Check List 10(4): 761–794, 2014

ISSN 1809-127X (available at *www.checklist.org.br*)

Check List
Journal of species lists and distribution

Lists of Species

Diversity and ecology of the macro-invertebrate fauna (Nemata and Arthropoda) of Kartchner Caverns, Cochise County, Arizona, United States of America

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Abstract: A two-year study of the diversity and ecology of the macro-invertebrate fauna (Nemata and Arthropoda) of Kartchner Caverns, near Benson, Arizona, USA, was conducted between September 2009 and September 2011. The study expands on the baseline study conducted twenty years earlier, from 1989-1991, which was one of several resource analyses conducted prior to development of Kartchner Caverns as an Arizona State Park. The recent study makes a significant contribution to the understanding of the invertebrate fauna and ecology of Kartchner Caverns and cave macro-invertebrates in the desert region of the southwestern United States and Northern Mexico. The initial study identified 39 macro-invertebrate species associated with the ecology of the cave. The recent study increased this number to 98 species, including 16 species new to science, seven of which are troglobites. Kartchner Caverns is now known to support the most species-rich macro-invertebrate ecology of any cave in Arizona.

DOI: 10.15560/10.4.761

Introduction

An initial baseline study of the macro-invertebrate cave fauna at Kartchner Caverns State Park (KCSP) near Benson, Arizona (Figure 1) was performed by W. Calvin Welbourn under contract to Arizona Conservation Projects, Inc. between 1989 and 1991, and the results were subsequently published in the Journal of Cave and Karst Studies (Welbourn 1999). The initial study was one of several resource analyses conducted prior to development of Kartchner Caverns as an Arizona State Park. The initial study included 164 in-cave hours of observation and sampling during 36 visits to the cave. The original paper states that 38 macro-invertebrate species were documented in the cave. A review of the paper reveals an actual total of 41 species, 39 of which we interpret as being integrally connected with the ecology of the cave. It was reported that the majority of the invertebrates in the cave are supported by bat guano deposited annually by the summer resident cave myotis (*Myotis velifer* Allen, 1890) maternity colony. Our recent study revealed that the ecology of the cave is more complex, and that there are additional anastomosing food webs operating in the cave that are independent of the bat guano nutrient source. Many of these food webs are associated with natural entrances to the cave, which provide other sources of energy input and allow ingress and egress of invertebrates and other small animals. We currently recognize 98 macro-invertebrate species that are elements of the ecology of Kartchner Caverns.

Figure 1. Location of Kartchner Caverns State Park, Arizona, USA.

This study was initiated in 2009 by Luis Espinasa/ Marist College, Poughkeepsie, New York and Robert Pape (RBP)/University of Arizona, Tucson, Arizona. Barry M. OConnor (BMOC)/University of Michigan, Ann Arbor, Michigan, joined the project shortly after its initiation as the co-principal investigator.

Materials and Methods

This study was conducted at the request of Arizona State Parks (ASP). The ASP project access and sampling permit was dated September 10, 2009. The original permit was for a two-year period, and has been extended for continuing studies. We refer the reader to Figure 13 for text references to place locations within the cave.

Because of the on-going crisis with the white-nose syndrome (WNS) fungal epidemic that has had a devastating effect on bat populations in the eastern half of the United States since 2006, this project followed the following ASP protocols to preclude introduction of the fungus:

- Most equipment and clothing used in the cave for this project was dedicated to the project.
- No equipment or clothing that had been used at any mine, cave, or other bat-occupied site east of the Mississippi River was allowed on the project, irrespective of whether use was in WNS-identified localities or not.
- Use of equipment that had been used in regional caves (west of the Mississippi River) was permitted provided current United States Fish and Wildlife Service (USFWS) decontamination protocols were applied to the equipment/clothing off of Kartchner Caverns State Park premises prior to use in the Park.
- All project personnel were educated about WNS and project protocols prior to their beginning activities on the project.
- All project personnel were provided with a combination sign-in and acknowledgement sheet regarding WNS information and protocols.

Arizona State Parks and the Arizona Game and Fish Department defer to the USFWS decontamination protocols for treatment of clothing and equipment to minimize the potential introducing WNS in Arizona.

We looked exclusively at macro-invertebrate species and did not address the fauna of drip waters, fungi, or microbial life such as bacteria. Fungal and microbial studies are currently being conducted in the cave by other research teams (Legatzki *et al.* 2009; Vaughan *et al.* 2011). Kartchner Caverns is a National Science Foundation designated Microbial Observatory, and is the only cave resource in that network.

Since reinitiating studies of macro-invertebrates at Kartchner Caverns in 2009, we have conducted a total of 29 trips into the cave, with at least one visit each month during the first two years of these efforts. Through September of 2011 total person in-cave time was approximately 374 hours, approximately 210 hours (56%) of which represented actual searching, observation and sampling time.

Our sampling approach emphasized low impact techniques of observation of invertebrates within the cave in their natural environment. Three principal methods were employed for locating invertebrates in the cave. The primary method was a general visual search of habitat including ceilings, walls, and floors of the cave, with particularly attention paid to searching beneath pieces of floor debris, but also at bat guano deposits and water sources. After observations were made and samples taken, pieces of floor debris were replaced in their original position to conserve invertebrate habitat.

The second method was the placement and intermittent monitoring of a single 5 cm x 1.9 cm x 0.6 cm raw hardwood block at 37 invertebrate stations we established throughout the cave. Each station was marked with a white plastic knife labeled with the station number and date of placement written in indelible ink (Figure 2). As the blocks decayed an ecological succession of resident invertebrates came to these bait stations.

The third method was the use of Berlese funnel extraction of bat guano. We repeated the sampling of the two major bat guano deposits in the cave (the Lunch Spot and the Maternity Roost sites) using the same methodology employed for the initial study (Figure 3). We sampled both sites each month for two years with the exception of July of each year, when the annual brood of young *M. velifer* is present and bonding with their parents.

Because of the importance of entrance areas in the movement of nutrients into the cave, and the often-complex ecological food webs that occur in these areas, we spent a significant portion of our in-cave time studying these areas. At the time of the initial study only two surface connections were recognized: the historic Entrance Sink and an unidentified surface connection in the Granite Dells area (Welbourn 1999). We now know of 7 surface connections with the cave that are accessible to invertebrates (Figure 13). Measured micro-climatic parameters and the presence of a diverse biota in the Throne and Rotunda Rooms (Figure 13), which was not present during the time of the initial study some 20 years previous, suggest another surface connection in that portion of the cave.

To preclude any significant impacts to potentially small populations of cavernicolous species, only the minimum number of specimens needed for identification

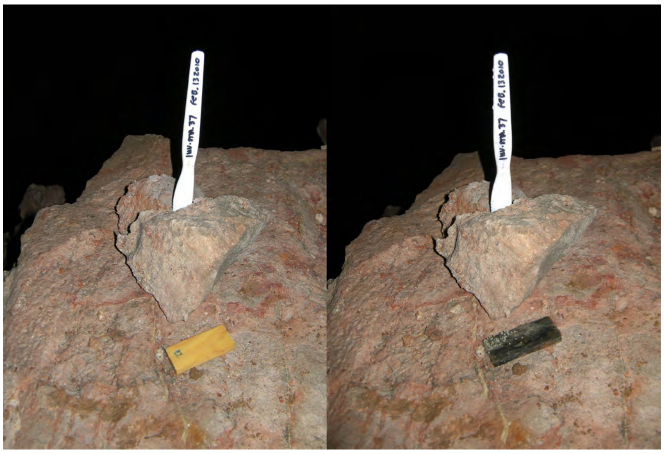

FIGURE 2. Invertebrate station with small wood block and plastic knife marker in the Pyramid Room, February 13, 2010 (left); same location five months later (July 17, 2010), showing mold development on the wood block.

FIGURE 3. Sampling fresh bat guano at the Lunch Spot in the Big Room, Kartchner Caverns State Park.

was sampled. Invertebrates were sampled by hand, with forceps, or with a camel hair brush moistened with denatured ethyl alcohol (ETOH). Samples were placed in ETOH in glass vials with plastic-seal screw cap lids. Each specimen was assigned a unique inventory number in the laboratory.

Subsequent to the initial study additional information on macro-invertebrates occupying the cave was limited to occasional sampling by KCSP staff. We reviewed these archived materials and incorporated our findings into the results of the recent study.

Voucher specimens were primarily placed in the resident institutions of taxonomists performing identifications, as appropriate. Specimens from the initial study are archived in the Florida State Collection of Arthropods, Gainesville, Florida. Voucher specimens, repositories, and accession numbers are listed in Appendix A.

Results

Macro-invertebrates that occur in caves are typically assigned to ecological groups using a somewhat superficial methodology based on their level of use of, and dependency on, the cave environment or resources contained therein. The ecological groups that have historically seen the most use, and seem to have the greatest utility, are trogloxene, troglophile, and troglobite. The initial study employed these terms, and we elected to retain them for the recent study. We define a trogloxene as 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. Accidentals are animals that wander or fall into caves, do not normally occur in such habitats, and obtain no benefit from their presence in caves. Species for which we do not currently understand their ecological association we list as unknown.

With the completion of this two-year study the list of macro-invertebrates that have a positive association with the cave currently stands at 98 taxa. This is an addition of 59 taxa to the 39 species reported in the initial study. There are an additional ten species recorded from the cave that we consider accidentals, and we have included these in Table 1. It is prudent to record all taxa observed within the cave for the primary reason that ecological associations are not always readily apparent, and species that might appear to be accidental may actually have some cryptic association that gives them a nexus with the cave. Our recent efforts have proved this to be true in several cases for species that had been considered to be accidentals at the time of the initial study (*e.g.* the thread-legged bug [*Phasmatocoris labyrinthicus* (troglobite)], the two New World army ants [*Neivamyrmex* spp. (troglophiles)], and the Vaejovid scorpion [*Pseudouroctonus* nr. *apacheanus* (undescribed species?) (troglobite)], among others).

Table 1 is a list of all macro-invertebrate taxa that have been recorded from Kartchner Caverns consolidated from the initial study (Welbourn 1999), the samples taken by KCSP staff between 2002 and 2009, a single record from the recent University of Arizona nematode study, and those from our recent study. In addition to assigning each species to an ecological group, we also assign each species to a guild that it occupies in the ecology of the cave; fungivore (including bacterial feeders), decomposer, scavenger, predator, parasite, herbivore, or unknown. Since accidental species are not an integral part of the ecology of the cave no guild is assigned for these animals. The two species that are tentatively listed as accidentals (accidental?), since there is some potential for an ecological association with the cave, have their guild listed as unknown. A question mark after any of the descriptors in Table 1 indicates the probable or suspected, but unconfirmed assignment of the characteristic. Species that were documented in the cave during the initial study (Welbourn 1999) are preceded by an asterisk in the species column of Table 1.

The status (relative abundance) of each species in the cave is assigned according to the following definitions:

Abundant – A species that can usually be found during most of the year, is present in at least several areas of the cave, and for which the number of individuals in a relatively small area may range from several to many.

Common – A species that may be observed regularly in the cave, either through most of the year or seasonally, and that occurs in multiple areas of the cave, but is usually not represented by large numbers of individuals in a small area.

Uncommon - A species that is found occasionally, but may be restricted to certain habitats, areas of the cave, or seasons, and is more likely not to be seen on any given trip into the cave, but may be observed during every third to tenth visit.

Rare - Rare species are those that we have observed no more than three times during the recent study (and/or a similar level of observation during the initial study or combination of both studies), may not be seen for extended periods (commonly more than ten cave visits on average), and includes those that we know from only a single record or few records from a single location in the cave.

Species Accounts

This section contains a brief species account for each taxon documented from the cave and describes details of its biology and ecology as they are currently understood. Ecological notes from the initial study (Welbourn 1999) are incorporated into the discussions as appropriate. Photographs of many of these taxa are accessible at the Kartchner Caverns Website at: http://azstateparks.com/Parks/KACA/science.html.

Phylum Nemata
Family Thabditidae
Rhabditis spp.

Two species of nematodes (*Rhabditis*) were identified from samples taken from the Big Room during an independent study by the University of Arizona Microbial Team in 2009: one from a fresh bat guano deposit of the resident cave myotis maternity colony and the other from clay soil floor deposits (Holohan and Stock 2009). No nematodes were found in any of the guano samples taken for Berlese analysis for the current project. Based on their buccal morphology both species of *Rhabditis* from the cave are bacterial feeders (Holohan and Stock 2009). They are likely prey for small predators in the guano, primarily mite species. The species from the guano deposit is considered a bacteriovore-guanophile in the cave, and is probably generally common despite the lack of its appearance in the Berlese samples. Nematodes were recorded in the initial study from fresh bat guano in the Big Room (Welbourn 1999).

Phylum Arthropoda
Class Arachnida
Order Palpigradi
Family Eukoeneniidae?

Undetermined genus and sp.

This animal is known in the cave from a single immature specimen taken in the Big Room during the initial study (Welbourn 1999). We made a concerted effort to relocate this species during this study, searching in many areas of the cave, and particularly in habitat resembling that occupied by the only other known cave palpigrade population in Arizona, at Papago Springs Cave (RBP personal observation). No palpigrades were found during the two years of the recent study, and we conclude that the species is apparently rare in the cave.

Order Scorpionida
Family Vaejovidae
Pseudouroctonus nr. *apacheanus* (Savary; personal communication)

Scorpions were encountered only rarely during the initial study, and were observed primarily in the entrance area ("…on several occasions."), with the only observations deeper in the cave limited to one animal found in the Scorpion Passages ("…near Grand Central Station."), and one at the guano pile beneath the bat maternity roost in the Big Room (Welbourn 1999). The supposition in the initial study was that the animals were accidentals, occurring primarily near the cave entrance, and that individuals found deeper in the cave represented vagrants. We assume that the original observations represent a single species, and that it is the *Pseudouroctonus* that is currently found in the cave. A nocturnal surface reconnaissance conducted in the vicinity of the cave Entrance Sink on August of 2012 failed to locate *Pseudouroctonus* outside of the cave. The surface scorpion fauna in the vicinity of the cave was found to be dominated by another vaejovid scorpion, the stripe-tailed scorpion (*Hoffmannius spinigerus* Wood, 1863). We have never found *H. spinigerus* in the cave proper, but we did find it in the bottom of the open portion of the cave Entrance Sink.

In addition to the presence of young, finding juvenile exuviae, and the incipient troglomorphy[†] exhibited by the species in the form of a reduction in body pigmentation, the single most significant indication that the species is a cave endemic is the occasional presence of the animals deep in the cave. Findings for the few species that have been studied, particularly burrowing species, show that scorpions have very limited home ranges. A 16-meter diameter home range is considered large for a scorpion, with ranges for most species limited to a few meters (Polis 1990; Benton 1992). The species has been found in the middle of the Big Room at the bat maternity roost site and in the middle of the Rotunda/Throne Room area of the cave. The former location is 75 meters from the nearest cave surface connection, a distance nearly five times what is considered a large home range for scorpions. The Rotunda/Throne Room location is even deeper within the cave.

[†]Troglomorphy in animals is a convergent morphology involving reduction of cuticular pigmentation and eye structure and enhancement or attenuation of extra-optic sensory structures associated with long-term habitation of naturally occurring aphotic environments (Pipan and Culver 2012).

Based on our current understanding of the ecology of this animal we believe the Kartchner Caverns scorpion is, at the very least, a disjunct troglobitic population of *P. apacheanus*, and may be a distinct species. Additional studies on this population are currently under way.

Order Pseudoscorpiones
Family Chernetidae
Dinocheirus (*arizonensis*?)

The initial study recorded two species of pseudoscorpions in the cave (see following discussion), but did not identify them beyond order. We have encountered only a single pseudoscorpion species in the cave during the recent study, represented by six observations of single individuals. Both males and females were observed, all but one appearing to be adults. The single juvenile was found as prey in the chelicerae of an adult female *Achaearanea canionis* in its web in the Crinoid Room. This pseudoscorpion apparently does not occur deep in the cave, and is primarily associated with areas near surface entrances where the humidity is comparatively low, and where its probable main prey, the barklouse *Psyllipsocus ramburii*, also occurs. The deepest location in the cave for a pseudoscorpion recorded during the initial study (likely this species) was in the southern end of the Anticipation Room. We found the species somewhat deeper in the cave, in the central portion of Grand Central Station, on a couple of occasions. Based on the few animals found during the study, the population of the species in the cave is apparently small, and the species is considered uncommon and localized in the cave. There is no apparent morphological evidence of cave adaptation in this species, and it is most likely a troglophile in the cave. Interbreeding with an epigean population of the species may occur.

Family Unknown
Undetermined genus and sp.

The initial study reported a second species of pseudoscorpion from the cave, also recorded as occurring "near the cave entrance". No information is available to confirm its identity, or whether indeed a second species is present. The only pseudoscorpion we found during the recent study is *Dinocheirus* (*arizonensis*?). Since the sexes of many pseudoscorpions [including *D.* (*arizonensis*?)] are variably dimorphic, it may be that males and females of this species were misconstrued as separate species during the initial study. We suspect this only since our extended efforts in this part of the cave revealed only the one species. The presence of a second pseudoscorpion species in the cave is certainly not precluded, and we retain the original reference on the list of species for the cave.

Order Araneae
Family Theraphosidae
Aphonopelma sp.

The disarticulated remains of a single tarantula were found on the top of the main breakdown block in the lower portion of the Tarantula Room (Figure 4). This is the same individual that was the source of the name given to this room by the original explorers (Gary Tenen, personal communication). No other tarantulas, live or otherwise, were observed in the cave during the current two year study. The theraphosid record from the initial study occurs only in the list, and there is no information in the text of the paper whether a live animal was found in the cave, or whether they encountered the same remnants that we found, and that still remain, in the Tarantula Room.

Family Filistatidae
Kukulcania sp.

We have only a single record of this species in the cave, from the observation of a distinctive hackled-band web that is the characteristic architecture of the webs constructed by this family of spiders. The web was located at the top of the Jackrabbit Shaft, and contained about a hundred newly hatched spiderlings. No adults were present at the time. This was the interior of the nest, which is seldom so readily observed. Due to the size of the web structure, this is apparently a large species, which makes it likely that it belongs to genus *Kukulcania*, since the genus contains the only large members of this family known in North America.

