area

The Morrinho Cave (40°55′05″W 10°12′32″S) is located at an altitude of 600 m in the Laje dos Negros (Campo Formoso City), northeastern Bahia State, Brazil. The vegetation around the cave is composed of deciduous plant species common in this dry region, called caatinga (RIZZINI 1992). The cave entrance is horizontal (7 m wide and 2 m high) and its only conduit, almost completely flat, has only two constrictions along its 475 m. These constrictions, formed by internal collapses, partially obstruct the passage. The cave is formed in pure dolomite interspersed with thick nodules of chert (silicates) (RUBBIOLI & PILÓ 1995). It is permanently dry, and the main food resource for invertebrates is guano from frugivorous and haematophagous bats. No insectivorous guano pile was found in the cave.

Procedures

All the 23 deposits (11 frugivourous and 12 haematophagous guano piles) found in the cave were sampled in January, 1997. Invertebrates from each pile were sampled twice: the observable ones were sampled on the first visit, while a Berlese-Tullgren sample was collected from each deposit on the second visit. Measurements of the physical-chemical parameters were made on 8 subsequent visits (area, distance from the cave entrance, Development of Margin Index, pH, organic substance, moisture, etc.).

Sampling arthropods

The arthropods associated with the 23 guano deposits were collected manually with the aid of forceps, brushes and a magnifying glass, and fixed in 70% alcohol. Arthropods from 11 of the deposits were also sampled with Berlese-Tullgren extractors (following BERNARTH & KUNZ 1981). This methodology was not applied to the other 12 deposits due to their solid consistency. Overall *total* richness (number of species obtained by visual collection and Berlese-Tullgren extractors) and *volumetric* diversity (diversity expressed as total richness per unit volume of guano) were obtained only for the 11 piles sampled both ways. Only *visual* richness and *visual* diversity per unit surface area were estimated for the communities of the deposits collected manually.

The sampling area for micro-invertebrates was standardized at 10% of the total area of each guano pile. This area was further divided into sub-samples of 400 cm^2 according to Ferreira & Martins (1999a). Hence the actual number of sub-samples in each guano pile was larger in large guano piles. Each sub-sample was removed randomly from each guano pile. The sub-samples were placed individually into Berlese-Tullgren extractors and all the invertebrates removed were fixed in 70% alcohol. All organisms collected during this study were sorted into different morphospecies and identified to the lowest possible taxonomic level. The number of invertebrates of each morphospecies was divided by the volume of guano from each sub-sample, giving a measure for diversity per cc of guano in that sub-sample. The total volume of the guano pile was then estimated using the average volume per sub-sample (i.e. per 400 cm^2) multiplied by total surface area. The average number of morphospecies/cc was then multiplied by the total volume in the pile to give an estimate of the total number of individuals of each morphospecies in each pile.

Distance from the cave entrance, area and shape

The 23 guano piles were individually marked with small aluminium tags. The distance was measured from the cave entrance to the centre of each pile. The area of each pile was calculated using Simpson's formula, which integrates the measures of 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. Although the depth of guano piles often determines the structure of some associated communities (Herrera 1995), this parameter was not measured in this work. All the guano piles were extremely shallow, and the associated fauna was always in the piles' surface.

Percentage of organic substance, moisture content and pH

Three samples of each guano pile were taken from the centre, border and middle surface area of each pile.

The guano moisture content was taken from three samples (20 g) from each guano deposit, which were dried in an oven at 100 °C for 24 hr. The moisture content was equivalent to the weight lost after drying. The same three samples from each guano deposit were then placed in a muffle furnace and burned at 550 °C for 3 hr. The organic matter content was equivalent to the weight lost after incineration. The pH was measured from three other sub-samples from each guano pile (2.5 g each) placed in bottles with 20 ml of distilled, deionized water. These mixtures were homogenized for 1 min and the pH of the solutions was measured with a pH meter.

Richness and diversity analyses

Correlations between the physical and chemical parameters of the 23 guano piles were tested by linear regression. The relationships between the physical and chemical parameters and biodiversity measures were also tested by Canonical Correspondence Analysis (CCA). The DMI (Development of Margin Index) was excluded from this analysis since the number of valid cases (23) allowed only five independent variables. This excluded variable was tested separately by linear regression with the biological parameters, in both treatments. All the variables lacking normal distribution were transformed to natural logarithms. Analyses were performed separately for frugivorous and haematophagous guano piles to determine the influence of the guano type on the community response. The CCA was not used in this case, since

the number of valid cases (11 frugivorous guano piles and 12 haematophagous guano piles) was insufficient for that analysis. The guano type was tested by logistic regression upon the biological parameters (ZAR 1996). The Jaccard similarity Index was calculated between all the guano piles to verify possible preferences for a specific guano type (WOLDA 1981).

RESULTS

In total, 12,356 individuals in 85 morphospecies belonging to at least 26 families of Acarina, Araneida, Pseudoscorpionida, Isopoda, Coleoptera, Collembola, Diptera, Ensifera, Heteroptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Psocoptera, Siphonaptera, Thysanoptera, and Zygentoma were sampled in the guano piles. Acarina was the richest order with 43 out of 85 morphospecies (50.59%). Silverfishes were the most abundant in guano (n = 6,379; 51.6% of the total abundance of morphospecies), followed by mites (n = 4,682; 37.9%) and barklice (n = 1,102; 8.9%). Of all the species found, only three were troglomorphic (two springtails and one mite).

