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BIOLOGY AND ECOLOGY OF BAT CAVE, GRAND CANYON NATIONAL PARK, ARIZONA

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Abstract: A study of the biology and ecology of Bat Cave, Grand Canyon National Park, was conducted during a series of four expeditions to the cave between 1994 and 2001. A total of 27 taxa, including 5 vertebrate and 22 macro-invertebrate species, were identified as elements of the ecology of the cave. Bat Cave is the type locality for *Eschatomoxys pholeter* Thomas and Pape (Coleoptera: Tenebrionidae) and an undescribed genus of tineid moth, both of which were discovered during this study. Bat Cave has the most species-rich macro-invertebrate ecology currently known in a cave in the park.

Introduction

This paper documents the results of a biological and ecological analysis of Bat Cave on the Colorado River within Grand Canyon National Park conducted during four expeditions to the cave between 1994 and 2001. The study focused on the macro-invertebrate elements present in the cave and did not include any microbiological sampling, identification, or analysis. Access to caves in the park is strictly regulated and requires either an approved research permit or a cave entry permit, granted through the Grand Canyon Division of Science and Resource Management.

Cave Invertebrates in Grand Canyon National Park

Grand Canyon National Park has extensive cave resources, but there has been little research on cave-inhabiting invertebrates in the park. The earliest effort was conducted by the Cave Research Foundation at Horseshoe Mesa in 1977 and 1978 (Welbourn, 1978). The scope of that project was not strictly biological, but did include a search for invertebrates in eight caves contained in the Mooney Falls member of the Redwall limestone. The effort produced a total of fourteen invertebrate species, including a new species of garypid pseudoscorpion (*Archeolarca cavicola* Muchmore). The lack of species diversity was attributed to the lack of available moisture in the caves. Peck (1980) looked at three caves in the Grand Canyon, all of which, like Bat Cave, were in the Muav limestone. All three of these caves contain active streams that have their outfall in major tributaries to the main gorge of the Colorado River below the North Rim of Grand Canyon. Peck's effort identified a total of 15 invertebrate species from the 3 caves. One of those caves, Roaring Springs Cave, was revisited by Drost and Blinn in 1994 and 1995 (Drost and Blinn, 1997), and their effort increased the invertebrate species recorded from that cave from the original 10 found by Peck to 19, including the first records of aquatic invertebrates from a Grand Canyon Cave. A review of cave-invertebrate studies in the park, which included 9 reports addressing 16 caves, was prepared by Wynne et al. (2007). Their compilation resulted in a list of approximately 37 species of cave macro-invertebrates currently known from caves there. Wynne and others have recently performed invertebrate surveys in caves in the Grand Canyon–Parashant National Monument, and have already encountered several undescribed cave-inhabiting macro-invertebrate species, including three new genera. These include a camel cricket (Rhaphidophoridae), a barklouse (Psocoptera), and a macrosternodesmid millipede, *Pratherodesmus* (Shear et al., 2009; Wynne and Drost, 2009).

Bat Cave

Bat Cave is located in the north wall of the main gorge of the Colorado River within Grand Canyon National Park (Fig. 1, insert). The entrance is at an elevation of 580 meters, approximately 260 meters above the river. The cave is formed along a major vertical fault in the Cambrian Muav limestone and consists of just over one thousand meters of surveyed passage, mostly along the single main trunk passage. From the entrance, the cave trends a few degrees east of north (Fig. 1). The cave is essentially horizontal, with a total vertical relief of only 75 meters.

Bat Cave is named for the large maternity colony of Mexican free-tailed bats (*Tadarida brasiliensis* I. Geoffroy) that resides there. The first record of the cave is from the 1930s. Shortly thereafter, there were efforts to mine the bat guano for fertilizer. These early efforts were mostly unproductive. In 1958, the property was purchased by the U.S. Guano Corporation. U.S. Guano invested 3.5 million dollars in the setup of the mining operation, only to find that the extent of the guano deposit was only 1 percent of their original estimate. Difficulties with the haul system across the canyon, and specifically the lack of a significant guano deposit, forced the abandonment of the mining operation in 1960 (Billingsley et al., 1997). The support towers for the haul system's cables are still present on the top of the south rim of the canyon and below the cave on the