Family Pholcidae
Physocyclus sp.

This pholcid spider occurs only in the entrance areas of the cave, but certainly completes its life cycle within the cave, and is therefore considered a troglophile. We found this species only in the Crinoid Room, which is just inside the historic collapsed Entrance Sink. Here, where they are active year-round, they construct their irregular webs among breakdown blocks in the collapse area of the sink. The pholcid is a generalized predator of invertebrates that become trapped in its web. The species is considered common where it occurs locally in the cave. This species was not recorded in the original published study (Welbourn 1999), but was alluded to in the 1992 report to Arizona State Parks as "…. surface spiders were noted in the entrance area…." which is probably this species.

Figure 4. Disarticulated remains of tarantula (*Aphonopelma* sp.) in the Tarantula Room.

Family Sicariidae
Loxosceles sp.

This species has so far been recorded only from the Jackrabbit Shaft. The spiders live in the top part of the shaft and prey primarily on surface invertebrates entering the cave via small openings to the surface. The species is uncommon and has apparently not colonized the cave to any significant depth. They should also be present at other cave surface connections, particularly in the collapsed Entrance Sink. Species of *Loxosceles* are relatively common in caves in southern Arizona, sometimes occurring in large numbers as a significant predator in these habitats. They appear to be sensitive to repeated human disturbance. Caves that have robust populations of the spiders seem to be those that receive little human visitation, while the spiders never seem to be common in caves that are regularly visited by large numbers of people (RBP personal observation). Based on our observations this species is probably primarily a trogloxene in Kartchner Caverns, but *Loxosceles* are known to be troglophilic in other caves (RBP personal observation), and this species may occasionally be troglophilic here.

Family Theridiidae
Achaearanea canionis

This small species occurs in the cave only near entrance areas and shares these areas with the pholcid spiders. They are somewhat less common than the pholcids, and they typically spin their webs among rocky rubble in collapse areas near entrances, or between rocks and the cave floor. Observed prey of this species in the cave includes the spider beetle (*Niptus ventriculus*) and the pseudoscorpion *Dinocheirus* [*arizonensis*?]. This species is a troglophile in Kartchner Caverns.

Family Theridiidae
Undet. genus and sp.

We have found two unidentified juvenile theridiids, both in the interior of the cave. We are uncertain if they represent one or two species, and we are unable to determine if they are *A. canionis* or represent one or two additional theridiid species. Because they were found in the cave interior they are considered unlikely to be *A. canionis*. Alternatively, they may be accidentals that entered the cave on tour visitors.

Family Nesticidae
Eidmanella pallida

This nesticid spider is wide ranging, occurring from far south central Canada throughout most of the USA and south to Central America and the West Indies (Paquin and Hedin 2005). It is common in cool, damp habitats such as deep litter, boulder piles, and other similar habitats as well as being a common resident of caves in these regions. Some cave populations show evidence of troglomorphy (Paquin and Hedin 2005). The Kartchner Caverns population does not exhibit obvious troglomorphy.

The spiders occur anywhere in the moister areas of the cave where adequate prey supports the species. Contrary to what was reported in the initial study (Welbourn 1999), we found the species particularly common in areas that receive the annual guano deposits from the resident bat maternity colony. On the guano deposits they will erect their webs in voids among rocks embedded in the guano, but more commonly occupy drip cones in the guano. They are most likely primarily consuming various mites that bloom in enormous numbers when the bats return to the cave each spring, but likely supplement their diet with other invertebrates that they can capture, including the sciarid and cecidomyiid gnats that breed in the fresh guano.

The spiders suspend their round, bright-white egg cases in their web matrix. Eggs and young were observed in the webs with females between November and February. The initial study reported that egg cases were present in May and October. We suspect the species typically has a single generation per year in the cave, although in areas away from the annual guano piles this may vary. *E. pallida* is a common troglophile in Kartchner Caverns.

Family Linyphiidae
Undetermined genus and sp.

This species is known from a single juvenile that was taken in the Jackrabbit Gallery. It is fully eyed but is somewhat de-pigmented, is likely a rare troglophile in the cave, and may occur only near surface connections. Because it was a juvenile the animal could not be identified beyond the family level.

Family Hahniidae
Neocryphoeca sp. #1 (undescribed species; Ubick, personal communication)

This species is known from a single adult male that was sampled in the Pirate's Den by Steve Willsey in March of 2008. The species is fully troglomorphic, being totally blind and de-pigmented, and with its limbs and tactile hairs exhibiting moderate attenuation. The species is likely endemic to Kartchner Caverns, and is apparently very rare in the cave. No individuals of this species could be found during the recently completed study.

Family Hahniidae
Neocryphoeca sp. #2 (undescribed species; Ubick, personal communication)

This undescribed spider is less morphologically cave-adapted than *Neocryphoeca* sp. #1. The species has less attenuation of the limbs than the previous species, and exhibits minor expression of pigmentation and remnants of eye structure in some individuals. It is however a troglobitic species, and may be endemic to Kartchner Caverns. The species is more common and widespread in the cave than *Neocryphoeca* sp. #1.

Family Corinnidae
Undetermined genus and sp.

Corinnid spiders are mostly ground-dwelling species of rocky areas and leaf litter. A single female of this species was sampled in the Jackrabbit Gallery in August of 2010. The species is likely a trogloxene in the cave, entering entrance areas where they may search for prey.

Family Gnaphosidae
Zelotes sp.

Gnaphosid spiders are mostly nocturnal, ground-dwelling, foraging species that occur among rocks, leaf litter, and grasses, and are common in desert environments. Based on its dark pigmentation this species is likely an epigean species that may occasionally hunt in cave entrance areas. A single individual was recorded from the Jackrabbit Shaft.

Subclass Acari
Order Actinedida
Family Cheyletidae
Cheyletus sp.

Cheyletus are predators of mites and other small arthropods (Welbourn 1999; Fain and Bochkov 2001). A few immature individuals of a species of *Cheyletus* were found on some of the old bat guano piles in the Big Room during the initial study (Welbourn 1999). This mite was not found during the recent study, but we did not sample the older guano piles to the extent conducted during the initial study.

Family Erythraeidae
Charletonia sp.

This mite is known from a single specimen sampled by KCSP staff in July of 2007 from the Rotunda electric utility room. Larval erythraeid mites are parasitic on other arthropods, while nymphs and adults are predators on other small arthropods. We have no knowledge of the potential host for this species, and its presence in the cave could be accidental.

Family Neothrombiidae
Ceuthothrombium cavaticum

The larval instar of *Ceuthothrombium* species is parasitic on cave crickets, whereas the free-living deutonymph and adult stages are predators of mites and other arthropods (Welbourn 1999). The mite larvae attach around the base of the limbs of the crickets (at the coxal/thoracic junction) or under the lateral edges of the thoracic terga (BMOC – based on *C. pima* hosts examined from other caves) where they feed. Welbourn (1999) reported from 1 to 8 of the mites on almost all crickets examined. We found a similar situation during the recent study, with up to 12 mites found on one cricket. The deutonymphs and adults probably live in soil or leaf litter outside of the cave, where they encounter foraging crickets, and the larvae may find their host in this manner.

What were originally thought to be several species of *Ceuthothrombium* in the Southwestern United States are now considered to probably all be *C. cavaticum* (Welbourn, personal communication).

Family Pygmephoridae
Undet. genus and sp.

Most pygmephorids are fungivores, and many are phoretic on various insects including scarab beetles, alates of ants, flies, and others, and on mammals and birds (Rodrigues *et al.* 2001; Krivolutsky *et al.* 2004; Whitaker *et al.* 2007; Mumcuoglu and Braverman 2010; Uppstrom and Klompen 2011). These phoretic associations provide dispersal for the mites to new mold sources. A few individuals of an unidentified pygmephorid mite were found on bat guano in the Big Room during the initial study. The original report did not specify if they occurred on fresh or old bat guano deposits. No pygmephorid mites were found during the recent study.

Family Rhagidiidae
Poecilophysis sp.

Poecilophysis mites are predators that occur in soil, leaf litter, and caves (Welbourn 1999). Species of *Poecilophysis* recorded from caves include at least one troglophile (*P. weyerensis*; Elliott 2007) and one cave obligate species (*P. wolmsdorfensis*; Culver *et al.* 2003). Two specimens of a species of *Poecilophysis* were found during the initial study in the LEM Room and Main Corridor. No *Poecilophysis* were found during the recent study.

Family Stigmaeidae
Eustigmaeus lirella

Most species of *Eustigmaeus* are predators that occurs in soil and leaf litter (Welbourn 1999), and a few feed on mosses (Kethley 1990). *E. lirella* has been taken from a wood rat (*Neotoma* sp.) nest in California (Welbourn 1999). One species of *Eustigmaeus* (*E. johnstoni*) is a known parasite on tropical phlebotomine flies (Zhang and Gerson 1995). An association of *E. lirella* with the phlebotomine fly (*Lutzomyia* [*californica*?]) present in Kartchner Caverns is considered unlikely since the mite is apparently involved in the ecology of the bat guano deposits far from where the flies have been found in the cave. *E. lirella* was found to occur uncommonly on fresh bat guano deposits in the cave during both the original and current studies.

Family Tarsonemidae
Neotarsonemoides sp.

A species of *Neotarsonemoides* was found on bat guano in the Big Room during the initial study. The original report did not state whether this species was found on fresh or older guano. No representatives of this species were found during the recent study. Known species of *Neotarsonemoides* are fungivorous (Eickwort 1990), and the species is likely associated with fungi on the bat guano in the cave (Welbourn 1999).

Order Astigmata
Family Acaridae
Sancassania sp.

Sancassania mites are omnivorous, feeding primarily on decaying organic materials and fungi but also on insect eggs and larvae, and occasionally on nematodes (Welbourn 1999). The initial study reported *Sancassania* as the most abundant mite species on the fresh bat guano deposits. *Sancassania* remains a significant element, and is seasonally the most populous arthropod species present on the bat guano. All life stages were recovered, including the dispersing deutonymph. Deutonymphs were not found in phoretic association with any of the larger arthropods occurring in the cave.

Family Histiostomatidae
Histiostoma nr. *guanophilum* sp. #1 (Undescribed species; OConnor)

Many species of *Histiostoma* inhabit naturally occurring water films, or are associated with manure (including guano) or decaying vegetable or fungal substrates (OConnor 1982; 2009). An undescribed species of *Histiostoma* was reported from pool edges in a gypsum cave in southeastern New Mexico (Cokendolpher and Polyak 1996). *Histiostoma* nr. *piloseta* was reported associated with a fresh guano deposit of a maternity roost of *Myotis austroriparius* in South Carolina (Reeves 2001). *Histiostoma* species have been recorded from bat guano deposits in other caves in Brazil (Ferreira *et al.* 2000) and Arkansas (Graening *et al.* 2006). This and the following species occurring in Kartchner Caverns are both undescribed species. *H.* nr. *guanophilum* sp. #1 is the smaller of the two *Histiostoma* species occurring in the cave but has fewer, larger cheliceral teeth, suggesting that they may feed directly on soft incompletely digested insect parts in the guano. They occur on fresh bat guano deposits in the Big Room. Like *Sancassania*, histiostomatid mites have a specialized dispersing deutonymph that is typically phoretic on insects. Two distinct *Histiostoma* deutonymphs were among the species originally recorded from the cave (Welbourn, 1999), probably corresponding to the two species represented by adults. In the absence of reared or pharate individuals, this remains speculative. No histiostomatid deutonymphs were recovered during the present sampling effort.

Histiostomatidae
Histiostoma nr. *guanophilum* sp. #2 (Undescribed species; OConnor)

H. nr. *guanophilum* is a larger, undescribed species of histiostomatid mite. This species has a large number of very fine cheliceral teeth like most *Histiostoma* species that filter microorganisms from water films. The species occurs on fresh bat guano deposits in the Big Room.

Family Rosensteiniidae
Nycteriglyphus sp.

A few individuals of *Nycteriglyphus* sp. were found in one of the older bat guano deposits in the Big Room during the initial study. *Nycteriglyphus* spp. are normally associated with guano of many species of insectivorous bats, including *M. velifer* (Whitaker and Easterla 1975; Reisen *et al.* 1976). Where they occur, *Nycteriglyphus* are usually present in large numbers in the guano deposits below roosts (Welbourn 1999). Welbourn suggested that the few individuals found in Kartchner Caverns probably indicate the species is not a permanent resident in the cave. He suggested that the high humidity in the cave (99.4 percent) may preclude *Nycteriglyphus* from becoming established (Welbourn 1999). No *Nycteriglyphus* were found during the recent study, but we conducted only limited sampling of the older (recent, but drier) bat guano deposits.

Order Ixodida
Family Argasidae
Carios yumatensis

This soft tick species has been found on *M. velifer* and several other bat species in the southwestern United States (Bradshaw and Ross 1961; Dooley *et al.* 1976). We observed *C. yumatensis* on six occasions during the recent study. Each observation was of a single individual. Since both nymphs and adults of this species were found in the cave during the recent study we suspect that the animals breed in the cave. Nymphs and adults of argasid ticks spend most of their time in the roost, only feeding on the hosts for short periods of time. Five of the animals were observed on the Maternity Roost guano pile, and one was located in the LEM Room where the individual was found beneath a small piece of floor debris.

Carios (formerly *Ornithodoros*) nr. *hasei*

Ticks were found on two bat guano piles in the Big Room during the initial study. They were not found on the two major guano deposits (Lunch Spot and Maternity Roost), but about 10 meters west of the Maternity Roost site. Since he found only immatures of the species Welbourn suggested that they were brought into the cave by bats, but were probably not reproducing in the cave (Welbourn 1999). Intuitively, it seems reasonable that only one species of *Carios* is involved here, and since we had adult animals for identification, we know that *C. yumatensis* is currently present in the cave. However, without specimens from the initial study we cannot preclude the occurrence of *C.* nr. *hasei* in the cave. Welbourn (1999) mentions a record of *C. hasei* taken from *M. velifer* in the state of Sinaloa, Mexico. We know of no confirmed records of this Neotropical species from the U.S. (BMOC).

Order Mesostigmata
Family Laelapidae
Gaeolaelaps sp.

Predatory laelapid mites present in the cave during the initial study were attributed to *Gaeolaelaps* sp. At that time the taxonomy of this group of laelapid mites was still in flux, and *Gaeolaelaps* and *Stratiolaelaps* were not considered discrete taxa by some acarologists. We currently have three species of laelapid mites present in the cave, including *Gaeolaelaps* sp. and the following two species (see below). During the recent study we found only a single individual of *Gaeolaelaps* sp. at invertebrate station 10 in the Millipede Tomb Room in May of 2012. Specimens of "*Gaeolaelaps*" from the initial study (Figure 7 in Welbourn, 1999) were provided to BMOC by Cal Welbourn for review and were found to be *Stratiolaelaps scimitus*. Like other free-living laelapids, *Gaeolaelaps* are predators.

Stratiolaelaps scimitus

The primary prey of some *Stratiolaelaps* species are thrips (Insecta: Thysanoptera), but they also feed on other soil arthropods and nematodes (Walter 2006). *S. scimitus* is a cosmopolitan soil-inhabiting, generalist, predatory mite species that has been transported around the world by humans (BMOC). The species is sold in the agricultural industry to control dark-winged fungus gnats (Diptera: Sciaridae) in greenhouse operations (Cabrera *et al.* 2005). Two undescribed species of *Stratiolaelaps* were reported from Hidden Cave in the Guadalupe Mountains of southeastern New Mexico (Polyak *et al.* 2001).

Stratiolaelaps mites are the dominant small predators on the fresh bat guano deposits in the cave where they likely feed on nematodes and a variety of micro-arthropods, including other mite species. One unidentified laelapid mite was observed with an entomobryid collembolan in its chelicerae at Millipede Meadows.

We currently have two species of predatory *Stratiolaelaps* mites in the cave. Since the initial study only listed a single species of laelapid mite (identified as *S. scimitus* by a review of the original materials), we do not know if both *Stratiolaelaps* species were present at that time. *S. scimitus* is commonly moved around by anthropogenic means. Since the species was present at the time of the initial study, it may have arrived in the cave on its own, or been accidentally introduced by early explorers of the cave.

Interestingly, there is a complete segregation of the two *Stratiolaelaps* species at the two major bat guano deposits in the cave. The Lunch Spot guano deposit supports only *S. scimitus*, and the Maternity Roost site supports only the undescribed *Stratiolaelaps* discussed below. Some cosmopolitan predatory invertebrates (such as *S. scimitus*) are successful because they are more aggressive than indigenous predatory species. Whether *S. scimitus* may eventually colonize the Maternity Roost guano site is a question that should be investigated.

Stratiolaelaps sp. (Undescribed species; OConnor)

This species is currently recorded only from the Maternity Roost guano location. The species was curiously absent from the Berlese guano samples in June and August (and possibly also July). We do not know why the species would not be present during that period. Since the mites are common on the deposit, a sampling anomaly seems unlikely. This species was not recorded in the initial study, and it is possible that it was introduced.

Family Macrochelidae
Macrocheles nr. *penicilliger* (Undescribed species; OConnor)

Macrocheles is the largest genus in this family of predatory mites. They are primarily predators on small invertebrates in dung deposits. Many species are ecologically tied to dung beetles (primarily species of scarab beetles), which they use phoretically for dispersal (Krantz 1998). This mite was found in the front part of the cave in the Crinoid Room. These mites may be associated with the feces of the white-throated wood rats that live in the boulder complex of the collapsed entrance sink. They could also potentially find forage on ringtail or other mammalian scat in this same area of the cave. The species is likely to be uncommon in the cave, but should be present year-round, and probably completes its life cycle in the cave. We consider *Macrocheles* nr. *penicilliger* to be a troglophile in the cave. The animal is apparently an undescribed species (BMOC).

Family Macronyssidae
Macronyssus crosbyi

This mite is a common ectoparasite on a North American vespertilionid bat species; *Myotis* spp. (including *M. velifer*), *Eptesicus fuscus* (Beauvois, 1796), *Corynorhinus townsendii* (Cooper, 1837) and *Perimyotis subflavus* (Menu, 1984) (Reisen *et al.* 1976; Whitaker *et al.* 1983). This species was not encountered during the initial study, and we found it only once, in a Berlese sample taken from the Lunch Spot guano pile in June of 2010. *Macronyssus* species are obligate, blood-feeding parasites that spend most of their time in crevices in the roost near their hosts.