The total abundance of invertebrates associated with guano in Morrinho Cave was estimated to be 59,864 individuals. Mites were the most abundant

Table 1.

Significant linear regressions between physical-chemical variables and biological variables for haematophagous and frugivorous guano.

		F	R	*P*
Hematophagous bat guano visual parameters	Area × Richness	$F_{1,10}=7.302$	0.650	0.022
	pH × Richness	$F_{1,9}=6.398$	0.645	0.032
	Area × Diversity	$F_{1,10}=5.732$	−0.604	0.038
	Distance × Equitability	$F_{1,10}=7.755$	0.661	0.019
	Area × Equitability	$F_{1,10}=10.150$	−0.071	0.009
Hematophagous bat guano total and volumetric parameters	IDM × Richness	$F_{1,3}=105.140$	−0.986	0.002
	pH × Richness	$F_{1,2}=19.582$	−0.952	0.047
	Area × Diversity	$F_{1,3}=71.364$	0.980	0.003
	Organic × Diversity	$F_{1,3}=21.923$	0.938	0.018
	Organic × Equitability	$F_{1,3}=82.926$	0.982	0.003
Frugivorous bat guano visual parameters	Moisture × Richness	$F_{1,9}=7.926$	0.684	0.020
	Distance × Diversity	$F_{1,9}=5.784$	0.625	0.040
	Moisture × Diversity	$F_{1,9}=10.431$	0.733	0.010
	Distance × Equitability	$F_{1,9}=6.880$	0.658	0.028
	Moisture × Equitability	$F_{1,9}=7.154$	0.665	0.025
Frugivorous bat guano total and volumetric parameters	Area × Richness	$F_{1,4}=25.362$	0.929	0.007
	Area × Diversity	$F_{1,4}=22.047$	0.920	0.009
	Area × Equitability	$F_{1,4}=26.509$	0.932	0.007

Table 2.

Measured variables for each guano pile (F, Frugivorous; H, Haematophagous).

Pile	Type	Distance from entrance (m)	Perimeter (cm)	Area cm²	DMI	pH	% Organic content	% Moisture	Richness (visual)	Total richness	Diversity (visual)	Volumetric diversity	Equitability (visual)	Total equitability
1	F	43.7	437	3978.0	1.95	7.5	66.39	29.49	7	*	1.06	*	0.55	*
2	H	48.55	396	5670.64	1.48	7.77	67.4	39.93	5	7	1.5	0.81	0.93	0.42
3	F	49.6	1160	28155.33	1.95	6.85	74.83	23.4	4	18	0.06	1.65	0.05	0.57
4	H	50.15	480	7724.53	1.54	8.37	64.99	27.56	5	*	0.28	*	0.17	*
5	H	53.3	812	24712.0	1.46	7.75	78.07	36.94	2	9	0.05	1.27	0.08	0.58
6	H	47.75	1382	99602.67	1.24	7.05	76.9	31.16	11	33	0.09	1.64	0.04	0.47
7	F	51.05	710	11158.8	1.9	7.9	75.54	23.48	3	12	0.04	0.77	0.04	0.31
8	H	51.05	720	13650.0	1.74	7.34	68.44	14.33	7	*	0.2	*	0.1	*
9	F	52.9	654	14608.53	1.53	7.58	78.61	20.07	5	14	0.19	1.21	0.12	0.46
10	H	56.55	177	5030.67	0.7	7.45	69.71	39.74	3	*	0.3	*	0.27	*
11	F	60.3	818	22571.67	1.54	7.79	67.25	20.44	5	20	0.17	2.11	0.11	0.7
12	F	64.55	326	5521.6	1.24	7.09	60.6	17.19	2	*	0.14	*	0.21	*
13	H	85.75	416	6233.33	1.49	8.07	33.65	42.46	4	*	0.69	*	0.5	*
14	F	102.65	330	6993.0	1.11	7.67	55.16	20.08	5	10	0.66	0.65	0.41	0.28
15	F	104.35	288	4953.33	1.15	7.75	57.05	18.31	5	10	0.55	0.4	0.34	0.17
16	F	104.85	400	3369.0	1.94	9.61	54.11	30.33	5	*	0.39	*	0.24	*
17	F	108.15	376	5525.33	1.43	8.06	72.47	28.24	7	*	0.94	*	0.48	*
18	H	120.45	192	1423.33	1.44	8.09	40.88	37.03	4	7	1.21	0.08	0.88	0.04
19	H	122.65	220	2066.4	1.37	8.24	46.24	35.14	4	*	0.9	*	0.65	*
20	H	136.95	372	4136.0	1.63	8.31	50.55	41.87	4	*	1.39	*	1	*
21	H	136.95	334	3793.06	1.53	8.25	30.35	23.31	2	*	0.5	*	0.72	*
22	F	158.25	432	11737.73	1.13	9.55	80.57	39.04	7	*	1.78	*	0.92	*
23	H	299.05	433	9520.66	1.25		57.01	66.13	5	28	1.22	0.71	0.76	0.25

* No data available.

Table 3.

Canonical roots extracted from the Canonical Correspondence Analysis.