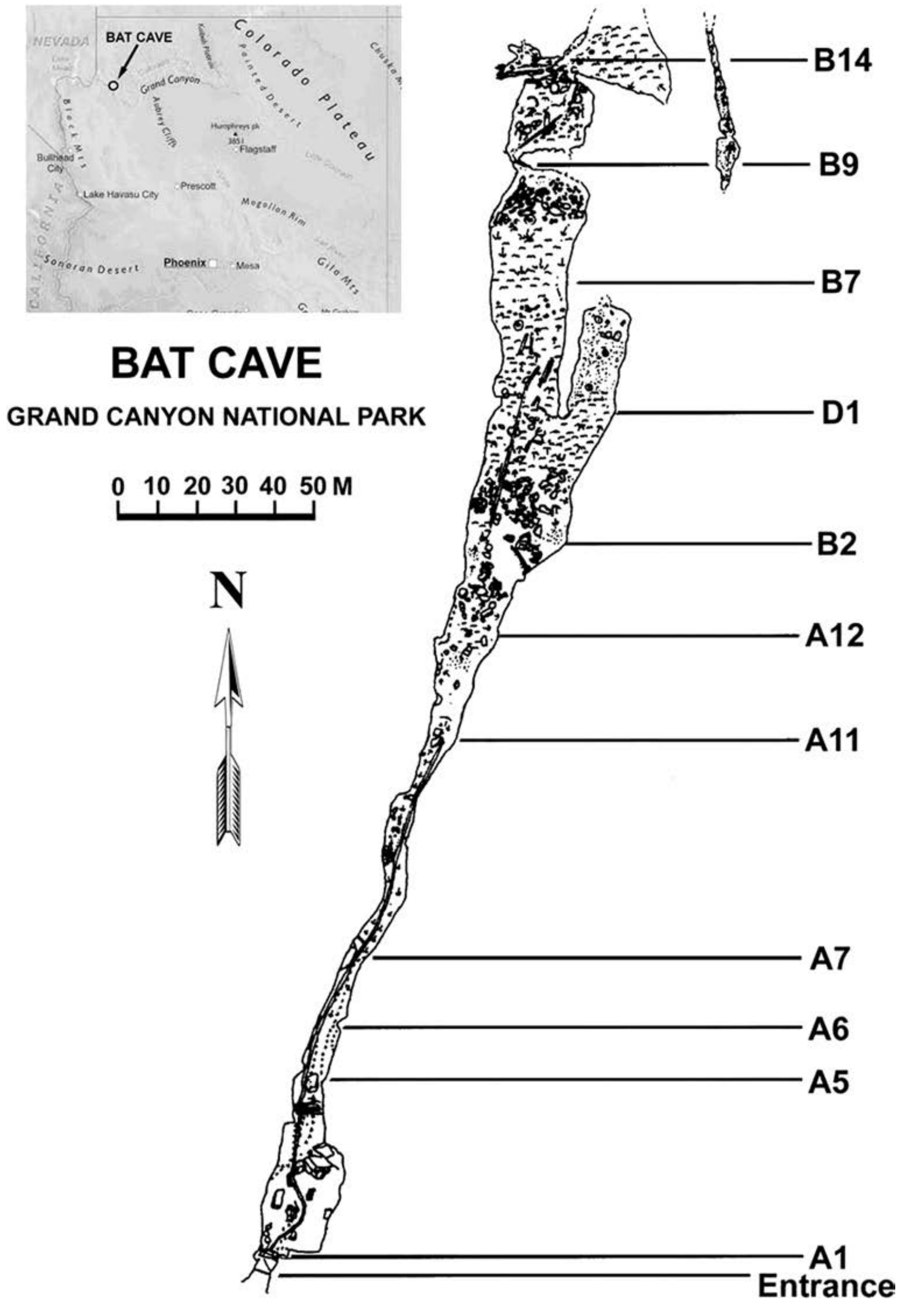

Figure 1. Map of the biologically active front portion of Bat Cave, Grand Canyon National Park, showing regional location (inset) and survey stations mentioned in the text.

north side of the river. A wooden plank-way, portions of which are elevated, traverses approximately the first 145 meters of the cave from an elevated entrance platform. Sections of large flanged pipe approximately 30 cm in diameter and other mining equipment remain in the cave. Most of the animal species associated with the cave are arthropods tied directly to the bat guano-supported food web.

Materials and Methods

The four expeditions to Bat Cave were conducted on March 12, 1994; March 29 and 30, 1996; October 24, 1997; and October 26, 2001. Access to the cave was made up the river by boat from Lake Mead. Visits to the cave were scheduled seasonally and temporally to avoid disturbance to the resident bat population. Even so, at least some bats were present on all visits to the cave. During the March visits, no more than a few hundred bats were present at any time, mostly around the roost at survey station D1 (Fig. 1). All efforts were made to keep disturbance to the bats at a minimum. This roost is at the east edge of the main trunk passage, and the roost area can be skirted with minimal disturbance to the bats.

The 5 visits involved approximately 34 hours of observation and sampling of invertebrates in the cave. The methods were low impact, consisting of a visual search of passage floors, walls, crevices, ledges, and breakdown-boulder accumulations. Additional habitat niches have been created in Bat Cave by the presence of wooden walkways and machinery remaining from the abandoned mine operation. Particular attention was paid to floor debris, under which many invertebrates commonly shelter. Debris that was overturned was replaced after examination to minimize impact to microhabitats. The principal benefits of this type of documentation are minimal habitat disturbance, low animal population impact, and ease of sampling in the cave environment. Since obligate cave invertebrate populations may be small and may be adversely impacted by over-sampling, no pitfall or other trapping devices were used. Pitfall traps should only be utilized where the traps can be regularly monitored.

Initial sampling of specimens was kept to a minimum, and no more than six individuals of each type were taken. Both males and females were included in these samples for species where their sex was readily evident. Additional sampling for type-series specimens was later performed for the tenebrionid beetle and the undescribed tineid moth. Specimens were sampled with forceps or a camel hair brush dampened with ethanol. Specimens were placed in vials of ethanol for transport to the laboratory.

Two approximately 0.3 kg samples of fresh bat guano were taken on March 29, 1996, for Berlese extraction. Each of these samples was a composite of smaller sub-samples taken in closely spaced areas within an approximately 0.5 m^2 area near the apex of the guano deposits. One sample was taken at each of the two main roosts, near survey stations D1 and B7. Specimens were sampled under two park permits (9503-09-02 and GRCA-2001-SCI-0043).

Relative-humidity and ambient air-temperature measurements were recorded at several points along the main trunk passage of the cave on March 29, 1996 using a digital temperature/humidity meter (Hanna Instruments model HI 8565).

Results and Discussion

A total of 27 taxa, including vertebrates, were identified from Bat Cave during this study. Table 1 is a taxonomic summary of the species documented and lists the assigned ecological group (trogloxene, troglophile, troglobite, or accidental), guild (scavenger, fungivore, predator, parasite, or phytophage), and relative abundance (abundant, common, uncommon, or rare) for each species. Ecological groups used in this paper are defined as follows: A trogloxene is an animal that enters caves to fill some ecological need, such as obtaining food, water, shelter, etc., but that cannot survive without returning to the surface to meet some of its life-cycle requirements. A troglophile is an animal that is capable of completing its life cycle within caves, but may also do so elsewhere. A troglobite is an obligate cave animal, which cannot live outside of the cave environment. The occurrence of parasites in the cave is in association with other species of animals, but because of their presence in the cave during part of their life cycle we consider them to be trogloxenes. Accidentals are just what the label implies, animals that wander or fall into the cave, would not normally occur in such habitats, and obtain no benefit from their presence in the cave.

Species Accounts

Phylum: Chordata
Class: Aves
Order: Passeriformes
Family: Troglodytidae

Catherpes mexicanus Swainson

A single canyon wren was observed in the entrance room of the cave on October 26, 2001. Canyon wrens are common in cave entrance areas, where they forage, shelter, and occasionally nest.

Class: Mammalia
Order: Chiroptera
Family: Vespertilionidae

Myotis californicus Audubon & Bachman

The presence of this insectivorous bat at Bat Cave is known from acoustic monitoring that was conducted at the entrance in 1997 (Charles Drost, pers. comm). It is assumed that only small numbers of these bats use the cave. Their contribution to the nutrient input to the cave is greatly overshadowed by the population of the Mexican free-tailed bat.

Myotis yumanensis H. Allen

The presence of this insectivorous bat at Bat Cave is known from acoustic monitoring that was conducted at the entrance in 1997 (Charles Drost, pers. comm). It is assumed that only small numbers of these bats use the cave. Their contribution to the nutrient input to the cave is greatly overshadowed by the population of the Mexican free-tailed bat. This species almost always occurs near a permanent water source, and it is likely a relatively common animal in caves and crevices along the Colorado River.