Family Rhodacaridae
Rhodacarella cavernicola

Rhodacarid mites are predators of small invertebrates, primarily other arthropods and nematodes, in a variety of habitats including soil, plant litter, ocean beach debris and small mammal nests (Moraza 2004; Silva *et al.* 2004). A few individuals of this mite were found on older bat guano deposits in the Big Room during the initial study. At the time, the species was placed as an unidentified species of *Rhodacarus* (Welbourn 1999). The materials sampled and prepared by Welbourn in 1990 were subsequently described as a new genus and species, *Rhodacarella cavernicola* (Moraza 2004). The species has not been recorded elsewhere, and as far as is known is an endemic limited to Kartchner Caverns. We did not relocate this species during the recent study, probably due to the limited sampling efforts conducted at the older bat guano deposits.

Order Oribatida
Family Damaeidae
Parabelbella sp.

Relatively little is known about the ecology of damaeid mites. Some species are microphytophages, and some of these feed on fungi and bacteria (Norton 1990). These mites were found exclusively on moldy wood in the cave, both at the recently placed invertebrate stations, and on older wood found in the cave, presumably from the commercial development of the cave. They are most likely feeding on fungi or bacteria.

Family Oppiidae
Multioppia sp.

Welbourn (1999) listed four species of oribatid mites taken from the cave, but did not elaborate on their taxonomy or provide any ecological discussion, so we do not know if they occurred on fresh, older, or all bat guano deposits (or in other situations). He listed the group as rare in the cave, which may explain why we encountered only a single species. The single *Multioppia* species we found was from Berlese samples taken from fresh bat guano sites in the Big Room. Many oribatid mites are either saprophytic or fungivorous in their habit (Norton *et al.* 1988), and we suspect the species in the cave are likely all fungivores on the bat guano deposits.

Family Undetermined
Undetermined genus & sp. (three spp.)

It is assumed that the *Multioppia* sp. discussed above is one of the four oribatid species found during the initial study. We did not find any of the other oribatid mites during the recent study, but this may be due to limited sampling of older bat guano deposits. We have no specimens or information on the other species noted in the initial study. We assume that the four species were all associated with bat guano deposits.

Class Malacostraca
Order Isopoda
Family Trichoniscidae
Brackenridgia nr. *sphinxensis*

This is one of the two truly troglobitic species that was recognized as such in the initial study (Welbourn 1999). We do not know whether the Kartchner population represents a new species, or is a disjunct population of *B. sphinxensis*, which was originally described from "Sphinx" (ne - Spinks) Cave in the Chiricahua Mountains in Arizona (Schultz 1984).

Brackenridgia are generalist scavengers and they occur in most areas of the cave wherever organic nutrient resources are available within areas of suitable habitat. The animals seem to be present only at sites where obvious fungi and molds have developed, such as on bat guano deposits, on decaying wood, and on dead animals including bats and invertebrates. During the current two-year study they were never observed on the two primary bat guano deposits, and may avoid these areas due to threat of predation, a high level of competition for resources, or other factors. The animals appear tolerant of saturated surface conditions, and do not occur in drier areas of the cave such as the vicinity of the Entrance Sink.

A review of our two years of data for this species has shown that there is an increase in the animals' activity in response to the influx of autogenic meteoric waters from both periods of our regional bimodal precipitation regime. Based on 65 sightings of the animals during all months of the year, the population peaked in April subsequent to the winter/spring precipitation season and again from September through November after the summer rains. The species is locally and seasonally common in the cave.

Juveniles are present year round and reproduction is probably either opportunistic, associated with adequate available food sources, or possibly consisting of two overlapping generations associated with the two peaks of activity coupled with the regional precipitation regime.

Family Porcellionidae
Porcellio laevis

P. laevis is an introduced species from southern Europe that is common and widespread in the United States and Canada (Muchmore 1990; McLaughlin *et al.* 2005). This species is essentially an epigean animal, occurring among surface debris, beneath rocks, and in the epikarst, but it is relatively common in the less humid portions of the cave near surface connections, where they come to forage. The species has been recorded primarily in the entrance series of rooms near the historic Entrance Sink and as far into the cave as Grand Central Station and the southern half of Main Corridor. It is also found in the Scorpion Passages and at Granite Dells, each of which have their own connections with the surface. We seldom encountered juveniles of *P.*

laevis, and the animals typically do not go deep into the cave. A clutch of very small individuals was found on a ringtail scat in the Scorpion Passages during a visit to the cave in May of 2012. Based on this evidence some of the animals apparently breed in the cave, and we thus consider the species an occasional troglophile in the cave.

There is very little overlap in the distribution of the two isopod species in the cave. *Brackenridgia* prefers interior, moister regions of the cave and *P. laevis* is typically found closer to entrances. *Brackenridgia* is probably intolerant of less humid atmospheres and drier surface conditions, while *P. laevis* is apparently tolerant of a wider range of environmental conditions. We suspect that the main reason that *P. laevis* does not often occur in the deeper regions of the cave is that it is essentially a surface species, but one that commonly occurs also in the epikarst and cave environments. They forage in cave entrance areas simply because these areas are integrally connected with their typical habitat.

Class Diplopoda
Order Polydesmida
Family Macrosternodesmidae
Nevadesmus ? (Undescribed species; Pape)

This apparently rare animal was first discovered in the cave in December of 2009 when a single adult female was taken from the underside a damp, deteriorating, and somewhat moldy large wood shim that was lying on the cave floor near the far west wall of the Big Room. We assume that the shim was an abandoned piece of debris from the original commercial development of the cave. We subsequently found three juveniles among developing mold on one of the wood blocks placed at one of the invertebrate stations, about 3.5 meters from the original sampling site. The species is totally de-pigmented and blind, and is a true troglobite. The animal is quite small, about 3 millimeters in length, and ranks among the smaller of the known cave Polydesmida.

Millipedes may feed on a variety of materials, but many species are primarily saprophagous, feeding on decomposing vegetable debris including wood or other plant parts. Some millipedes will also feed on fecal materials and dead invertebrates (David 2009; RBP personal observation). Some cave millipedes, particularly smaller species of *Speodesmus* (Polydesmidae) are apparently soil burrowing species (Elliott 2004). It is possible that the Kartchner Caverns species is a soil inhabiting species, and other methods of sampling will need to be employed to obtain the specimens needed for taxonomic placement of this species.

Order Spirostreptida
Family Cambalidae
Undetermined genus and sp. (Undescribed species?; Pape)

This troglobitic millipede is only known from a couple of areas in the cave, including three individuals from a small area in the Mud Flats and the vicinity of the Fallen Giant formation (both at the east end of the Big Room), and from a single animal found in the west end of the Anticipation Room just southeast of Main Corridor. Only these four individuals have been found and unfortunately, all were dead when found. All four appear to have been adults, and all of them had died on wet (active), off-white colored calcite formations.

We identified this species from parts (approximately the first two dozen body segments) salvaged from the first animal found. The species is totally eyeless and appears to be mostly (or entirely) de-pigmented, the body color (based on dead material), being remarkably similar to the off-white color of the formations on which all four carcasses have been found.

Our knowledge of the ecology of this species is limited to assumptions based on the situations where the dead animals have been found. We suspect the species may be associated with a wet bio-film community on active calcite formations in the cave. The species may be only seasonally active, and is apparently quite rare. The current long term drought in Southeast Arizona (about 12 years; Breshears *et al.* 2005) may have impacted the population of this species, and could explain why we have not found live animals.

Class Chilopoda
Order Scutigeromorpha
Family Scutigeridae
Dendrothereua nr. *homa*

Species in the genus *Dendrothereua* are primarily Neotropical in their distribution, with only a single species (*Dendrothereua homa*) currently recognized as occurring in the United States (Edgecombe and Giribet 2009). However, this species probably represents a handful of distinct taxa in the southern U. S., which may eventually be sorted out by future taxonomic studies.

This centipede species has only been observed in the cave on four occasions, and only in the Jackrabbit Shaft. Two adults and two juvenile animals have been observed. Scutigerid centipedes commonly occur in humid environments such as cellars, wells, and similar situations where they feed on a variety of invertebrates. Here in Kartchner Caverns this centipede is probably feeding on the Australian cockroach (*Periplaneta australasiae*), which is an introduced species in the cave. The centipede likely competes for a variety of invertebrate prey with the Western Banded Gecko (*Coleonyx variegatus* Baird, 1858), which also occurs primarily in the Jackrabbit Shaft. A related species, which commonly occurs in domestic situations, is the cosmopolitan, American house centipede (*Scutigera coleoptrata*). *S. coleoptrata* is an effective predator of invertebrates, and is even capable of feeding on one prey while holding another with some of its legs (Acosta 2003). It is reasonable to assume that the species of *Dendrothereua* found in Kartchner Caverns also has this capability.

This species was not reported in the initial study, and it seems likely that it was not found at that time due to its apparently highly localized habitat within the cave. We consider it unlikely that this species occurs in the Park outside of the cave(s) since suitable habitat is otherwise not present (on the surface).

Order Scolopendromorpha
Family Scolopendridae
Scolopendra heros var. *arizonensis*

Centipedes in the genus *Scolopendra* are predators of a wide variety of invertebrates and the larger species manage to capture small vertebrates including amphibians, lizards, snakes, small rodents, birds, and rarely bats (McCormick and Polis 1982; Schal *et al.* 1984; Elzinga 1994; Molinari *et al.* 2005). Scolopendrids are not uncommon in cave entrances, and these areas are a natural element of their habitat in karst environments. We consider most occurrences of scolopendrid (and other) centipedes occurring in caves to be trogloxenes.

A single adult of this large, colorful desert centipede was observed in the bottom of the Jackrabbit Shaft in May of 2012 (Figure 5). This powerful predator likely finds ample food in the Jackrabbit Shaft with some of its prey potentially including the Western Banded Gecko, the endemic scorpion (*Pseudouroctonus* nr. *apacheanus*), the scutigerid centipede (*Dendrothereua* nr. *homa*), the field cricket (*Gryllus multipulsator*), the introduced cockroach (*Periplaneta australasiae*) and a variety of medium-sized spiders.

Family Scolopendridae
Undetermined genus and sp.

A single scolopendrid centipede was observed in Grand Central Station during the initial study, and was presumed to be an accidental occurrence (Welbourn 1999). We suspect that the scolopendrid observed during the initial study may have been *S. h.* var. *arizonensis*, but since we have no documenting evidence for this, we have retained this record as a potential second species of the family recorded from the cave.

Class Insecta
Order Collembola
Family Onychiuridae
Tullbergia iowensis

This eyeless, de-pigmented species occurs primarily in soils, caves and on the ground surface where it feeds among cryptobiotic crusts (Brantley and Shepherd 2004). The species ranges widely throughout much of North America, the Caribbean and south as far as Brazil, and also occurs in Europe (Bolger 1986; Palacios-Vargas 1997; Culik and Zeppelini-Filho 2003). The species is recorded from caves in Arkansas (Christiansen and Bellinger 1998), Georgia (Reeves *et al.* 2000), Iowa (Peck and Christiansen

Figure 5. Adult giant desert centipede (*Scolopendra heros* var. *arizonensis*) in the Jackrabbit Shaft.

1988), Cuba (Díaz Aspiaszu *et al.* 2003), and Nova Scotia, where it was associated with a guano deposit of the North American porcupine (*Erethizon dorsatum* Linnaeus, 1758) (Calder and Bleakney 1965).

The single record of the species we have from Kartchner Caverns was taken from a piece of partially buried wood in the floor of the Jackrabbit Gallery area near the Jackrabbit Shaft in May of 2011. Because of the wide distribution of this species, and its presence in both cave and non-cave habitats, it is difficult to assess the origin of this species in the cave. The species may be more common than our single record indicates, and additional sampling of collembola in the cave (in general) is needed.

Family Isotomidae
Folsomia candida

This parthenogenetic springtail is pan-global in distribution, having been transported around the globe by humans, primarily contained in soils associated with plants. The species is common in the soil horizon, often being the dominant springtail in such associations, but is also regularly found in caves and mines. The original species description (in 1902) was of a single animal taken from the surface of a pool in a cave in Belgium. *F. candida* is white and blind, but because it occurs commonly in non-cave habitats we consider it a troglophile in the cave. We sampled only a single individual of this species, from one of our invertebrate stations at the far west end of the Big Room adjacent to Millipede Meadows. We suspect the species is likely more common in the cave than our one specimen would indicate.

Family Entomobryidae
Coecobrya tenebricosa

This species is the second most common springtail in the cave. *C. tenebricosa* is a very common springtail species and is the most widely distributed species in the genus in the world (Zhang *et al.* 2009). It is one of the few species of *Coecobrya* found outside of the Oriental region, and may be the only one found in North America (Soto-Adames personal communication). This pure white, blind species is apparently primarily a cave-inhabiting animal, but also occurs in similar habitats, and in greenhouses (Christiansen and Bellinger 1998). Because it also occurs in non-cave environments we consider it a troglophile in the cave. The species was probably introduced into the cave.

Family Entomobryidae
Entomobrya unostrigata

This is primarily an epigean species, but it also occurs in caves. The only record we have from the cave is from a Berlese sample of the Maternity Roost bat guano deposit taken in August of 2010. Because the entomobryomorph collembola documented during the initial study were found mostly between the Babbitt Gate and Main Corridor (and not in the deeper reaches of the cave), we believe this species is a new record for the cave. There is some potential that this animal is an introduced species that may have become established during the commercial development of the cave.

Family Entomobryidae

Entomobryoides guthriei

This species is the most common springtail in the cave and is found in damp to wet situations such as on decaying wood and on dead animals. *E. guthriei* is a common and widespread species in western North America, with a few disjunct records from South Dakota, Iowa, and Louisiana (Christiansen and Bellinger 1998). The species is also previously recorded from caves (Cokendolpher and Polyak 1996). We suspect that this is the entomobryid referred to in the initial study. The initial study stated that collembola were generally uncommon in the cave. Currently the population of *E. guthriei* in the cave is more robust and more widely distributed. The increase in the presence of this species may be attributable to the introduced lampenflora associated with lights in the tour areas of the cave.

Family Entomobryidae

Sinella sp.

The single record of this species from the cave was a juvenile and was not identifiable beyond the generic level. The animal was found at one of our invertebrate stations in the Rotunda Room. There are about 18 species of Nearctic *Sinella*, including some cavernicolous forms (Christiansen and Bellinger 1998). Additional sampling and study will be required to determine the status of this species in the cave.

Family Sminthuridae

Arrhopalites caecus

This small, globular springtail species is known from cave and surface habitats in Europe and North America (Moore *et al.* 2005). We have observed it at mold sources in the cave, including on the wood blocks at the established invertebrate stations. Some of the sminthurids in the cave occur in wet areas, including active formations, small drip pools, and around hose bibs along the tour trails.

We suspect the wet formation biofilm food webs in the cave may be partially supported by bacteria present in autogenic meteoric waters. This small, dispersed food web type apparently contains two or possibly three macro-invertebrate species. In addition to the sminthurids we have observed small spiders in webs they constructed on wet stalagmites, where they are likely preying on the sminthurids. A third member of this biofilm food web may be the cambalid millipede. The sminthurids were apparently present in small numbers during the time of the initial study, and the size of their population in the cave appears to be unchanged.

Family Sminthuridae

Pygmarrhopalites nr. *dubius* (Undescribed species; Soto-Adames, personal communication)

P. dubius is apparently a cave-limited species that has been recorded from caves in Arkansas, Iowa, and Minnesota (Slay and Graening 2009; Zeppelini *et al.* 2009). The Kartchner Caverns population, which likely represents an undescribed species near *P. dubius*, is likely also cave-limited, and may be endemic to Kartchner Caverns or regional caves. The single specimen we obtained was taken from the moldy wood block at invertebrate station 13 in the Rotunda Room Attic in June of 2011. The species is likely more widely distributed in the cave.

Family Oncopoduridae

Oncopodura nr. *yosiiana* (Undescribed species; Soto-Adames, personal communication)

At the time of Christiansen and Bellinger's monograph on the Collembola of North America (1998) there were 13 distinct species of *Oncopodura* known in North America, two of which were undescribed. Most North American *Oncopodura* are blind and de-pigmented cavernicolous species. *O. yosiiana* is recorded from California and Asia; however, the specimens from California attributed to this species were incomplete, and the determination uncertain. The California records were from both cave and epigean habitats (Christiansen and Bellinger 1998). The Kartchner Caverns species could be the same one that is recorded from California (which may not be *O. yosiiana*), or it may be a distinct species, which may be endemic to the cave.

Order Zygentoma

Family Nicoletiidae

Speleonycta anachoretes

Cave adapted nicoletiids are currently known from only two disjunct cave populations in Arizona, the one at Kartchner Caverns, and the other at Arkenstone Cave in Colossal Cave Mountain Park, 32 kilometers east of Tucson near Vail, Arizona. The two caves are separated by a distance of 36 kilometers. It is currently not known whether the Arkenstone Cave population is a sister population to the one at Kartchner Caverns, or whether it represents a separate species. Our comparison of individuals from each site revealed that they are morphologically indistinguishable (Espinasa *et al.* 2012). DNA sequencing of fresh specimens from Arkenstone Cave will be required to make a final determination whether the populations represent one or two species. Arkenstone Cave has been closed to research since 2004.

Only three nicoletiids were observed in Kartchner Caverns during the original two-year study 20 years ago, and all three were found near the entrance to the Red River Passage. We have yet to observe a nicoletiid near the entrance to the Red River Passage, which is approximately 30 meters from the Jackrabbit Gallery. We have identified the Jackrabbit Gallery as the apparent center of the main contemporary population of the species in the cave. The 40 individual observations we have made of *S. anachoretes* since initiation of the recent study consisted of 20 adults and 20 juveniles. Some of these observations may represent the same animals over a period of months, but in March of 2010 we confirmed at least 8 different individuals in the Jackrabbit Gallery.