	Visual parameters		Total and volumetric parameters	
	Root 1	Root 2	Root 1	Root 2
Distance	0.4667	– 0.1841	0.9245	–15.948
Area	– 0.4246	0.6394	– 13.153	0.7660
pH	– 0.2652	– 0.2381	– 0.0941	0.0912
Organic content	– 0.2417	–11.861	12.309	– 27.254
Moisture content	0.4198	– 0.2594	0.3014	– 10.126
Richness	– 0.1689	0.5786	– 0.8257	– 16.517
Diversity	– 0.7507	– 34.989	0.2579	62.296
Equitability	16.148	30.343	– 66.106	– 54.017
Canonical R	0.8649	0.7480	0.9914	0.9091
χ^2	411.386	183.946	273.903	90.667
df	15	8	15	8
P	0.00031	0.01848	0.02576	0.13334

(40,571 individuals), followed by barklice (9,947 individuals) and silverfish (6,653 individuals).

Amongst the mites, four morphospecies totaled 98% (n = 4,602) of all sampled invertebrates. One troglomorphic Criptostigmata was highly abundant, representing 58% (n = 2,728) of the total individuals; 82% (n = 2,241 individuals) of this species were found on frugivorous bat guano.

The frugivorous and haematophagous guano types showed different correlations among the tested parameters (Table 1). The relationships were quite distinct in the different types, but two correlations were significant in both cases: distance from the cave entrance versus equitability (visual parameters) and area versus diversity (volumetric parameters).

There was no significant correlation between the guano type and the biological parameters tested.

Biotic and abiotic attributes of the bat guano piles exhibited considerable variability (Table 2). Several physical and chemical parameters were related in Morrinho Cave. The logarithm of the distance from the cave entrance was negatively correlated with the logarithm of the pile area ($F_{1,21}$ = 4.769; R = – 0.430; P < 0.040), pH ($F_{1,20}$ = 14.782; R = – 0.652; P < 0.001) and organic content ($F_{1,21}$ = 7.598; R = – 0.515; P < 0.011), and positively correlated with moisture content ($F_{1,21}$ = 8.112; R = 0.664; P < 0.001). Thus, guano piles farther from the cave entrance were smaller, more acidic, had less organic content and were moister.

The Canonical Correspondence Analysis showed a significant relationship between the physical-chemical and biological parameters for both visual and total/volumetric treatments of the biological parameters (Table 3). The Canonical R for the first root in the visual treatment was 0.865 (SS^2 = 41.139; df = 15; P < 0.000). The distance from the cave entrance (0.467), the area of the guano piles (– 0.425) and the moisture content (0.420) were the most important variables related to those biological parame-
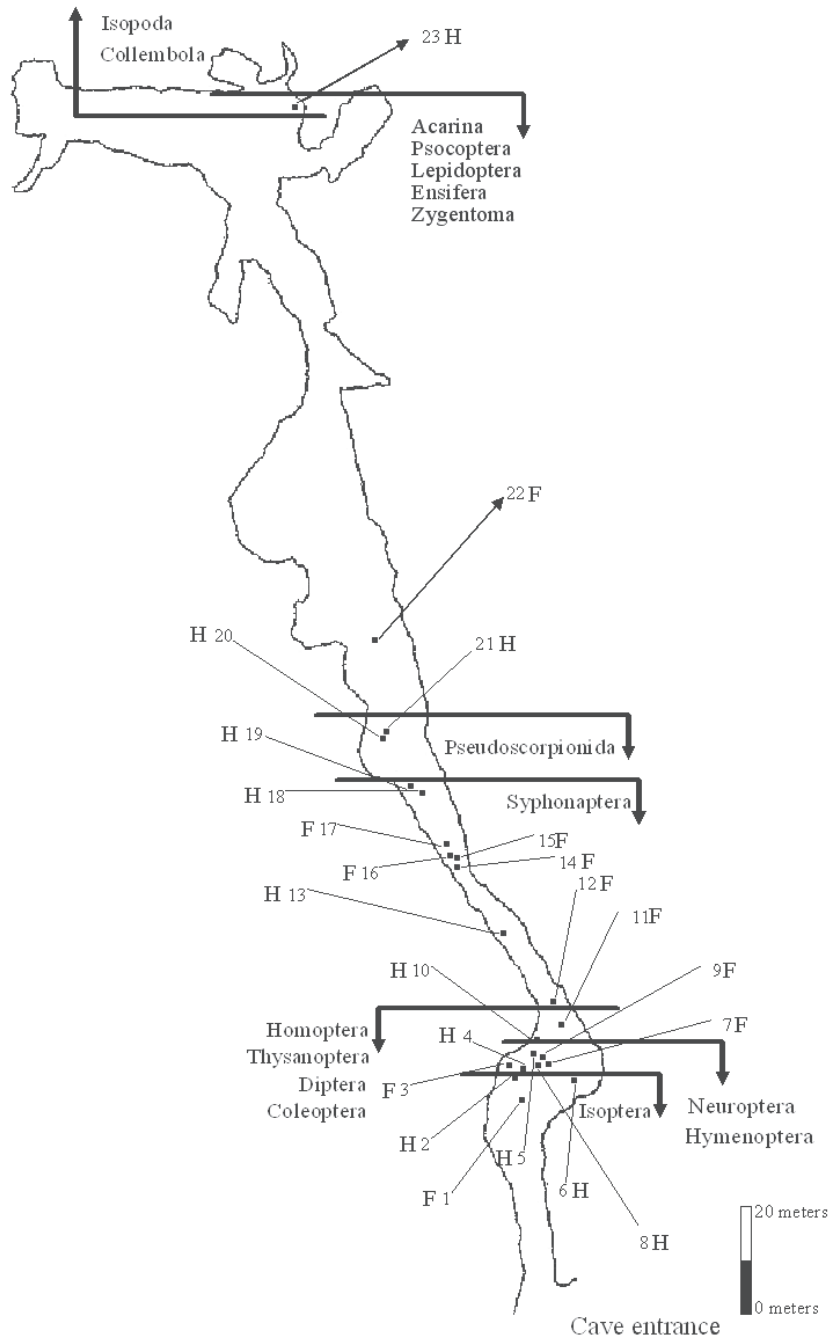
Fig. 1. — Spatial distribution of the orders associated with the guano piles in Morrinho Cave. The dark lines indicate the distance into the cave that the different orders were found (F, Frugivorous guano; H, Haematophagous guano).
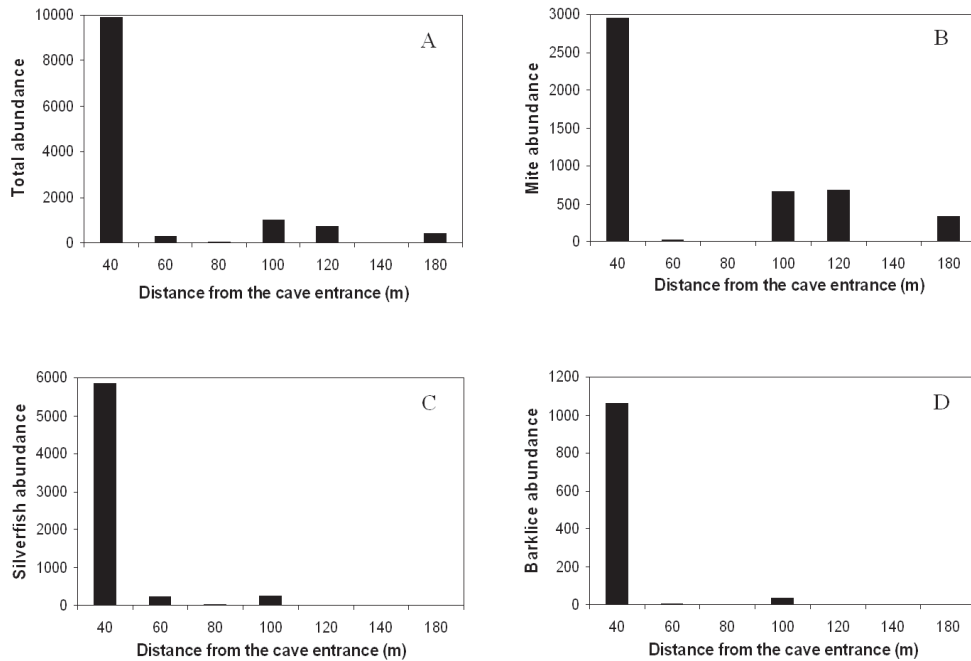
Fig. 2. — Abundance (number of individuals) of some taxa in relation to the distance from the cave entrance: (A) Total abundance; (B) Mites abundance; (C) Silverfish abundance and (D) Barklice abundance.

