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Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves

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The trophic structure and natural history of bat guano invertebrate communities in Brazilian caves was compared with information concerning bat guano communities in other caves throughout the world. The basis of Brazilian cave guano food webs are detritivorous organisms that directly consume guano, and microorganisms that live off deposits. These include mites, the most common organisms on guano, and others such as springtails (*Acherontides eleonorae* Palacios-Vargas & Gnaspini-Netto 1992), booklice (e.g. Psyllipsocidae), beetles (e.g. Dermestidae, Cholevidae), moths (e.g. Tineidae) and flies (e.g. Phoridae, Milichiidae). Facultative detritivores are also common, forming large populations when other organic substrata, such as vegetable debris, become scarce, as in the case of permanently dry caves. These are isopods (e.g. *Trichorrhina* sp.), diplopods (e.g. *Pseudonannolene* sp.), cockroaches, crickets (e.g. *Endecous* sp.), and silverfish (e.g. *Coletinia brasiliensis* Mendes & Ferreira in press). Other detritivores, like flatworms, earthworms, gastropods and harvestmen, are rarely found. Detrivores are in turn consumed by a wide range of predators, like pseudoscorpions (e.g. Chernetidae), spiders (e.g. *Loxosceles similis* Moenkhaus 1898, *Oecobius annulipes* Lucas 1846), and heteropterans (Reduviidae *Zelurus variegatus* Costa-Lima 1940). Facultative predators, like scorpions and whip-scorpions attracted by prey items, are also occasionally abundant. Food webs of bat guano communities in Brazilian caves are richer in species than those elsewhere.

KEY WORDS: Brazil, caves, bat guano, trophic structure, invertebrate communities, richness, food webs.

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INTRODUCTION

Knowledge of the natural history of bat guano invertebrates in neotropical caves is insufficient to allow generalizations (Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira 1998, Ferreira & Martins 1999, Gnaspini & Trajano in press), but it is more than what is known for other regions of the world, like Australia (Richards 1971), North America (Bernarth & Kunz 1981), Asia (Deharveng & Leclerc 1989) and Africa (Braack 1989) where only glimpses of the natural history of guano organisms have been published.

Feces and dead bodies of bats, various cave dwelling organisms, and other organisms (plant or animal) that have been deposited by chance are widely considered an important source of organic matter in caves in general (Harris 1970, Decu 1986, Ferreira & Martins 1999 and in press). In tropical caves, especially permanently dry ones, bat guano piles are the most common source of organic matter, forming the trophic base for the structure of many invertebrate communities (Decu 1986, Ferreira 1998, Ferreira & Martins 1999 and in press). Less frequently, guano deposits of birds such as the guácharo, *Steatornis caripensis* Humboldt 1817, can also support communities in South American caves (e.g. Venezuela) (Herrera 1995).

The diversity of feeding habits of bats in tropical regions is remarkable (Herzig-Straschil & Robinson 1978, Gnaspini & Trajano in press). According to the feeding habits, there are three main types of bat guano: (i) frugivorous, with small undigested seeds and occasional larger seeds, sometimes with pulp still attached to the feces; (ii) hematophagous, which has a pasty consistency and a reddish color when fresh, becoming black and often powdery when older (Gnaspini-Netto 1989); (iii) insectivorous, peculiar in containing chitinous pieces of insects or other arthropods. This variability allows comparisons among community compositions on different types of bat guano. The physical and nutritional properties of guano piles change with time, the particular environment of each cave, and the type of animal that produces the guano. Due to the great diversity of food, the feeding ecology of bats, the type of bat roosts (caves, buildings, tree hollows and many others), and geographic distribution, the communities of guano invertebrates differ throughout the world. The composition of communities in bat guano in caves of Africa (Braack 1989), Asia (Deharveng & Leclerc 1989), Australia (Richards 1971), North America (Martin 1976), Trinidad (Hill 1969, 1981), Romania (Decou & Decou 1964, Negrea & Negrea 1971, Decu & Tufescu 1976) and in buildings of North America (Bernarth & Kunz 1981, Whitaker et al. 1991) demonstrates such differences, which are further emphasized when compared to those of Brazilian caves.

Bat guano cave communities are important for ecological studies mainly because of their condensed and relatively contained structures (both physically in the guano pile itself and in the overall cave), and to the great number of easily-defined interactions with the overall cave environment. These features allow one to divide larger cave community interactions into units that become more easily studied. Bat guano communities are often considered "isolated" but in fact are not, since a high number of cave invertebrate groups associate and interact with them. The comparisons among communities associated with guano piles in caves or other bat roosts all over the world are, however, very difficult, since such communities are poorly known. Many relevant aspects, such as latitudinal variations and differences among guano communities in different roost types (caves, buildings, tree hol-

lows, etc.) cannot be satisfactorily explored, since the amount of information that these comparisons require is virtually non-existent in the literature.

This paper summarizes and presents new information about the natural history of bat guano invertebrate communities in Brazilian caves. The features of the guano deposits were related, when possible, to the presence or preference of each group associated with them. Another objective was to compare the present information with that of bat guano invertebrate communities in caves throughout the world.

METHODOLOGY

This research was conducted from March, 1996 to January, 1998 in 248 guano piles of frugivorous, insectivorous and hematophagous bats located in caves in the Brazilian states of Minas Gerais (12 caves), Bahia (4 caves), and Goiás (5 caves), and to a lesser extent in Mato Grosso (1 cave), and São Paulo (1 cave) (Table 1). Physico-chemical features of a great variety of guano deposits were observed in these cave environments and were related, when possible, to the presence of each group.

Guano deposits varied greatly in size, shape, thickness, and location in relation to the cave entrances. In many caves, organisms were collected and features of each deposit (type, size and distance from the cave entrance) were recorded. However, in a few caves, some data were recorded during brief and cursory field trips.

Larger organisms were sometimes collected with the aid of a magnifying glass, forceps and small brushes. Berlese-Tullgren funnels were used to separate smaller organisms from guano (Bernarth & Kunz 1981). Some guano piles were visually divided into sub-samples of 400 cm^2, and as many of these sub-samples were randomly removed as was necessary to correspond to 10% of the total area of the pile. All organisms from each sub-sample were preserved in 70% alcohol. Taxa were identified as precisely as possible but in many cases identifications were limited to families.