Family: Molossidae

Tadarida brasiliensis I. Geoffroy

The Mexican free-tailed bat maternity colony at Bat Cave is the major source of nutrient input into the cave, with its guano serving as the foundation of the cave's invertebrate

Table 1. Summary of fauna documented at Bat Cave, Grand Canyon National Park, Arizona.

Taxon	Ecological Group	Guild	Abundance
Class Aves			
Order Passeriformes			
Troglodytidae			
Catherpes mexicanus	Trogloxene	Predator	Uncommon
Class Mammalia			
Order Chiroptera			
Vespertilionidae			
Myotis californicus	Trogloxene	Predator	Uncommon?
Myotis yumanensis	Trogloxene	Predator	Uncommon?
Molossidae			
Tadarida brasiliensis	Trogloxene	Predator	Abundant
Order Carnivora			
Procyonidae			
Bassariscus astutus	Trogloxene	Predator	Common
Class Arachnida			
Order Sarcoptiformes			
Glycyphagidae			
Glycyphagus sp.	Troglophile	Fungivore	Uncommon
Rosensteiniidae			
Cubaglyphus sp.	Guanophile	Scavenger	Common
Suidasiidae			
Sapracarus tuberculatus	Troglophile	Scavenger?	Rare
Order: Mesostigmata			
Macronyssidae			
Chiroptonyssus robustipes	Troglophile	Parasite	Abundant
Mitonyssoides stercoralis	Troglophile	Predator	Common
Order: Trombidiformes			
Pterygosomatidae			
Pimeliaphilus sp. (Undes.?)	Trogloxene	Parasite	Common
Order Araneae			
Filistatidae?			
(*Kukulcania* sp.?)	Troglophile	Predator	Rare
Plectreuridae			
Kibramoa suprenans	Troglophile	Predator	Common
Sicariidae			
Loxosceles sp.	Troglophile	Predator	Uncommon
Pholcidae			
Psilochorus sp.	Troglophile	Predator	Uncommon
Selenopidae			
Selenops sp.	Trogloxene	Predator	Uncommon
Order Pseudoscorpiones			
Chernetidae			
Neoallochernes stercoreus	Troglophile	Predator	Abundant
Class Hexapoda			
Order Psocoptera			
Psyllipsocidae			
Psyllipsocus ramburii	Troglophile	Fungivore	Common
Order Neuroptera			
Myrmeleontidae			
Eremoleon pallens	Troglophile	Predator	Common

Table 1. Continued.

Taxon	Ecological Group	Guild	Abundance
Order Coleoptera			
Dermestidae			
Dermestes carnivorus	Troglophile	Scavenger	Rare
Tenebrionidae			
Eschatomoxys pholeter	Troglophile	Scavenger	Abundant
Curculionidae			
Smicronyx imbricatus	Accidental	Phytophage	Uncommon
Order Siphonaptera			
Ischnopsyllidae			
Sternopsylla distincta	Trogloxene	Parasite	Common
Order Diptera			
Muscidae			
Fannia sp.	Trogloxene?	?	Rare?
Order Lepidoptera			
Tineidae			
New genus and species	Troglophile	Scavenger	Common
Tinea (*pallescentella*?)	Troglophile?	Scavenger	Rare
Order Hymenoptera			
Sphecidae			
Sceliphron caementarium	Trogloxene	Predator	Uncommon

food web. During the period the field work was conducted, the summer population of the bats was estimated at 285,000 (Charles Drost, pers. comm). The bats currently roost at two major sites within the cave. The primary site is at survey station B7, 265 meters from the entrance. The second, smaller roost is located at survey station D1, 229 meters into the cave. Overflow bats from these roosts probably congregate in wider sections in the main corridor closer to the entrance, between survey stations A11 and B2. Recent guano deposits in the front sections of the cave are not extensive. Currently, the bats seldom go deeper into the cave than the passage constriction at survey station B9, 308 meters from the entrance. No recent guano deposition was observed beyond survey station B9.

A large fossil guano deposit is present at the back of the cave beginning at survey station B14. Over a period of time the main cave passage was gradually cut off at a passage constriction at survey station B9. The bedrock ceiling of the cave passage at this point dips steeply downward. Evidently the annual accumulations of guano deposited at the roost centered at survey station B7 eventually increased in depth until the slope of the deposit met with the ceiling at survey station B9, isolating the back portion of the cave. Based on the presence of old mining pipes at this point, the back section of the cave was apparently reopened during the last mining efforts. A sample of the top of the fossil bat guano beyond station B9 was dated at 6.5 ka, and the bottom of the fossil guano deposit was dated at 14.5 ka (Wurster et al., 2008). The more recent date would represent the time of last regular use of the back portion of the cave by the large *Tadarida* colony.

Order: Carnivora

Family: Procyonidae

Bassariscus astutus Lichtenstein

Ringtail scats and tracks were observed throughout the front half of the cave, back to the active bat roosts at survey stations D1 and B7. A ringtail was observed on two of the five visits into the cave. Both were nocturnal sightings, which is the normal activity period for the animals. One sighting was at 1929 hrs on March 29, 1996, along the east wall of the cave adjacent to survey station B2, where a single animal was observed headed deeper into the cave. At the time there were a few hundred free-tailed bats active at the roost at survey station D1. A second sighting was at 1930 hrs on October 24, 1997, between survey stations A5 and A6, where the main passage narrows. Along the west wall of the cave at this point there is a wooden walkway support structure that extends toward the middle of the passage. We had earlier noted that there were several dead *Tadarida* lying on and around this small structure (Fig. 2). There were abundant ringtail scats present along the west wall here. The ringtail was observed perched on the east edge of the support structure. This put it near the center of the walkway area and well within the flight path of any low-flying bats. There were still a few bats leaving the cave at this time. The ringtail was not observed attempting to take bats out of the air, but it is probable that is how it was capturing live bats. It is unknown why the several dead bats on the support structure noted earlier in the day had not been consumed by the ringtail. With the abundant bats as a dependable food source from at

Figure 2. Dead *Tadarida* killed by ringtail near survey stations A5 and A6; scale is 15 cm.

least April through October and the natural shelter provided by the cave, it is possible that ringtails may also den in the cave. Ringtails would probably use the front entrance room for denning, since there is a jumble of rocks which could provide a secluded area for that purpose. Other rock-pile accumulations occur near survey station B2.