The animals have been observed in four rather widely separated areas of the cave during the recent study. The highest density occurs in the Jackrabbit Gallery (34 observations), with an apparently smaller population in Granite Dells (4 observations), and single observations at the Big Room Overlook and in the entrance to the River Passage (not the Red River area of the cave). Based on the numbers of animals we have observed, we consider the species to be localized, but common in the cave. We refer the reader to Espinasa *et al.* (2012) for additional details regarding this species.

Order Orthoptera
Family Rhaphidophoridae
Ceuthophilus pima

This is one of several species of cave (or camel) crickets that inhabit caves in southern Arizona. All known populations documented from caves in Arizona are trogloxenic. *C. pima* is recorded from one other cave in the Whetstone Mountains, and from two caves in the Santa Rita Mountains. Hubbell's 1936 monograph on *Ceuthophilus* listed the species as occurring only in the Santa Catalina and Santa Rita Mountains. Specimens in the University of Arizona collection are from these two ranges plus the Pinaleño Mountains southwest of Safford, Arizona.

Cave crickets (both *Ceuthophilus* spp. and *Hadenoecus* spp.) are important in the delivery of allochthonous nutrient input to many cave environments, and are keystone species in the macro-invertebrate ecology of some caves (Hubbell and Norton 1978; Muchmore and Pape 1999; Fagan *et al.* 2007; Lavoie *et al.* 2007). Their fecal material is their primary contribution in these situations, but they are also prey for a variety of predators and their dead bodies recycle nutrients into the caves. Species of *Ceuthophilus* are rather omnivorous in their diets, feeding primarily on plant materials, but also on fungi, detritus, insects, dead animals, and even engage in cannibalism of injured individuals (Fagan *et al.* 2007; Lavoie *et al.* 2007).

Cave crickets seek shelter in caves from climate extremes, particularly in northern latitudes and at high elevations, where seasonal and nighttime temperatures may be well below temperatures where most invertebrates can function. They use caves for similar reasons in the arid southwest, where low humidity and high summer temperatures create equally unfavorable conditions. Some cave cricket populations have annual cycles, but others breed in caves year-round. This is apparently the case at Kartchner Caverns, which is evident from the presence of all age classes of crickets in the cave year-round. Perennially breeding populations may be correlated with suitable epigean foraging conditions during most of the year, where a nearly continuous availability of nutrients allows for egg production to continue unabated. It seems intuitive that populations occurring at lower elevations may more commonly fall into this category.

The initial study recorded population counts of this species in the area between the historic Entrance Sink and the ingress route junction with Main Corridor of between 300 and 800 individuals at various times during the year. During the two years of the recent study we found no more than 55 crickets at one time in this same section of the cave. The current population of the crickets in this area of the cave is therefore an order of magnitude lower than the observed pre-commercial development population. We have not determined the reason(s) for the decline in the cave cricket population at Kartchner Caverns. Other groupings of these crickets occur at all of the known cave surface connections with the exception of the one in the Tarantula Room, which may be too constricted to allow movement of adults of the species in and out of the cave.

The large population of *C. pima* that was present in the cave at the time of the initial study must have been responsible for a significant contribution to the nutrient input to the cave. The drastic reduction in the cave cricket population has no doubt had a negative impact on the macro-invertebrate ecology of the cave. Because cricket guano is derived primarily from plant materials its nutrient content per volume is probably greater than that of bat guano, which contains a high percentage of chitinous remains of insects, which most invertebrates are incapable of digesting.

Family Gryllidae
Gryllus multipulsator

This species is the common *Gryllus* field cricket in the southwestern U.S. and Mexico. The species was recently split from *G. assimilis*, which in the U.S. has been found to be restricted to areas east of the continental divide (Weissman *et al.* 2009). This species seems to only be present in the cave after initiation of the summer rainy season, and has so far been found only in the Jackrabbit Shaft, Jackrabbit Gallery, and the vicinity of the Tarantula Room. They normally live beneath debris such as rocks or downed trees that occur on the surface above the cave. The animals are apparently attracted to the moisture present in the cave. They are uncommonly encountered in the cave, and we consider the species to be an occasional trogloxene. When these animals die in the cave they provide nutrients for other invertebrates in the cave food web. Some of the dead crickets observed supported developing scuttle fly larvae (*Megaselia* sp. : Phoridae).

Order Isoptera
Family Undetermined
Undetermined genus and sp.

Even though many termite species are subterranean in their habits, living primarily within the soil horizon, as a group they are poorly represented in cave invertebrate records in the southwest. Termite soil tunnels were found at Kartchner Caverns at the highest point of the upper portion of the Tarantula Room in August of 2010. This portion of the Tarantula Room comes within about a half meter of the surface, and essentially intrudes as a pocket into the soil profile of the hill above the cave. In that sense the termites at this location are simply living within their normal habitat. They had built their earthen tunnels over plant roots (upon which they were apparently feeding) that extended from the soil horizon into the open air voids of the cave. Some of their tunnels extend out from beneath the edges of flowstone remnants onto the exposed bedrock wall where the roots had grown (Figure 6).

Termites have been observed in one other cave in southern Arizona, within which their soil tunnels extended 11 meters down the bedrock wall of the entrance shaft of the cave (RBP personal observation). Termites are known to go to great depth (up to 30 meters) to obtain water necessary for their survival (Howarth and Stone 1990). Because of extreme arid conditions in the desert southwest during some seasons, one would anticipate that permanent water sources available in caves would be capitalized on by termites on a regular basis. Based on observations in many caves in Arizona and New Mexico this generally appears not to be the case in the region (RBP personal observation).

FIGURE 6. Soil termite tunnels in the upper Tarantula Room. The tunnels had been constructed over plant roots that entered the cave.

FIGURE 7. Adult female *Phasmatocoris labyrinthicus* with adult female *Eidmanella pallida* prey near the Jackrabbit Shaft door on August 14, 2010.

Order Blattodea
Family Blattidae
Periplaneta australasiae

P. australasiae is an omnivorous scavenger that is not native to North America, but which has become widespread in the southern U.S. The species has a global distribution, is thought to have a tropical African lineage and was likely not "Australasian" in its origin (Helfer 1953). This species was not recorded during the initial study, but was likely established during the commercial development of the cave, where the animals and/or their egg cases may have been among construction supplies or equipment brought to the site. Interestingly, the animals seem to be primarily limited to peripheral areas of the cave such as the entrance tunnels. Few have been found very far into the cave, and the occasional records in the cave interior are likely to be individuals that have ridden in on visitors, followed the tour tails, or flown into the deeper portions of the cave because they were attracted to the tour lights. Since this species has likely been established in the cave since the construction era, and there appear to be no identifiable adverse effects to the ecology of the cave resulting from its presence, it probably does not represent a significant potential impact on the ecology of the cave.

Order Psocoptera
Family Psyllipsocidae
Psyllipsocus ramburii

This barklouse (psocid) is a cosmopolitan species that occurs in caves, cellars and many epigean, often dry, habitats throughout the United States and much of Europe. The species has been moved to many far places of the globe by the activities of man (Mockford 1993). The species is commonly found in caves in southern Arizona, but their populations never seem substantial. This is the status of the species in Kartchner Caverns as well, even though there appears to be plentiful habitat suitable for the species in the cave. Welbourn (1999) considered the species common in the cave, but stated that he usually saw only 1 or 2 animals at a given time. So, while they are apparently regularly present, they are dispersed in their distribution within the cave, and almost always occur in small numbers in a given area. They are primary consumers and in the cave they are likely detritivores where they occur in association with organic materials. They may be preyed upon by small invertebrate predators in the cave including any of the spider species, the pseudoscorpion, and the larger of the two resident army ants (*Neivamyrmex graciellae*).

Order Hemiptera
Family Reduviidae
Triatoma recurva

This species is a haematophagous (bloodsucking) parasite of vertebrates. *T. recurva* was observed in the cave on only three occasions during the recent study, but we suspect it is likely more common that our data indicates. Several species of *Triatoma* in the southwestern U.S. are primarily or exclusively associated with species of wood rats, and while *T. recurva* is recorded feeding on the white-throated wood rat (*Neotoma albigula* Harley, 1894) (Ibarra-Cerdeña *et al.* 2009), according to Lent and Wygodzinsky (1979), it is more commonly a parasite of the rock squirrel (*Spermophilus variegatus* Erxleben, 1777). We observed a single rock squirrel inside the cave just inside the Blowhole Gate in April of 2010. KCSP personnel have live-trapped rock squirrels in the entrance area while attempting to control ringtails that were predating bats.

Family Reduviidae
Phasmatocoris labyrinthicus

This thread-legged bug was first recorded in the cave during the initial study in 1990, when it was observed in several widely separated areas of the cave. Welbourn (1999) considered it an accidental in the cave, and not a part of the regular cave fauna. Early in the recent study we found several dead adults of this species, but we were unable to locate a live animal. A concerted effort to find live individuals of this species in portions of the cave where most of the dead animals were found proved successful 9 months into the study, in August of 2010. On that date we located three live adult animals, one (the first, a male) in the upper Tarantula Room, and two females in the Jackrabbit Gallery. We made an adult female nesticid spider (*E. pallida*) available to one of the females, and it was readily accepted as prey by the animal (Figure 7). Based on our observations we suspect that *P. labyrinthicus* is an opportunistic predator and is preying on any animals that it can capture, whether the prey is a cave resident, occasional visitor, or an accidental. We have observed three live juveniles of *P. labyrinthicus.* in the cave, all in the Jackrabbit Room.

Since we have confirmed that this species has a long-term presence in the cave, still occurring twenty years after it was originally observed, and with the additional evidence of shed skins (indicating presence of the animals as they develop), juveniles active in the cave, and feeding of the animals on at least one resident invertebrate of the cave (*E. pallida*), we have demonstrated that this species in not an accidental, but an active element of the ecology of the cave. We believe the species does not occur outside of the cave, is a true troglobite at Kartchner Caverns, and is likely a relictual population. *P. labyrinthicus* is distinctly different morphologically form any known species in the genus. It is also the northernmost and first Nearctic species in this primarily Neotropical genus. See Pape (2013) for additional information on the ecology of this species.

Family Cimicidae
Cimex incrassatus

Cimicids are blood-feeding parasites of mammals and birds. A single adult cimicid was retrieved from the Maternity Roost guano pile in the Big Room in August of 2011. Like other cimicids (popularly known as bedbugs), this species probably spends most of its time in the roost away from the hosts. This animal was apparently groomed off one of the cave myotis that were still present in the cave at the time. *C. incrassatus* is a nearctic species that is recorded from southern California, Arizona, and Mexico. The species has been recorded from the following vespertilionid bats: pallid bat (*Antrozous pallidus* LeConte, 1856), big brown bat (*Eptesicus fuscus*), fringed myotis (*Myotis thysanodes* Miller, 1897), cave myotis (*M. velifer*), Yuma myotis (*M. yumanensis* Allen, 1864), and western pipistrelle (*Parastrellus hesperus*) (Usinger 1966).

They are apparently uncommon in the bat population at Kartchner Caverns since two guano piles were examined and sampled nearly every month for two years with only this single observed occurrence of the species. It is possible that they are more common, but are not often sampled since they are living in crevices among the roosting bats.

The individual specimen is somewhat anomalous due to two morphological variables that do not completely follow the key in Usinger (1966), but we consider it unlikely that this is an undescribed species, and rather, represents a morph within a variable species.

Family Cydnidae
Dallasiellus californicus

This species is not uncommon in cave entrance areas in southern Arizona (RBP unpublished data), and we found a single individual in the Jackrabbit Shaft in April of 2011. They are feeders on plant roots, and occur in cave entrance areas associated with roots that penetrate cave interiors where the cave overburden is shallow, typically in entrance areas. We consider *D. californicus* to be a trogloxene in the cave.

Family Lygaeidae
Undetermined genus and sp.

A single individual of this species of true bug was found in the Crinoid Room just below the Entrance Sink gate in May of 2010. This species is probably a plant feeder, and is almost certainly an accidental in the cave.

Order Coleoptera
Family Carabidae
Lebia subgrandis

This small, colorful predatory ground beetle is a surface species, which was encountered as a single individual just inside the cave in the Crinoid Room in April of 2011. The species is an accidental in the cave.

Family Staphylinidae
Stamnoderus sp. (Undescribed species; Margaret Thayer/ Chicago Field Museum, personal communication)

The mostly Neotropical genus *Stamnoderus* is currently represented by 15 described species (Newton *et al.* 2005). Many species of staphylinids live in habitats, including the epikarst, where they occur in proximity to caves. Because of this, they are relatively common in caves, particularly in entrance areas, where most are trogloxenes. Both larvae and adult staphylinids are typically predators of small arthropods. Cave adapted species are concentrated in the Mediterranean and North African regions, and cave species are generally poorly represented in other areas (Bordoni and Oromi 1998). The only cave record we found for *Stamnoderus* was an undescribed species from Cebada Cave in Belize (Reddell and Veni 1996).

The first known record of this animal in the cave is from June of 2001, when it was observed during algae cleaning efforts around lights in the Rotunda/Throne tour access tunnel. The animal was not recorded in the cave during the initial study, but is currently well-established in the cave in the Rotunda and Throne Rooms, where it is a breeding troglophile. We suspect the species may have been introduced to the cave, but we do not know if it occurs in the Park outside of the cave.

Family Staphylinidae
Undetermined genus and sp.

This species is represented by a single animal that was sampled from an environmental monitoring station (EMS) evaporation pan in the Big Room near the Sombrero Formation by KCSP park staff in April of 2005. The species shows no obvious morphological adaptations for living in caves. The initial study reported a single unidentified staphylinid beetle observed near the Maternity Roost guano pile. There is apparently no specimen for this earlier record, so we do not know if it is the species that was found in the cave in 2005. We suspect these records may both be accidental occurrences in the cave. Staphylinid beetles are good fliers and are highly mobile. They are certain to be common in the Park outside of the cave, and with the cave being opened repeatedly to admit tours these beetles are one group we would expect to occasionally find in the cave. Surface surveys should be conducted to see which staphylinid beetle species occur in the epigean environment in the Park.

Family Scarabaeidae
Genuchinus ineptus

This scarab beetle species has only been found in Kartchner Caverns once, sampled in the Throne Room by Park staff in July of 2006. *G. ineptus* is known to be predatory on a variety of adult and larval insects (Alpert 1994). It is an accidental occurrence in the cave.

Family Buprestidae
Acmaeodera cazieri

This metallic wood-boring beetle species is recorded from a single record sampled in September of 2007 by Steve Willsey from the trail curb in the Throne Room. Adults of *Acmaeodera* species are commonly found on flowers where they feed on pollen and/or other floral structures (Westcott *et al.* 1979). This species is an obvious accidental in the cave.

Family Anobiidae
Niptus ventriculus

Species of spider beetles are fairly common in drier parts of cave entrance areas in the southwest (RBP personal observation), where they are probably scavengers. They are commonly found in association with wood rat middens, where they may feed on feces, mold, or organic nest materials. Endemic cave species of *Niptus*, which have reduced eyes, are recorded from a few caves in California and Utah (Aalbu and Andrews 2005). The Kartchner Caverns population has well-developed eyes and shows no obvious morphological adaptations for a subterranean existence.

N. ventriculus is reported from wood rat middens in north central Baja California near Cataviña (Clark and Sankey 1999), and in the Puerto Blanco Mountains in southwestern Arizona (Hall *et al.* 1990). The species occurs only in the drier portions of Kartchner Caverns near entrances, and possibly only where there is an association with nesting rodents. We have two observations of the species in the Crinoid Room, one of which was taken from the web (as prey) of a female *Achaearanea canionis*.

Family Scraptiidae
Anaspis nr. *rufa* (Undescribed species; Pape)

A. rufa is reported to be mycetophagous (Majka 2010). The species was reported as a fossil from late Quaternary wood rat middens at Bida Cave in northern Arizona. Its presence in middens was interpreted as a potential commensal association, with the beetles likely feeding on wood rat nest materials or the midden waste pile (Elias *et al.* 1992). The single live individual that we found was in the Crinoid Room, which is proximal to the cave Entrance Sink where wood rats are present. Between 2005 and 2011 eight of the beetles were found drowned in water at the EMS evaporation pan in Grand Central Station, some 60 meters from the cave entrance, and far from any area used by wood rats. We consider this species to be a troglophile in the cave, and believe that it is an undescribed species.

Family Tenebrionidae
Argoporis alutacea

A variety of tenebrionid beetle species in the southwestern U.S. are associated with small burrowing mammals, where they forage among nesting materials and/or feed on waste of the host animals. It should come as no surprise then that many of these beetles are also occasionally found in caves, where the mammals they associate with also often make their homes. We found this species only once, in the rear parallel passage in the Jackrabbit Gallery, in August of 2012. The species is probably uncommon in the cave, and is likely to be found only near surface connections. The species is a scavenger and a trogloxene in the cave.

Family Tenebrionidae
Conibius gagates

We have encountered this species on two occasions, with two or three of the beetles present at each observation. So far this species has been found only in the Jackrabbit Shaft and in the Jackrabbit Gallery near the shaft door. Many of the species in this genus are scavengers, and some are known from dry caves or associations with ant nests (Aalbu and Triplehorn 1985). We have activity of two species of ants in the Jackrabbit Shaft; *Pheidole rhea* and *Trachymyrmex arizonensis*. A portion of the nest of the latter species is incorporated into a fracture in the bedrock wall of the Jackrabbit Shaft. There is some possibility of an association of *C. gagates* with *T. arizonensis* in the cave. We consider *C. gagates* to be a trogloxene in the cave.

Family Tenebrionidae
Eleodes knullorum

This species has been observed only once in the cave, in the Crinoid Room in November of 2009. The species is a scavenger and a trogloxene in the cave.

Family Tenebrionidae
Eleodes longicollis

The presence of tenebrionid beetles, including species of *Eleodes*, is not unusual in caves, and a few *Eleodes* (subgenus *Caverneleodes*) are cave-adapted to various degrees (Triplehorn 1975). We have at least one cave-adapted troglophilic tenebrionid beetle in Arizona (*Eschatomoxys pholeter*), which occurs in a few caves in Grand Canyon National Park (Pape *et al.* 2007).