RESULTS

The basis of the food web in bat guano communities in the sampled caves are detritivorous organisms that directly consume guano and microorganisms that live off deposits (Figs 1-4). These include mites, the most common organisms on guano, and other invertebrates including: springtails (e.g. Entomobryidae, Hypogastruridae, Isotomidae and Arrhopalitidae); booklice (mainly Psyllipsocidae); beetles, specifically larvae (Dermestidae, Tenebrionidae, and Leiodidae, the most abundant families, followed by Carabidae, Trogidae, and Histeridae); moths (mainly Tineidae larvae); and fly larvae in fresh guano (Drosophilidae, Phoridae, Milichiidae, and Fanniidae). Facultative detritivores are also common, forming large populations, when other organic substrata, such as vegetable debris, become scarce, as in permanently dry caves. Examples are isopods (e.g. Armadillidae, Plathyartridae, and Styloniscidae), diplopods (mainly Spirostrepida), chilopods (mainly Geophylomorpha), cockroaches, crickets (mainly Phalangopsidae), and silverfish (Lepismatidae, Nicoletiidae). Other detritivores, like flatworms, earthworms, gastropods and harvestmen, were rarely found.

Detritivores are in turn consumed by a wide range of predators. Pseudoscorpions (mainly Chernetidae), spiders (e.g. Theridiidae, Sicariidae, and Oecobidae), mites (e.g. Macrochelidae), and bugs (primarily Reduviidae) were the most common

Table 1.

Caves sampled in the study, with number and type of guano piles (H, hematophagous; I, insectivorous; F, frugivorous).

Cave	State	City	Co-ordinates	Type and number of guano piles sampled
01. Lavoura	Minas Gerais	Matozinhos	44°02'14"W 19°31'27"S	26 H
02. Piriás	Minas Gerais	Matozinhos	—	08 H
03. Taboa	Minas Gerais	Sete Lagoas	—	13 H, 07 I
04. Moinho	Minas Gerais	São José da Lapa	—	05 H
05. Lapa Vermelha	Minas Gerais	Confins	43°59'44"W 19°36'42"S	06 H
06. Morena	Minas Gerais	Cordisburgo	44°20'27"W 19°09'48"S	15 H
07. Ossos	Minas Gerais	Itacarambi	—	12 H
08. Bonita	Minas Gerais	Itacarambi	44°14'20"W 15°06'23"S	08 H
09. Caboclo	Minas Gerais	Itacarambi	43°51'24"W 18°17'14"S	13 H
10. Carlúcio	Minas Gerais	Januária	44°15'43"W 15°05'01"S	09 H
11. Rezar	Minas Gerais	Januária	44°13'06"W 15°08'28"S	14 H
12. Brejal	Minas Gerais	Januária	44°15'39"W 15°05'07"S	08 H
13. Morrinho	Bahia	Campo Formoso	40°55'05"W 10°12'32"S	12 H, 11 F
14. Boa Vista	Bahia	Campo Formoso	40°51'39"W 10°09'36"S	05 H, 10 F
15. Convento	Bahia	Campo Formoso	10°02'56"W 40°43'37"S	10 H, 04 I
16. Cesário	Bahia	Campo Formoso	10°01'01"W 40°42'02"S	06 H
17. Angélica	Goiás	São Domingos	46°23'20"W 13°31'24"S	10 H
18. Indio I	Goiás	Uruaçu	—	05 H
19. Indio II	Goiás	Uruaçu	—	02 H, 04 I
20. Riacho Fundo	Goiás	Niquelândia	—	05 H, 08 I
21. Lagoas	Goiás	Niquelândia	—	03 H, 02 I
22. Aroe Jari	Mato Grosso	Chapada Guimarães	52°27'W 55°35'S	02 I
23. Paivas	São Paulo	Iporanga	48°27'32"W 24°16'24"S	05 H

predators. Facultative predators, like scorpions and whip-scorpions, were also found. All the groups that were found in guano piles during this work are listed in Table 2.

Nematodes were mainly found in deposits of fresh guano. Gastropods occurred, at low frequency, in some guano deposits. Such associations always occurred in saturated caves in which deposits (even the old ones) were very wet.

Many orders of Arachnida were found in guano deposits in the sampled caves. Scorpions (Scorpionida) were observed only in a single cave (Riacho Fundo) in the north of Goiás State which contains both large guano piles from insectivorous bats and smaller ones from hematophagous bats. Individuals of *Tytius* sp. were distributed in a wide range of substrates, including guano, but only on insectivorous guano piles. They likely were feeding on crickets or cockroaches (which were abundant) or other medium-size detritivores.

Whip-scorpions (Amblypygi) were associated with guano piles only when they were hunting for potential prey items, mainly crickets and roaches. Individuals of the three main families occurring in Brazilian caves (Phrinidae, Damonidae, and Charontidae) were found in guano piles.

Harvestmen (Opilionida) were abundant in several caves and were both directly and indirectly associated with bat guano. Individuals were always observed in old hematophagous and frugivorous guano deposits, likely feeding on the guano itself.

Pseudoscorpions (mainly Chernetidae) were frequently found in guano deposits, mainly older ones. Many individuals were observed and collected in all three types of guano deposits, though they were more common in hematophagous ones. Populations of pseudoscorpions associated with guano were generally small, but some may have had tens of individuals. They prey upon mites, springtails, and the young of other organisms, such as silverfish. In some situations, individuals were seen moving between guano piles, possibly searching for a greater abundance of prey items.

Spiders (Araneida) were found in nearly all types of guano in nearly all conditions. However, they rarely occurred in fresh guano piles. Different families of spiders, however, seemed to prefer different types and ages of guano in the sampled caves.

Theridiids were the most abundant spider group. These small spiders lived in small holes in the guano, feeding on small detritivores such as psocopterans, crickets, roaches, and probably springtails. Some species (*Netiscodes rufipes* Lucas 1846) were preferentially found in guano piles near the cave entrances.

Sicariids were also frequently associated with guano deposits. *Loxosceles* spp. occurred in many substrata, and are clearly cave generalists; they were found roughly equally on all types of guano, except for fresh deposits, which they avoided. These spiders were generally found at the edge, but sometimes near the middle