ters. The Canonical R for the first root in the total/volumetric treatment was 0.991 (SS^2 = 27.390; df = 15; P < 0.026). The area of the guano piles (– 1.315) and the organic content (1.231) were the most important variables related to those biological parameters.

The resource basis for the guano food web in the Morrinho Cave consists of detritivorous organisms that directly consume guano and microorganisms that live in the deposits. These include mites, the most common organisms on guano, springtails (Entomobryidae), barklice (Psyllipsocidae), beetles (Leiodidae, Tenebrionidae, Dermestidae), silverfishes (Lepismatidae), moths (Tineidae, Pyralidae) and flies (Psychodidae, Phoridae, Milichiidae, Cecidomyiidae). Facultative detritivores also occurred, such as woodlice (Platyarthridae) and crickets (Phalangopsidae: *Endecous* sp.). Detritivores were in turn consumed by predators like pseudoscorpions (Chernetidae), spiders (*Loxosceles similis* Mankhaus 1898, *Oecobius annulipes* Lucas 1846, *Nesticoides rufipes* Lucas 1846, *Sicarius tropicus* Mello-Leitão 1936) and ant-lion larvae (Myrmeleontidae). Rare groups included Homoptera, Hymenoptera, Isoptera, Siphonaptera, and Thysanoptera.

The different orders of organisms from the guano deposits, directly or indirectly, exhibited various distributions (Fig. 1). Acarina, Araneida, Isopoda, Collembola, Ensifera, Lepidoptera, Psocoptera and Zygentoma were found in guano throughout the cave. In contrast, other orders were found only in piles close to the entrance (Coleoptera, Diptera, Homoptera, Hymenoptera, Isoptera, Neuroptera and Thysanoptera). Pseudoscorpions and fleas occurred from the entrance through piles close to the middle of the cave.

Table 4.

Richness and guano type preferences of the groups found in Morrinho Cave (H, Haematophagous; F, Frugivorous).

