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CAVE-DWELLING ARTHROPODS AND VERTEBRATES OF NORTH RIM GRAND CANYON, WITH NOTES ON ECOLOGY AND MANAGEMENT

J. Judson Wynne[1] and Kyle D. Voyles[2]

ABSTRACT.—Prior to this study, there was no information on arthropods, bats, and other vertebrates of caves in northwesternmost Arizona. Based on invertebrate and vertebrate inventory work conducted during 2005 and 2006, we provide future directions for conservation and management for caves on Grand Canyon–Parashant National Monument, northwestern Arizona. Baseline investigations to find and identify arthropods, bats, and other vertebrates were conducted at 7 of the largest known caves on the monument. We identified 52 morphospecies including 44 arthropods, 4 bats, and 4 other vertebrates. Of the cave-dwelling arthropods, we found 10 eisodophiles, 6 troglophiles, 8 questionable troglophiles, 7 trogloxenes, 8 accidentals, 3 taxa of unknown cave affiliations, and 2 mammalian parasites. We made several contributions to the entomological record including 2 new genera, 6 new species, 3 possible new species, one range extension, and one possible range extension. Also, we identified 5 bat roosts—1 hibernaculum, 2 night roosts, and 3 summer roosts of unconfirmed use. Observed arthropod richness per cave ranged from 1 to 14 morphospecies, and observed bat and other vertebrate (combined) richness was 1–3 morphospecies. We did not detect any cave-adapted arthropods during this investigation. For the caves sampled, we are uncertain whether the lack of cave-adapted taxa is due to (a) low nutrient input and high cryptoaridity associated with many southwestern cave systems or (b) lack of intensive sampling. Despite the lack of cave-adapted species, 5 of the 7 caves inventoried are considered of high management concern. Additional research at these caves will be required to obtain the data necessary to best manage and protect these systems.

RESUMEN.—Anterior a este estudio, no había información sobre los artrópodos, murciélagos y otra fauna en las cavernas al noroeste de Arizona. Basados en el inventario de invertebrados y vertebrados realizados durante 2005 y 2006, nosotros proveemos las futuras direcciones para la investigación y gestión de cavernas del Grand Canyon–Parashant National Monument, noroeste de Arizona. Investigaciones iniciales fueron realizados en artrópodos, murciélagos y fauna en 7 de las más grandes cavernas conocidas. Identificamos 52 morfoespecies incluyendo 44 artrópodos, 4 murciélagos y 4 fauna silvestre. De los artrópodos, hubo 10 eisodofilos, 6 troglofilos, 8 pseudo-troglofilos, 7 trogloxenos, 8 accidentales, 3 desconocidas y 2 ectoparásitos. Realizamos varias contribuciones al registro entomológico incluyendo 2 nuevos géneros, 6 nuevas especies, 3 posibles nuevas especies, una expansión distribucional y una posible expansión distribucional. También, identificamos 5 refugios de murciélagos: 1 hibernáculo, 2 dormideros nocturnos y 3 dormideros estivales de uso indeterminado. La riqueza observada de artrópodos oscilo entre 1–14 morfoespecies y la riqueza combinada para murciélagos y fauna vario entre 1–3 morfoespecies. Durante este trabajo, no fueron encontrados artrópodos troglomorficos. En las cavernas muestreadas, se desconoce si la falta de taxones adaptados a las cavernas es debido a (i) el bajo aporte de nutrientes y la alta cripto-aridez asociada generalmente con los sistemas de cavernas del suroeste, o (ii) el insuficiente muestreo. A pesar de ello, 5 de las 7 cavernas inventariadas son consideradas como de alto interés de gestión. Investigaciones adicionales en estas cavernas serán necesarios para obtener los datos requeridos para una mejor gestión y protección de estos sistemas.

Information related to the biospeleology of northern Arizona is limited. Prior to this study, no investigations on cave use by arthropods, bats, and other vertebrates in northwestern Arizona had been undertaken. Based on our literature review, most of the work on the southern Colorado Plateau (within northern Arizona) has been baseline in nature, and these studies were largely focused on Wupatki National Monument and Grand Canyon National Park. Given limited information and the desire to provide a regional summary of cave biology, we present a brief overview of the taxa reported during previous work.

At Wupatki National Monument, Welbourn (1976) conducted 1–2 site visits at 5 earth cracks (volcano-tectonic fissures) and identified 19 arthropods, including 5 troglophiles, 13 trogloxenes, and 5 accidentals; no troglobites were identified during his work (see below for definitions on cave specificity functional groups). From Welbourn's inventory (1976), Muchmore

[1]Department of Biological Sciences, Colorado Plateau Biodiversity Center, Colorado Plateau Research Station and Landscape Conservation Initiative, Northern Arizona University, Box 5614, Building 56, Suite 150, Flagstaff, AZ 86011. URL: http://www.jutwynne.com
[2]Saint George Field Office, Bureau of Land Management, 345 E. Riverside Dr., St. George, UT 84790.

(1981) described an endemic pseudoscorpion (*Archeolarca welbourni*) from 2 earth cracks.

Bat research has been conducted on a nearly decadal scale at Wupatki. Gustafson (1964) collected one Townsend's big-eared bat (*Corynorhinus townsendii*) during the summer near the bottom of an earth crack. Welbourn (1976) identified *C. townsendii* at 4 earth cracks (one of the earth cracks was the same visited by Gustafson [1964]). Day roost activity was documented at all features in September, and 2 earth cracks were identified as hibernacula. Bain (1986) documented winter use of 7 earth cracks (confirming continued use of the one previously visited by Gustafson and 4 visited by Welbourn [1976]) by *C. townsendii.* Concerning other vertebrate species, Welbourn (1976) identified the remains of 2 accidental morphospecies in Wupatki earth cracks: Rodentia (from 2 earth cracks) and Lagomorpha (from one earth crack).

Wynne et al. (2007) compiled a review of cave-dwelling arthropod research in Grand Canyon National Park (GRCA) and synthesized information from 15 caves representing 9 studies (conducted between 1975 and 2001). At least 47 cave-dwelling arthropods, including 3 troglobites, one stygobite (aquatic cave-adapted animals), 7 trogloxenes, 16 troglophiles, and 16 unidentified cavernicoles (presumed troglophiles) were identified (Wynne et al. 2007). Additionally, bats known to use GRCA caves include the Brazilian free-tailed bat (*Tadarida brasiliensis*) from 2 caves (Pape 1998, Hill et al. 2001) and *C. townsendii* from 2 caves (Welbourn 1978). Other cave-dwelling vertebrates known to occur in GRCA include *Neotoma* sp. from 4 caves (Peck 1980, Bodenhamer 1989, Drost and Blinn 1998, Hill et al. 2001), brush mouse (*Peromyscus boylii*) from one cave (Drost and Blinn 1998), American porcupine (*Erethizon dorsatum*) from one cave (Hill et al. 2000) and ringtail (*Bassariscus astutus*) from 4 caves (Peck 1980, Bodenhamer 1989, Pape 1998, Hill et al. 2000, 2001).

Peck (1982) conducted invertebrate surveys and reported on the largely depauperate fauna ($n = 2$ morphospecies) occurring in 4 lava tube caves at Sunset Crater National Monument and in the greater Flagstaff region.

Although much of the biospeoleological research over the past several decades has been baseline in nature, these studies combined with our present work begin to produce a regional picture of the natural history of caves on the southern Colorado Plateau.

Here we report the first regional all-taxa biological inventory of known caves in Grand Canyon–Parashant National Monument, Arizona. Our objectives were to conduct baseline inventories by (1) sampling cave-dwelling arthropods; (2) identifying bat use of caves either directly or by examining previous evidence of use; (3) documenting all other vertebrate activity observed within each cave; and (4) identifying caves of high management concern for further study.