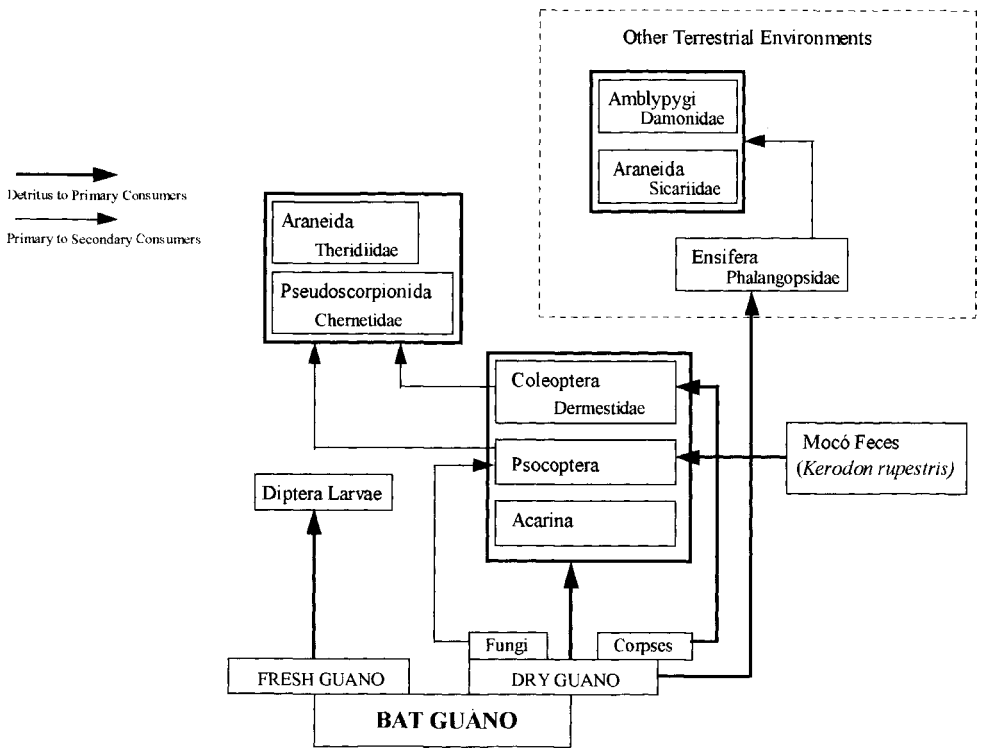

Fig. 1. — Food web of a bat guano community in Ossos cave, north Minas Gerais State.

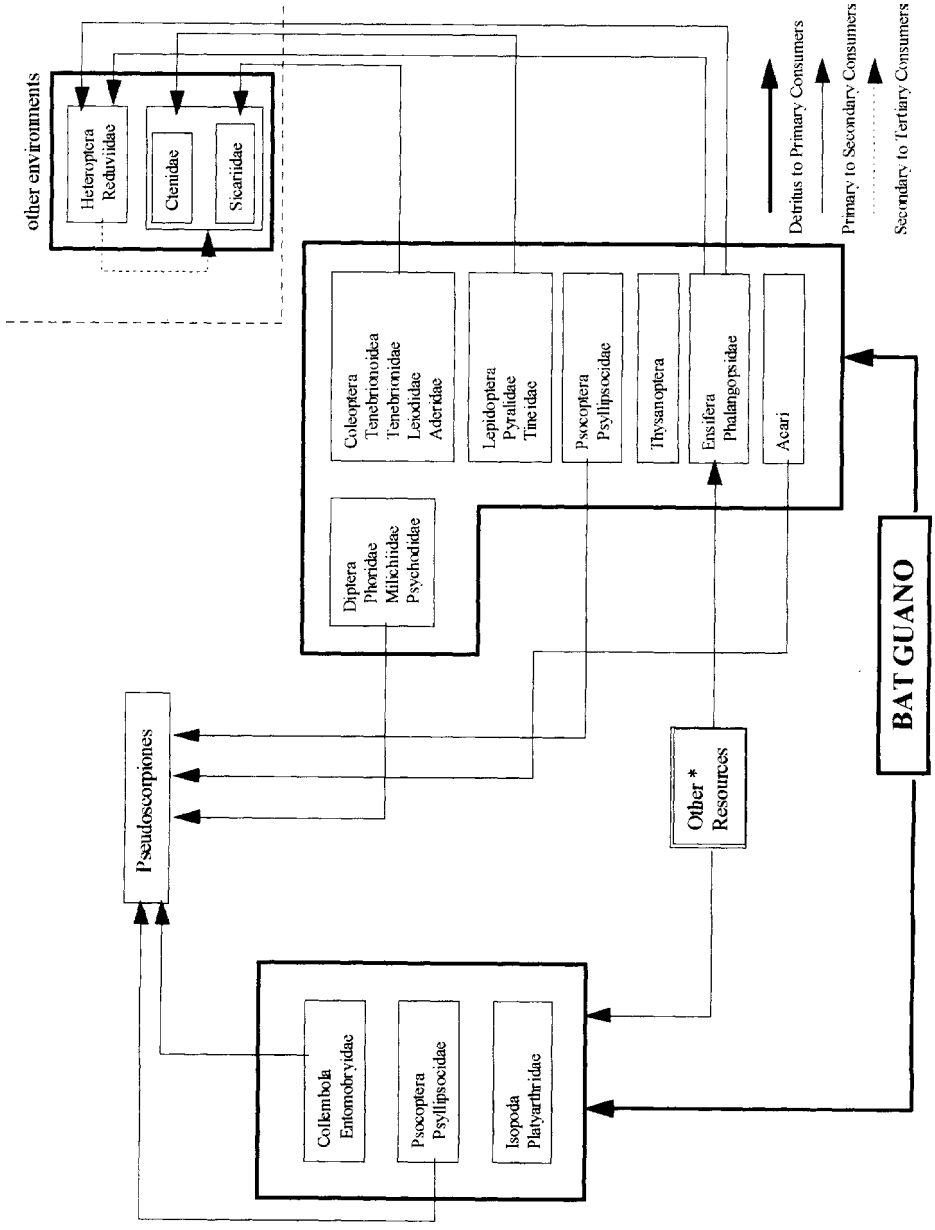

Fig. 2. — Food web of a bat guano community in Lavoura cave, central Minas Gerais State.

of guano piles. Prey items include crickets, roaches, bugs, silverfish, and harvestmen. In contrast to *Loxosceles* spp., *Sicarius* spp. preferred to stay in the middle of old frugivorous deposits, where they buried themselves with their legs and waited for prey, the same items used by *Loxosceles* spp.

Oecobids were found in some caves, as in north Bahia State. In these caves, they were often abundant on the guano pile surface or in small holes in it, and fed on small detritivores such as silverfish, psocopterans, and perhaps springtails.

Members of Theridiosomatidae, Corinnidae, and Theraphosidae were less commonly found in guano. Like these families, which are not typically associated with guano, Ctenidae (*Ctenus* spp. and *Enoploctenus* spp.) and Pholcidae (*Blechroscelis* spp.) were also observed.

Mites practically occurred everywhere guano was found. However, there were family level preferences for specific types of bat guano. Families like Ameroseiidae, Laelapidae, Macronyssidae, Phytoseiidae (Gamasida), Aphelacaridae, Microzetidae and Sphaerochthoniidae (Oribatida) were preferentially found in old hematophagous piles. In fresh guano, individuals of the sub-order Ixodida (mainly Argasidae, e.g. *Ornithodoros* spp.) were found.