Taxon	Visual richness	Total richness	Guano type
— ARTHROPODA	28	85	
— ARACHNIDA	9	51	
— Araneida	5	7	
Loxosceles similis	1	1	H F
Oecobius annulipes	1	1	H F
Nesticoides rufipes	1	1	H F
Sicarius tropicus	1	1	H
Corinidae	1	1	H
sp. 1	0	1	H F
sp. 2	0	1	H F
— Pseudoscorpionida	1	1	
Chernetidae	1	1	H
— Acarina	3	43	H F
— CRUSTACEA	1	1	
— Isopoda	1	1	
Platyarthridae	1	1	H
— INSECTA	18	33	
— Collembola	1	1	H
Entomobryidae	1	1	
— Ensifera	1	1	H F
— Phalangopsidae	1	1	H F
— Psocoptera	2	3	
Psyllipsocidae	2	3	H F
— Thysanoptera	0	2	H F
— Coleoptera	3	4	
Tenebrionidae	1	1	H F
Leiodidae	1	1	F
Dermestidae	1	1	F
sp. 1	0	1	H F
— Lepidoptera	6	6	
Tineidae	3	3	H F
Pyralidae	2	2	F
sp. 1	1	1	H F
— Diptera	2	7	

(continued)

Table 4. *(continued)*

Taxon	Visual richness	Total richness	Guano type
Psychodidae	0	2	H
Phoridae	0	1	H
Milichiidae	1	1	H F
Cecidomyiidae	0	1	H
Streblidae	1	1	H
larva sp.	0	1	H F
— Hymenoptera	0	1	
Formicidae	0	1	H F
— Homoptera	0	3	H F
— Zygentoma	1	1	H F
— Siphonaptera	1	1	
Pulicidae	1	1	H
— Isoptera	0	1	
Nasutitermitidae	0	1	H
— Neuroptera	1	1	
Myrmeleontidae	1	1	H F
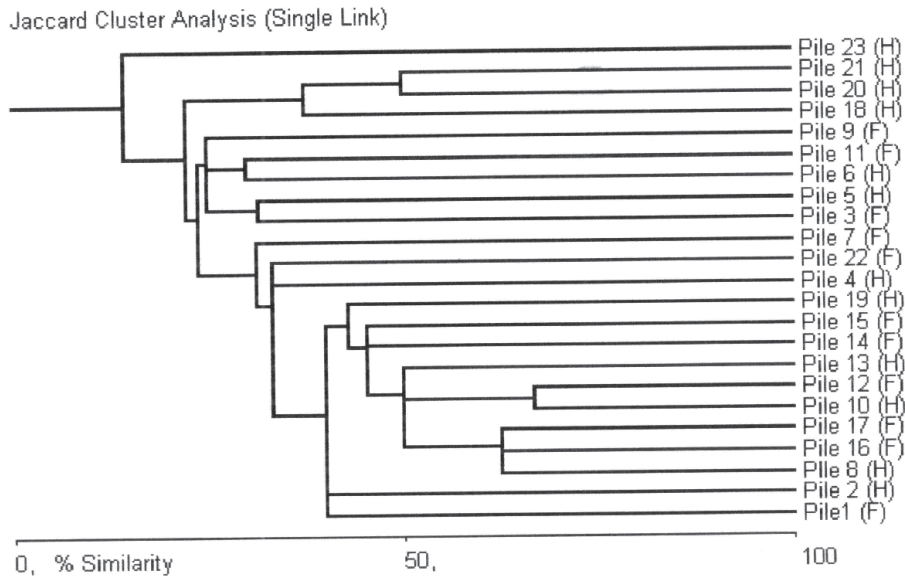
Fig. 3. — Cluster of similarity between all the guano piles in Morrinho Cave.

Table 5.

Similarity matrix between all the guano piles (F, Frugivorous; H, Haematophagous guano).