METHODS

Cave-Dependency Functional Groups

We divided Grand Canyon–Parashant cave-dwelling taxa into 7 cave-dwelling organism groups and one special case category. The following definitions were taken from Barr (1968), Howarth (1983), and Wynne (2013): (1) *troglobites,* obligate cave dwellers who can only complete their life cycle within the hypogean environment; (2) *troglophiles,* species that occur facultatively within caves and complete their life cycles there, but also exist in similar dark and humid epigean microhabitats; (3) *trogloxenes,* species that frequently use caves for shelter but forage in the epigean realm; (4) *accidentals,* morphospecies that occur in caves but cannot survive within the hypogean environment; (5) *eisodophiles,* species that facultatively use cave entrances and twilight zones and may complete their life cycles there, but also exist in similar partially sheltered epigean environments; (6) *eisodoxenes,* species that frequently use cave entrances and twilight zones for shelter but forage on the surface; (7) *unknown,* species for which information is lacking to place them within one of the 6 aforementioned groups; and, (8) *parasites,* a special-case group, which includes parasitic arthropods detected in caves due to the presence of their host (e.g., bats or other mammals).

Study Site

Located in northwestern Arizona, Grand Canyon–Parashant National Monument (hereafter shortened to Parashant) is jointly managed by the National Park Service and the Bureau of Land Management. Encompassing 1.1 million acres, Parashant is characterized by rugged terrain containing deeply incised

canyons, mesas, and mountains. Two geological provinces converge here: the Basin and Range and the Colorado Plateau. Vegetation zones include Mojave Desert at lower elevations, grading through grassland and juniper shrubland to ponderosa pine forest on Mt. Trumbull (elevation 2447 m).

Parashant caves were selected for inventory if they contained deep zone–like conditions. Cave deep zones are characterized by complete darkness, stable temperature, water-saturated atmosphere, and limited to no airflow (see Howarth 1980, 1982). This zonal environment serves as habitat for cave-adapted arthropods. Two of 7 caves met all the deep zone criteria. However, caves meeting most of these criteria (i.e., complete darkness, stable temperature, limited airflow) were also included in our study. Because troglomorphic animals often represent rare and endemic taxa, caves supporting these animals are considered of high management and conservation value. Therefore, we sampled caves with deep zones and deep zone–like conditions.

To safeguard caves and their resources, we referred to all of the caves in this study by using an alphanumeric coding system developed by the National Park Service (NPS) rather than actual cave names. Parashant headquarters in St. George, Utah, has the cipher table with cave codes and names. A copy of this paper with actual cave names is on file with both the National Park Service in St. George and the National Cave and Karst Research Institute, Carlsbad, New Mexico.

We sampled arthropods, bats, and other vertebrates in the following date ranges: 4–14 August 2005 and 16–26 September 2005. Winter roost surveys for hibernating bats were conducted during 4–10 March 2006.

Arthropod Sampling

Based on our site visits, we identified 6 caves that were believed to support deep zone–like conditions, and we included one additional cave due to the presence of a summer bat roost. Five caves (PARA 1801, PARA 2602, PARA 2204, PARA 1001, and PARA 1401) were sampled using a combined baited and unbaited pitfall trapping approach and direct intuitive searches. Two caves (PARA 0802 and PARA 2202) were sampled using direct intuitive searches and opportunistic hand-collecting throughout each cave's length.

In caves sampled with pitfall traps, we deployed traps for 4 days, with 2 traps placed within each of the 3 primary zones—light, twilight, and dark. Because the location of the twilight zone shifts temporally and seasonally, we estimated the location of this photic zone during summer. Pitfall trap construction consisted of two 32-ounce stacked plastic containers (13.5 cm height, 10.8 cm diameter rim and 8.9 cm base). We used approximately 4.9 mL of peanut butter as bait and placed it in the bottom of the exterior container. At the bottom of the interior container, we made several dozen holes so the bait could "breathe" to attract insects. We buried containers to the rim when possible, built rock ramps to the trap rim in other cases, and covered all traps with a caprock. Prior to removing traps at the end of the sample period, we searched around each trap to identify and capture individuals attracted to the bait but not captured within the trap (Poulson and Culver 1969).

No pitfall traps were placed in PARA 2202 due to safety issues associated with a return visit. Although PARA 0802 lacked deep zone–like conditions and we considered the presence of cave-adapted arthropods unlikely, we sampled the cave for arthropods because of the presence of a bat roost (and thus guano).

We searched each cave in areas deemed most likely to contain certain arthropods. These areas included detritus deposits, areas with condensed water and mud, guano deposits, and active speleothems. We searched for arthropods for at least 40 minutes (2 observers $\times$ 20 min each) in each zone (i.e., light, twilight, and dark). We also opportunistically collected arthropods by traversing the length of the cave and searching for and collecting arthropods as encountered (2 observers per cave).

Arthropod Identification

We used a combination of existing keys and worked with staff members at both the Colorado Plateau Museum of Arthropod Biodiversity and the Colorado Plateau Research Station at Northern Arizona University (NAU) to identify arthropods to the lowest taxonomic level possible. For several taxonomic groups, we sent specimens to experts, including Rolf Aalbu (Coleoptera: Tenebrionidae), Thomas Barr Jr. (Coleoptera: Rhadine), Earnest Bernard (Collembola), Theodore Cohn (Orthoptera: Rhamphidophoridae), Carl Dick (Diptera:

TABLE 1. Arthropods, bats and other vertebrates identified across all cave specificity functional groups, Grand Canyon–Parashant National Monument.

	Eisodophiles	Eisodoxenes	Troglophiles	Troglophiles?	Trogloxenes	Accidentals	Unknown	Parasites
Arthropods	10	—	6	8	7	8	3	2
Bats	—	—	—	—	4	—	—	—
Other vertebrates	—	2	1	—	—	1	—	—

Nycteribiidae), Mark Harvey (Pseudoscorpiones: Chernetidae), Robert Johnson (Hymenoptera: Formicidae), Edward Mockford (Psocoptera), Pierre Paquin (Arachnida), William Shear (Opiliones), Jon Gelhaus (Diptera: Tipulidae), and Chen Young (Diptera: Tipulidae). Voucher specimens for most arthropod groups identified through this work are deposited at the Museum of Northern Arizona, Flagstaff.

Vertebrate Sampling

BATS.—During August and September 2005, we surveyed for bats by employing a combination of techniques including (i) mist-netting and harp-trapping at cave entrances during evening emergence; (ii) hand-netting within one cave; (iii) visually identifying bats as encountered within each cave; and (iv) examining caves for evidence of bat use. For each bat captured, we determined sex, age, weight, and reproductive status (Kunz 1982). Cave entrances were presumed to serve as night roosts if we documented guano and/or insect parts on the cave floor within 5 m of a cave's entrance.

We set 2 mist nets and a harp trap within the entrances of PARA 1801, PARA 0802, and PARA 1401. Mist nets and harp traps were deployed before sunset and removed 2 hours after bats had started their evening emergence. We used 6-m, 2-shelf Avinet mist nets (www.avinet.com) and a G6 Cave Catcher harp trap (Bat Management, www.batmanagement.com; maximum catch area 3.35 m^2). We hand-netted bats within PARA 2602.

During late winter (4–10 March 2006), each cave was visited once to search for and count hibernating bats. When possible, we visually identified all bats encountered to species. No hibernating bats were handled during this work.

OTHER VERTEBRATES.—Within each cave, we searched for and recorded the presence of all other vertebrates. Sign of other vertebrates included direct observation, scat, feathers, and skeletal remains.

RESULTS

We detected 52 cavernicolous taxa, including 44 arthropods, 4 bats, and 4 other vertebrates (see the Annotated List of Morphospecies, page 8). Of these, arthropods comprised 10 eisodophiles, 6 troglophiles, 8 questionable troglophiles, 7 trogloxenes, 8 accidentals, 3 unknowns

TABLE 2. Total number of arthropods observed per photic zone by cave.