Based on sightings and an abundance of their scats, ringtails apparently regularly use caves in the southwestern U.S. They use caves for shelter, as a source of water and some foods, and probably den in caves, at least occasionally. Ringtails are opportunistic in their feeding, taking equally from animal and plant materials seasonally. Birds, wood rats, bats, mice, and other small rodents are commonly taken (Taylor, 1954; Murie, 1974; Poglayen-Neuwall and Toweill, 1988). Ringtails probably regularly take dying adult bats and young that fall onto cave floors below roosts. Records for lizards and snakes from two-thousand-year-old ringtail scats were documented in caves in the western part of Grand Canyon by Mead and Van Devender (1981). Arthropods make up a significant part of the diet of ringtails (Toweill and Teer 1977; Poglayen-Neuwall and Toweill, 1988). I found cave cricket (*Ceuthophilus* nr. *pinalensis*) parts in a ringtail scat at Arkenstone Cave in southern Arizona. Taylor (1954) also recorded *Ceuthophilus* sp. from ringtail scats. A microscopic examination of ringtail scats from Bat Cave revealed abundant body parts of the Bat Cave tenebrionid beetle (*Eschatomoxys pholeter*). The only other invertebrate of adequate abundance in Bat Cave that might be used as food by ringtails is the plectreurid spider (*Kibramoa suprenans* Chamberlin). Ringtails are known to take arachnids (Poglayen-Neuwall and Toweill, 1988), and it is doubtful that they would be intimidated by spider-web silk in pursuing this species.

Phylum: Arthropoda
Class: Arachnida
Order: Sarcoptiformes
Family: Glycyphagidae

Glycyphagus sp.

This dust mite is likely fungivorous and likely feeds on molds associated with the bat guano.

Family: Rosensteiniidae

Cubaglyphus sp.

This animal is an undescribed species of *Cubaglyphus* (Barry OConnor, pers. comm.).

Family: Suidasiidae

Sapracarus tuberculatus Fain & Philips

This is a species of very small mites that is known from a variety of habitats, including caves (Barry OConnor, pers. comm.). The feeding habits of the species are not known (Barry OConnor, pers. comm.). Other mite records from caves in Grand Canyon National Park are an anystid mite from several of the Horseshoe Mesa caves (Welbourn, 1978) and a rhagidiid mite (*Rhagidia* cf. *hilli*) from Roaring Springs Cave (Peck, 1980).

Order: Mesostigmata
Family: Macronyssidae

Chiroptonyssus robustipes Ewing

This mite is an obligate parasite of the Mexican free-tailed bat. The bats groom them off their bodies and the mites drop to the guano pile below. It is not known whether any of the mites manage to return to the bats. Many of them are likely consumed by the various invertebrate predators in the guano pile. The mite population in the guano piles was not at its peak during our visits to the cave since the number of bats present was generally low. The fresh guano accumulation was quite limited when the Berlese samples were taken.

Mitonyssoides stercoralis Yunker, Lukoschus, and Giesen

This mite is the only species in its family (Macronyssidae) that is not a blood-feeding parasite on a vertebrate host, but is predatory on the rosensteiniid mites that occur in bat guano. *M. stercoralis* is found in the guano of both molossid and vespertilionid bats. The previously known range of the species was from Indiana in the U.S. to southern Brazil (Radovsky and Krantz, 2003). Presence of *M. stercoralis* in Grand Canyon National Park is a significant range extension for the species.

Order: Trombidiformes
Family: Pterygosomatidae

Pimeliaphilus sp.

Species of *Pimeliaphilus* are parasitic on lizards and a variety of arthropods (Field et al., 1966; Anderson, 1968; Ibrahim and Abdel-Rahman, 2011; Delfino et al., 2011). A single deutonymph and larvae of an undetermined species of *Pimeliaphilus* were sampled from *Eschatomoxys pholeter*

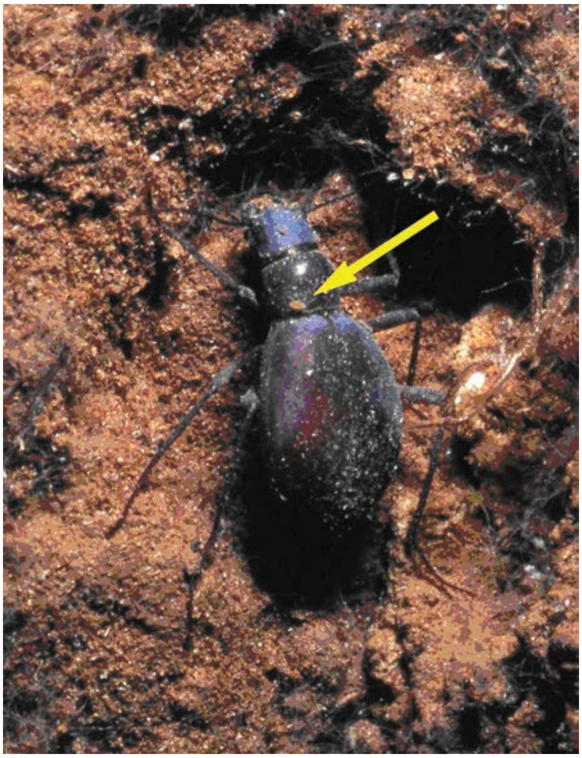

Figure 3. Undescribed *Pimeliaphilus* sp. mite on thorax of *Eschatomoxys pholeter*.

in the cave (Fig. 3). These mites are relatively common on the beetles, and are typically parasitic at these stages. This animal may be a new species of *Pimeliaphilus* (Barry OConnor, pers. comm).

Order: Araneae

Family: Filistatidae?

Kukulcania sp.?

A single large, blackish spider was found in the apron of its web on the north side of a large boulder in the middle of the main trunk passage of the cave at survey station A5. The spider eluded capture, but is believed to be *Kukulcania* sp.