E. longicollis is known to be associated with harvester ants, where the beetles scavenge off the organic matter deposited at the periphery of the ant nest (Slobodchikoff 1979). *E. longicollis* may be the most common tenebrionid species in the cave, and has been observed on four occasions: twice in the Crinoid Room, once in the LEM Room and the single deep penetration of the cave in the far north end of the Big Room. The initial study recorded a species of *Eleodes* from the “entrance area” of the cave, but did not specify whether this was in the breakdown rubble in the open Entrance Sink, in the first room (Crinoid Room), or elsewhere in the front part of the cave. We do not know if the original observation represents this species, but this seems probable.

Order Lepidoptera
Family Tineidae
Undetermined genus and sp.

We found a single larva of this species in the bottom of the Jackrabbit Shaft in December of 2010. We are uncertain as to the ecological group or guild this species may occupy in the cave, if any.

Family Undetermined
Undetermined genus and spp. #1 & #2

The initial study reported three observations of moths in the cave, but did not state whether they represented more than one species. They were recorded near the Entrance Sink (2) and one in Granite Dells. During the recent study we have observed two species of small moths in the cave. The smaller of the two species is some kind of microlepidopteran. We have found these as an occasional dead animal in the cave, some having drowned in water in EMS evaporation pans.

A second small moth (Undet. genus and sp. #2) was observed flying in the Big Room in September of 2011, but could not be captured. This second animal was considerably larger, with broader wings, and with a wingspan of approximately 1.5 cm, but still a rather small species. This larger moth may be an accidental, which may have entered the cave through the human access portals.

Both of these species are too small to be the same as the larvae found in the Jackrabbit Shaft. We have no evidence to support the presence of a guano moth associated with the bat guano deposits in the cave. Tineid populations associated with bat guano deposits in caves are typically present in larger numbers. In those situations they are usually readily evident in the vicinity of the major guano deposits, and this is not the case in Kartchner Caverns.

Order Siphonaptera
Family Ischnopsyllidae
Myodopsylla collinsi?

Larvae of a species of bat flea were found on the Maternity Roost guano pile in August of both 2010 and 2011. No adults were found, and the larvae have not been positively identified to species. However, of the 11 species of bat fleas recorded from North America, only *Myodopsylla collinsi* has been recorded from the cave myotis, including several records from Arizona (Jameson 1959; Bradshaw and Ross 1961; Ubelaker 1966; Whitaker and Easterla 1975; Reisen *et al.* 1976; Lewis and Lewis 1994). We suspect that the larvae are probably this species.

Family Pulicidae
Undet. genus and sp.

A variety of species of fleas are common in caves, typically near entrances, where they are associated with mammals that inhabit these areas. This species was observed only once as a couple of individuals that climbed onto two of us in the Crinoid Room. Only one individual was captured. We assume that it is a parasite on one or more of the mammals that are present in the entrance area of the cave. Potential hosts include ringtail, rock squirrel, white-throated wood rat, kangaroo rat (*Dipodomys* sp.), mice, and gray fox (*Urocyon cinereoargenteus* Schreber, 1775).

Order Diptera
Family Psychodidae
Lutzomyia (*californica*?)

This phlebotomine sand fly species was a rather unexpected surprise as a resident in a Nearctic cave. Adult sand flies are blood-feeding ectoparasites of mammals, including bats (Williams 1987; Lampo *et al.* 2000), and the larvae breed in a very wide variety of both wet and dry habitats, including forest leaf litter, rodent and other animal burrows, caves, decaying manure, domestic animal shelters, bird nests, termite mounds and many other ecotopes (Feliciangeli 2004). Sand flies are rather common in caves in the tropics, where they occur in association with bats and other mammals, typically rodents. Many species are important vectors of tropical diseases among vertebrate hosts including bacterial diseases, arboviruses and protozoan parasites (including leishmaniasis) (Carvalho *et al.* 2011).

We have only two records of this psychodid from the cave: a single adult female sampled near the "Big Wall" of the Throne Room in November of 2006 and a single larva taken in July of 2011 off the molding wood block at the invertebrate station in Granite Dells. We assume the larva and the adult are the same species. The species is apparently rare in the cave.

Species of *Lutzomyia* are known to occur in caves, where adults obtain blood meals from bats, and the larvae breed in the associated bat guano deposits. Since both the larva and adult of this species have been found only in areas of the cave that do not support any bats (Granite Dells and the Throne Room respectively), we preclude that association. We suspect the species is probably associated with rodents near cave entrance areas.

Family Cecidomyiidae
Bremia? sp.

We have identified at least three species of cecidomyiids in the cave, representing three genera in the tribe Cecidomyiidi. All of the species found in the cave are associated with the bat guano deposits, and specimens were obtained from Berlese samples of the two main guano deposits, the Lunch Spot and the Maternity Roost. Species of *Bremia* are usually associated with decaying materials, but probably more likely fill a predatory niche in the guano deposits (Gagné personal communication). There are records of *Bremia* sp. recorded from caves in Arkansas, Georgia, and Missouri (Reeves *et al.* 2000; Barnes *et al.* 2009). These records do not mention an ecological association.

Family Cecidomyiidae
Clinodiplosis sp.

Larvae of *Clinodiplosis* spp. are commonly associated with decaying plant and animal matter and finding them associated with bat guano would not be unexpected. *Clinodiplosis* was recorded by Peck (1988) from Mount Nemo Cave in Alberta, Canada. There is no ecological information with this record, so it is not know if it is potentially a guanophile. *Clinodiplosis* (*araneosa*) is recorded from the entrance area of Cueva de los Riscos in the State of Durango, Mexico (Reddell 1982). The ecological status of this record is not known.

Family Cecidomyiidae
Lestodiplosis sp.

Larvae of *Lestodiplosis* are predators, some exclusively on mites, and others are polyphagous (Gagné personal communication). Some of our specimens were not identifiable, and there is some potential there is a second species of *Lestodiplosis* represented in the sampled materials. There is a record of a *Lestodiplosis* sp. from Cueva de la Puente in San Luis Potosi, Mexico (Elliott and Reddell 1973), and from caves in Missouri (Barnes *et al.* 2009). None of these records provide ecological associations for *Lestodiplosis* spp. in caves.

Family Mycetophilidae
Subfamily Keroplatinae?

Fungus gnats in the family Mycetophilidae are small, delicate flies that are often common in caves. They typically occur in association with organic materials near cave entrances, or on such materials that have been washed into the cave, where the larvae feed on fungi present on the decaying materials. There are a few species with predaceous larvae.

We have a single record of a rather large (approximately 12 mm long) mycetophilid larvae from beneath a cobble partially embedded in the clay floor in Grand Central Station (Figure 8). Based on its size we assume the larva was mature. It had created a linear mucous runway with many finer lateral mucous strands that covered much of the irregular clay-soil substrate beneath the cobble. Easily visible beads of mucous were irregularly spaced along many of the strands. The function of the beads is probably for trapping of microfauna, which would indicate a predatory habit of the larvae. Larvae that create mucous webs occur in three subfamilies of the Mycetophilidae; Diadocidiinae, Keroplatinae, and Sciophilinae, but only the Keroplatinae are known to contain predatory species. The extremely slender, smooth, oligochaete-like body form of this animal along with its mucous spinning habit and probable predatory nature likely place it within the subfamily Keroplatinae (Vockeroth 1981).

Because some larvae in this subfamily are luminescent, we took a 10 minute open-shutter photograph of the animal in April of 2011, but no luminescence was detected. We monitored the larva for several months so that the adult fly could be reared from the pupa and allow identification of the species. Unfortunately, the last time we looked for the animal it had completely disappeared along with all of its mucous strands. We could not locate the fly pupa. We assume the strands and mucous beads were all consumed by the larva as a resource conservation measure prior to its entering the pupal stage.

Figure 8. Mature larva of *Keroplatine*(?) fungus gnat beneath cobble in Grand Central Station within Kartchner Caverns. Note mucous strands and beads.

Family Sciaridae
Lycoriella sp.

Adult sciarids are relatively common in the cave, and are often attracted to lights. The initial study reported two unidentified species of these dark-winged fungus gnats in the cave. This *Lycoriella* species is one of two sciarids that have been observed during the recent study. Sciarid larvae have been found in the bat guano (Maternity Roost site) on several occasions, and we assume both sciarid species breed in the annual fresh bat guano deposits.

Family Sciaridae
Plastosciara sp.

This dark-winged fungus gnat is sympatric in the cave with *Lycoriella*, and is assumed to also breed in the annual fresh bat guano deposits.

Family Asilidae
Cophura painteri?

This species was sampled in the Throne Room in July of 2006 by KCSP staff. It represents an accidental occurrence in the cave.

Family Phoridae
Megaselia sp. (Undescribed species; Disney, personal communication)

The scuttle fly genus *Megaselia* is one of the largest (number of species) genera of flies known (Disney and Campbell 2010), and there are many records of *Megaselia* spp. from caves worldwide. They are recorded from caves in the U.S. in Georgia (Reeves *et al.* 2000), Arkansas and Oklahoma (Barnes *et al.* 2009), Nevada (Disney *et al.* 2011) and Arizona (RBP unpublished data).

This species has been observed in Kartchner Caverns on three occasions. Most occurrences were associated with dead field crickets (*Gryllus multipulsator*), but the species was also sampled from a dead kangaroo rat (*Dipodomys* sp.). All observations of the species have been in August. The initial study mentions the presence of unidentified fly larvae on a dead cave cricket in Grand Central Station (Welbourn 1999). This initial record could be *Megaselia* sp. This species is probably the resident dipterous decomposer of dead arthropods in the cave. Because we found these flies only near a cave entrance (Jackrabbit Shaft), we suspect it is primarily a surface species. However, since the animal is capable of reproducing in the cave, it probably completes its life cycle in the cave at least occasionally. We therefore classify it as a troglophile.

Family Phoridae
Puliciphora sp.

Species of *Puliciphora* are very common scavenging flies, and have been recorded from caves in Trinidad (Disney and Sinclair 2008) and Mexico (Reddell and Elliot 1973). Members of the genus are probably a widely dispersed but poorly recorded group in caves. We have only a single record of this species from the cave, a female, taken by KCSP staff in November of 2006. The specimen label says "off dead cricket", but we do not know if this refers to *Gryllus multipulsator* or *Ceuthophilus pima*.

Family Anthomyiidae
Pegomya sp.

Species of *Pegomya* are primarily leaf miners as larvae, but a few species attack pine cones, and there are also fungivorous species. There are records of *Pegomya* from caves (Peck 1988; Barnes *et al.* 2009; RBP unpublished data), but associations are all with entrance areas where there is proximity to vegetation, often in karst features such as sinkhole entrances. There is no lush vegetation in the Kartchner Caverns Entrance Sink, so anthomyiid flies that commonly occur in many cave entrance areas would be less likely to be present here. This species is most likely an accidental in the cave. We found only a single animal in the Main Corridor in June of 2010. We think a fungal association for this species is unlikely, or we would likely have found more than a single individual.

Family Streblidae
Trichobius major

Bat flies are obligate blood-feeding ectoparasites. *T. major* is an ectoparasite of several species of bats, primarily species of *Myotis*, and is commonly recorded on the cave myotis (*Myotis velifer*) (Jameson 1959; Bradshaw and Ross 1961). The few occurrences on other species of bats are thought to be due to these species roosting in association with *Myotis* spp. (Ubelaker, 1966; Wenzel and Peterson 1987). The fly larvae pupate on the walls and ceilings of roost sites (Wenzel and Peterson 1987).

There are two records of *T. major* occurring in the cave (September of 2004 and October of 2006), with both records in proximity to the major bat roosts. This species was not observed during the original or current studies. This fly is likely more common than observations would indicate. The flies may stay close to the roost areas, which are high above the floor of the cave. The flies are probably primarily present only during the period the bats are in residence, and travel with the bats to their winter hibernaculum. These parasites are good fliers, and those that get groomed off of bats can quickly return to the colony.

Family Muscidae
Undetermined genus and sp.

This is a record from the initial study, with no identification beyond family level. Muscids are uncommon in caves, but members of several other calyptrate muscoid families, notably the Calliphoridae (blow flies), Sarcophagidae (flesh flies), Tachinidae (tachinid flies), and Anthomyiidae (anthomyiid flies) are often common in caves, particularly in entrance areas. Many of these flies have a superficial resemblance to muscid flies, particularly if merely observed in flight. Without the specimen for confirmation, we suspect this record may not actually belong in the family Muscidae, but would more likely belong to another of the above-listed fly families. We do have the single record of *Pegomya* sp. (Anthomyiidae) from the recent study, and there is some potential the original record could be this species. However, without the original specimen, we cannot make this determination, and we have retained Muscidae in the record of species from the cave due to a lack of contrary evidence.

Family Tachinidae
Undetermined genus and sp.

This species is documented from a single empty pupal case found in the far west end of the Granite Dells area of the cave in August of 2012. I (RBP) have observed evidence for the presence of an internal calyptrate dipterous parasite(s) of *Ceuthophilus* in two other caves in southern Arizona. I first observed two large larvae, presumably of a species of tachinid fly, excreted by a single cave cricket in Ida Cave in October of 1989. Clayptrate pupal cases, presumably of a tachinid fly, are also found individually scattered throughout the front portions of Arkenstone Cave, where the presence of an internal parasite is presumed to periodically parasitize the resident population of *Ceuthophilus* nr. *pinalensis*. Since these pupal cases are typically found as scattered individuals in caves, they are unlikely to be the remains of calliphorids present at carcasses, since those flies typically occur in large numbers in such situations. Additionally, the surface connections in the Granite Dells area of Kartchner Caverns are presumed not to be large enough to admit vertebrates, and this precludes a possible association with fly species occurring on dead vertebrates in that portion of the cave. The pupal cases are very persistent in caves, potentially lasting for many years, and the low numbers present indicate that this parasite is not common where it has been observed in caves in southern Arizona. The cave crickets may ingest the eggs of the flies while foraging on vegetation outside of the cave. Alternatively, the flies may actively lay their eggs directly on the crickets, or the planidial larvae may attach themselves to the crickets, when they forage outside of the cave

Order Hymenoptera
Family Sphecidae
Chlorion aerarium

This species was found as a single dead individual in the Jackrabbit Room in November of 2009 (Figure 9). This species is a cricket hunting species, and may have been attracted to the songs of the field crickets (*Gryllus multipulsator*) in the Jackrabbit Shaft area. Since it is

Figure 9. Cricket-hunting sphecid wasp (*Chlorion aerarium*) found dead in the Jackrabbit Gallery.

probable that the presence of this wasp was the result of its hunting for prey in the cave, we consider this occurrence of *C. aerarium* to be a trogloxene in the cave.

Family Mutillidae
Undetermined genus and sp.

This record is from a single dead female that was found in the very top of the Tarantula Room. Since none of the known invertebrates recorded from the cave are likely to be suitable prey for this parasitic wasp, we consider it an accidental in the cave. The specimen is missing several parts, including the head and most of its legs, and while it is almost certainly a mutillid, it could also belong in the related family Bradynobaenidae. The body structures diagnostic for separation of these two families are not present among the pieces of the specimen retrieved.

Family Pompilidae
Pepsis sp.

A single dead individual of this species was found on the tour trail in the Big Room in September of 2009 (Figure 10). The species is an accidental that probably came into the cave through the tunnel entrances with a cave tour. Alternatively, but less likely, it could have entered the cave through the historic Entrance Sink and eventually made its way into the heart of the cave, and could not find its way back out.

Family Pompilidae
Agenioideus biedermani

A. biedermani is known from California east to Kansas and south to the State of Hidalgo, Mexico (Wasbauer and Kimsey 1985). *A. biedermani* is known in Kartchner Caverns from a single dead individual that was found in August of 2010. The animal was found on the floor of the cave high in the top of the Tarantula Room. Foraging pompilid wasps search along the ground for spiders. They also search among vegetation, beneath objects on the ground, in animal burrows, in earth cracks and in caves (Evans and Shimizu 1996; RBP personal observation). It is therefore not unusual for some species of pompilids to enter caves either to seek prey or rarely, to nest. The only prey record for *A. biedermani* is of *Loxosceles devius* (Sicariidae) in Texas (Evans 1959). The presence of a species of *Loxosceles* in Kartchner Caverns along with an individual of *A. biedermani* may be evidence that this wasp occasionally hunts in caves. Because of this potential association, we consider *A. biedermani* to be a trogloxene in the cave.

Figure 10. Dead pompilid wasp found on the tour trail in the Big Room. Note the yellow fungal fruiting bodies on the carcass.

Family Formicidae
Neivamyrmex graciellae

Ants were not actually observed during the initial study, but their presence was inferred from what appeared to be old ant trails in the soil floor of the cave just outside and just inside of the entrance to the Red River Passage. These old trails are still visible today. We found what are obviously more recent ant trails in the Red River Passage (Figure 11). There is little doubt that army ants are responsible for these trails, since this is precisely the type of trail structure that they create both on forest floors in the tropics (Figure 5.9 in Schneirla, 1971; Plate 12 in Gotwald, 1995), and in caves (Figure 8 in Reddell and Cokendolpher 2001; trail of *Labidus coecus*). The trails are constructed by removing vegetation and litter from the ground surface (epigean environments), and piling soil particles at the sides, resulting in an uncluttered trench (in both epigean and hypogean environments).

During the recent study, we observed *N. graciellae* active in the cave only once (in June of 2011), when we encountered a sparse column of them running along a trail near the junction of Main Corridor and the Anticipation Room. Approximately a dozen ants could be seen at any given time along this stretch.

Species of *Neivamyrmex* have been recorded previously from caves only incidentally, from Texas and Mexico, and the ants in these occurrences were considered accidentals (Reddell and Cokendolpher 2001). However, two species of *Neivamyrmex* were previously observed actively foraging in Arkenstone Cave (RBP personal observation), and *Neivamyrmex* is now also known from Kartchner

Figure 11. Army ant trail (likely of *N. graciellae*) in the front portion of the Red River Passage. The black and white scale is in centimeters.

Caverns (also two, but different species). These records from two Arizona caves are the only non-accidental cave occurrences documented for *Neivamyrmex* spp. The presence of *Neivamyrmex* spp. in caves in the southwest is probably more common than has been documented. There are no known troglobitic ant species (Holldobler and Wilson 1990; Decu *et al.* 1998).