	Pile 2 (H)	Pile 3 (F)	Pile 4 (H)	Pile 5 (H)	Pile 6 (H)	Pile 7 (F)	Pile 8 (H)	Pile 9 (F)	Pile 10 (H)	Pile 11 (F)	Pile 12 (F)	Pile 13 (H)	Pile 14 (F)	Pile 15 (F)	Pile 16 (F)	Pile 17 (F)	Pile 18 (H)	Pile 19 (H)	Pile 20 (H)	Pile 21 (H)	Pile 22 (F)	Pile 23 (H)
Pile 1 (F)	40.00	9.52	1.40	0.60	11.11	11.76	40.00	23.53	11.11	13.04	12.50	10.00	21.43	23.08	18.18	16.67	7.69	10.00	10.00	12.50	16.67	4.17
Pile 2 (H)	*	9.52	20.00	14.29	11.11	18.75	27.27	16.67	11.11	13.04	12.50	10.00	13.33	23.08	18.18	16.67	7.69	10.00	10.00	12.50	16.67	0.00
Pile 3 (F)	*	*	10.53	31.58	11.36	21.74	4.55	25.00	5.56	25.00	5.88	11.11	4.00	13.64	4.76	9.52	4.55	0.00	0.00	0.00	9.52	6.25
Pile 4 (H)	*	*	*	16.67	11.76	6.25	33.33	11.76	14.29	14.29	16.67	12.50	25.00	16.67	22.22	20.00	9.09	12.50	12.50	16.67	33.33	4.55
Pile 5 (H)	*	*	*	*	13.51	11.76	6.67	21.05	9.09	21.74	10.00	18.18	5.56	20.00	7.14	14.29	6.67	0.00	0.00	0.00	14.29	3.85
Pile 6 (H)	*	*	*	*	*	15.38	14.29	17.50	9.09	30.00	6.06	12.12	16.22	16.67	11.43	14.29	11.11	5.71	5.71	2.94	8.11	10.87
Pile 7 (F)	*	*	*	*	*	*	11.76	23.81	15.38	19.23	16.67	23.08	10.00	16.67	12.50	18.75	5.56	0.00	0.00	0.00	11.76	7.14
Pile 8 (H)	*	*	*	*	*	*	*	23.53	42.86	13.04	28.57	22.22	41.67	33.33	62.50	40.00	16.67	37.50	10.00	12.50	27.27	13.64
Pile 9 (F)	*	*	*	*	*	*	*	*	13.33	17.86	14.29	20.00	14.29	21.05	11.11	16.67	5.00	0.00	0.00	0.00	5.00	3.23
Pile 10 (H)	*	*	*	*	*	*	*	*	*	10.00	66.67	40.00	30.00	33.33	50.00	42.86	0.00	16.67	0.00	0.00	11.11	10.53
Pile 11 (F)	*	*	*	*	*	*	*	*	*	*	5.00	9.52	11.54	21.74	13.64	18.18	8.33	9.52	4.55	5.00	13.04	8.82
Pile 12 (F)	*	*	*	*	*	*	*	*	*	*	*	50.00	20.00	22.22	33.33	28.57	0.00	0.00	0.00	0.00	12.50	5.26
Pile 13 (H)	*	*	*	*	*	*	*	*	*	*	*	*	16.67	30.00	25.00	37.50	10.00	0.00	0.00	0.00	10.00	12.00
Pile 14 (F)	*	*	*	*	*	*	*	*	*	*	*	*	*	26.67	45.45	41.67	21.43	16.67	7.69	9.09	13.33	8.00
Pile 15 (F)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	36.36	45.45	14.29	18.18	8.33	10.00	23.08	14.29
Pile 16 (F)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	42.50	18.18	42.86	11.11	14.29	30.00	8.70
Pile 17 (F)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	16.67	22.22	10.00	12.50	16.67	13.64
Pile 18 (H)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	22.22	37.50	28.57	16.67	10.00
Pile 19 (H)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	14.29	20.00	22.22	4.76
Pile 20 (H)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	50.00	10.00	0.00
Pile 21 (H)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	12.50	8.70
Pile 22 (F)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	8.70

The most abundant orders were generally concentrated relatively close to the cave entrance (~ 40-50 m; Fig. 2A). Mites (Fig. 2B), silverfish (Fig. 2C) and barklice (Fig. 2D) were very abundant in the first 40 m of the cave.

Distinct groups have different preferences for the types of guano. Only one family of Lepidoptera (Pyralidae) and two of Coleoptera (Dermestidae and Leiodidae) were found exclusively in frugivorous bat guano. Conversely many families were found exclusively on haematophagous bat guano, such as Sicariidae (*Sicarius tropicus*) and Corinidae (Araneida), Chernetidae (Pseudoescorpionida), Platyarthridae (Isopoda), Entomobryidae (Collembola), Psychodidae, Phoridae, Cecidomyiidae, Streblidae (Diptera), Pulicidae (Syphonaptera) and Nasutitermitidae (Isoptera). The other groups were found both in haematophagous and frugivorous bat guano (Table 4).

The values of similarity between different piles were variable, ranging from zero to 66.67 (Table 5). The values of similarity did not indicate that communities associated with frugivorous guano are distinct from those found in haematophagous guano (Fig. 3). Furthermore, the highest value of similarity was found between a frugivorous and a haematophagous pile (66.67; piles 12 and 10).

DISCUSSION

Invertebrate communities associated with guano piles in caves are poorly known throughout the world, and most of the knowledge about these communities consists of descriptions of food webs and species composition (DECOU & DECOU 1964, HARRIS 1970, NEGREA & NEGREA 1971, POULSON 1972, DECOU et al. 1974, DECU & TUFESCU 1976, MARTIN 1976, BERNARTH & KUNZ 1981, STRINATI 1982, GNASPINI-NETTO 1989, FERREIRA & MARTINS 1999a, GOMES et al. 2000, BAHIA & FERREIRA 2005). The few ecological data concerning such communities are very recent but contain important information about physical-chemical and biological factors that influence the structure of guano communities (HERRERA 1995, FERREIRA & POMPEU 1997, FERREIRA et al. 2000, BAHIA & FERREIRA 2005).

Inter-relations of the physical-chemical parameters

The distance from the cave entrance had a clear association with other parameters, such as pile area, pH, organic content and moisture content. The negative correlation between distance from the entrance and area, pH and organic content indicates that the bats prefer sites near the entrance instead of sites in the deep zone of the cave. Therefore, the biggest piles are concentrated near the entrance and many of these piles are, in general, fresh (as indicated by the high pH and organic content). The moisture content of the guano, however, is higher far from the entrance; this is as expected, since the external environment is extremely dry and thus most influences the sites near the cave entrance.

General patterns of richness and diversity

A positive relationship between the area of the guano piles and the richness and diversity of the communities was found in earlier studies (FERREIRA & POMPEU

1997, Ferreira & Martins 1998, Ferreira et al. 2000, Bahia & Ferreira 2005). The numbers of individuals or species that use faecal deposits tend to be proportional to the availability of the fecal matter (Doube 1986). However, in large guano deposits, faecal matter accumulates without being consumed, as the organisms remain mostly on the surface. Consequently, one would expect some area effect of greater potential microhabitat variability over a larger surface. Larger deposits with a high diversity of microhabitats (like small holes and cracks) have more associated species, as suggested by the present and other works (Ferreira & Pompeu 1997, Ferreira & Martins 1998). In the present study, richness was positively correlated to pile area. However, the visual diversity and equitability were higher in smaller piles. This relationship is because, in larger piles, huge populations of some species (mainly mites and silverfish) clearly reduce equitability and, thus, diversity. These huge populations are more frequent in bigger piles due to the amount of guano available.