Family: Plectreuridae

Kibramoa suprenans Chamberlin

The population of this spider at Bat Cave is pale in color and may represent a troglophilic population (Darrell Ubick, pers. comm). No troglophilic plectreurid spider population has been previously recorded (Ribera and Juberthie, 1994). This spider is the only large invertebrate predator in the cave-invertebrate food web here. The primary food of the older, larger spiders is the tenebrionid beetle *Eschatomoxys pholeter*. Below their webs an accumulation of the beetle bodies is often evident (Fig. 4). The spiders are abundant wherever there is support for their webs. They build their webs along the base of the cave walls, among rock piles, and in and under the walkway and machinery left from the guano-mining operation. Some recesses in the walls of the cave are festooned with old webs containing their ecdysed skins, old egg cases, and carcasses of *E. pholeter* (Fig. 5). A close-up view of an individual abandoned web is shown in Fig. 6.

Figure 4. Numerous carcasses (white arrows) of *Eschatomoxys pholeter* in debris pile at the base of an old *K. suprenans* web; scale is 15 cm.

The juvenile spiders spin their webs across small depressions on the cave walls or in recesses or depressions in the guano deposits on the floor of the cave. The latter generally occur at the edge of the active guano deposition areas where they are proximal to smaller invertebrates present on the surface of the guano. Interestingly, this species has not been recorded in other caves in the park.

Family: Sicariidae

Loxosceles sp.

There are several troglophilic and a few troglobitic species in this genus that occur in the tropics (Ribera and Juberthie, 1994). This species exhibits no obvious morphological modifications that would indicate that it is adapted for living in a cave environment, and it is probably an epigean form. This may be the same species recorded from Thunder Cave by Peck (1980) and from Roaring Springs Cave by Drost and Blinn (1997).

This spider is not a prominent member of the biota within the cave, but is probably relatively common outside

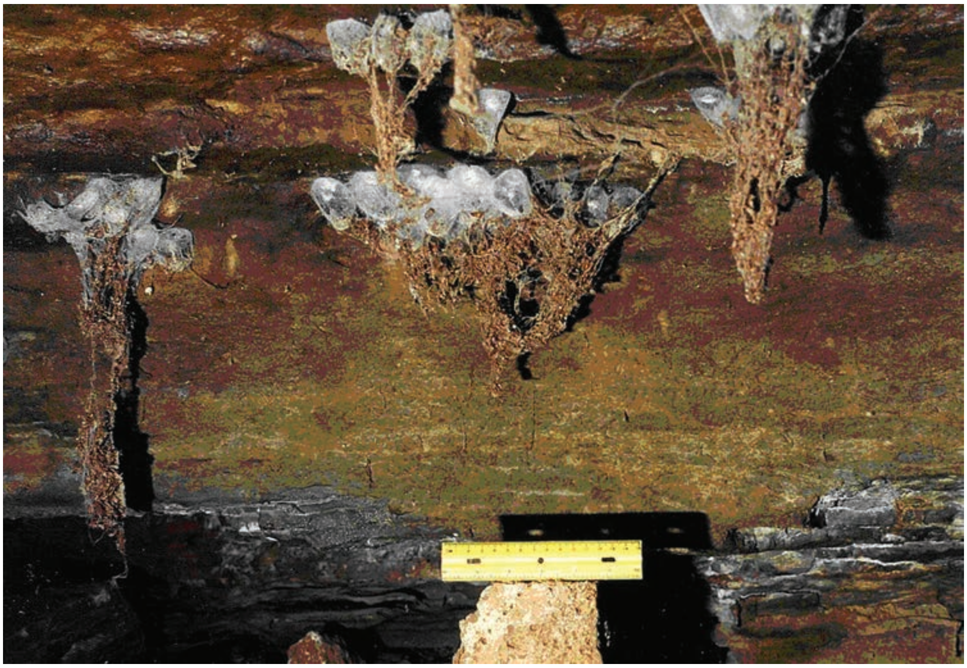

Figure 5. Several old webs of *Kibramoa suprenans* hanging from a wall in the cave; scale is 15 cm.

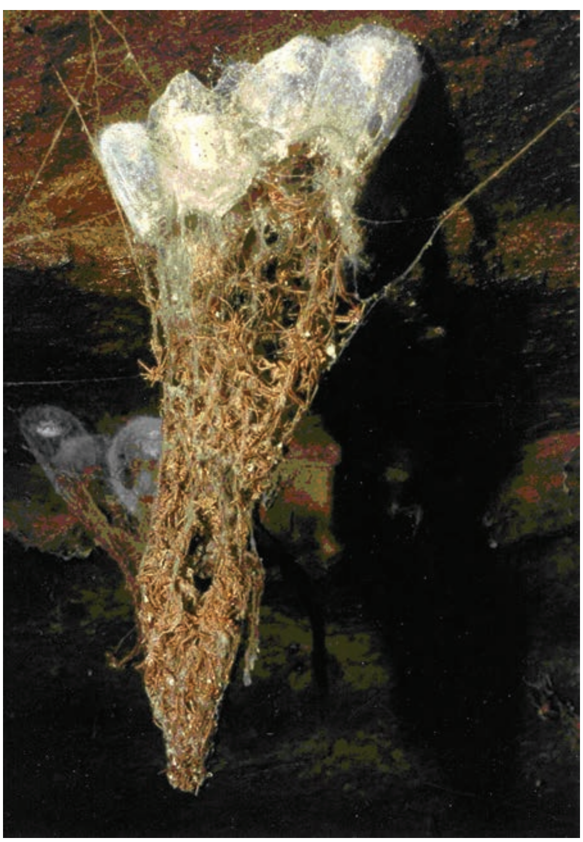

Figure 6. Single old web structure of *Kibramoa suprenans* showing white egg-case enclosures at top and aggregation of shed spider skins trapped in lower portion.

the cave in rocky areas along the cliff faces. The single female found was located on the cave floor at the base of the west wall of the passage, approximately 64 meters from the cave entrance. A reduction of cave passage dimensions in this area has an ameliorating affect on the cave microclimate. Closer to the entrance, where passage dimensions are considerably larger, hot, dry desert air from outside the cave easily mixes with the cave atmosphere, resulting in significant drying of the front part of the cave. The area of this initial passage constriction is where invertebrates of the guano food-web are first encountered. The brown spider has encroached on the periphery of the active food web, where it is not in competition with the dominant plectreurid spider. When first observed, this spider had a muscid fly (*Fannia* sp.) in its chelicerae.

Family: Pholcidae

Psilochorus sp.