There have been occasional sightings of ants in the cave by KCSP staff, and they are probably usually *N. graciellae.* We suspect that *N. graciellae* is more common in the cave than *N. leonardi*. This is based primarily on the assumption that the army ant trails that have been observed in the Red River Passage area all belong to *N. graciellae*. We infer this from the large size, both in depth and width of the trails, which would appear to not be a match with the smaller, more "delicate" *N. leonardi*. However, there are currently 19 species of *Neivamyrmex* recorded from Arizona (Snelling and Snelling 2007), and there is always the possibility that another *Neivamyrmex* species that we have not found in the cave may be involved with the ant trails that we have observed. Another New World army ant species *L. coecus* is fairly common in caves in Texas and Mexico, where they make very prominent entrenched trails (Reddell and Cokendolpher 2001). *L. coecus* has so far not been recorded from Arizona.

Family Formicidae
Neivamyrmex leonardi

N. leonardi is a small, pale yellow, eyeless species of native army ant, for which there are only two previous Arizona records, one sampled at Nogales in 1947, and a second in Tucson in 1965, and (Snelling and Snelling 2007; 2012). There is so far only a single observation of this species from Kartchner Caverns, in December of 2006, where they were found at a leaking hose bib in the Big Room. It is not known weather this species may forage at the nearby guano deposit, but none were observed there during the recent study. This species is probably not responsible for the observed formicine trenches in the cave (see previous species account). *N. leonardi* is apparently rare in the cave. It has also been recorded elsewhere in the southwest (not in caves) from western Nevada, southern California, east central Texas, and Baja California, Mexico (Watkins 1985; Snelling and Snelling 2007).

Family Formicidae
Pheidole rhea

P. rhea is an important seed harvester of xeric habitats where they occupy open, rocky slopes of foothills at the base of mountain ranges from southern Arizona and south into Mexico (Wilson 2003). While the species is primarily a seed harvester, it is not totally dependent on these resources, and is an active predator as well (Holldobler and Wilson 1990; Wilson 2003). They have been observed in the cave on a few occasions, mostly in the Jackrabbit Shaft and the adjacent portion of the Jackrabbit Gallery. We do not know at this time why this species enters the cave. Their presence may be a simple case of proximity to a nest in the soil horizon near the top of the Jackrabbit Shaft. We have found dead individuals of this species on the floor of the cave beneath live *Phasmatocoris labyrinthicus*, by which we suspect the ants may have been taken as prey.

Family Formicidae
Pheidole sp.

A single specimen of this ant was sampled in the Throne Room in May of 2007 by Steve Willsey. We do not know anything about the ecology of this species in the cave.

Family Formicidae
Trachymyrmex arizonensis

Members of the ant tribe Attini are fungus-gardening species, and are obligate fungivores (Vo *et al.* 2009). The Attini are primarily tropical, and *T. arizonensis* is one of only 9 species of attines recorded from Arizona (Rabeling *et al.* 2007). *Trachymyrmex* construct their sheltered gardens in the ground or beneath surface objects such as rocks.

All observations of this species have been in the Jackrabbit Shaft. The first two records, in April of 2010 and June of 2011, were of a single individual. In September of 2011 RBP observed a group of about 18 individuals near the top of the shaft, where they were observed moving chaff from their fungus garden to a refuse midden at the side, near the top of the shaft where there is a break in the wall between the drilled bedrock and the concrete cap of the shaft. The chaff had overflowed this repository and had cascaded down into the shaft. The yellowish-grey color of the chaff is diagnostic for this species (Rabeling *et al.* 2007). It appears the ants were using the shaft as an ant "landfill". RBP observed the ants excavating a nest in a crack in the bedrock wall about 2.5 meters below the top of the shaft in May of 2012. There were about two dozen of the ants actively working the hole and removing pieces of soil, and a spoils pile had accumulated on part of the metal framework for the shaft ladder system. By August of 2012 the colony had expanded its presence in the cave and there were numerous individuals of the species operating out of the nest in the wall of the Jackrabbit Shaft. With its long-term presence in this part of the cave *T. arizonensis* is apparently at home in a karst environment. Because of their nesting presence in the cave we consider the species a trogloxene.

Army ants (*Neivamyrmex* spp.), many of which are primarily predators of other ant species, have been recorded preying on *T. arizonensis* in southern Arizona (Rabeling *et al.* 2007). Our records of *Neivamyrmex* in the cave are not in proximity to the Jackrabbit Shaft. If *N. graciellae* does prey on *T. arizonensis*, it likely occurs outside of the cave proper, in the soil profile. *N. leonardi* is probably too small a species to successfully predate *Trachymyrmex* spp.

Discussion

The Cave Environment

Survival of cave-adapted species is predicated on maintenance of cave microclimatic parameters that are often in precarious balance with the influence of surface environmental conditions. This is particularly true in arid environments such as the southwestern U.S., where the combination of extreme summer temperatures and low humidity most of the year result in evaporation rates at the surface that greatly exceed annual precipitation. Aggravating the effects of surface conditions on the cave environment are the effects of air flow in caves. Caves with multiple entrances commonly suffer from a “chimney effect” air circulation pattern, which can result in drying of the cave, adversely affecting the habitat of resident invertebrates. Additional pressures on regional cave ecosystems include a recent, ongoing drought (Breshears *et al.* 2005) and the effects of regional and global climate change.

In many respects Kartchner Caverns is typical of caves in southern Arizona. The cave does not have significant aquatic components such as a perennial stream or much in the way of other persistent waters such as perched pools. Because of this there is no obvious aquatic macro-invertebrate component of its resident biota. The cave is still active, however, with autogenic meteoric waters infiltrating the cave from above depositing calcite as speleothems, and allogenic waters periodically flooding portions of the cave during extended or stochastic precipitation events higher in the watershed. Water from these surface runoff events enters the cave from ephemeral desert streams that flank the cave hill on its west and south sides. The flooding can be extensive, and may reach depths up to 2.4 meters in some areas of the cave. Interestingly, the floodwaters last only about a few weeks at most before penetrating to humanly inaccessible lower levels of the sedimentary section within which the cave is developed.

One of these major flood events occurred during the initial study, and it was observed that organic debris such as leaves and twigs had entered the cave with the floodwaters. Invertebrates, particularly the terrestrial cave isopod (*Brackenridgia* nr. *sphinxensis*), were observed feeding on these materials (Welbourn 1999). By chance, a major flood event of almost identical magnitude occurred during the recent study, and no associated coarse organic materials were observed in the cave. We suspect that there may have been a change in the influx hydrology of the cave such that coarse materials now get filtered out before reaching the cave interior. These flood events certainly bring some dissolved carbon and other nutrients into the cave, but these may be inadequate to support a regular presence of macro-invertebrates in these areas.

A significant component of these occasional cave flood events is suspended sediments, primarily clays, which are deposited as a thin layer over the entire substrate with each event. Due to the accumulation of these sediments there are no exposed pieces of debris on the floors that provide shelter habitat for invertebrates in areas of the cave subject to flooding. The exposed post-flood substrate consists of large-scale polygonal blocks of accumulated sediments, which typically remain saturated for long periods (Figure 12). The polygonal structure of the substrate indicates that these areas do occasionally dry to a point adequate for the formation of these shapes (desiccation cracks), which result from shrinkage of clays as moisture is lost from the soil. We suspect that the combination of an apparent limited nutrient supply along with the lack of shelter habitat is sufficient evidence to explain the absence of macro-invertebrates in areas of the cave subject to occasional stochastic flood events. Other unidentified factors may also be involved.

The average air temperature in a given cave typically stabilizes at the mean annual surface temperature, which is a function of the elevation and latitude where the cave is located. Based on these criteria, the air temperature expected in Kartchner Caverns should be 15.4°C. However, while the temperature in the cave fluctuates it always remains above this level (between 18.6°C and 21.3° C). Buecher (1999) suggested that the elevated air temperature in Kartchner Caverns may be due to proximity to geothermal waters in the San Pedro Valley, where the cave is located. Other factors may be responsible or may contribute to this effect. Relative humidity in the cave varies primarily in association with proximity to surface connections. Values in the deeper reaches of the cave are relatively constant, and during the initial study averaged 99.42 percent (Buecher 1999).

Nutrient Sources

Compared with epigean habitats cave environments are often nutrient poor and resources that do occur are mostly transported into caves from allochthonous sources. Methods of nutrient energy transfer into caves vary, but often include infusion of organic materials transported by animals, or through physical processes such as allogenic stream flow and autogenic meteoric waters percolating through the overburden above the cave. Influx of autogenic meteoric waters, which historically was not considered an important source of nutrient transport into caves, has recently been recognized as a source of significant quantities of organics that are derived from the epikarst (Culver and Pipan 2009; Romero 2009).

Animals that use caves for a portion of their life cycle, but which feed primarily outside of caves, are an important element of organic nutrient input to cave ecosystems. Therefore, unimpeded movement of biota, including both invertebrates and vertebrates, is often critical to the maintenance of many cave food webs. A significant portion of the organic nutrients brought into Kartchner Caverns is contributed by animals. The primary source of these nutrients (by volume) is the annual influx of bat guano provided by the cave myotis maternity colony. Other animals that bring measurable amounts of nutrients

Figure 12. Polygonal cracking of clay soils in the flood-prone area of the cave. The object in the center of the photo is a plastic flask that had been relocated by the 2010 flood event from a nearby, old environmental monitoring station. The flask is about 20 cm in height.

into the cave in their feces include cave crickets, ringtails (*Bassariscus astutus* Lichtenstein, 1830), and rodents that occasionally enter the cave. Animals occurring as accidentals in the cave, including invertebrates and the occasional vertebrate, which fail to find their way out of the cave, become a food source for resident species as prey or carcasses. Natural death of resident invertebrates retains nutrients that are recycled within the cave food webs.

Based on our observations we conclude that coarse organic debris, such as plant litter, is not a major nutrient resource available to cave macro-invertebrates living near cave surface connections at Kartchner Caverns. This condition is not unusual for caves in desert southwestern region of the U.S.

Autochthonous nutrients present in the cave are probably limited to microbial elements. Some of the primary consumers in the cave, particularly collembola, may use these resources to some degree. Otherwise, most macro-invertebrates in the cave probably subsist primarily on allochthonous nutrient input from the sources previously discussed.

The presence of large numbers of people moving through caves on tours of commercially-developed caves inevitably results in the cumulative deposition of lint composed of clothing fiber and human hair and skin elements. This unintended input provides nutrients for microbes and arthropods. This input is minimized at Kartchner Caverns by the curbed trails, which contain much of this litter, and the regular washing down of the trail system.

Artificial lighting in show caves provides energy for the development of phototrophic lampenflora. Lampenflora are initially comprised of prokaryotic cyanobacteria and eukaryotic algae which form on surfaces of rock and speleothems adjacent to the lights (Mulec and Kosi 2009). Lampenflora provide a nutrient base for microbes and primary consumer level arthropods.

Ecology of the Macro-invertebrates of Kartchner Caverns

There are two major categories of habitats that may support macro-invertebrates in caves: aquatic and terrestrial. Aquatic habitats in Kartchner Caverns are very limited as there are very few perennial water sources in the cave. Temporary waters collect seasonally in very small pools in response to the influx of autogenic meteoric waters during the two regional precipitation seasons. While some of these pools may last for many months, they are not perennial. Most of the few perennial pools occurring in the cave are at the base of the Big Wall in the Throne Room. On an irregular basis when there is adequate sustained

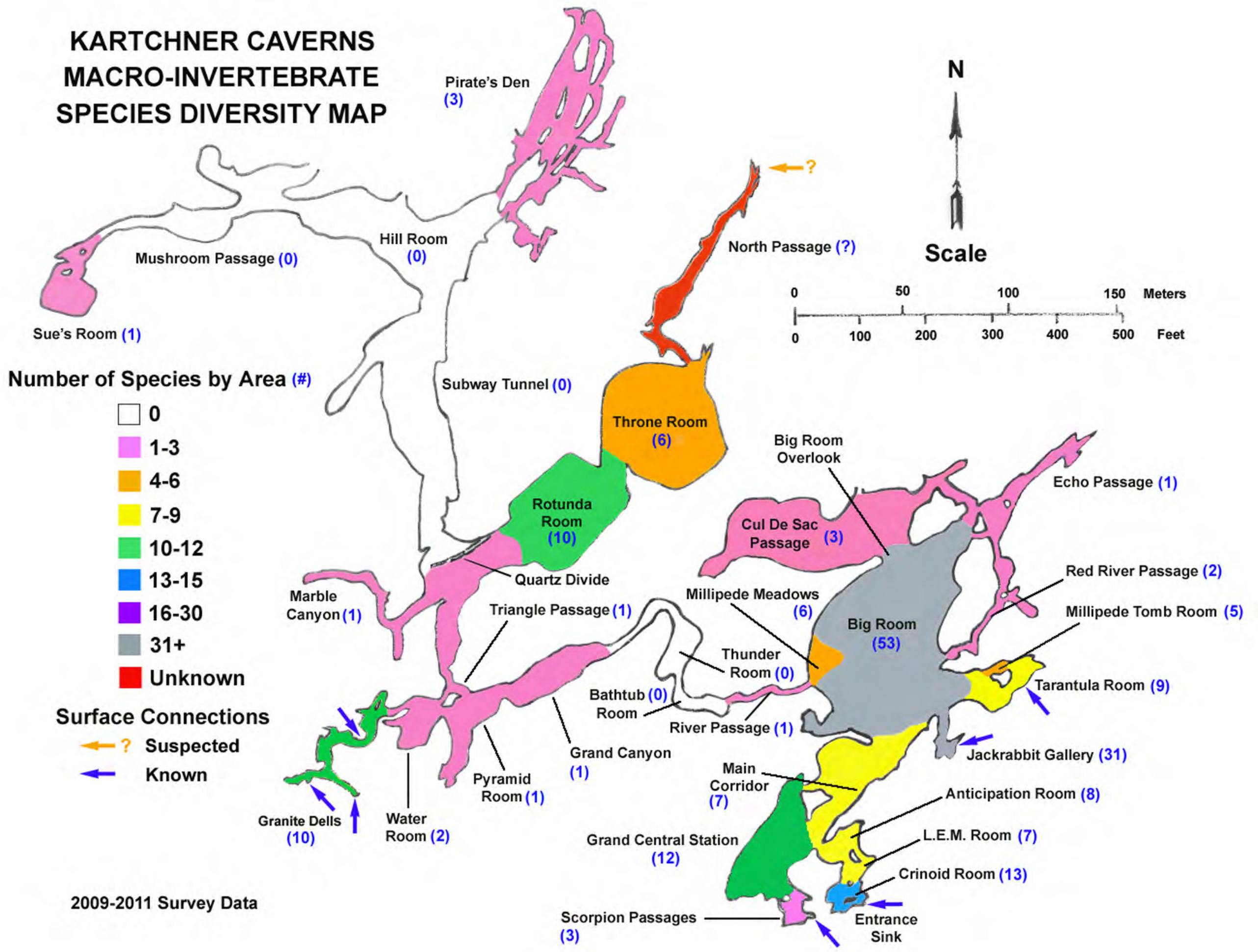

FIGURE 13. Macro-invertebrate species diversity (numbers of species) in the cave by area. The blue numbers accompanying each named area are the totals recorded from those locations, and include the historic records from the initial study. Areas with similar numbers of species have been artificially grouped to show a visual relative diversity of species richness in the cave. We used the same ranges that Welbourn used in the initial study (Figure 1 in Welbourn, 1999) for the first five ranges, and have added two additional ranges due to the considerable increase in the total taxa. Surface connections accessible to macro-invertebrates are shown by arrows.

flow down the ephemeral surface washes in the Park there can be significant flooding of portions of the cave. As mentioned previously, these waters infiltrate completely after several months, and are thus also not perennial in humanly accessible portions of the cave system.

There are almost certainly copepods (Crustacea: Copepoda) and other micro-invertebrates that live in the epikarst that are transported into the cave by the seasonal influx of autogenic meteoric waters. These animals may persist on wet flowstone and in the temporary pools in the cave as long as free water is present. These animals may be an important food source for the few macro-invertebrates that live on wet formations in the cave. The only invertebrates that we have regularly observed on wet formations are sminthurid collembolans and small unidentified spiders that spin their webs at these sites, and likely prey on the collembolans. The sminthurids have also been found on the surface of small pools of water, again possibly making use of microfauna in the water. Although all four individuals of the cambalid millipede we found in the cave were dead, they were found on wet formations. We suspect that the cambalid millipede may be part of the ecology of a wet flowstone biofilm community that is supported by autogenic meteoric waters. Although associated with wet environments, these arthropods are considered terrestrial animals.

Food webs in the cave are partitioned by a combination of various microclimatic conditions and available nutrients. The bat guano deposits are mostly a contained ecosystem, and one that is totally dependent on the annual influx of fresh nutrients brought into the cave each year by the bat colony. There are species, primarily mites, which are found only on the bat guano deposits. And, there are several invertebrates that are associated with the guano deposits, but are only present peripherally, apparently avoiding the highly competitive environment of the guano deposits.

Most of the macro-invertebrate activity in the cave is associated with areas that do not flood and that provide nutrient resources of some kind. In these higher, "drier" portions of the cave the macro-invertebrates can establish and maintain themselves undisturbed for many generations. These areas are more stable and hospitable to cave life than the portions of the cave that are subject to occasional stochastic flooding events. These areas typically also contain an abundance of breakdown blocks and a multitude of floor debris consisting of small to large rocks and pieces of broken calcite formations that provide shelter habitat for macro-invertebrates. Some floor areas that are covered with flowstone have sub-floor areas that also provide habitat for invertebrates, such as occurs in the Jackrabbit Gallery.

Overall, we found that the surface connection areas are some of the most ecologically significant areas of the cave, cumulatively supporting a number of non-accidental species (48) nearly equal to that of the bat guano habitats (53) in the Big Room (Figure 13). If one were to remove the significant mite component of 16 species directly associated with the bat guano deposits in the Big Room, the surface connection areas would then exceed the number of species supported by bat guano.

One habitat present in a few areas of the cave, but which is apparently underutilized by macro-invertebrates, is exposed plant roots that penetrate the cave and hang from walls or ceiling areas. This nutrient resource is often used by invertebrates in caves. The best example of this habitat in the cave is in the south end of the Big Room at Sharon's Saddle (Figure 14). Here, the roots are seasonally wet and have enough biomass to theoretically support small numbers of invertebrates. Other areas where roots are exposed include the upper Tarantula Room and two of the surface connections in the Granite Dells area. Some of the roots in the upper Tarantula Room have been used as food by termites, but only where the roots are in contact with wall surfaces, which allows the termites to enclose them with their soil tunnels that they have extended from the soil horizon into the cave (Figure 6).