	Light	Twilight	Dark
PARA 1801	20	16	2
PARA 2202	—	~1000	4
PARA 2602	14	6	13
PARA 2204	9	~1000	13
PARA 0802	—	1	—
PARA 1401	—	—	1
PARA 1001	>500	>500	6
TOTAL	543[a]	2523[a]	39

[a]The values were estimated for large populations of crickets (PARA 1001) and harvestmen (PARA 2202 and PARA 2204) and were likely underestimated for each cave.

and 2 parasites; all bats were trogloxenes, and other vertebrates included one troglophile, one accidental, and 2 eisodoxenes (Table 1). Observed arthropod richness ranged from one to 14 morphospecies per cave. The rank order of caves by arthropod species richness was PARA 1801 (14), PARA 2602 (13), PARA 1001 (11), PARA 2204 (8), PARA 2202 (5), PARA 0802 (1), and PARA 1401 (1). We detected bats in most caves (71.4%); PARA 0802, PARA 1401, and PARA 2602 all contained at least 2 bat morphospecies. Numbers for other vertebrates ranged from one to 2 morphospecies per cave; both PARA 1001 and PARA 2202 supported 2 vertebrate species.

Arthropods

Taxonomically, the most morphospecies-diverse groups of arthropods were spiders (Araneae; $n = 14$), beetles (Coleoptera: 6 different families; $n = 7$), cave crickets (Orthoptera: Rhaphidophoridae; $n = 5$), ants (Hymenoptera: Formicidae; $n = 4$), flies (Diptera: 4 different families; $n = 4$), and book lice (Psocoptera: 3 different families; $n = 3$). Other groups of particular interest due to their ecological and evolutionary relationships to cave environments include harvestmen (Opiliones; $n = 1$), mites (Acari; $n = 2$), and springtails (Collembola; $n = 1$). The remaining arthropods detected within caves include true bugs (Hemiptera; Reduviidae; $n = 1$), fleas (Siphonaptera; $n = 1$) and bristletails (Thysanura; $n = 1$).

On a regional level, several taxonomic groups were represented by 4 or more morphospecies. Spiders were the most commonly detected animal in all caves visited, representing ~30% of the arthropods detected. PARA 1801 and PARA 2202 contained the highest diversity of spiders, 5 and 4, respectively. Other notable groups include beetles (7 morphospecies from 5 caves), crickets (5 morphospecies from 3 caves), Psocoptera (3 morphospecies from 3 caves), and ants (4 morphospecies from 3 caves). All ants that we detected represent accidental occurrences (R. Johnson, personal communication, 2006).

Across all arthropod groups, most morphospecies were limited to a single observation within a single cave. However, both *Leiobunum townsendii* and *Entomobrya zona* were encountered across 3 caves.

When we considered total numbers of observed individuals per light zone, we found that the twilight zone contained the largest number of individuals (~2523), followed by the light (~543) and dark zones (~39; Table 2). PARA 1001 contained a large cricket roost (estimated to contain >1000 individuals). Although the crickets occurred throughout PARA 1001, most were detected within the light and twilight zones. They were often found denning in large groups along the walls and ceilings and within several ceiling fissures. PARA 2202 and PARA 2204 supported large numbers of *Leiobunum townsendii* (estimated in the hundreds) denning in packed clusters in large overhead fissures within the twilight zones of each cave. When we shined our light on these clusters, the harvestmen would rock, sway, and often aggregate into tighter clusters.

This work resulted in discovery of 2 new genera, 6 new species, 3 possible new species, 1 range extension, and 1 possible range extension. The 2 new genera (comprising 2 new species) are a book louse (Psocoptera: Sphaeropsocidae: *Troglosphaeropsocus voylesi*, Mockford 2009) and a cave cricket (Rhaphidophoridae: cf *Ceuthophilus* n. gen. n. sp., Cohn and Swanson, unpublished data). Additional new species included the following: a new pseudoscorpion (Chernetidae: *Tuberochernes* n. sp., det. M. Harvey), a cave cricket (*Ceuthophilus* n. sp., det. T. Cohn); a carabid beetle (*Rhadine* n. sp., *Perlevis* species group, det. T. Barr), and 2 tenebrionid beetles (*Eschatomoxys pholeter* Thomas and Pape 2007 [Pape et al. 2007] and *Eleodes* [*Caverneleodes*] *wynnei* Aalbu 2012 [Aalbu et al. 2012]). Images of select taxa are provided in Fig. 1. Two additional *Ceuthophilus* sp. (n. sp.? a and n. sp.? b) from PARA 1801 may represent new species; the specimens are "distinctive, and both may be undescribed" (T. Cohn, personal communication, 2006).

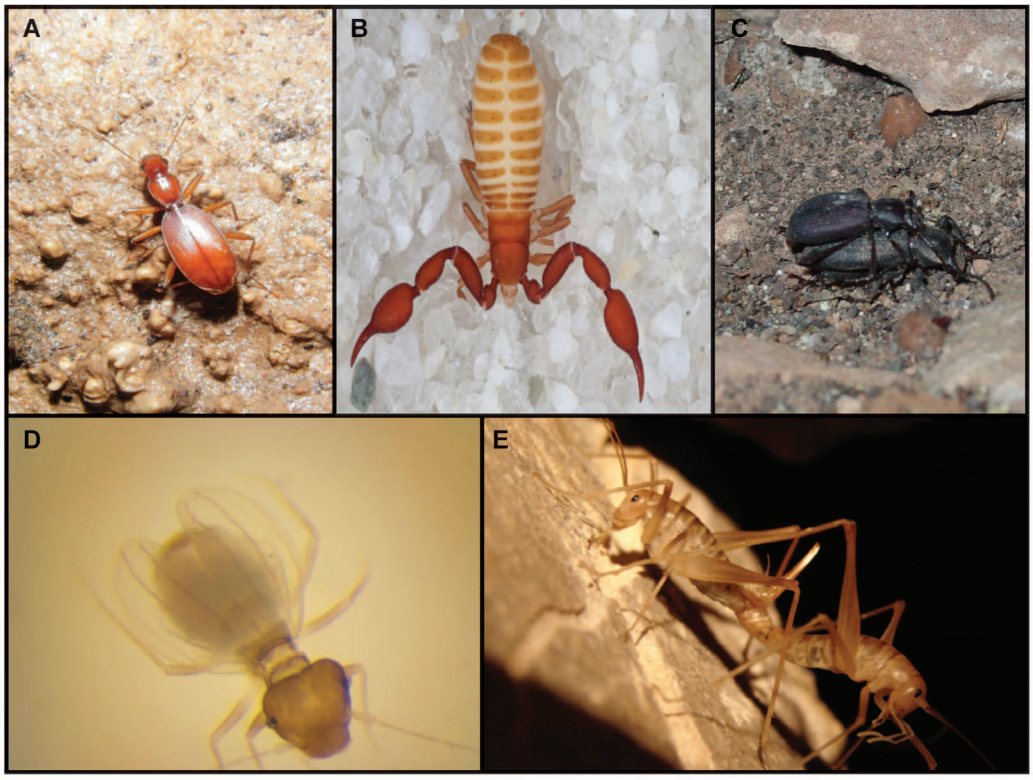

Fig. 1. Five new species (including 2 new genera) discovered on Grand Canyon–Parashant National Monument, Arizona: **A,** *Rhadine* n. sp., *Perlevis* species group, on cave floor of PARA 2204; **B,** high resolution postmortem image of *Tuberochernes* n. sp.; **C,** a breeding pair of *Eleodes* (*Caverneleodes*) *wynnei* (Aalbu et al. 2012) from PARA 1001; **D,** postmortem image of *Troglosphaeropsocus voylesi* (courtesy of E. Mockford); **E,** a breeding pair of cf *Ceuthophilus* n. gen. n. sp. from PARA 1001.

Our efforts extended the range of the *Speleketor flocki* (Psocoptera: Psyllipsocidae), which was previously known from 2 other localities in the southwest: Tucson Mountains, southern Arizona, and southeastern Nevada. One accidental ant species, *Paratrechina hystrix*?, may represent the first record of this species in Arizona (R. Johnson, personal communication, 2006). Specimens match the description of *P. hystrix* in part; however, because no workers were collected, this identification cannot be confirmed (R. Johnson, personal communication, 2006).

Bats

Five of the 7 caves (71.4%) contained bats. Of these, we identified 3 roosts of an unknown function, 2 night roosts, and a hibernaculum. PARA 1401 serves as both a summer roost and hibernaculum.