The patterns of variation of richness and diversity of the guano communities in relation to distance from the cave entrance are similar to those found by Ferreira & Pompeu (1997). These authors found a reduction in richness and diversity with increasing distance in the Taboa Cave (Sete Lagoas, Minas Gerais State). Ferreira & Martins (1998) also found a reduction in richness and diversity of spiders associated with guano in Morrinho Cave. However, Ferreira et al. (2000) and Bahia & Ferreira (2005) did not find linear effects between distance from the cave entrance and richness and diversity of guano communities in Lavoura Cave (Matozinhos, Minas Gerais State) and in Mil Pérolas cave (Sete Lagoas, Minas Gerais State) respectively.

Since most invertebrates associated with guano piles are troglophiles and some troglobites, the colonization of each deposit may occur from any place inside the cave. However, in Morrinho Cave, many species associated with guano piles that are usually troglophiles may have been acting as trogloxenes, eventually looking for additional resources in the epigean environment, which would explain the observed relationship found. Furthemore, many big deposits are concentrated near the cave entrance and, since area is a strong factor that determines the structure of the associated communities, the effect of reduction of richness and diversity in deep zones could be only a guano pile area effect. It is important to point out that, although very consistent in many cases, the effect of reduction in richness and diversity of guano communities in deep cave zones may not always be the rule.

The influence of the cave entrance on guano communities (when present) is probably more related to the presence of organic matter that accumulates in the cave entrance (e.g. branches, leafs), which provides additional food resources and increases habitat complexity, attracting some groups (Prous et al. 2004, Prous 2005).

Shape effects

The lack of correlation between the DMI and richness and diversity of the guano piles suggests that many species are able to locate the guano piles by chemotaxy, which corroborates the results found by Ferreira et al. (2000) and Bahia & Ferreira (2005). If colonization occurred exclusively at random, we would expect to find a positive correlation between the DMI and the richness and diversity of the guano piles, since more dendritic deposits would be found more easily and colonized than round deposits of similar area. The only correlation found (IDM × total richness) was not considerable, since it was found specifically for haematophagous bat guano communities and was tested in only four deposits.

Physical-chemical effects

The physical-chemical composition is important in determining richness and abundance of communities on organic deposits (Cornaby 1974; Denno & Cothran 1976; Kuusela & Hanski 1982; Kneidel 1984a, 1984b). The reduction of guano pH over time is well-known (Herrera 1995, Ferreira & Martins 1999a, Gnaspini & Trajano 2001). Fresh guano is alkaline and becomes acidic due to ammoniac fermentation (Hutchinson 1950). However, as Ferreira et al. (2000) showed, pH does not always reflect guano age, since these deposits are open systems that could be affected by chemical (percolation of water, floods, etc.) and physical (landslides, sedimentation, etc.) processes inherent to cave environments.

Except for some rich alkaline piles from Morrinho Cave, the relationship between guano pH and richness is quite similar to that found in Lavoura Cave (Ferreira et al. 2000). However, the diversity and equitability were slightly higher in alkaline piles. This may indicate that alkalinity acts as a barrier to the establishment of huge populations of some species. If a huge population could become established in an alkaline pile, this certainly would reduce diversity and equitability, since it would increase the dominance of a few species. The relationship between guano pH and richness was explained in two, not mutually exclusive, ways (Ferreira et al. 2000). The first is related to the existence of optimum and intermediate values of pH, and the second is related to age of the guano piles (in those cases in which pH actually indicates age). In a general way, both possibilities would be true for Morrinho Cave, but the two rich alkaline piles seem to invalidate both. The two alkaline piles were rapidly colonized and had high richness, even in the apparently extreme pH conditions. However, the richest piles were generally those of moderate pH.

The negative correlation between organic content and total richness suggests that in conditions of high organic content, only a few species were favoured, which developed huge populations thus reducing the equitability of the associated communities. As seen in this and other studies (see Ferreira et al. 2000), more diverse communities were found in guano piles with higher organic content. This effect is expected, since guano deposits with higher amounts of organic matter have potentially richer and diverse communities.

The guano moisture content influences the richness and diversity of the associated communities in Morrinho Cave. Dry deposits are probably restrictive to many populations but favourable for some species, whose populations can become very large.

Taxon-specific pattern

The specific traits of each order influence its distribution and abundance in the cave. In general, the total abundance was higher near the cave entrance, probably due to the large number of piles located within 50 m of the cave entrance. The high number of species and abundance of mites found in these guano deposits corroborate the results of other authors, namely that Acarina are the most abundant and diverse invertebrates in guano (Decou & Decou 1964, Poulson 1972, Harris 1973, Decou et al. 1974, Decu & Tufescu 1976, Martin 1976, Bernath & Kunz 1981, Strinati 1982, Gnaspini-Netto 1989, Whitaker et al. 1991, Ferreira & Pompeu 1997, Ferreira & Martins 1999a, Ferreira et al. 2000, Gnaspini & Trajano 2001, Webster & Whitaker 2005).