This troglophile is a small relative of the common cellar spider. Members of this family are often a common element of invertebrate biota of caves in the western U.S. *Psilochorus* has not previously been recorded from caves in the park, but is likely to be present in habitats similar to that present in Bat Cave. There is some depigmentation in this species, but no observable reduction of the eyes. Only a small population of these delicate spiders is found in the cave, and they typically occur away from areas of intense invertebrate activity at the fresh guano deposits. Their more delicate webs and the situations where they build may indicate that mostly small airborne prey are taken. No prey debris was observed in their webs. Their diet may include the guano moth and small dipterous species associated with the fungus-covered guano and dead bats in the cave.

Family: Selenopidae

Selenops sp.

The presence of *Selenops* sp. in the cave was limited to a couple of shed skins found on the walls of the first room of the cave within the first six meters from the entrance. These spiders are foragers that typically occur in rocky habitats, spending most of their time in rock piles, crevices, and caves. Their presence here is not a surprise. They apparently do not go deeply enough into the cave to capitalize on prey supported by the bat guano deposit, where *Kibramoa suprenans* is the dominant predator.

Order: Pseudoscorpiones

Family: Chernetidae

Neoallochernes stercoreus Turk

This is the first record of this pseudoscorpion associated with a bat colony in Arizona (William Muchmore, pers. comm). This species is apparently the common pseudoscorpion associated with active Mexican free-tailed bat guano deposits, and is found in many caves in Texas where free-tailed colonies reside (Muchmore, 1992). A mean density of 135 individuals/dm^2 was recorded for this species at Fern Cave, Val Verde Co., Texas (Mitchell and Reddell, 1971). The estimated density of this species in Bat Cave at the time of sampling is approximately one fourth that value. However, the sampling was not done during the summer peak of the bat population and active guano deposition.

Interestingly, the species has not been found at Carlsbad Caverns National Park, which has a free-tailed colony of approximately 700,000 bats. The pseudoscorpion species present there is *Dinocheirus astutus* Hoff (Muchmore, 1992). Likely prey of *N. stercoreus* in Bat Cave includes mites, the psocid, and collembola, if they are present. No collembola were observed on or sampled from the guano.

The only other pseudoscorpion known from a cave in Grand Canyon National Park is *Archeolarca. cavicola* from Cave of the Domes on Horseshoe Mesa (Welbourn, 1978). *A. cavicola* shows slight morphological modifications for its subterranean habit (Muchmore, 1981). Other species in that genus have been reported from caves at Wupatki National Monument, Arizona, and Guadalupe Mountains National Park, Texas (Muchmore, 1981).

Pseudoscorpions are a common element of cave and guano deposit ecosystems. I have observed them in many caves in the southwestern U.S., often in caves that are quite dry and where food resources seem to be minimal. Overall, the group appears to be more tolerant of arid conditions than other arthropod predators. Additional studies in caves in the park should reveal additional pseudoscorpion species.

Class: Hexapoda

Order: Psocoptera

Family: Psyllipsocidae

Psyllipsocus ramburii Selys-Longchamps

This barklouse seems to be the common psocid found in caves in the southwestern U.S., and indeed, has a worldwide distribution (Badonnel and Lienhard 1994). Psocids occurring in cave environments are probably detritivores, feeding on microflora or other organic sources (Mockford, 1993). The guano deposits at Bat Cave likely provide a whole suite of potential nutrient sources for this species. *P. ramburii* is associated with cave cricket (*Ceuthophilus* nr. *pinalensis*) guano at Arkenstone Cave in southern Arizona. There it is the prey of the cave-adapted pseudoscorpion *Albiorix anophthalmus* Muchmore (Mockford, 1993; Muchmore and Pape, 1999). It is likely to be a prey species for *Neoallochernes stercoreus* in Bat Cave. Psocids (Psyllipsocidae) were recorded from several of the Horseshoe Mesa caves (Welbourn, 1978), and they are likely the same species. *P. ramburii* was also recorded from a single specimen at Tapeats Cave (Peck, 1980).

Order: Neuroptera

Family: Myrmeleontidae

Eremoleon pallens Banks

The larval pits of this antlion species are common in the dry, silty soils of the entrance room of the cave. Adults were seen flying in the evenings in the main passage in the vicinity of survey station A7, and small groupings of their wings were found clustered on the floor of the passage where *Tadarida* had captured the animals in flight and hung up on the ceiling to feed on the insects. This is a new county record for *E. pallens* in Arizona (Mohave County), and the only record of the species from a cave. The type species for *E. pallens* was from a mine shaft on Picacho Peak in southern Arizona. At least one species of *Eremoleon* (*E. longior* Banks) has previously been recorded from caves (Adams, 1956).

Order: Coleoptera

Family: Dermestidae

Dermestes carnivorus Fabricius

Dermestid beetles are common faunal elements on bat-guano deposits in the New World and Asia (Mitchell and Reddell, 1971; Decu et al., 1998; Gnaspini and Trajano, 2000). Where they occur in association with bat guano, they are typically the dominant decomposer, and they may be present in enormous numbers. No dermestid species is established in the cave, and colonization attempts by dermestids, which likely occur on occasion, are apparently repelled by predatory or scavenging elements in the guano community, possibly including *Eschatomoxys pholeter*, which could feed on eggs and/or young larvae of dermestids. Only a single *D. carnivorus* was found in the cave, on October 26, 2001. The animal was probably attracted to the odor of the guano deposit, which is detectable even by humans at great distance. The beetle was found near the front part of the cave (near survey station A5).

Family: Tenebrionidae

Eschatomoxys pholeter Thomas and Pape

This beetle species was described using specimens taken at Bat Cave during this study. The species also occurs in other caves in western Grand Canyon National Park and the Grand Canyon–Parashant National Monument (Pape et al., 2007). The species is probably not strictly a cave species, and likely also occurs in dry situations among cliffs, where it is probably associated with fecal materials in rodent nests. This is similar to the habit of *E. tanneri* Sorenson and Stones, which has been recorded in southern Utah (Sorenson and Stones, 1959) and in Marble Canyon, Arizona (Pape et al., 2007). Peck (1980) recorded a single specimen of *Eschatomoxys* sp. from Thunder Cave, also in the Grand Canyon. The location of this record is about midway between the known distributions of *E. pholeter* and *E. tanneri*. The Thunder Cave record probably represents one of these two species, but since the disposition of the specimen is unknown it could not be examined. The specimen was taken off a wall of a dry upper passage above some (bat?) guano (Peck 1980).