We documented a fringed myotis (*Myotis thysanodes;* Fig. 2C) colony (~30 individuals) at PARA 1801 during the September 2005 survey. We trapped one nonreproductive female using a harp trap. We were unable to determine the function of this roost based upon the one individual captured. Given the presence of a fresh guano pile, we ascertained the general location of the roost, which was at the back of the cave.

We confirmed 2 pallid bat (*Antrozous pallidus;* Fig. 2B) roosts during August surveys. In PARA 0802 and PARA 2602, we observed ~50 and ~100 individuals, respectively. We captured one postlactating female, 4 nonreproductive females (1 juvenile, 1 adult, and 2 undetermined), and one nonscrotal male, using a harp trap and mist nets at PARA 0802. These bats were not marked, so there was the possibility of double counting. In PARA 2602, we captured one nonreproductive female and one nonscrotal male with handheld nets. We tentatively identified a pallid bat (on the basis of its light brown color and size) flying within PARA 2202.

Fig. 2. Three cave-roosting bat species confirmed on Grand Canyon–Parashant National Monument, Arizona: **A,** 3 hibernating *Corynorhinus townsendii* from PARA 1401; **B,** 3 *Antrozous pallidus* from PARA 0802; **C,** *Myotis thysanodes* in hand during harp-trapping and mist-netting operations at the entrance of PARA 1801.

In August 2005, we counted approximately 10 *Myotis* sp. emerging from PARA 1401. Numerous lepidopteran wings were documented within the entrance and twilight zones of PARA 0802 and PARA 2602. *Corynorhinus townsendii* is one of the more common trogloxenic bats in northern Arizona. This bat uses cave entrances as night roosts, where it has been documented removing the wings of moths prior to consuming the abdomen (e.g., Lopez-Gonzalez 2005). In West Virginia, Sample and Whitmore (1993) have shown this species to preferentially consume moths over other arthropods. Because of this documented diet preference and the large accumulation of moth wings, we suggest these caves are probably used as night roosts by *C. townsendii.*

During our early March 2006 surveys, we observed 9 *C. townsendii* (Fig. 2A) hibernating within the deep zone of PARA 1401 at mid-cave.

Other Vertebrates

We identified woodrat (*Neotoma* spp.) middens in 4 caves, American porcupine use (*Erethizon dorsatum*) at 2 caves, owl use of one cave, and small carnivore use of one cave. We documented *Neotoma* spp. middens in the entrance and twilight zone of 4 caves (PARA 2202, PARA 2602, PARA 2204, and PARA 0802). Woodrats and their middens are commonly observed along sheltered rock outcrops, crags, rock shelters and cave entrances; thus, woodrats are considered troglophiles. Because we did not trap small mammals during this study, we were unable to provide species-level identifications.

Three woodrat species are known to occur within Parashant. The Mexican woodrat (*Neotoma mexicana*) occurs within rocky outcrops and slopes and is found in open woodland and transition-zone vegetation (Cornely and Baker 1986). Stephen's woodrat (*Neotoma stephensi*) is often found in association with juniper trees (*Juniperus* spp.; Jones and Hildreth 1989). Also, the white-throated woodrat (*Neotoma albigula*) may also occur at the mid-elevations of the monument (Macêdo and Mares 1988). Thus, woodrat activity may represent one or more of these species at any given site.

We found significant use by American porcupine in both PARA 1001 and PARA 1401. Woods (1973) indicates that porcupines den in caves, hollow trees, and logs. However, we did not find evidence of recent activity in either cave. In PARA 1001, we confirmed use by porcupine based on an extensive deposition of scat and quills, extending from the middle portion to the back of the cave. We found scat and quills littering the entrance of PARA 1401, as well as a fully articulated porcupine skeleton in the cave. Evidence of owl roosting activity (i.e., pellets) was documented in the twilight zone of PARA 2202.

We found scat from a small carnivore (possibly ringtail) in the dark zone of PARA 2202. This could be one of 3 small carnivores known to use caves in the Southwest, including ringtail (*Bassariscus astutus;* e.g., Peck 1980, Bodenhamer 1989, Pape 1998, Hill et al. 2000, 2001, Strong 2006), skunks (Mephitidae), or raccoon (*Procoyon lotor;* e.g., Winkler and Adams 1972).

ANNOTATED LIST OF MORPHOMETRICS

The following is an annotated list of morphospecies detected from 7 caves on Grand Canyon–Parashant National Monument, Arizona.

Phylum Arthropoda
Class Arachnida
Order Araneae
Family Pholcidae

Undetermined genus and species.
Det. P. Paquin. Eisodophile.

One juvenile specimen was collected from the twilight zone of PARA 1801. Because the specimen was an immature, it could not be identified beyond family level (P. Paquin, personal communication, 2006).

Physocyclus sp.
Det. P. Paquin. Eisodophile.

One male specimen was collected from the light zone of PARA 2204.

Psilochorus sp.
Det. P. Paquin. Troglophile?

One female specimen was collected from the dark zone of PARA 2602. Given that it was collected from the dark zone, we suggest this spider may be a troglophile.

Family Theridiidae

Achaearanea sp. Det. P. Paquin. Eisodophile.

One female specimen was removed from a web within the light zone of PARA 1801. Peck (1980) suggests this genus occurs in caves, as well as in more mesic epigean environments in Arizona, California, New Mexico, and Utah.

Family Linyphiidae

Undetermined genus and species.
Det. P. Paquin. Eisodophile.

Two juvenile specimens belonging to the same genus and species were collected from the light zone of PARA 1801. Because they were juveniles, they could not be identified beyond family level.

Agyneta sp.
Det. P. Paquin. Troglophile?

We collected one female specimen from the dark zone of PARA 2204. Given that it was collected from the dark zone, we suggest this spider may be a troglophile.

Family Tetragnathidae

Metellina sp. Det. P. Paquin. Eisodophile.

Two juvenile specimens were collected from the light zone of PARA 1001.

Family Tengellidae

Undetermined genus and species a.
Det. P. Paquin. Troglophile?

One juvenile specimen was collected from the dark zone of PARA 2202. Given that it was collected from the dark zone, we suggest this spider may be a troglophile.

Undetermined genus and species b.
Det. P. Paquin. Troglophile?

We collected 2 juvenile specimens of a genus and species different from the aforementioned specimen from the dark zone of PARA 2202. Given that these specimens were collected from the dark zone, we suggest this spider may be a troglophile.

Undetermined genus and species c.
Det. P. Paquin. Eisodophile.

One juvenile specimen was collected from the light zone of PARA 1801.

Family Plectreuridae

Plectreurys sp.
Det. P. Paquin. Eisodophile.

We collected one specimen from a web within the twilight zone of PARA 2202.

Family Uloboridae

Uloborus sp.
Det. P. Paquin. Eisodophile.

One female specimen was collected from the light zone of PARA 1001.

Family Oecobiidae

Oecobius sp. Det. P. Paquin. Eisodophile.

One juvenile wall spider was collected from the twilight zone of PARA 2602.

Order Opiliones
Family Sclerosomatidae

Leiobunum townsendii Weed, 1893.
Det. W. Shear. Trogloxene.

We collected 3 specimens in the light zone of PARA 1801. In the twilight zones of both PARA 2204 and PARA 2202, several hundred individuals were observed within ceiling fissures. These individuals were denning close together in large masses. We suspect these opillionids den in fissures during the day, and exit to forage at night. This species was also observed throughout the length of PARA 1001.

Order Pseudoscorpiones
Family Chernetidae

Tuberochernes n. sp.
Det. M. Harvey. Troglophile?

We collected 3 specimens from the dark zone of PARA 1001. These specimens are with a taxonomist and will ultimately be described.

Subclass Acari

Acari species a.
Specimens misplaced by taxonomist. Unknown.

Two specimens were collected from the twilight zone of PARA 2602.

Acari species b.
Specimens misplaced by taxonomist. Unknown.

Two specimens were collected from the light zone of PARA 1801.

Class Entognatha
Subclass Collembola
Order Entomobryomorpha

Family Entomobryidae

Entomobrya zona Christiansen and Bellinger, 1980. Det. E. Bernard. Troglophile.