A lampenflora faunal community has been introduced into the cave and is artificially distributed incidental to the placement of the tour lights. Ultimately, species of mosses and ferns could potentially colonize these areas, but this level of lampenflora development is not often observed (or tolerated) in commercial caves. Because lampenflora can develop over a wide humidity range, these communities are less constrained by moisture requirements than some of the other food web habitats.

There is a suite of macro-invertebrate taxa that are commonly present in caves in southern Arizona. Peculiarly, none of the caves apparently supports all of these species, and few caves have the same mix of these species as elements of their fauna. Kartchner Caverns fits within this pattern. Taxa that are commonly represented in this core of cave residents in the region include a cave cricket (*Ceuthophilus* sp.), a laniatore harvestman (*Sitalcina* sp.), a trichoniscid isopod (*Brackenridgia* sp.), a cave carabid beetle (*Agonum* sp. [subgenus *Rhadine*]), and one or more small spider species (some of which are cave-adapted), usually in the families Hahniidae (*e.g. Neocryphoeca* sp.), Leptonetidae (*e.g. Leptoneta* sp.), Nesticidae (*e.g. Eidmanella* sp.), or Theridiidae (*e.g. Achaearanea* sp. and *Thymoites* sp.). The species in these groups present in Kartchner Caverns include *Ceuthophilus pima* (Hubbell,

Figure 14. Plant roots at Sharon's Saddle. These resources in the cave appear to be mostly unused by macro-invertebrates.

1936), *Brackenridgia* sp., two undescribed species of *Neocryphoeca*, *Eidmanella pallida* (Emerton, 1875), and *Achaearanea canionis* (Chamberlin & Gertsch, 1929). We have found no representative species of *Sitalcina*, *Rhadine*, or *Leptoneta*.

Significance of the macro-invertebrate faunal studies of Kartchner Caverns State Park

The long history of cave science in Europe, which began initially in France and Romania (roughly 1890-1920), predated significant studies in the U.S. (which began in about 1955) by at least 50 years (Belles 1992; Barr *et al.* 1994; Romero 2009). Regionally, the biota of Texas caves has been studied extensively since the 1960s, and is considerably better known than the Arizona cave fauna. Compared to other regions, the caves of Arizona have received little study. Much of the early work done on cave invertebrates in Arizona was concentrated in the Grand Canyon region, and there is work ongoing in that area today, primarily by J. J. Wynne and others. However, most studies of macro-invertebrates in caves in Arizona have involved single visits or brief efforts, and many of these were incidental to other resource documentation activities. Work on invertebrates was conducted in 14 caves on the Coronado National Forest in southern Arizona by RBP between April of 1993 and November of 1994 (RBP unpublished data). However, similar to so many studies of regional cave invertebrates, most caves in that study were visited only a single time. Exceptions to these more limited efforts are the studies of Bat Cave in Grand Canyon National Park (Pape, in press) and at Arkenstone Cave in Colossal Cave Mountain Park by RBP (unpublished data). The Bat Cave study involved five expeditions to the cave spanning 8 years (1994-2001). The Arkenstone Cave biological studies represent the longest extended effort studying the cave macro-invertebrates at a single cave in Arizona (124 cave visits over 14 years). With the extensive effort that was made at Arkenstone Cave, the suite of species recorded there is considered essentially complete for the cave, and the cave may be used as a baseline reference for comparison with other caves in the region.

With the addition of our recent efforts, a total of 65 visits have been conducted in Kartchner Caverns to research macro-invertebrates (36 from the initial study and 29 from the recent study). Kartchner Caverns remains the second-most studied cave in Arizona for its macro-invertebrate richness and ecology.

Our recent study has greatly increased the number macro-invertebrate taxa known from Kartchner Caverns. However, even with a total of four years of study in the cave between the two studies, it is inevitable that not all the species that use the cave have been found. The amount of labor required to reach a level of confidence in the completeness of a list of invertebrates that are present in any given cave requires an extended effort over many years. We plotted search effort in hours against total accumulated taxa found during the studies, and the resultant curve does not approach an asymptote (Figure 15). Thus, we know that additional species are present in the cave.

Summary

Caves are non-renewable resources that provide a sustainable environment for unique aggregations of interdependent and often cave-adapted subterranean invertebrate (and vertebrate) species. A thorough understanding of invertebrate resources is critical to appropriate management strategies for these animals and their habitat. Information gathered from the recent study provides insight on the relationships of invertebrates with the cave environment and with species in the various cave food webs. This knowledge allows for a more informed implementation of existing management protocols, and may potentially identify actions needed to preserve these resources at Kartchner Caverns.

Efforts of ASP staff in the years subsequent to the initial study, combined with the results of the recent study, have resulted in an increase in the non-accidental macro-invertebrates species recorded at Kartchner Caverns from the original 39 species to 98 species. Kartchner Caverns currently supports the most species-rich macro-invertebrate ecology of any cave studied in Arizona.

Overall the health of the macro-invertebrate ecology of the cave is good. There appear to have been some losses, primarily several of the mite species from the bat guano food web, but most of the rest of the taxa that were present during the initial study 20 years ago, prior to the commercial development of the cave, are still present. The population of the cave cricket *C. pima* is greatly reduced since the initial study, but the cause(s) of this are not understood. Certainly the species persists in the cave, and is presently using three of the seven known surface connections to access the cave. The cave isopod (*Brackenridgia*) has a greatly reduced presence in the areas of the cave that are subject to major flooding. We suspect that this is due to a change in the subsurface hydrology of the cave, which currently precludes the influx of coarse organic nutrients that once supported a more robust population of the species in flood-prone areas of the cave. We now have several introduced macro-invertebrate species in the cave, but none of these appear to present an immediate or significant threat to the ecology of the cave. Finally, the nicoletiid *S. anachoretes* and the thread-legged bug *Phasmatocoris labyrinthicus*, both of which have their known distribution in the cave concentrated in the area of the Tarantula (access) Tunnel (Tarantula Room and Jackrabbit Gallery area), apparently survived (or rebounded from) the effects of the commercial development of the cave. This may be a reflection of the durability of what may be the two most charismatic invertebrate species at Kartchner Caverns.

Table 1. Macro-invertebrate taxa of Kartchner Caverns, Cochise County, AZ, USA. Compiled data from the initial study (Welbourn 1999) and the recent study (Pape and OConnor 2012). Species documented during the initial study are preceded by an asterisk in the species column.

PHYLUM NEMATA					
CLASS SECERNENTIA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Rhabditida	Thabditidae	*Rhabditis* (Dujardin, 1845) sp. 1	Troglophile	Fungivore	Common?
		Rhabditis (Dujardin, 1845) sp. 2	Troglophile	Fungivore	Common?
PHYLUM ARTHROPODA					
CLASS ARACHNIDA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Palpigradi	Eukoeneniidae?	*Undet. genus and sp.	Troglophile	Predator	Rare
Scorpionida	Vaejovidae	**Pseudouroctonus* nr. *apacheanus* (Gertsch & Soleglad, 1972)	Troglobite	Predator	Uncommon
Pseudoscorpiones	Chernetidae	**Dinocheirus* (*arizonensis*?) (Banks, 1901)	Troglophile	Predator	Uncommon
	Undet. family	*Undet. genus and sp.	Unknown	Predator	Rare?
Araneae	Theraphosidae	**Aphonopelma* sp. (Pocock, 1901)	Accidental	NA	Rare
	Filistatidae	*Kukulcania* sp. (Lehtinen, 1967)	Trogloxene	Predator	Rare
	Pholcidae	*Physocyclus* sp. (Simon, 1893)	Troglophile	Predator	Common
	Sicariidae	*Loxosceles* sp. (Heineken & Lowe, 1832)	Trogloxene	Predator	Uncommon
	Theridiidae	*Achaearanea canionis* (Chamberlin & Gertsch, 1929)	Troglophile	Predator	Uncommon
		Undet. genus and sp.	Troglophile?	Predator	Rare?
	Nesticidae	**Eidmanella pallida* (Emerton, 1875)	Troglophile	Predator	Common
	Linyphiidae	Undet. genus and sp.	Troglophile	Predator	Rare
	Hahniidae	*Neocryphoeca* (Roth, 1970) sp. #1	Troglobite	Predator	Rare
		Neocryphoeca (Roth, 1970) sp. #2	Troglobite	Predator	Uncommon
	Corinnidae	Undet. genus and sp.	Trogloxene	Predator	Rare
	Gnaphosidae	*Zelotes* sp. (Gistel, 1848)	Trogloxene	Predator	Rare
Actinedida	Cheyletidae	*Cheyletus* sp. (Latreille, 1796)	Troglophile	Predator	Rare
	Erythraeidae	*Charletonia* sp. (Oudemans, 1910)	Trogloxene	Fungivore?	Uncommon?
	Neothrombiidae	**Ceuthothrombium cavaticum* (Robaux, Webb & Campbell, 1976)	Trogloxene	Predator/Parasite	Common
	Pygmephoridae	*Undet. genus and sp.	Troglophile	Fungivore?	Rare
	Rhagidiidae	**Poecilophysis* sp. (Cambridge, 1876)	Troglobite?	Predator	Rare
	Stigmaeidae	**Eustigmaeus lirella* (Summers and Price, 1961)	Troglophile	Predator	Common
	Tarsonemidae	**Neotarsonemoides* sp. (Kaliszewski, 1984)	Troglophile	Scavenger	Rare
Astigmata	Acaridae	**Sancassania* sp. (Oudemans, 1916)	Troglophile	Scavenger	Abundant
	Histiostomatidae	**Histiostoma* nr. *guanophilum* (Mahunka, 1982) sp. #1	Troglophile	Scavenger	Rare
		**Histiostoma* nr. *guanophilum* (Mahunka, 1982) sp. #2	Troglophile	Scavenger	Rare
	Rosensteiniidae	**Nycteriglyphus* sp. (Zachvatkin, 1941)	Guanophile	Scavenger	Rare
Ixodida	Argasidae	*Carios yumatensis* (Cooley & Kohls, 1941)	Trogloxene	Parasite	Uncommon
		**Carios* nr. *hasei* (Schulze, 1935)	Trogloxene	Parasite	Uncommon
Mesostigmata	Laelapidae	**Gaeolaelaps* sp. (Evans and Till, 1966)	Troglophile	Predator	Uncommon?
		Stratiolaelaps scimitus (Womersley, 1956)	Troglophile	Predator	Common
		Stratiolaelaps sp. (Berlese, 1916)	Troglophile	Predator	Common

Table 1. *Continued.*

	Macrochelidae	*Macrocheles* nr. *penicilliger* (Berlese, 1904)	Troglophile	Predator	Uncommon?
	Macronyssidae	*Macronyssus crosbyi* (Ewing & Stover, 1915)	Trogloxene	Parasite	Rare?
	Rhodacaridae	**Rhodacarella cavernicola* (Moraza, 2004)	Troglophile	Predator	Rare
Oribatida	Damaeidae	**Parabelbella* sp. (Bulanova-Zachvatkina, 1967)	Troglophile	Fungivore	Uncommon
	Oppiidae	*Multioppia* sp. (Hammer, 1961)	Troglophile	Scavenger	Uncommon
	Family Undet.	*Undet. genus and sp.	Troglophile?	Scavenger	Rare
	Family Undet.	*Undet. genus and sp.	Troglophile?	Scavenger	Rare
	Family Undet.	*Undet. genus and sp.	Troglophile?	Scavenger	Rare
CLASS MALACOSTRACA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Isopoda	Trichoniscidae	**Brackenridgia* nr. *sphinxensis* (Schultz 1984)	Troglobite	Scavenger	Common
	Porcellionidae	**Porcellio laevis* (Collinge, 1917)	Troglophile	Scavenger	Common
CLASS DIPLOPODA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Polydesmida	Macrosternodesmidae	*Nevadesmus*? (Shear, 2009)	Troglobite	Scavenger	Rare
Spirostreptida	Cambalidae	Undet. genus and sp.	Troglobite	Scavenger	Rare
CLASS CHILOPODA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Scutigeromorpha	Scutigeridae	*Dendrothereua* nr. *homa* (Chamberlin, 1942)	Troglophile	Predator	Rare
Scolopendromorpha	Scolopendridae	**Scolopendra heros* var. *arizonensis* (Kraepelin, 1903)	Trogloxene	Predator	Rare
		Undet. genus and sp.	Trogloxene	Predator	Rare
CLASS INSECTA					
ORDER	**FAMILY**	**SPECIES**	**GROUP**	**GUILD**	**STATUS**
Collembola	Onychiuridae	*Tullbergia iowensis* (Mills, 1932)	Troglophile	Fungivore	Uncommon?
	Isotomidae	*Folsomia candida* (Willem, 1902)	Troglophile	Fungivore	Uncommon
	Entomobryidae	*Coecobrya tenebricosa* (Folsom, 1902)	Troglophile	Fungivore	Common
		Entomobrya unostrigata (Stach, 1930)	Troglophile	Fungivore	Rare?
		**Entomobryoides guthriei* (Mills, 1931)	Troglophile	Fungivore	Common
		Sinella sp. (Brook, 1882)	Troglophile	Fungivore	Rare?
	Sminthuridae	**Arrhopalites caecus* ((Tullberg, 1871)	Troglophile	Fungivore	Uncommon?
		Pygmarrhopalites nr. *dubius* (Christiansen, 1966)	Troglobite	Fungivore	Rare?
	Oncopoduridae	*Oncopodura* nr. *yosiiana* (Szeptycki, 1977)	Troglophile	Fungivore	Uncommon?
Zygentoma	Nicoletiidae	**Speleonycta anachoretes*	Troglobite	Scavenger	Common
Orthoptera	Rhaphidophoridae	**Ceuthophilus pima* (Hubbell, 1936)	Trogloxene	Scavenger	Common
	Gryllidae	*Gryllus multipulsator* (Weissman, 2009)	Trogloxene	Scavenger	Uncommon
Isoptera	Undet. family	Undet. genus and sp.	Trogloxene	Decomposer	Uncommon
Blattodea	Blattidae	*Periplaneta australasiae* (Fabricius, 1775)	Troglophile	Scavenger	Common
Psocoptera	Psyllipsocidae	**Psyllipsocus ramburii* (Selys-Longchamps, 1872)	Troglophile	Scavenger	Common
Hemiptera	Reduviidae	*Triatoma recurva* ((Stål, 1868)	Trogloxene	Parasite	Uncommon
		**Phasmatocoris labyrinthicus* (Pape 2013)	Troglobite	Predator	Uncommon
	Cimicidae	*Cimex incrassatus* (Usinger and Ueshima, 1965)	Trogloxene	Parasite	Rare

Table 1. *Continued.*

	Cydnidae	*Dallasiellus californicus* ((Blatchley, 1929)	Trogloxene	Herbivore	Rare
	Lygaeidae	Undet. genus and sp.	Accidental	NA	Rare
Coleoptera	Carabidae	*Lebia subgrandis* (Madge, 1967)	Accidental	NA	Rare
	Staphylinidae	*Stamnoderus* sp. (Sharp 1886)	Troglophile	Predator	Common
		*Undet. genus and sp.	Troglophile?	Predator	Rare
	Scarabaeidae	*Genuchinus ineptus* (Horn, 1885)	Accidental	NA	Rare
	Buprestidae	*Acmaeodera cazieri* (Knull, 1960)	Accidental	NA	Rare
	Anobiidae	*Niptus ventriculus* (LeConte, 1859)	Troglophile	Scavenger	Uncommon
	Scraptiidae	*Anaspis* nr. *rufa* (Say, 1826)	Troglophile	Unknown	Uncommon
	Tenebrionidae	*Argoporis alutacea* (Casey, 1890)	Trogloxene	Scavenger	Uncommon
		Conibius gagates (Horn, 1870)	Trogloxene	Scavenger	Uncommon
		**Eleodes longicollis* (LeConte, 1851)	Trogloxene	Scavenger	Uncommon
		Eleodes knullorum (Triplehorn, 1971)	Trogloxene	Scavenger	Rare
Lepidoptera	Tineidae	Undet. genus and sp.	Unknown	Unknown	Rare
	Undetermined family	*Undet. genus and sp. #1	Unknown	Unknown	Rare
		Undet. genus and sp. #2	Unknown	Unknown	Rare
Siphonaptera	Ischnopsyllidae	*Myodopsylla collinsi*? (Kohls, 1937)	Trogloxene	Parasite	Common
	Pulicidae	Undet. genus and sp.	Trogloxene	Parasite	Uncommon
Diptera	Psychodidae	*Lutzomyia* (*californica*?) (Fairchild and Hertig, 1957)	Troglophile	Parasite	Rare
	Cecidomyiidae	*Bremia*? (Rondani, 1860) sp.	Troglophile	Predator?	Common
		Clinodiplosis (Kieffer, 1895) sp.	Troglophile	Scavenger	Common
		Lestodiplosis (Kieffer, 1894) sp.	Troglophile	Predator	Common
	Mycetophilidae	Undet. genus and sp.	Troglophile	Predator	Rare
	Sciaridae	**Lycoriella* sp. (Frey, 1942)	Troglophile	Scavenger	Common
		**Plastosciara* sp. (Berg, 1899)	Troglophile	Scavenger	Common
	Asilidae	*Cophura painteri*? (Pritchard, 1943)	Accidental	NA	Rare
	Phoridae	*Megaselia* sp. (Rondani, 1856)	Troglophile?	Scavenger	Uncommon
		Puliciphora sp. (Dahl, 1897)	Troglophile?	Scavenger?	Rare
	Anthomyiidae	*Pegomya* sp. (Robineau-Desvoidy, 1830)	Accidental?	Unknown	Rare
	Streblidae	*Trichobius major* (Coquillett, 1899)	Trogloxene	Predator	Uncommon
	Muscidae	*Undet. genus and sp.	Accidental?	Unknown	Rare
	Tachinidae	Undet. genus and sp.	Trogloxene	Parasite	Rare
Hymenoptera	Sphecidae	*Chlorion aerarium* (Patton, 1879)	Trogloxene	Predator	Rare
	Mutillidae	Undet. genus and sp.	Accidental	NA	Rare
	Pompilidae	*Pepsis* sp. (Fabricius, 1804)	Accidental	NA	Rare
		Agenioideus biedermani (Banks, 1910)	Trogloxene	Parasite	Rare
	Formicidae	**Neivamyrmex graciellae* (Mann, 1926)	Troglophile	Predator	Uncommon
		Neivamyrmex leonardi (Wheeler, 1915)	Troglophile	Predator	Rare
		Pheidole rhea (Wheeler, 1908)	Trogloxene	Herbivore/Predator	Uncommon
		Pheidole sp. (Westwood, 1841)	Trogloxene	Predator?	Rare?
		Trachymyrmex arizonensis (Wheeler, 1907)	Trogloxene	Fungivore	Uncommon