Peck (1980) recognized that *Eschatomoxys* spp. show morphological adaptations to a subterranean habitat. The head and pronotum are narrowed, and there is a definite attenuation of the legs and antennae. He suggested that this morphology represents adaptation for scavenging in animal nests and burrows rather than being associated with caves. This seems reasonable, considering most records of the genus have not been from caves, except for *E. pholeter*, which has so far been recorded only from caves. The species probably colonizes caves opportunistically from adjacent shelter and crevice habitats where they are probably associated with rodents.

The greatest density of the beetles in the cave is on the active bat-guano deposits. Otherwise they are thinly distributed throughout the front portion of the cave, except in the entrance room, which may be too dry. They scavenge over the surface of the guano and probably feed on a variety of foods, including dead bats. They were observed feeding on the dead bats presumed to have been caught by a ringtail near the front part of the main passage of the cave (Pape et al., 2007: figure 9). There were no larvae of *E. pholeter* found in the guano deposits, and they were not present in the two guano samples removed from the cave. The larvae may be present only during times of the year when bat activity is at its peak. The beetle is the primary prey of the spider *Kibramoa suprenans* at Bat Cave.

E. pholeter is the only invertebrate species that was observed beyond the passage constriction at survey station B9. Only a couple of individuals were present there, and it is probable these were vagrants from the nearby active guano deposit. A search of the fossil guano deposit for invertebrate activity gave negative results, and the deposit is likely depleted of useable nutrients.

Family: Curculionidae

Smicronyx imbricatus Casey

This weevil has been recorded from the Gulf coastal plain and "central lowlands" (north-central plains) in Texas to the Sierra Nevada and coast-range sections of the Pacific mountain system, and it is widely distributed in the basin and range province (Anderson, 1962). I assume the weevils emerge in the cave from seeds contained in scats deposited by ringtails. *S. imbricatus* was found in moderate abundance at the peak of the guano deposit at survey station D1. The natural proclivity of many weevils is to climb up vegetation and other objects. The only thing available for them to climb in the cave is a mountain of guano, so they congregate at the top along with other invertebrates. The presence of this species is coincidentally associated with ringtail use of the cave.

Order: Siphonaptera

Family: Ischnopsyllidae

Sternopsylla distincta Rothschild

This flea is known from throughout the southern portion of the United States, where it is associated primarily with the Mexican free-tailed bat and the western bonneted bat (*Eumops perotis* Schinz) (Hubbard, 1968). It is found in large numbers on the active guano piles at Bat Cave when the bats are present. The bats groom the fleas off their bodies, and the fleas drop to the guano pile. There is no way for the fleas to return to the host once they are removed, and some may become prey of predators on the guano piles. There are currently no other records of fleas from caves in the park, but associations with birds, rodents, bats, and other cave-frequenting mammals makes their presence likely.

Order: Diptera

Family: Muscidae

Fannia sp.

A single individual of this muscid fly was found in the cave. It had been captured by the single female *Loxosceles* spider observed in the cave. Its association with the ecology of the cave, if any, is not known.

Order: Lepidoptera

Family: Tineidae

Tineid moth (new genus and species)

This animal is a new genus and species (Don Davis, pers. comm.). This small, weakly flying moth is common in the cave. They are readily noticed because their wing scales reflect a silvery color in the light from headlamps. The larvae of the moths probably derive nourishment directly from the fresh guano (Vandel, 1965) and would then be considered guanobionts. Alternatively, they may be fungivores. They may be preyed upon by spiders present in the cave (*Psilochorus* sp., *Kibramoa suprenans*, and *Loxosceles* sp.). The moths were apparently attracted to the dead *Tadarida* found near the front of the cave. This association is not understood. The only other record of a tineid moth from a cave in the park is from one of the caves on Horseshoe Mesa (Welboun, 1978).

Tinea (*pallescentella*?)

A single individual of this animal was found in the cave. The moth is larger and distinctly different from the undescribed species listed above. The specimen was damaged and was not positively identifiable to species, but may be *T. pallescentella*. Its association with the ecology of the cave is not known.

Order: Hymenoptera

Family: Sphecidae

Sceliphron caementarium Drury

The presence of this sphecid wasp was evident from the abundant multi-celled mud nests observed throughout the entrance area. Nests were present on the walls of the cave and on the wooden walkway supports, pulleys, and cables left from the guano mining operation. One of the nests contained sixteen cells. None of the nests were in use during our visits to the cave. *S. caementarium* provisions its nests with spiders. Due to the dry, sheltered environment inside the cave entrance, the old nest cells may have accumulated over a very long time.

Cave Microclimate

A series of temperature and relative humidity measurements were taken in the cave on March 29, 1996, beginning at the cave entrance (at 1617 hrs), and progressing deeper into the cave to the bat-occupied roost areas. Temperature and humidity at the cave entrance (drip line) were 17 °C and 15.4 percent, respectively. Both of these climatic parameters increased toward the rear of the cave at the time of our visit. The lower values at the cave entrance were the result of the large size of the entrance and its proximity to, and air exchange with, the arid desert environment outside of the cave. The microclimate of the cave at the bat roosts is greatly influenced by the presence of the bats, particularly when they are in residence in large numbers. Their presence results in a localized increase in both relative humidity and ambient air temperature. At the first bat roost (229 meters from the entrance; Fig. 1, survey station D1), where a few hundred bats were present, the values were 26 °C and 89.0 percent at fifteen centimeters above the guano deposit. Deeper in the cave, along the main trunk passage, the air temperature drops slightly at the high point in the cave at the main bat roost (265 meters from the entrance; Fig. 1, between survey stations B7 and B9). Here the air temperature was 25 °C and the relative humidity 100.0 percent. The slightly lower air temperature at this location may have been due to a larger volume of air that was less affected by the small number of bats present at the time the measurements were taken. Additionally, air movement along the main trunk passage may have caused some minor mixing with cooler air from the front part of the cave.

Bat Cave Food Web

The food web in the cave is supported primarily by the annual deposition of guano introduced by the Mexican free-tailed bat colony. While some bats are present throughout much of the year, the greatest numbers are in residence from April through September. The bats leave the cave after sunset each evening to feed on insects and return to roost in the cave and digest their food. Their urine and fecal pellets drop to the floor and build into large deposits over many years. The annual guano layer supports most of the arthropod activity, with layers from previous years, depleted of nutrients, showing little or no arthropod activity.

Adult bats that die of natural causes fall to the guano pile and provide additional nutrients. During the summer, juvenile bats that lose their grasp on the ceiling and are unable to fly also drop to the guano deposit and are consumed by arthropods and, probably, ringtails. Parasites that are groomed from the bats drop to the guano pile, where they become food sources for other microfauna. Ringtail scats provide a small amount of additional allochthonous nutrient input to the cave. The lack of a rhaphidophorine cave cricket at Bat Cave may be due to inadequate vegetation in proximity to the cave.