Specimens from this family were collected in the light ($n = 3$) and twilight ($n = 10$) zones of PARA 1801; the light ($n = 4$), twilight ($n = 1$), and dark ($n = 7$) zones of PARA 2602; and the light zone ($n = 4$) of PARA 2204. We observed this collembolan in the light zones of 3 caves and the twilight zones of 2 caves. We suggest this animal is a troglophile because (1) it was found throughout the lengths of 2 caves; (2) it is a largely nonvagile edaphic organism, and (3) collembolans are routinely found in caves.

Class Insecta
Order Coleoptera
Family Anobiidae

Undetermined species.
Det. C. Drost. Accidental.

We collected 3 specimens from the light zone of PARA 1801. Most members of the family of death watch or spider beetles occur in dry vegetation (Triplehorn and Johnson 2005). Members of this family are occasionally noted in caves where they may occur in packrat midden material.

Family Carabidae

Rhadine n. sp. (*Perlevis* species group).
Det. T. Barr. Troglophile.

A total of 6 specimens were collected, consisting of 3 males and one female from PARA 2204 and one male and one female from PARA 2202. These specimens represent an undescribed species (T. Barr, personal communication, 2007).

Family Bruchidae

Undetermined species.
Det. R. Delph. Accidental.

We collected 2 specimens from the light zone of PARA 1801. This seed-boring beetle was detected within the cave entrance but is not expected to use caves unless seeds are transported into the cave by aeolian currents.

Family Leiodidae

Undetermined species.
Det. J. Wynne. Troglophile?

Twelve specimens were collected from 2 Parashant caves. The specimens consist of one from the light zone of PARA 1001 and 10 from PARA 2204 (4 from the light zone and 6 from the twilight zone). This beetle species was observed denning in large numbers within the fissures in the twilight zone and in association with *Leiobunum townsendii.* Most leiodid beetles are habitat generalists and feed as both adults and larvae on certain fungi or microorganisms associated with decaying organic matter (e.g., Majka and Langor 2008). We suggest these beetles may have a commensal relationship with harvestmen (opilionid spiders) and may feed on fungi growing on spiders' feces. There is a literature, rich with examples of troglomorphic species, that confirms that leiodids use caves (e.g., Peck 1974, 1978). We suggest this morphospecies may be a troglophile.

Family Mordellidae

Undetermined species.
Det. R. Delph. Accidental.

Fifteen specimens were collected including 3 specimens from PARA 2602 (2 from the dark zone and one from the light zone) and 12 specimens from PARA 2204 (2 from the dark zone and 10 from the twilight zone). Mordellid larvae feed on decaying wood and vegetation, while adults feed on flowers (Triplehorn and Johnson 2005). Because both of these caves were dry and detritus deposition was low, we suggest this morphospecies is accidental.

Family Tenebrionidae

Eschatomoxys pholeter Thomas and Pape 2007 (new species). Troglophile.

This species was newly discovered and described through this research. This beetle was collected from the twilight zone of PARA 2602. Pape et al. (2007) considered this beetle a troglophile. Representing the fourth documented locality, this species was also collected in Rampart, Bat, and Christmas Tree Caves, Grand Canyon National Park (Pape et al. 2007).

Eleodes (*Caverneloedes*) *wynnei* Aalbu, Smith & Triplehorn 2012 (new species). Troglophile.

This species was newly discovered and described through this research. Three specimens were collected from the twilight zone of PARA 1801 and the light zone of PARA 1001. Also, we collected tenebrionid larvae within PARA 1801. All *Caverneleodes* species are considered troglophiles (Aalbu et al. 2012).

Order Diptera
Family Nycteribiidae (formerly known as Hippoboscidae)

Basilia antrozoi Townsend, 1893.
Det. C. Dick. Parasite.

One female specimen was removed and collected from a captured *Antrozous pallidus* at the entrance of PARA 0802.

Family Phoridae

Undetermined species.
Det. J. Wynne. Troglophile?

We collected 2 specimens from the dark zone of PARA 1001. This cave contains cricket guano and decaying vegetation. Adults of this species may be feeding on the fungus growing on these 2 nutrient sources.

Family Sciaridae

Undetermined species.
Det. J. Wynne. Troglophile?

We collected one specimen from the dark zone of PARA 1001. This cave contains cricket guano and decaying vegetation. Larvae of this morphospecies are likely feeding on the fungus growing on these 2 nutrient sources. Additionally, larvae of some of these sciarid species are known to be predaceous (Cole and Schlinger 1969, Triplehorn and Johnson 2005). No larvae were detected within PARA 1001.

Family Tipulidae

Tipula kaibabensis Alexander 1946.
Det. J. Gelhaus and C. Young. Trogloxene.

One specimen was photographed in the twilight zone of PARA 1001, and one was collected from PARA 0802. Tipulids use dark damp places for dens during the day (J. Gelhaus, personal communication, 2013). Peck (1981) and Reeves et al. (2000) considered Tipulids detected in caves in the SE United States to be trogloxenes.

Order Hemiptera
Family Reduviidae

Triatoma cf *rubida.*
Det. J. Wynne. Accidental.

We collected one specimen from the light zone of PARA 1001. Given that this species is sanguinivorous and that we didn't observe any vertebrates within this cave, we suggest the occurrence is accidental.

Order Hymenoptera
Family Formicidae

Note: All ant morphospecies were detected within cave entrances and in only association with baited pitfall traps. We consider all of these ants to be accidental.

Solenopsis xyloni McCook, 1879.
Det. R. Johnson. Accidental.

Five specimens were collected from the entrance of PARA 2602.

Pheidole vistana Forel, 1914.
Det. R. Johnson. Accidental.

We collected 3 specimens from the entrance of PARA 2602.

Paratrechina cf *hystrix.*
Det. R. Johnson. Accidental.

We collected 2 specimens from the entrance of PARA 1801. R. Johnson (personal communication, 2006) suggests it may be *P. hystrix.* If so, this record is the first for Arizona (R. Johnson, personal communication, 2006). *Paratrechina hystrix* is a northern species known to occur in Nevada and Utah. R. Johnson (personal communication, 2006) suggests the specimens match the description in part; however, because we did not collect any workers, a reliable identification is not possible.

Pheidole sp.
Det. R. Johnson. Accidental.

One specimen was collected from the entrance of PARA 2204. R. Johnson indicated the specimen was a single minor worker. Minors are often difficult to identify to species, and the specimen was not examined further (R. Johnson, personal communication, 2006).

Order Orthoptera
Family Rhaphidophoridae

cf *Ceuthophilus* n. gen. n. sp.
Det. T. Cohn and A. Swanson.
Trogloxene.

Nine specimens (8 females and one male) were collected from the light and twilight zone of PARA 1001. T. Cohn (personal communication, 2006) indicated that this new genus has clasping cerci with unique short spines on their base, a subgenital plate that matches no other specimens in his collection, and a distinctive last tergite.

Ceuthophilus n. sp.
Det. T. Cohn.
Trogloxene.

One male was collected from the twilight zone of PARA 2204. T. Cohn (personal communication, 2006) suggests that the structures on this specimen are unique and that the specimen represents an undescribed species.

Ceuthophilus n. sp. a?
Det. T. Cohn. Undescribed?
Trogloxene.

We collected one female from the entrance of PARA 1801. Although we will require adult males for confirmation, T. Cohn (personal communication, 2006) indicated that the female has distinctive characters and may be undescribed.

Ceuthophilus n. sp. b?
Det. T. Cohn. Undescribed?
Trogloxene.

Another female was collected from the entrance of PARA 1801. T. Cohn (personal communication, 2006) indicated that the female has an "extraordinarily elongate and curved ovipositor" and is distinctive and may be undescribed. Male specimens will be required to confirm this.

Undetermined *Ceuthophilus* sp.
Det. T. Cohn.
Trogloxene.

There was at least one undetermined immature female *Ceuthophilus* species collected in PARA 1401. Because the specimen was an immature, it was not possible to identify it beyond genus. However, it may also represent a new species (T. Cohn, personal communication, 2006).

Order Psocoptera
Family Sphaeropsocidae

Troglosphaeropsocus voylesi Mockford 2009
(new genus and species).
Det. E. Mockford. Unknown.