The high total abundance of spiders living on guano observed in this study is similar to that found in other studies (Ferreira & Pompeu 1997, Ferreira & Martins 1998, Ferreira et al. 2000). The high spider abundance emphasizes the importance of guano as habitats where these predators can find abundant prey. The irregular distribution of Sicariidae (*Loxosceles similis*, *Sicarius tropicus*) in the main conduit of the cave reflects the great mobility of these species when searching for crickets, silverfish and other arthropods (Ferreira & Martins 1998, Ferreira at al. 2005).

Barklice are common in older guano piles (Negrea & Negrea 1971, Bernarth & Kunz 1981, Strinati 1982, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira & Martins 1999a). The abundance of this group in this cave is probably due to the number of old guano deposits. The fact that abundance of barklice decreased consistently with the distance from the cave entrance, is likely due to the amount of apparently old guano piles close to the cave entrance.

Silverfish are sometimes abundant in guano piles (Ferreira & Martins 1999a), though only rarely. The hundreds of individuals of *Ctenolepisma* sp. (Lepismatidae) observed in older frugivorous and haematophagous guano deposits were probably due to a lack of other resources in the epigean system, since the area has is a semi-arid climate. In other caves in the same region, troglobitic individuals of Nicoleti-idae (*Coletinia brasiliensis*, Mendes & Ferreira 2002) were found to be associated with guano deposits. However, these organisms were associated with all types of organic substrates in these caves (primarily corpses of animals accidentally entering the cave) and were only infrequently observed on guano piles.

Preference for guano types

Although there was an apparently high preference for haematophagous guano (11 exclusive species in contrast to 3 exclusive species in frugivorous guano), this might be due merely to the area of each type. Haematophagous guano piles had an average area of 15,296.3 cm^2, while corresponding value for frugivorous guano piles was 10,779.3 cm^2.

The area of the guano piles and their distance from the cave entrance are undoubtedly important variables determining the diversity of guano communities. This becomes clear when we observe that both frugivorous and haematophagous guano communities exhibit a relationship with those parameters.

The observed similarity values reinforce the idea that the species associated with guano do not exhibit a strong preference for one or another type, being able to colonize and use different kinds of guano.

Invertebrate preferences for different guano types (insectivorous, frugivorous or hematophagous guano) proposed by Gnaspini-Netto (1989) for some Brazilian caves do not apply to Morrinho Cave. Dermestids, which he considered to be specific to insectivorous bat guano, were also found in frugivorous guano. Isopods and psocopterans, considered to be specific to frugivorous guano, were also found in haematophagous guano. Finally, pseudoscorpions and mites were considered specific to insectivorous guano, whereas we found these organisms on haematophagous bat guano. Many invertebrates associated with guano piles are generalistic detritivores, able to consume different types of organic resources (Ferreira & Martins 1999a, 1999b). Therefore, the dependence of some invertebrate groups on specific guano types is probably not as strong as previously thought. Conversely, these patterns of association could be strongly determined by the kind and amount of

resources available in each particular cave system and also by the epigean distribution of the potential cave colonizers that use one or another guano type. GNASPINI & TRAJANO (2001) assumed that blood feeders have a more homogeneous food source than frugivores, especially in dry areas of Brazil. The present data do not corroborate this assumption, since the differences found between the communities associated with haematophagous and frugivorous bat guano were weak.

Community dynamics and species flux

The concept of metacommunity was first used by GILPIN & HANSKI (1991) to represent a set of local communities from different sites connected by dispersion of one or more of its components. According to these authors, a metacommunity follows the same dynamics as a metapopulation, being subject to local extinctions and recolonizations. There is some evidence that the studied system is a metacommunity. The low abundance of organisms in some old piles enhances local extinctions and possible colonization can occur in other guano piles. FERREIRA et al. (2000) suggested that larger deposits can act as sources of colonization for smaller ones. As the guano become older, its quality as a resource decreases and the associated community progressively leaves the pile. Those organisms may colonize other piles to maintain their populations. However, the dynamics of between-pile movements remain largely unknown and merit further research.

Similarity cannot be used to indicate the flux of organisms between communities. However, considering the small distance between deposits and the fact that they are (in the case of Morrinho Cave) the main resource in the system, it is reasonable to accept that the observed values of similarity could reflect the flux of organisms among communities from different piles, a feature typical of metacommunity systems. A high similarity could indicate frequent individual flux, suggesting a single community whose component populations can use many piles to acquire resources. On the other hand, if the observed similarity was equal or very close to zero, such a system would be composed of small isolated communities, each one restricted to one or a few close piles.

Concluding remarks

One of the most important aspects of the structure of guano invertebrate communities is the importance of specific guano traits in determining the structure of the communities that live in caves. Communities from caves in different areas and biomes are dependent on the guano pile area, organic content and other traits inherent to the guano itself. Therefore, the structure of a guano community is more dependent on the microenvironment provided by the guano than on the cave environment as a whole. This is reinforced when cave guano communities are compared to those in other roosts, such as buildings. The structure of guano communities in buildings is quite similar to those found in caves (BERNARTH & KUNZ 1981), even when located in very distinct meso-environments.

Therefore, communities associated with bat guano are more dependent on the guano microenvironment itself than on the cave environment. However, the specific degree of influence of each guano pile trait on the structure of these communities is expected to be variable in different caves.

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