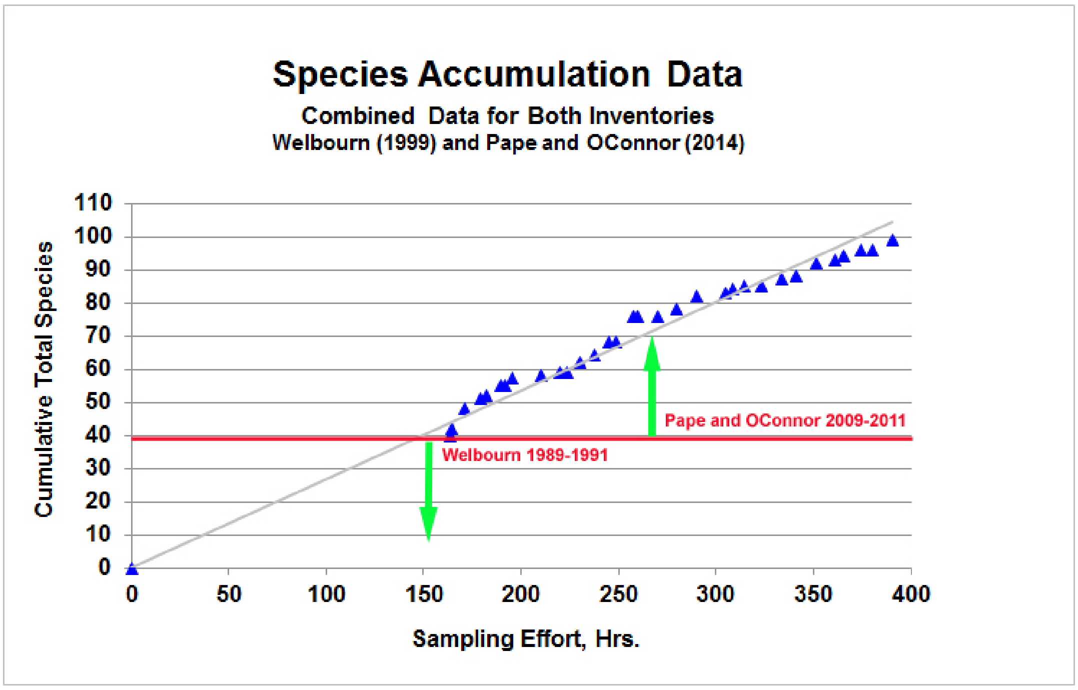

Figure 15. Search effort in hours plotted against total accumulated taxa found during the studies. The resultant curve does not approach an asymptote. Thus, we know that additional undocumented species are present in the cave.

Acknowledgments: We sincerely thank Dr. Robert Casavant, Arizona State Parks (ASP) Research and Science Manager and the ASP staff at Kartchner Caverns State Park for providing the opportunity to conduct this study in the cave. Steve Willsey, former ASP Ranger at Kartchner Caverns and currently an ASP - Resource, Inventory and Monitoring (RIM) Program senior resource specialist, was responsible for site visit logistics, was present on all in-cave trips, and made several significant discoveries both prior to, and during the study. Luis Espinasa of Marist College, Poughkeepsie, New York, contributed to the initial project development, participated in in-cave studies, described the endemic nicoletiid, and provided a review of an earlier version of this manuscript. We gratefully acknowledge the contributions of the other members of the KCSP personnel: Ginger Nolan, Mary Kumiega and Heidi Lauchstedt. We thank Carl Olson/University of Arizona, Department of Entomology for his review of this manuscript. Esty Pape proofread the manuscript. We sincerely thank the following international team of professional invertebrate taxonomists for their donations of time and expertise: Darrell Ubick/California Academy of Sciences (Araneae), Felipe Soto-Adames/ University of Illinois (Champaign) (Collembola), Raymond Gagné/ USDS-ARS-Systematic Entomology Laboratory (Beltsville, Maryland) (Cecidomyiidae), Luis Espinasa/Marist College (Nicoletiidae), Warren E. Savary/California Academy of Sciences (Scorpionida), R. Henry L. Disney/ University of Cambridge (*Megaselia*: Phoridae), James Cokendolpher/ Texas Tech University (Lubbock) (Pseudoscorpionida), and Brian Brown/ Natural History Museum of Los Angeles County (Phoridae). We thank W. Calvin Welbourn, (FSCA) for the loan of specimens from his earlier study of the cave fauna. We thank Kerry Gainor, Alanna Henneberry, Michael Mormando, and Terrence Turner, undergraduate students from Marist College for their assistance with the study during the March 2010 week-long field expedition. Partial support for Luis Espinasa and the aforementioned students came from the School of Science and a VPAA grand from Marist College. We thank Donald A. McFarlane at the Claremont McKenna College, California, and one anonymous reviewer for their comments, which improved the manuscript. Last, but certainly not least, we thank the cave discovery team of Gary Tenen and the late Randy Tufts for their many years of dedication to the preservation of what became Kartchner Caverns State Park. Without their efforts, which resulted in the protection of this unique natural resource, the unique fauna of Kartchner Caverns may not have been preserved.

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Received: July 2013
Accepted: July 2014
Published online: September 2014
Editorial responsibility: Ana Lúcia Tourinho

Appendix A: List of voucher specimens
Abbreviations used in the table for repositories are:

UA = University of Arizona – Entomology Department – Tucson, Arizona (USA);
UM = University of Michigan – Museum of Zoology - Insect Division – Ann Arbor, Michigan (USA);
CAS = California Academy of Sciences – San Francisco, California (USA);
TT = Texas Tech University – Lubbock, Texas (USA);
LAMNH = Los Angeles Museum of Natural History – Los Angeles, California (USA);
IL = University of Illinois – Champaign, Illinois (USA);
AMNH = American Museum of Natural History – New York, New York (USA);
UC = University of Cambridge – Museum of Zoology – Collection of World Phoridae – Cambridge, England (UK);
FSCA = University of Florida – Florida State Collection of Arthropods – Division of Plant Industry Gainesville, Florida (USA); specimens from the initial Welbourn study conducted between 1989-1991 are archived there.

Note: Photo vouchers are found in the main body of this paper associated with the species account.

PHYLUM NEMATA				
CLASS SECERNENTIA				
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Rhabditida	Thabditidae	*Rhabditis* (Dujardin, 1845) sp. 1	UA	Previous record
		Rhabditis (Dujardin, 1845) sp. 2	UA	Previous record
PHYLUM ARTHROPODA				
CLASS ARACHNIDA				
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Palpigradi	Eukoeneniidae?	Undet. genus and sp.	FSCA	Previous record
Scorpionida	Vaejovidae	*Pseudouroctonus* nr. *apacheanus* (Gertsch & Soleglad, 1972)	CAS	CASENT 9050717 & 9052215
Pseudoscorpiones	Chernetidae	*Dinocheirus* (*arizonensis*?) (Banks, 1901)	TT	TTU-Z 60729
	Undet. family	Undet. genus and sp.	FSCA	Previous record
Araneae	Theraphosidae	*Aphonopelma* sp. (Pocock, 1901)	Photo	This paper
	Filistatidae	*Kukulcania* sp. (Lehtinen, 1967)	Observation	This paper
	Pholcidae	*Physocyclus* sp. (Simon, 1893)	CAS	CASENT 9052209
	Sicariidae	*Loxosceles* sp. (Heineken & Lowe, 1832)	CAS	CASENT 9052210
	Theridiidae	*Achaearanea canionis* (Chamberlin & Gertsch, 1929)	CAS	CASENT 9052212 & 9052214
		Undet. genus and sp.	CAS	CASENT 9052211 & 9052213
	Nesticidae	*Eidmanella pallida* (Emerton, 1875)	CAS	CASENT 9052204-9052208
	Linyphiidae	Undet. genus and sp.	CAS	CASENT 9052203
	Hahniidae	*Neocryphoeca* (Roth, 1970) sp. #1	CAS	CASENT 9052198
		Neocryphoeca (Roth, 1970) sp. #2	CAS	CASENT 9052199-9052202
	Corinnidae	Undet. genus and sp.	CAS	CASENT 9052196
	Gnaphosidae	*Zelotes* sp. (Gistel, 1848)	CAS	CASENT 9052197
Actinedida	Cheyletidae	*Cheyletus* sp. (Latreille, 1796)	FSCA	Previous record
	Neothrombiidae	*Ceuthothrombium cavaticum* (Robaux, Webb & Campbell, 1976)	UM	BMOC 11-0928-003-1

Appendix A. *Continued.*

	Pygmephoridae	Undet. genus and sp.	FSCA	Previous record
	Rhagidiidae	*Poecilophysis* sp. (Cambridge, 1876)	FSCA	Previous record
	Stigmaeidae	*Eustigmaeus lirella* (Summers & Price, 1961)	UM	BMOC 11-0928-025-2
	Tarsonemidae	*Neotarsonemoides* sp. (Kaliszewski, 1984)	FSCA	Previous record
Astigmata	Acaridae	*Sancassania* sp. (Oudemans, 1916)	UM	BMOC 11-0928-007-1
	Histiostomatidae	*Histiostoma* nr. *guanophilum* (Mahunka, 1982) sp. #1	UM	BMOC 11-0928-021-1
		Histiostoma nr. *guanophilum* (Mahunka, 1982) sp. #2	UM	Previous record
	Rosensteiniidae	*Nycteriglyphus* sp. (Zachvatkin, 1941)	FSCA	Previous record
Ixodida	Argasidae	*Carios yumatensis* (Cooley & Kohls, 1941)	UM	BMOC 11-0928-027
		Carios nr. *hasei* (Schulze, 1935)	FSCA	Previous record
Mesostigmata	Laelapidae	*Gaeolaelaps* sp. (Evans and Till, 1966)	UM	BMOC 12-0624-002-1
		Stratiolaelaps scimitus (Womersley, 1956)	UM	BMOC 11-0928-006-1
		Stratiolaelaps sp. (Berlese, 1916)	UM	BMOC 11-0928-007-1
	Macrochelidae	*Macrocheles* nr. *penicilliger* (Berlese, 1904)	UM	BMOC 11-0928-005-1
	Macronyssidae	*Macronyssus crosbyi* (Ewing & Stover, 1915)	UM	BMOC 11-0928-017-1
	Rhodacaridae	*Rhodacarella cavernicola* (Moraza, 2004)	FSCA	Previous record
Oribatida	Damaeidae	*Parabelbella* sp. (Bulanova-Zachvatkina, 1967)	UM	BMOC 12-0624-001-1
	Oppiidae	*Multioppia* sp. (Hammer, 1961)	UM	BMOC 11-0928-029-1
	Family Undet.	Undet. genus and sp.	FSCA	Previous record
	Family Undet.	Undet. genus and sp.	FSCA	Previous record
	Family Undet.	Undet. genus and sp.	FSCA	Previous record
Trombidiformes	Erythraeidae	*Charletonia* sp. (Oudemans, 1910)	UM	BMOC 11-0928-018-1
		CLASS MALACOSTRACA		
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Isopoda	Trichoniscidae	*Brackenridgia* nr. *sphinxensis* (Schultz 1984)	UA	KCSP 0050
	Porcellionidae	*Porcellio laevis* (Collinge, 1917)	UA	KCSP 0042
		CLASS DIPLOPODA		
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Polydesmida	Macrosternodesmidae	*Nevadesmus*? (Shear, 2009)	UA	KCSP0056
Spirostreptida	Cambalidae	Undet. genus and sp.	UA	KCSP0103
		CLASS CHILOPODA		
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Scutigeromorpha	Scutigeridae	*Dendrothereua* nr. *homa* (Chamberlin, 1942)	UA	KCSP0053
Scolopendromorpha	Scolopendridae	*Scolopendra heros* var. *arizonensis* (Kraepelin, 1903)	Photo	This paper
		Undet. genus and sp.	FSCA	Previous record
		CLASS INSECTA		
ORDER	**FAMILY**	**SPECIES**	**REPOSITORY**	**ACCESSION NUMBER(S)**
Collembola	Onychiuridae	*Tullbergia iowensis* (Mills, 1932)	IL	551675
	Isotomidae	*Folsomia candida* (Willem, 1902)	IL	551656
	Entomobryidae	*Coecobrya tenebricosa* (Folsom, 1902)	IL	551651; 551659; 551670-551672
		Entomobrya unostrigata (Stach, 1930)	IL	551657-551658
		Entomobryoides guthriei (Mills, 1931)	IL	551653-551,655; 551668-551669
		Sinella sp. (Brook, 1882)	IL	551673
	Sminthuridae	*Arrhopalites caecus* (Tullberg, 1871)	IL	551676
		Pygmarrhopalites nr. *dubius* (Christiansen, 1966)	IL	551677
	Oncopoduridae	*Oncopodura* nr. *yosiiana* (Szeptycki, 1977)	IL	551674
Zygentoma	Nicoletiidae	*Speleonycta anachoretes* (Espinasa, Pape, Henneberry & Kinnear, 2012)	AMNH	1ZC00114297
Orthoptera	Rhaphidophoridae	*Ceuthophilus pima* (Hubbell, 1936)	UA	KCSP0199
	Gryllidae	*Gryllus multipulsator* (Weissman, 2009)	UA	KCSP0106
Isoptera	Undet. family	Undet. genus and sp.	Photo	This paper
Blattodea	Blattidae	*Periplaneta australasiae* (Fabricius, 1775)	UA	KCSP0075
Psocoptera	Psyllipsocidae	*Psyllipsocus ramburii* (Selys-Longchamps, 1872)	UA	KCSP0133
Hemiptera	Reduviidae	*Triatoma recurva* (Stål, 1868)	UA	KCSP0079
		Phasmatocoris labyrinthicus (Pape 2013)	AMNH	65999
	Cimicidae	*Cimex incrassatus* (Usinger & Ueshima, 1965)	UA	KCSP0168

Appendix A. *Continued.*

	Cydnidae	*Dallasiellus californicus* ((Blatchley, 1929)	UA	KCSP0147
	Lygaeidae	Undet. genus and sp.	UA	KCSP0071
Coleoptera	Carabidae	*Lebia subgrandis* (Madge, 1967)	UA	KCSP0146
	Staphylinidae	*Stamnoderus* sp. (Sharp 1886)	UA	KCSP0062
		Undet. genus and sp.	UA	KCSP0001
	Scarabaeidae	*Genuchinus ineptus* (Horn, 1885)	UA	KCSP0039
	Buprestidae	*Acmaeodera cazieri* (Knull, 1960)	UA	KCSP0027
	Anobiidae	*Niptus ventriculus* (LeConte, 1859)	UA	KCSP0091
	Scraptiidae	*Anaspis* nr. *rufa* (Say, 1826)	UA	KCSP0202
	Tenebrionidae	*Argoporis alutacea* (Casey, 1890)	UA	KCSP0212
		Conibius gagates (Horn, 1870)	UA	KCSP0061
		Eleodes longicollis (LeConte, 1851)	UA	KCSP0180
		Eleodes knullorum (Triplehorn, 1971)	UA	KCSP0048
Lepidoptera	Tineidae	Undet. genus and sp.	UA	KCSP0090
	Undetermined family	Undet. genus and sp. #1	FSCA	Previous record
		Undet. genus and sp. #2	FSCA	Previous record
Siphonaptera	Ischnopsyllidae	*Myodopsylla collinsi*? (Kohls, 1937)	UA	KCSP0099
	Pulicidae	Undet. genus and sp.	UA	KCSP0046
Diptera	Psychodidae	*Lutzomyia* (*californica*?) (Fairchild & Hertig, 1957)	UA	KCSP0029
	Cecidomyiidae	*Bremia*? (Rondani, 1860) sp.	UA	KCSP0157
		Clinodiplosis (Kieffer, 1895) sp.	UA	KCSP0094
		Lestodiplosis (Kieffer, 1894) sp.	UA	KCSP0189
	Mycetophilidae	Undet. genus and sp.	Photo	This paper
	Sciaridae	*Lycoriella* sp. (Frey, 1942)	UA	KCSP0015
		Plastosciara sp. (Berg, 1899)	UA	KCSP0102
	Asilidae	*Cophura painteri*? (Pritchard, 1943)	UA	KCSP0032
	Phoridae	*Megaselia* sp. (Rondani, 1856)	UC	UC Book 20, #161
		Puliciphora sp. (Dahl, 1897)	LAMNH	LACM ENT 275384
	Anthomyiidae	*Pegomya* sp. (Robineau-Desvoidy, 1830)	UA	KCSP0078
	Streblidae	*Trichobius major* (Coquillett, 1899)	UA	KCSP0038
	Muscidae	Undet. genus and sp.	FSCA	Previous record
	Tachinidae	Undet. genus and sp.	UA	KCSP0214
Hymenoptera	Sphecidae	*Chlorion aerarium* (Patton, 1879)	Photo	This paper
	Mutillidae	Undet. genus and sp.	UA	KCSP0084
	Pompilidae	*Pepsis* sp. (Fabricius, 1804)	Photo	This paper
		Agenioideus biedermani (Banks, 1910)	UA	KCSP0083
	Formicidae	*Neivamyrmex graciellae* (Mann, 1926)	UA	KCSP0021
		Neivamyrmex leonardi (Wheeler, 1915)	UA	KCSP0036
		Pheidole rhea (Wheeler, 1908)	UA	KCSP0076
		Pheidole sp. (Westwood, 1841)	UA	KCSP0076
		Trachymyrmex arizonensis (Wheeler, 1907)	UA	KCSP0069