This animal represents both a new genus and species discovered through this research. We collected one specimen from the twilight zone of PARA 2602 (located in the Mojave Desert). The cave is dry and dusty with little to no aeolian-deposited detritus; however, it is used as a summer roost by *Antrozous pallidus*. Until we have additional information on this psocid's occurrence within caves, we consider its cave affiliation to be unknown.

Family Psyllipsocidae

Psyllipsocus ramburii Sélys-Longchamps, 1872. Det. E. Mockford. Troglophile.

This species was trapped in the light, twilight, and dark zones of PARA 1801 and the dark zone of PARA 2602. Because psocids are routinely found living in caves, we suggest it is a troglophile.

Family Prionoglarididae

Speleketor flocki Gurney, 1943.
Det. E. Mockford. Troglophile.

We collected a nymph of this species from the dark zone of PARA 2602. E. Mockford (personal communication, 2006) indicated that although the specimen was a nymph, its head markings are unmistakable. This specimen represents the third locality for this species in the western United States. It has been confirmed from a cave in the Tucson Mountains and Gypsum Cave, southeastern Nevada.

This psocid routinely lives in caves, and because a nymph was found in the dark zone of this cave, we suggest it is probably a troglophile.

Order Siphonaptera

Undetermined family, genus, and species.
Det. J. Wynne. Parasite.

One specimen was collected from the dark zone of PARA 2602. This cave supports a possible maternity roost for *Antrozous pallidus*, which is likely the host of this siphonapteran and explains its occurrence.

Subclass Apterygota
Order Thysanura
Family Lepidotrichidae

Undetermined species.
Det. J. Wynne. Eisodophile.

We trapped one silverfish within the entrance of PARA 2602.

Phylum Chordata
Class Mammalia
Order Chiroptera
Family Vespertilionidae

Myotis sp.
Det. J. Wynne. Trogloxene.

Approximately 3 *Myotis* sp. were observed during exit counts at PARA 1401. According to Arizona Game and Fish Department's (AGFD) Heritage Data Management System, this observation is likely either *M. thyasanodes* or *M. yumanensis.* Only *M. yumanensis* is known to roost both in caves and human-made structures (AGFD 2003a, 2003b). Williams et al. (2006) suggest this species is commonly found near small- to moderately sized bodies of water, and of the 4 habitat types investigated, this species occurs in riparian woodland more than in all other habitats combined. Though there are 2 water tanks within 3 miles of PARA 1401, these tanks are intermittent water sources. We suggest the best candidate water source is probably Imlay Reservoir, approximately 8.85 km from the cave.

Myotis thysanodes Miller 1897. Fringed myotis. Det. J. Wynne. Trogloxene.

One nonreproductive female was captured in a harp trap at the entrance of PARA 1801. We estimated roost size between 20 and 30 individuals. We suggest PARA 1801 may be a maternity roost. This bat roosts in caves, mines, and buildings (O'Farrell and Studier 1980).

Antrozous pallidus Allen, 1862. Pallid bat.
Det. J. Wynne. Trogloxene.

Pallid bats were identified in PARA 2602, PARA 0802, and possibly PARA 2202. Two individuals (one adult female and one nonscrotal male) were captured and identified in a handheld net in PARA 2602. During our survey in August 2005, we observed ~100 individuals roosting in the boulder breakdown at the entrance of PARA 2602. At PARA 0802, we used a combined mist-netting/harp-trapping approach to capture 7 individuals (2 postlactating adult females, one nonreproductive juvenile female, 2 nonreproductive undetermined females, one nonscrotal juvenile male, and one nonreproductive adult female). This roost contained ~50 individuals and was located in the rock fissures in the ceiling within the cave's light zone. In PARA 2202, we observed a bat flying in the twilight zone whose pelage was consistent with *A. pallidus.* Although we did not confirm it was a pallid bat, the observation likely represented this species. While pallid bats are found roosting in caves, a majority of data suggest they roost primarily in rock crevices and outcrops (Hermanson and O'Shea 1983).

Corynorhinus townsendii Cooper 1837.
Townsend's big-eared bat.
Det. J. Wynne. Trogloxene.

Nine individuals were observed hibernating in the twilight zone of PARA 1401. This was the only documented hibernaculum on the Grand Canyon–Parashant National Monument. Lepidopteran wings were also observed within the entrance of PARA 2602 and PARA 0802, suggesting night use by this species of bat. *Corynorhinus townsendii* is a cave-roosting bat, but it also roosts in mines and buildings (Kunz and Martin 1982).

Order Rodentia
Family Cricetidae

Neotoma sp. Packrat or woodrat.
Det. J. Wynne and K. Voyles. Troglophile.

Midden activity was documented in the entrances and into the light zones of PARA 2202, PARA 2602, PARA 2204, and PARA 0802. Woodrats use cave entrances rock outcrops, rock fissures, and other suitable features for establishing dens.

Family Erythizontidae

Erethizon dorsatum Cuvier 1822. North American porcupine.
Det. J. Wynne. Eisodoxene.

Both PARA 1001 and PARA 1401 have been used extensively by porcupine. In PARA 1001, guano deposition of 2–10 cm was observed

throughout the cave; however, there were no signs of recent porcupine use. A fully articulated porcupine skeleton was photographed amid a deep deposition of guano in PARA 1401. Though the North American porcupine dens in caves, it also will den in other features offering similar microhabitats (e.g., hollow logs and trees). Strong (2006) indicates that this species is commonly documented in caves in the Chihuahuan Desert, New Mexico.

Order Lagomorpha
Family Leporidae

Lepus californicus Gray 1837. Black-tailed jackrabbit. Det. J. Wynne. Accidental.

A black-tailed jackrabbit skeleton was found approximately 5 m from the entrance of PARA 1001. This animal likely fell into the cave, became trapped, and eventually died. The carcass provided a pulsed food resource for scavenging cavernicoles.

Class Aves
Order Strigiformes

Undetermined family, genus and species. Det. K. Voyles and J. Wynne. Eisodoxene.

We documented owl pellets within the twilight zone of PARA 2202. Owls routinely roost in cave entrances and other suitable habitats both during the day, and also during the night between hunting outings.

DISCUSSION

This study represents the first regional all-taxa biological inventory of caves in the southwestern United States. Our study resulted in discovery of at least 2 new genera, 6 new species, and 3 potential new species (which will be described in future publications), as well as 2 range extensions and one possible range extension of arthropods. Additionally, we identified 5 bat roosts and cave use by several other vertebrates. Though our study has contributed significantly to the natural history of the region, cave biological research within Parashant remains incomplete.

Two of the most morphospecies-rich caves, PARA 1801 (14 morphospecies) and PARA 2602 (13 morphospecies), supported a largely epigean arthropod community. Both caves contained roosting bats, which provided nutrients via guano. PARA 1001 (11 morphospecies) contained water condensation on the ceiling and walls and supported the largest known cricket den in Arizona (likely on the order of thousands of individuals). Such a large number of crickets generate a significant nutrient load in the form of cricket eggs, nymphs, and guano. The ecological importance of cave crickets has been widely documented (e.g., Barr 1967, Howarth 1983, Taylor 2003, Culver 2005, Poulson 2005), and we suggest that the presence of crickets was why this cave supported a higher arthopod diversity. Additionally, given the significant nutrient loading provided by crickets and the presence of a cave deep zone, PARA 1001 may also support cave-adapted arthropods.

No troglomorphic taxa were identified during this survey. Detections of cave-adapted taxa are reportedly low for northwestern Arizona. However, there are cave-adapted taxa known regionally. For example, 3 troglobites and one stygobite are known from Grand Canyon National Park (Wynne et al. 2007), and a cave-limited millipede (Shear et al. 2009) and a cave-adapted copepod have been collected from the BLM–Arizona Strip lands adjacent to Parashant (J. Wynne unpublished data).