Several isopods were found in guano piles. Each family showed a preference for a different substratum. Armadillids, for instance, did not show preferences for a

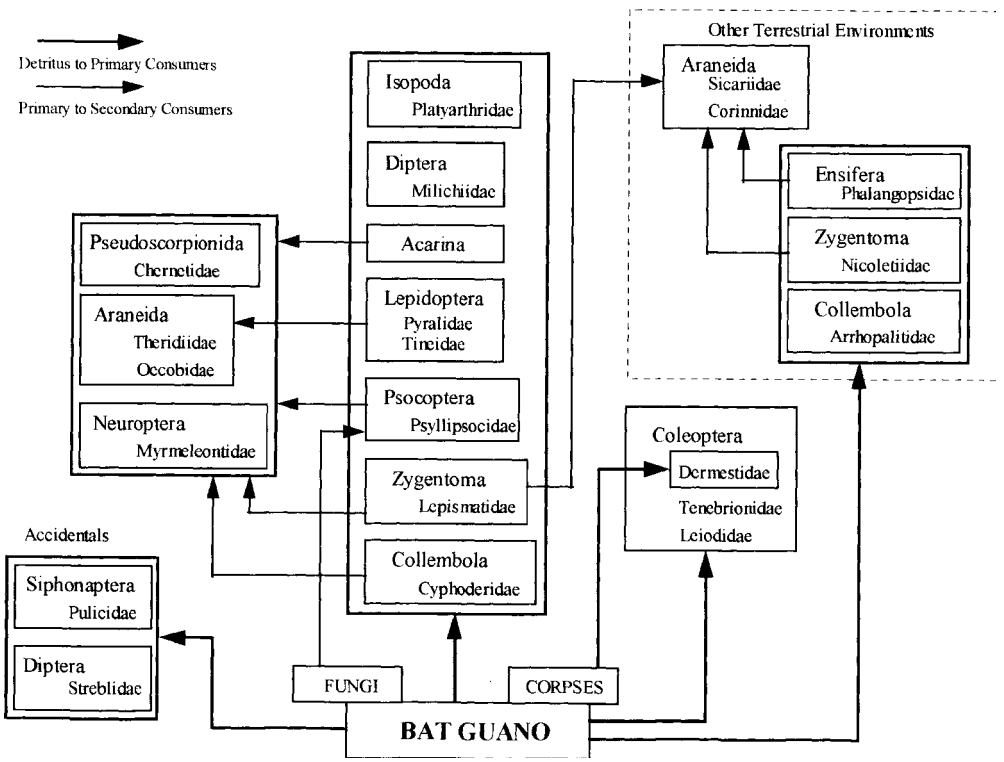

Fig. 3. — Food web of a bat guano community in Morrinho cave, north Bahia State.

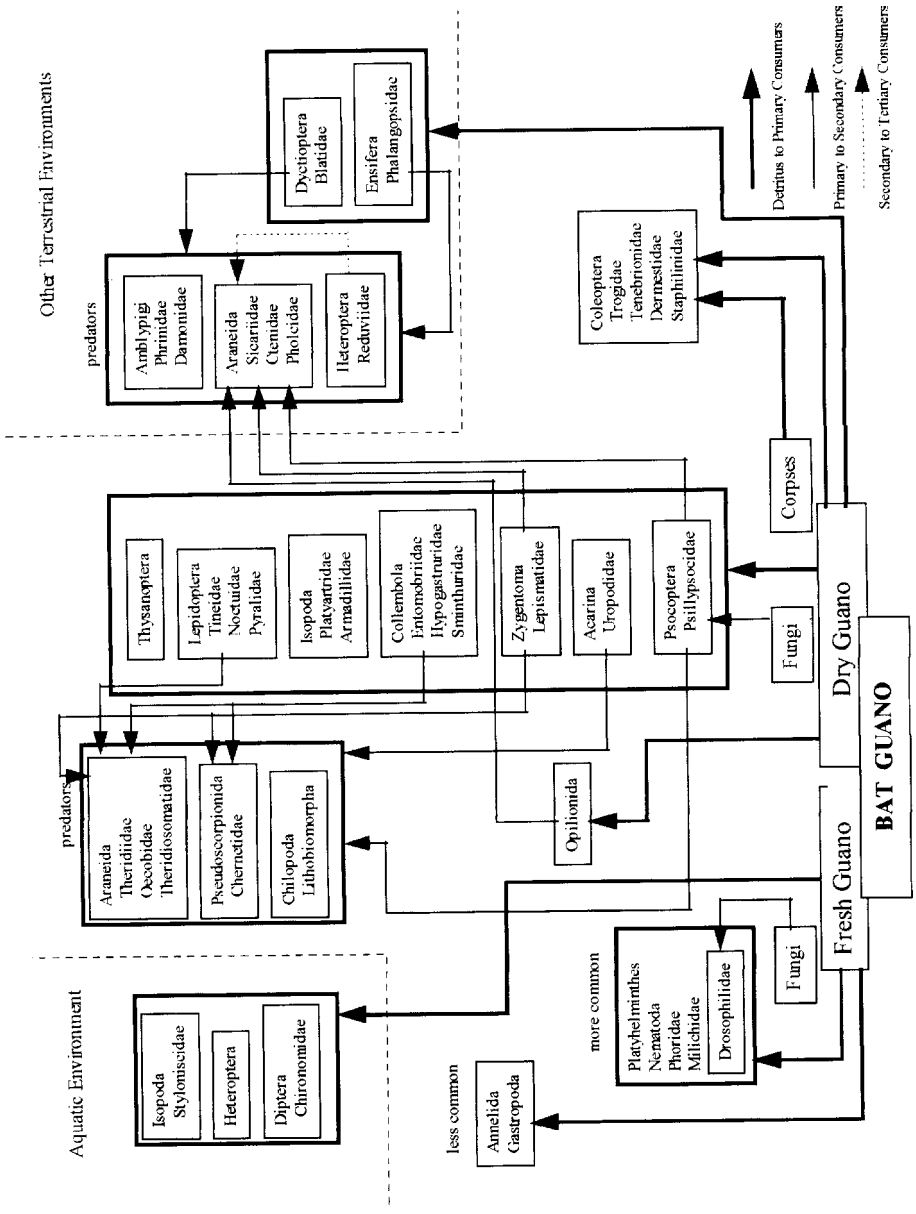

Fig. 4. — General food web of bat guano communities in Brazilian caves.

Table 2.

Taxa reported in bat guano piles in the sampled caves (numbers correspond to the caves listed in Table 1).