The diagram of the cave food web, as it is currently understood, is presented in Fig. 7. Most associations shown are assumed and are based on typical life habits of the taxa present. However, several of the associations were documented during the study, including the Mexican free-tailed bats feeding on the antlion (*E. pallens*), the ringtail feeding on both bats (*T. brasiliensis*) and the tenebrionid beetle *E. pholeter*, the plectreurid spider (*K. suprenans*) also feeding on *E. pholeter*, and the brown spider *Loxosceles* sp. feeding on the muscid fly (*Fannia* sp.).

Summary

The annual deposit of *Tadarida* guano is the only nutrient input of any consequence entering Bat Cave. The entrance to the cave is horizontal, and the ceiling at the entrance overhangs the debris slope from the cave, precluding allochthonous organic debris washing into the cave and contributing nutrients. Only very small quantities of water penetrate the thick bedrock overburden at the main fault along which the cave is developed. The only water observed in the cave was several small drip points concentrated in an area along the west wall 230 meters from the entrance and at the top of the large guano deposit 265 meters from the entrance and very small quantities of condensate water found in the fossil guano deposit approximately 360 meters from the entrance. No arthropods were found at any of these water sources.

Most of the invertebrates present in Bat Cave are associated directly with the active guano deposit. Previous annual guano layers beneath the freshly accumulating layer are drier and appear mostly devoid of arthropod activity.

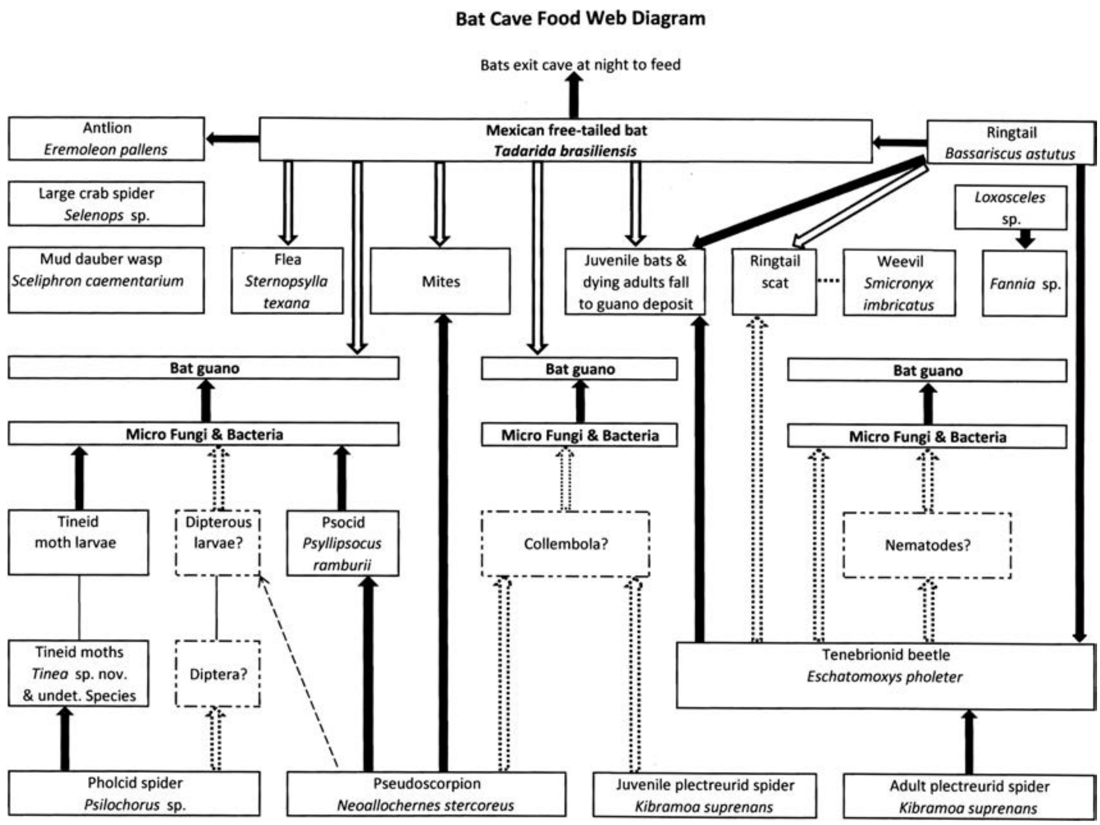

Figure 7. Bat Cave food web diagram. The associations are identified as follows: Solid-filled block arrows indicate direct consumption. Unfilled block arrows indicate deposition. Dashed-line block arrows indicate likely consumption associations. A narrow solid line is an intraspecies connection and a narrow dashed arrow is an assumed association. Documented taxa are shown as solid-bordered boxes and suspected taxa are shown as dash-bordered boxes.

However, the drier condition of the lower layers may provide suitable habitat for eggs, larvae, or pupae of some species inhabiting the guano. The drier guano may inhibit potentially harmful fungi associated with the higher moisture content of the fresh guano. No arthropod activity was present in the nutrient-depleted fossil guano deposit at the rear of the cave.

Except for the presence of the large bat colony and the associated guano deposit, Bat Cave would appear to follow the pattern described by Welbourn (1978) for the caves at Horseshoe Mesa and many other caves in Grand Canyon National Park. Because of the generally arid climate in the region during the last ten to twelve thousand years (Van Devender, 1990), many caves, especially those with multiple entrances, have dried to a considerable degree. Cave invertebrates that may have been present in more mesic, wetter times were likely extirpated during this extended drying period. While Bat Cave is nearly devoid of free water sources, the humidity in the cave increases from the front to the rear of the cave. This is due to the cave having a single entrance, which minimizes air exchange with the arid exterior environment, and moisture contributed by the bats through their respiration and urination.

A total of 27 taxa, including five vertebrates and 22 macro-invertebrate species, were identified as elements of the ecology of Bat Cave. Two of the macro-invertebrates, *Eschatomoxys pholeter* (Coleoptera: Tenebrionidae) and an undescribed genus of tineid moth are species first discovered during this study. Additional study would likely reveal additional macro-invertebrate species in the cave. Bat Cave has the most species rich macro-invertebrate ecology currently known in a cave in the park.

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