Concerning more regional patterns, we identified at least 18 arthropods with strong cave affinities (e.g., trogloxenes or troglophiles) and 21 accidentals or eisodophiles from 7 caves. Given the arid conditions of the desert Southwest, we suggest that few ground-dwelling arthropods in the Southwest are genetically predisposed to colonizing the often more mesic cave environment. Barr (1968) suggests that most troglobites were preadapted to the cave environment in that they previously inhabited similar mesic habitats such as leaf litter, moss, or deep soils. By extension, given that these more mesic habitats are nonexistent in the Mojave Desert and juniper shrublands within the study area, a contemporary preadapted pool of cave colonists seems to be lacking, and thus may be reflected by the low number of ground-dwelling cavernicoles observed.

Similarly, Peck (1978, 1980) suggests that the low numbers of cave-adapted taxa in southwestern U.S. caves may be due to the low nutrient input and high aridity associated with southwestern cave systems. At Wupatki National Monument, Welbourn (1976) indicated

that moisture was the most limiting abiotic factor in the earth cracks he sampled. While not completely excluding the likelihood that troglomorphic arthropod diversity will be low in northern Arizona, Wynne et al. (2007) suggested that the low numbers of cave-adapted taxa in Grand Canyon caves may reflect limited sampling effort and perhaps inappropriate techniques for detecting cave-adapted taxa.

While troglomorphic taxa in the Southwest may be depauperate in comparison to cave-obligate communities in the mesic central and eastern portions of the United States, we maintain that sampling effort and ineffective sampling techniques may still explain the lack of troglomorphic taxa detected in Parashant caves.

For future work, we recommend a multiyear systematic study design, including an increased number of sampling stations per cave for timed searches and baited pitfall trapping (see Wynne 2013), as well as direct intuitive searches and bait stations (provisioned with chicken liver, mushrooms, blue cheese, and sweet potato) within deep cave zones (e.g., Howarth et al. 2007). This approach would (a) provide us with a more thorough inventory of cave-dwelling arthropods, (b) provide for inferential statistical comparisons across sites, and (c) increase the likelihood of detecting cave-adapted organisms. Secondly, we suggest that sample size (i.e., the number of caves inventoried) may also be an issue. We provide the results from only 7 caves within Parashant. In the adjacent BLM–Arizona Strip lands and Grand Canyon National Park lands, there are approximately 250 and >400 known caves, respectively. As we expand our efforts into other management units in Arizona and obtain a larger sample of study sites, we hypothesize that more troglomorphic taxa will be discovered. Only through increased sampling effort and use of systematic techniques will we be able to make ecological comparisons to other regions in the southwestern United States and infer whether the American Southwest truly supports low troglomorphic diversity.

Management Implications

Through this research, we tentatively identified one cave as a high management priority because of the presence of cave-dwelling arthropods. PARA 1001 supports the only known type localities for the new cricket genus, cf *Ceuthophilus* n. gen. n. sp. Though this genus may occur elsewhere on and off Grand Canyon–Parashant National Monument, this has not been confirmed. To increase our knowledge of the current population and to better define its range, we recommend (1) conducting a multiyear census of the population during the most productive time of year—between the late monsoonal season and the early post-monsoonal season (mid-August to mid-September); (2) sampling additional caves within Parashant to search for this animal; and (3) conducting surface surveys in the region to estimate the actual geographic distribution of this new cricket. Additionally, we know of only one other cave in Arizona that supports such a large cricket population. Because cave crickets contribute important nutrients via guano, eggs, nymphs, and cricket carcasses and are a prey source for predaceous arthropods (e.g., Barr 1967, Howarth 1983, Taylor 2003, Culver 2005, Poulson 2005), the cricket population is likely an important component of this ecosystem. Given the population size within PARA 1001, we suggest that the presence of crickets likely has an important bottom-up effect on ecological structure and species richness and also suggest that the actual number of species will be higher than the observed richness presented in this study.

We recommend that all caves containing both summer roosts and hibernacula (PARA 0802, PARA 1401, PARA 1801, and PARA 2602) be closed to recreational use until these sites can be thoroughly studied and their functions determined. There is little argument that human disturbance to bat roosts is detrimental (e.g., Humphrey 1969, Mohr 1972, McCracken 1988, 1989, Harnish 1992, Brown et al. 1993, Boyles and Brack 2009). Additionally, there is a growing threat of white-nose syndrome (WNS), a disease caused by *Pseudogymnoascus destructans* (refer to Minnis and Lindner 2013), which will likely spread through the western United States. This psychrophilic fungus has resulted in the "most precipitous decline of North American wildlife in the past century" (BCI 2010). Furthermore, WNS has resulted in the mortality of over 7 million bats and has been detected in 23 states and 5 Canadian provinces (Wynne 2014).

Little is known concerning the habitat characteristics of bat hibernacula in the American Southwest. In Arizona alone, we lack baseline

information regarding the locations of cave-roosting hibernating bats (A. McIntire, Arizona Game and Fish, personal communication, 2010). Thus, resource managers can best prepare for the westward advance of WNS by intesifying their efforts to establish population estimates of nonmigratory cave-roosting bats and characterize habitat of cave roosts in the western United States.

To improve our knowledge regarding bat distributions in northwestern Arizona, we recommend the following: (1) additional surveys of summer roosts (at PARA 0802, PARA 1801, and PARA 2602) during the middle of the nursery period (mid- to late June) to determine whether these roosts are actually maternity/nursery sites; (2) establishment of annual or biennial winter bat censuses of the hibernaculum cave (PARA 1401); and (3) expanded searches to identify additional cave roosts, with follow-up inventories, roost monitoring, and habitat characterization as appropriate.

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LITERATURE CITED

AALBU, R.L., A.D. SMITH, AND C.A. TRIPLEHORN. 2012. A revision of the *Eleodes* (subgenus *Caverneleodes*) with new species and notes on cave breeding *Eleodes* (Tenebrionidae: Amphidorini). Annales Zoologica 62: 199–216.

[AGFD] ARIZONA GAME AND FISH DEPARTEMENT. 2003. *Myotis yumanensis.* Unpublished abstract compiled and edited by the Heritage Data Management System. AGFD, Phoenix, AZ. 5 pp.

BAIN, J. 1986. Winter roosts of Townsend's big eared bat *Plecotus townsendii* (Vespertilionidae) in Wupatki National Monument and vicinity, Arizona. Unpublished report to National Park Service, Wupatki National Monument, Flagstaff, AZ. 18 pp.

BARR, T.C., JR. 1967. Observations on the ecology of caves. American Naturalist 101:475–491.

_____. 1968. Cave ecology and evolution of troglobites. Pages 35–102 *in* T. Dobzhansky, M. Hecht, and W. Steere, editor, Evolutionary Biology. Volume 2. Appleton-Century-Crofts, New York, NY.

[BCI] BAT CONSERVATION INTERNATIONAL. 2010. White nose syndrome: a crisis for America's bats, BATFAQ. BCI, Austin, TX. Available from: http://www.batcon.org/pdfs/whitenose/WNSFACTSSHEET_Mar15_2010.pdf

BODENHAMER, H. 1989. Impacts to caves within Grand Canyon National Park, preliminary observations and research proposal. Unpublished report to National Park Service, Grand Canyon National Park, Grand Canyon, AZ. 100 pp.

BOYLES, J.G., AND V. BRACK JR. 2009. Modeling survival rates of hibernating mammals with individual-based models of energy expenditure. Journal of Mammalogy 90:9–16.

BROWN, P., R. BERRY, AND C. BROWN. 1993. Bats and mines: finding solutions. Bats 11:12–13.

COLE, F.R., AND E.I. SCHLINGER. 1969. The flies of western North America. University of California Press, Berkeley, CA. xi + 693 pp.

CORNELY, J., AND R. BAKER. 1986. *Neotoma mexicana.* Mammalian Species 262:1–7.

CULVER, D.C. 2005. Species interactions. Pages 539–543 *in* D.C. Culver and W.B. White, editors, Encyclopedia of caves. Elsevier, Burlington, MA.

DROST, C.A., AND D.W. BLINN. 1998. Invertebrate community of Roaring Springs Cave, Grand Canyon National Park, Arizona. Southwestern Naturalist 42: 497–500.