Taxon \ Cave	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
– NEMATODA						+	+																
– ARTHROPODA	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
– ARACHNIDA	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
– Acarina	+		+				+						+										
Actinedida													+										
Gamasida	+		+										+										
Ameroseiidae	+																						
Laelapidae	+																						
Macrochelidae													+										
Macronyssidae	+																						
Phytoseiidae	+																						
Uropodidae													+										
Oribatida	+		+				+					+	+										
Aphelacaridae	+																						
Microzetidae	+																						
Sphaerochthoniidae	+																						
– Amblypygi							+		+	+	+			+	+	+	+	+	+	+	+		
Charontidae																+							
Damonidae							+		+	+	+												
Phrynidae														+	+	+	+	+	+	+	+		
– Araneida	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+			+			
Corinnidae													+										
Oecobidae													+										
Ctenidae	+																						
Pholcidae	+											+											
Sicariidae	+	+			+	+	+	+	+	+	+	+	+	+	+		+	+	+	+			
Theraphosidae	+																						
Theridiidae		+	+				+		+			+	+		+	+	+			+			
Theridiosomatidae			+											+									
– Opilionida			+																				

(continued)

Table 2 *(continued)*

Taxon \ Cave	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
– Pseudoscorpionida	+	+	+			+	+	+	+	+	+		+	+	+								
Chernetidae	+	+	+			+			+				+	+	+								
Garypidae							+			+	+												
– Scorpionida																				+			
Buthidae																				+			
– Crustacea Isopoda	+	+	+	+	+						+	+	+										
Armadillidae											+	+											
Plathyarthridae	+	+	+										+										
Styloniscidae			+	+	+																		
– Myriapoda																	+						
– Diplopoda				+		+																	
– Chilopoda		+										+			+		+						
Lithobiomorpha		+													+								
Geophilomorpha												+											
Scutigeromorpha												+								+			
– Insecta	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
– Coleoptera	+	+	+			+	+	+	+	+	+	+	+	+			+						
Aderidae	+																						
Anobiidae									+														
Carabidae		+										+											
Dermestidae	+		+				+		+	+			+										
Elateridae										+													
Histeridae			+																				
Lampyridae												+											
Leiodidae	+		+										+				+						
Ptinidae										+	+	+											
Scarabaeidae									+														
Staphylinidae (+ Pselaphidae)								+				+											
Tenebrionidae	+					+	+	+	+	+	+	+	+	+									
– Collembola	+		+			+						+	+				+						

(continued)

Table 2. *(continued)*

Taxon \ Cave	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Arrhopalitidae												+	+										
Cyphoderidae												+	+				+						
Entomobryidae	+		+																			+	
Hypogastruridae																							
Isotomidae						+																	
Paronellidae			+																				
Sminthuridae						+																	
– Dictyoptera			+					+				+						+	+				
– Diptera	+	+	+			+			+	+		+	+		+		+						
Cecidomyiidae	+											+											
Drosophilidae		+										+											
Fanniidae			+																				
Milichiidae	+											+	+										
Muscidae					+							+	+										
Phoridae	+		+			+						+			+		+						
Psychodidae	+				+				+	+													
Sciaridae						+																	
Sphaeroceridae						+							+										
Stratiomyidae		+																					
Streblidae													+								+	+	
– Ensifera	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
– Heteroptera	+		+			+																	
Reduviidae	+		+																				
Veliidae						+											+						
– Hymenoptera	+																						
Formicidae												+	+										
Signiphoridae	+																				+		
– Lepidoptera	+	+			+	+	+	+	+	+	+	+	+	+	+		+			+			
Noctuidae	+																						
Pyralidae	+												+								+		
Tineidae	+	+			+	+	+	+	+	+	+	+	+	+	+		+			+			

(continued)

Table 2 *(continued)*

Taxon \ Cave	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
– Neuroptera												+	+										
Myrmeleontidae													+										
– Psocoptera	+		+			+	+	+	+	+	+	+	+	+	+		+						
Psyllipsocidae	+		+			+	+						+	+	+		+						
Trogiidae							+	+	+	+	+	+											
– Siphonaptera												+	+										
Pulicidae												+	+										
– Thysanoptera	+																						
– Zygentoma												+	+	+									
Lepismatidae												+	+	+									
Nicoletiidae												+	+	+									

specific age of guano, but seemed to prefer hematophagous bat guano deposits. Platyarthrids preferred old guano piles, probably consuming the guano itself or the fungi associated with it. Some genera (e.g. *Trichorhina* spp.) seemed to have distinct rather than overlapping generations, as individuals of two life stages (adult plus young) were never observed together. Some species of platyarthrids entered small holes in guano piles and could remain there for long periods of time. Styloniscids were always associated with immersed guano piles in travertine (small pools delimited by calcareous deposits). They seemed to prefer guano as a food source, even in the presence of other organic matter, such as corpses or vegetable debris. All observed occurrences of styloniscids were on hematophagous bat guano.

The most common chilopods in bat guano were lithobiomorphs, which tended to be associated with older deposits of hematophagous bat guano, but were rather rare. Scutigeromorpha (mainly Scutigeridae) were also rarely found but were observed several times near guano piles in caves in north Goiás State and in the valley of the Peruaçú River (north Minas Gerais State). Geophylomorpha were found in some hematophagous guano piles in Brejal cave (Minas Gerais State).

Diplopods were found frequently in hematophagous and frugivorous bat guano. Many Pseudonannolenidae (order Spirostrepida) were observed in/or near guano deposits of several caves. Individuals of this family (mainly *Pseudonannolene* spp.) were frequently found in some caves on other organic substrata (e.g. vegetable debris). Polydesmida (Chelodesmidae) were observed feeding in hematophagous guano piles.

Several orders of Insecta were found in bat guano deposits. Springtails (Collembola) were the most commonly found, which, like mites, were often quite abundant. Huge populations of hypogastrurids (e.g. *Acherontides eleonorae* were found in a single cave (Paiva) on hematophagous

guano. Podurids, typically rare in guano, were found in it when other organic substrata were scarce (dry caves). In addition to these, arrhopalitids were also commonly observed, including a troglomorphic species (*Arrhopalites* sp.) in Morrinho cave (Bahia State). Cyphoderids, entomobryids, paronellids and sminthurids were mainly found in hematophagous guano piles, some with large populations in bigger piles. Springtails, like booklice, were very important prey for many predators, especially spiders and pseudoscorpions.

Silverfish (Zygentoma) were very abundant in bat guano piles in some caves. Hundreds of individuals of the family Lepismatidae were observed in older frugivorous guano deposits in Morrinho cave (Bahia State, Fig. 3). In other caves in the same region, troglobitic individuals of Nicoletiidae (*Coletinia brasiliensis*, MENDES & FERREIRA in press) were found indirectly associated with guano deposits. These organisms were associated with all types of organic substrates in these caves (primarily corpses of accidentals) and were only infrequently observed on guano piles. Silverfish, like springtails, were commonly observed being eaten by spiders, pseudoscorpions, and other predators.

Crickets (mainly Phalangopsidae) were normally found near or in guano piles, being observed on frugivorous, insectivorous (in caves of Niquelândia city, Goiás), and hematophagous bat guano. The most common genus was *Endecous* sp., which has a wide distribution and high abundance in Brazilian caves. Crickets were seen directly feeding on the bat guano, and on corpses of bats or arthropods found on it.

The few individuals of roaches observed in this study were on older hematophagous and frugivorous piles, mainly in Minas Gerais State caves.

Booklice (mainly Psyllipsocidae) were normally found in guano in large numbers (tens of individuals). Populations of this order preferred older deposits, rarely being found in fresh guano, and apparently showed no preference for a specific guano type. Psocopterans were found in a variety of other organic substrates besides guano, such as rodent (*Kerodon rupestris* Wied. 1820) feces (always of older age), as observed in caves of the Peruaçú River valley (north Minas Gerais State, Fig. 1). Some individuals showed a clear preference for corpses of bats or other animals like diplopods (also old) which were commonly found on guano piles. Tens of individuals were seen several times under carcasses on guano piles, in addition to a few others spread throughout the guano. Some of these insects were likely feeding on fungi growing on the guano. Like other small insects, psocopterans are also very important prey items for cave predators.

Ant-lion larvae (Neuroptera Myrmeleontidae) in Morrinho cave (Campo Formoso-Bahia State) represent the first record of this order in guano piles. Individuals were found in older hematophagous guano deposits approximately 40 m from the cave entrance. In contrast with most myrmeleontid larvae, they did not form cone traps in the guano, but lived in small openings in the deposits. Unfortunately no individual was observed capturing a prey, and thus capture strategy (pursuit or passive) could not be recorded, though it is likely passive.

The few individuals of thrips (Thysanoptera) observed in this study were on old deposits, mainly of frugivorous bats. Only adult individuals were found, exclusively in permanently dry caves in which guano was the main source of organic matter.

Reduviidae were the most common heteropterans found in this study. Nymphs of *Zelurus* spp. were frequent in many guano piles, primarily older ones. These reduviids preyed upon detritivores found in guano deposits, feeding on different groups of insects (psocopterans, silverfish, crickets, etc.) according to their stage of development.

Many guano deposits contained a large variety of beetles (Coleoptera) from the families Dermestidae, Histeridae, Hydrophilidae, Leiodidae, Scarabaeidae (incl. Trogidae), Staphylinidae (incl. Pselaphidae), and Tenebrionidae. Trogine scarabs were found in very old deposits (mainly hematophagous), always close to bat carcasses. Tenebrionids (mainly larvae) were found in large numbers in old deposits of any type. Dermestids were abundant on old frugivorous guano piles, often in populations of several hundred, and were a primary food source for many predators (Table 3).

Ants (Hymenoptera Formicidae) were occasionally found near bat guano piles. One ant midden was found between two guano deposits in Morrinho cave (north Bahia State). The fauna in the ant midden was quite different from that of the nearby guano piles (around 50 cm away).

Several moth larvae, mainly noctuids, pyralids, and tineids, appeared very frequently in guano deposits. All of them were almost exclusively found in old guano piles as larvae, and adults of these families were rarely observed on guano. The larvae probably are a very important source of food for many predators. Tineids were usually very abundant (tens of individuals), and adults have been observed on frugivorous guano in caves in north Bahia State.

Flies (Diptera) were commonly found in guano. Some fresh guano deposits (mainly of hematophagous bat guano) contained numerous larvae, mainly Drosophilidae. Many other families, such as Muscidae, Psychodidae, Fanniidae, Sphaeroceridae, Milichiidae and Phoridae, were observed in this study. Most flies of these families preferred fresh hematophagous guano piles. Streblids were occasionally found in guano piles, e.g. some species of fleas (Siphonaptera).

Table 3.

Taxa reported in bat guano piles throughout the world (modified from Gnaspini & Trajano in press. The marked taxa* were observed in this study).

Taxon	South America	Africa	Australia	Asia	North America	Europe
– Platyhelminthes	+					
Dugesiidae	+					
– Nematoda*	+				+	
– Mollusca Gastropoda	+					+
Subulinidae	+					
Physidae	+					
– Annelida Oligochaeta	+					+
– Arthropoda	+	+	+	+	+	+
– Arachnida	+	+	+	+	+	+
– Acarina*	+	+	+	+	+	

(continued)

Table 3 *(continued)*

Taxon	South America	Africa	Australia	Asia	North America	Europe
Acaridida	+		+			
Actinedida*	+		+			
Gamasida*	+		+		+	+
Ameroseiidae*	+					
Laelapidae*	+					
Macrochelidae*	+					+
Macronyssidae*	+					
Phytoseiidae*	+					
Rhodacaridae	+					
Uropodidae*	+					+
Oribatida*	+	+				+
Aphelacaridae*	+					
Microzetidae*	+					
Sphaerochthoniidae*	+					
– Amblypygi*	+			+		
Charontidae*	+					
Damonidae*	+					
Phrynidae*	+					
– Araneida*	+	+	+	+	+	+
Clubionidae					+	
Corinnidae*	+					
Ctenidae*	+					
Oecobidae*	+					
Pholcidae*	+					+
Sicariidae*	+					
Theraphosidae*	+					
Theridiidae*	+					+
Theridiosomatidae*	+					
– Opilionida*	+	+				+
– Pseudoscorpionida*	+		+	+	+	+
Cheliferidae					+	
Chernetidae*	+		+	+		
Garypidae*	+					
– Ricinulei	+					
– Schizomida				+		
– Scorpionida*	+					
Buthidae*	+					
– Crustacea Isopoda*	+	+	+	+		+
Armadillidae*	+		+	+		
Cylisticidae						+
Mesoniscidae						+
Plathyarthridae*	+					
Phylosciidae	+					
Porcellionidae						+
Scleropactidae	+					
Styloniscidae*	+					
Trichoniscidae						+
– Myriapoda*	+	+	+	+	+	+

(continued)

Table 3 *(continued)*

Taxon	South America	Africa	Australia	Asia	North America	Europe
– Diplopoda*	+	+		+		+
– Chilopoda*	+			+	+	+
Lithobiomorpha*	+					+
Geophilomorpha*	+					
Scutigeromorpha*	+					
– Symphyla	+					
– INSECTA*	+	+	+	+	+	+
– Coleoptera*	+	+	+	+	+	
Aderidae*				+		
Anobiidae*	+					+
Anthicidae					+	
Carabidae*	+		+		+	+
Cerylonidae	+					
Cryptophagidae						+
Curculionidae	+					
Dermestidae*	+			+	+	
Elateridae*	+				+	
Histeridae*	+		+		+	+
Hydrophilidae	+	+		+		
Lampyridae*	+					
Leiodidae*	+		+			
Nitidulidae	+					
Ptiliidae	+					
Ptinidae*	+	+	+			
Scarabaeidae*	+		+	+		
Scydmaenidae	+					
Staphylinidae* (+ Pselaphidae)	+			+	+	+
Tenebrionidae*	+	+	+		+	
– Collembola*	+	+	+	+	+	+
Arrhopalitidae*	+					
Cyphoderidae*	+					
Dicyrtomidae	+					
Entomobryidae*	+			+		+
Hypogastruridae*	+			+		+
Isotomidae*	+					+
Onychiuridae	+					+
Oncopoduridae	+					+
Paronellidae*	+			+		
Sminthuridae*	+					
– Dermaptera	+					
– Dictyoptera*	+	+	+	+		
– Diplura						+
– Diptera*	+	+	+	+	+	+
Anthomyidae					+	
Cecidomyiidae*	+				+	
Ceratopogonidae	+					
Cypselidae						+