GUSTAFSON, T.A. 1964. The bats of Wupatki National Monument, Coconino County, Arizona. Unpublished report on file with National Park Service, Wupatki National Monument, Flagstaff, AZ. 12 pp.

HARNISH, H. 1992. Protecting the bats of Devil's Den: when endangered bats needed special protection from disturbance, a cave alarm system provided an effective and creative solution. Bats 10:13–18.

HERMANSON, J.W., AND T.J. O'SHEA. 1983. *Antrozous pallidus.* Mammalian Species 213:1–8.

HILL, C.A., V.J. POLYAK, D.C. BUECHER, R.H. BUECHER, AND C.G. GRAF. 2001. Trip report: Bat Cave, Grand Canyon National Park, Arizona, June 11, 2001. Unpublished report on file with National Park Service, Grand Canyon National Park, Grand Canyon, AZ. 48 pp.

HILL, C.A., V.J. POLYAK, D.C. BUECHER, R.H. BUECHER, AND P.P. PROVENCIO. 2000. Trip report: Tse'an Kaetan (Cave of Prayer Sticks), Grand Canyon National Park, Arizona, February 11, 2000. Unpublished report on file with National Park Service, Grand Canyon National Park, Grand Canyon, AZ. 46 pp.

HOWARTH, F.G. 1980. The zoogeography of specialized cave animals: a bioclimatic model. Evolution 34: 394–406.

_____. 1982. Bioclimatic and geological factors governing the evolution and distribution of Hawaiian cave insects. Entomologia Generalis 8:1–26.

_____. 1983. Ecology of cave arthropods. Annual Review of Entomology 28:365–389.

HOWARTH, F.G., S.A. JAMES, W. MCDOWELL, D.J. PRESTON, AND C.T. IMADA. 2007. Identification of roots in

lava tube caves using molecular techniques: implications for conservation of cave arthropod faunas. Journal of Insect Conservation 11:251–261.

HUMPHREY, S. 1969. Status, winter habitat, and management of the endangered Indiana bat, *Myotis sodalis.* Florida Scientist 41:65–76.

JONES, C., AND N. HILDRETH. 1989. *Neotoma stephensi.* Mammalian Species 328:1–3.

KUNZ, T. 1982. The ecology of bats. Plenum Press, New York, NY. 425 pp.

KUNZ, T.C., AND R.A. MARTIN. 1982. *Plecotus townsendii.* Mammalian Species 175:1–6.

LOPEZ-GONZALEZ, C. 2005. Use of abandoned mines by a community of temperate bats in Durango, Mexico. Acta Chiropterologica 7:285–292.

MACÊDO, R., AND M. MARES. 1988. *Neotoma albigula.* Mammalian Species 310:1–7.

MAJKA, C.G., AND D. LANGOR. 2008. The Leiodidae (Coleoptera) of Atlantic Canada: new records, faunal composition and zoogeography. Zookeys 2:357–402.

MCCRACKEN, G. 1988. Who's endangered and what can we do? Bats 6:5–9.

_____. 1989. Cave conservation: special problems of bats. National Speleological Society Bulletin 51:49–51.

MINNIS, A.M., AND D.L. LINDNER. 2013. Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans,* comb. nov., in bat hibernacula of eastern North America. Fungal Biology 117:638–649.

MOCKFORD, E.L. 2009. Systematics of North American species of Sphaeropsocidae (Psocoptera). Proceedings of the Entomological Society of Washington 11:666–685.

MOHR, C. 1972. The status of threatened species of cave-dwelling bats. National Speleological Society Bulletin 34:33–47.

MUCHMORE, W. 1981. Cavernicolous species of *Larca, Archeolarca* and *Pseudogarypus* with notes on the genera (Pseudoscorpionida, Garypidae and Pseudogarypidae). Journal of Arachnology 9:47–60.

O'FARRELL, M.J., AND E.H. STUDIER. 1980. *Myotis thysanodes.* Mammalian Species 137:1–5.

PAPE, R.B. 1998. Bat Cave, Grand Canyon National Park: baseline biological inventory, final report, May 1998. Unpublished report on file with National Park Service, Grand Canyon National Park, Grand Canyon, AZ.

PAPE, R.B., D.B. THOMAS, AND R.L. AALBU. 2007. A revision of the genus *Eschatomoxys* Blaisdell (Tenebrionidae: Pimeliinae: *Edrotini*) with notes on the biology. Coleopterists Bulletin 61:519–540.

PECK, S.B. 1974. Biology of the Idaho lava tube beetle, *Glacicavicola.* National Speleological Society Bulletin 36:1–3.

_____. 1978. New montane *Ptomaphagus* beetles from New Mexico and zoography of southwestern caves (Coleoptera; Leiodidae; Catopinae). Southwestern Naturalist 23:227–238.

_____. 1980. Climatic change and the evolution of cave invertebrates in the Grand Canyon, Arizona. National Speleological Society Bulletin 42:53–60.

_____. 1981. The invertebrate fauna of the caves of the Uinta Mountains, northeastern Utah. Great Basin Naturalist 41:207–212.

_____. 1982. Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. Great Basin Naturalist 42:405–412.

POULSON, T.L. 2005. Food sources. Pages 255–264 *in* D.C. Culver and W.B. White, editors, Encyclopedia of caves. Elsevier, Burlington, MA.

POULSON, T.L., AND D.C. CULVER. 1969. Diversity of terrestrial cave communities. Ecology 50:153–158.

REEVES, W.K., J.B. JENSEN, AND J.C. OZIER. 2000. New faunal and fungal records from caves in Georgia, USA. Journal of Cave and Karst Studies 62:169–179.

SAMPLE, B.E., AND R.C. WHITMORE. 1993. Food habits of the endangered Virginia big-eared bat in West Virginia. Journal of Mammalogy 74:428–435.

SHEAR, W., S. TAYLOR, J. WYNNE, AND J. KREJCA. 2009. Cave millipeds of the United States. VIII. New genera and species of polydesmidan millipeds from caves in the southwestern United States (Diplopoda, Polydesmida, Polydesmidae and Macrosternodesmidae). Zootaxa 2151:47–65.

STRONG, T.S. 2006. Vertebrate species use of cave resources in the Carlsbad Caverns region of the Chihuahuan Desert. Pages 270–276 *in* D. Harmon, editor, People, places, and parks: proceedings of the 2005 George Wright Society Conference on Parks, Protected Areas, and Cultural Sites. The George Wright Society, Hancock, MI.

TAYLOR, S.J. 2003. America, North: biospeleology. Pages 45–49 *in* J. Gunn, editor, Encyclopedia of caves and karst science. Fitzroy Dearborn, New York, NY.

TRIPLEHORN, C.A., AND N.F. JOHNSON. 2005. Borror and Delong's introduction to the study of insects. Cengage Learning. 888 pp.

WELBOURN, W.C. 1976. Preliminary report on the fauna of the earth cracks. Pages 32–41 *in* Wupatki National Monument Earth Cracks. Cave Research Foundation, Yellow Springs, OH.

_____. 1978. Preliminary report on the cave fauna. Pages 36–41 *in* Cave Research Foundation, editors, Cave resources of Horseshoe Mesa, Grand Canyon National Park. Unpublished report on file with National Park Service, Grand Canyon National Park, Grand Canyon, AZ. 71 pp.

WINKLER, W., AND D. ADAMS. 1972. Utilization of southwestern bat caves by terrestrial carnivores. American Midland Naturalist 87:191–200.

WOODS, C.A. 1973. *Erethizon dorsatum.* Mammalian Species 29:1–6.

WYNNE, J.J. 2013. Inventory, conservation, and management of lava tube caves at El Malpais National Monument, New Mexico. Park Science 30:45–55.

_____. 2014. The reign of the Red Queen: the future of bats hangs in the balance. The Explorers Journal 92:40–45.

WYNNE, J.J., C.A. DROST, N.S. COBB, AND J.R. RIHS. 2007. Cave-dwelling invertebrate fauna of Grand Canyon National Park, Arizona. Pages 235–246 *in* C. van Riper and M. Sogge, editors, Proceedings of the 8th Biennial Conference of Research on the Colorado Plateau. University of Arizona Press, Tucson, AZ. 33 pp.

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