(continued)

Table 3 *(continued)*

Taxon	South America	Africa	Australia	Asia	North America	Europe
Dolichopodidae	+					
Drosophilidae*	+					
Empididae	+					
Fanniidae*	+		+			
Heleomyzidae						+
Lycoriidae						+
Milichiidae*	+			+	+	
Muscidae*	+				+	+
Mycetophilidae					+	
Phoridae*	+		+	+	+	+
Psychodidae*	+	+				+
Scatopsidae	+					
Scenopinidae	+				+	
Sciaridae*	+				+	+
Sphaeroceridae*	+	+		+		+
Stratiomyidae*	+			+		
Streblidae*	+					
– Ensifera*	+	+	+	+		
– Heteroptera*	+	+		+	+	
Anthocoridae					+	
Cimicidae					+	
Cydnidae	+					
Lygaeidae	+					
Reduviidae*	+	+		+	+	
Veliidae*	+	+				
– Hymenoptera*	+	+			+	
Bethylidae					+	
Encyrtidae					+	
Formicidae*	+	+				
Signiphoridae*	+					
– Lepidoptera*	+	+	+	+		+
Lyonetiidae		+				
Noctuidae*	+					
Pyralidae*	+					
Tineidae*	+		+	+		+
– Neuroptera*	+					
Myrmeleontidae*	+					
– Psocoptera*	+		+	+		+
Liposcelidae					+	
Psyllipsocidae*	+					
Trogiidae*	+					
– Siphonaptera*	+				+	
Ischnopsyllidae					+	
Pulicidae*	+					
– Thysanoptera*	+					
– Zygentoma*	+	+				
Lepismatidae*	+					
Nicoletiidae*	+					

DISCUSSION

The only variable that excluded piles from the present study was size, since structured communities were only observed in guano piles larger than 400 cm^2. Smaller deposits rarely, if ever, support a large variety of species, and thus do not adequately reflect the true cave community composition and structure.

Compositions of communities of guano invertebrates vary among different regions of the world. As expected, certain invertebrate orders tend to be universal, but variations occur at the family level. These variations are further accentuated when organisms facultatively associated with guano are included in comparisons.

Flatworms (Platyhelminthes) and nematodes (as in this work) are found in deposits of fresh guano, and their presence has been recorded in Brazilian caves (Gnaspini & Trajano in press). Some species are likely carried in and deposited by bats. Since they are only found in fresh guano, they can be considered "pioneer" species.

Gastropods can potentially occur in guano deposits (Strinati 1982), but are rarely found in it. Thus it is difficult to determine their preference for a specific guano type. Guano age seems to be an important limiting factor to gastropod occurrence, since they are only found in older deposits. Their association with guano is likely facultative: they only make use of guano when other organic resources become rare or disappear. Subulinidae and Physidae are the gastropod families found so far in Brazilian bat guano deposits (Gnaspini & Trajano in press).

Although earthworms (Annelida Oligochaeta) were not found during this study, they have been recorded in caves in São Paulo State on hematophagous and frugivorous bat deposits (Gnaspini & Trajano in press). Otherwise they have been recorded throughout the world (Decou & Decou 1964, Decou et al. 1974, Decu & Tufescu 1976).

Different orders of Arachnida can also be found in guano deposits throughout the world (Decou & Decou 1964, Decu & Tufescu 1976, Decu 1986, Gnaspini-Netto 1989). For comparison between Brazilian and other caves, the occurrence of each order will be separately discussed.

The unique occurrence of scorpions (Scorpionida) in guano piles in Riacho Fundo cave is certainly due to their relatively uncommon frequency in Brazilian caves. The lack of prey items in other substrata in that cave seems to be an important factor in their association with guano.

The association of whip-scorpions (Amblypygi) with guano piles seems to occur primarily when prey in other areas of the cave become scarce. The fact that individuals of the three main families of Brazilian Amblypygi were found mainly in older guano deposits suggests a preference for these, likely based on the wider variety of prey in many older deposits, while there was no evident preference according to guano type.

Harvestmen (Opilionida) are abundant in several Brazilian caves (Ferreira & Pompeu 1997, Gnaspini & Trajano in press) which explains their presence in some caves associated with guano, as found in this work.

Pseudoscorpions are frequently found in guano deposits in caves or other bat-roosts, like buildings, all over the world, mainly in older piles (Martin 1976, Bernarth & Kunz 1981, Chapman 1983, Ferreira & Pompeu 1997, Gnaspini & Trajano in press). Their frequent association demonstrates their importance as predators of small size arthropods, not only in Brazilian caves, but in other caves throughout the world.

Spiders (Araneida) are found in nearly all types of guano in nearly all conditions in several caves in the world (Harris 1970, Decou et al. 1974, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira & Martins in press). The fact that spiders are not often found in fresh guano piles, seems to be due to the absence of suitable prey. The distinct preferences for a specific type of guano (in different families) is certainly due to the distinct life cicles and behavior, which are quite different between species and families.

As in the present work, mites are the most abundant organisms in guano (Decou & Decou 1964, Poulson 1972, Decou et al. 1974, Decu & Tufescu 1976, Martin 1976, Strinati 1982, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Gnaspini & Trajano in press). Gnaspini & Trajano (in press) cite Acarida, Actinedida, Oribatida, and Gamasida as frequently found in guano in Brazilian caves, the latter being the most prominent, as in Romania (Decou et al. 1974). Gamasida present in bat guano in Brazil include Macrochelidae, Phytoseiidae, Rhodacaridae, and Uropodidae (Gnaspini & Trajano in press). The sub-order Ixodida (*Ornithodoros* spp.) is only present in fresh guano when individuals are brought in by hematophagous bats.

Several isopods can be found in guano piles both in tropical and temperate caves (Decou & Decou 1964, Decou et al. 1974, Decu 1986, Souza-Kury 1993, Ferreira & Pompeu 1997, Ferreira & Martins in press). Gnaspini & Trajano (in press) cited three families found in guano deposits in Brazilian caves (Phylosciidae, Scleropactidae and Armadillidae), the latter having been observed in north Minas Gerais State, in addition to Platyarthridae and Styloniscidae. The remarkable preferences among families are certainly the consequence of their distinct biological cycles.

Chilopods in bat guano were detected in other Brazilian caves, e.g. lithobiomorphs in frugivorous bat guano in caves in São Paulo State (Gnaspini-Netto 1989). The records of chilopods in Brazilian caves indicate their widespread distribution in these environments.

Like chilopods, diplopods were also normally found in hematophagous and frugivorous bat guano. Their association with guano seems to occur if other organic sources are scarce. Gnaspini-Netto (1989) recorded individuals of Polydesmida (family Cryptodesmidae) on frugivorous and hematophagous bat guano in São Paulo State caves.

Several orders of Insecta can be found in bat guano deposits all over the world (Decou & Decou 1964, Poulson 1972, Decou et al. 1974, Decu 1986, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira & Martins in press, Gnaspini & Trajano in press).

Springtails (Collembola) are the most commonly found, which, like mites, are often quite abundant (Decou & Decou 1964, Poulson 1972, Decou et al. 1974, Decu 1986, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira & Martins in press, Gnaspini & Trajano in press). Gnaspini & Trajano (in press) stated that the families Cyphoderidae, Entomobryidae, and Isotomidae are the most common in all types of guano deposits in Brazilian caves. Bat guano is the primary food source for most families though preferences may vary among families.

Despite their apparent pre-adaptation to life in the cave environment, silverfish (Zygentoma), which occurred in abundance in some caves in the present study, have not been recorded on guano in other caves in the world.

Crickets are commonly found in guano throughout the world. Rhaphidophoridae is an important family occurring in Australian caves (Richards 1971). Gnaspini-Netto (1989) reported differential preferences for guano types in caves in São

Paulo State. *Endecous* spp. only occurred in hematophagous bat guano piles, while individuals of *Eidmanacris* spp. were only found in frugivorous bat guano.

Roaches (Dictyoptera Blattaridae) frequently inhabit neotropical caves and can be found on guano piles (Braack 1989, Ferreira & Pompeu 1997). Larger populations (tens of individuals) were observed in Pará State, Brazil, in an arenitic cave (Gnaspini & Trajano in press).

Records of booklice (Psocoptera) appear several times in the literature, unfortunately with few notes concerning their biology (Negrea & Negrea 1971, Bernarth & Kunz 1981, Strinati 1982, Gnaspini-Netto 1989, Ferreira & Pompeu 1997, Ferreira & Martins in press, Gnaspini & Trajano in press). Their remarkable presence in guano communities all over the world indicates their importance as prey for several invertebrate predators.

Thrips (Thysanoptera) are rarely found in guano (Strinati 1982, Gnaspini & Trajano in press). As cited previously, the absence of immature individuals in guano piles, indicates that they are unable to complete their life cycles in bat guano. Such insects are not necessarily rare in caves, as they are likely present in other substrates.

Bugs (Heteroptera) are frequently recorded (Bernarth & Kunz 1981, Braack 1989, Whitaker et al. 1991, Ferreira & Pompeu 1997). Cydnidae and Lygaeidae are only found in frugivorous bat guano in Brazilian caves (Gnaspini & Trajano in press), in contrast with *Zelurus* (Reduvidae) which is frequently found in hematophagous bat guano.

Several families of beetles (Coleoptera) are commonly associated with guano throughout the world (Decou & Decou 1964, Harris 1970, Richards 1971, Decou et al. 1974, Chapman 1983, Braack 1989, Gnaspini-Netto 1989, Whitaker et al. 1991, Ferreira & Pompeu 1997, Ferreira & Martins in press, Gnaspini & Trajano in press). This huge diversity of families is certaily due to the great diversity of potential colonizers in epigean environments. The generalistic feeding habits of several families can also contribute to their widespread distribution in guano all over the world. Contrary to Gnaspini & Trajano (in press), who suggested that leiodids are the most common beetles on bat guano in Brazil, it appears that dermestids are generally more abundant.

Ants (Hymenoptera Formicidae) may be found near bat guano piles, as recorded in this study. The difference found between the ant midden and the guano deposits in Morrinho cave (north Bahia State) reflects the different sources of colonization, with organisms in the ant midden probably originating in the ant colony itself, thus not being true cave organisms, as is most of the guano community.

Like beetle larvae, moth larvae are also very numerous in guano deposits throughout the world (Decou & Decou 1964, Harris 1970, Richards 1971, Decou et al. 1974, Decu & Tufescu 1976, Chapman 1983, Gnaspini-Netto 1989). All of them are almost exclusively found in old guano piles as larvae. Adults of these families are rarely observed on guano, as observed for some families in this work.

As recorded in this study, Diptera families such as Muscidae, Fanniidae, Psychodidae, Sphaeroceridae, Milichiidae, and Phoridae, are frequently found in guano all over the world (Decou & Decou 1964, Poulson 1972, Decou et al. 1974, Decu 1986, Gnaspini-Netto 1989, Whitaker et al. 1991, Ferreira & Pompeu 1997, Ferreira & Martins in press, Gnaspini & Trajano in press). Streblids only appear in guano when they drop off their hosts. Similarly, fleas (Siphonaptera) can occasionally be found in guano piles (Bernarth & Kunz 1981, Strinati 1982), but also only when they drop off their hosts.

The invertebrate communities that are found in gauno piles in buildings and/or churches are very similar in composition to those found in caves. The same groups that are found in caves (e.g. Tenebrionidae, Histeriade, Dermestidae, Milichiidae, Muscidae) can also be found in guano piles in human constructions (Bernarth & Kunz 1981, Whitaker et al. 1991). This fact may indicate their relatively low dependence on the cave environment, instead, probably being more related to the guano itself. This generalizations are, however, very restricted, since almost nothing is known about guano communities in buildings throughout the world.

The high number of taxa in South American guano communities (specially in Brazil) may be a consequence both of the diversity of feeding habits of neotropical bats, and the greater diversity of potential colonizer invertebrates of neotropical ecosystems. However, the few natural history studies hinder to comparisons among bat guano invetebrate communities in caves or other bat roosts all over the world.

Guano piles obviously are a very important resource that maintains the diversity of cave invertebrates. This is especially true in permanently dry caves in Brazil. Even a brief analysis of populations associated with these deposits reveals a wide range of trophic structures and inter-population interactions of varying complexities (see Figs 1-4). Since the health of the overall cave ecosystems can be strongly dependent on the existence of guano, it is crucial to focus on the study of these communities and, in a larger context, the preservation of the animals that produce the guano.

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