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Quantifying meso-mammal cave use in central Texas

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Knowledge of meso-mammal cave use is essential for natural resource managers, particularly in the management of endangered cave invertebrates. Scat left by meso-mammals represents significant nutrient inputs into the oligotrophic cave environment which can disrupt the invertebrate species composition and ecology. Since little is known about what constitutes typical timing or frequency of meso-mammal visitation, current management practices are largely speculative. Central Texas caves were historically associated with raccoons *Procyon lotor*, but with the loss of large predators and encroachment of woody vegetation, the now naturalized North American porcupine *Erethizon dorsatum* has become an established part of the local ecosystems whose effect on cave biology remains unknown. Our objective with this study was to quantify meso-mammal cave use according to seasons, time of day, weather conditions, as well ecological and physical cave characteristics. We monitored 30 caves by placing trail cameras at cave entrances for one year on Joint Base San Antonio-Camp Bullis military base just north of San Antonio, Texas. North American porcupines, raccoons, and Virginia opossums *Didelphis virginiana* were the three most commonly photographed meso-mammals (>87%). All meso-mammal groups showed significantly different cave use according to season, weather, and cave characteristics. Data suggested most meso-mammals were using caves for denning while raccoons and Virginia opossums also were feeding on resident invertebrate and rodent populations. In particular, Virginia opossum and raccoon, both potential predators of endangered species, showed greater use of caves containing endangered species. The results from our study represent an initial step in understanding meso-mammal cave use in central Texas.

Meso-mammal cave use is an important, but relatively little-studied aspect of cave ecology. Caves are found in many parts of Texas, but the caves located north of San Antonio on the Joint Base San Antonio-Camp Bullis military base (hereafter Camp Bullis) are particularly significant because approximately 20% are inhabited by three federally-listed endangered invertebrates (*Cicurina madla, Rhadine exilis, Rhadine infernalis*). Cave biologists have long noted extensive cave use by meso-mammals including North American porcupines *Erethizon dorsatum*, raccoons *Procyon lotor*, and ringtails *Bassariscus asstutus*, but little is known about the frequency or motivations of their visits. Studies (Woods 1973, Roze 1987, 2009, Griesemer et al. 1998, Morin et al. 2005) have shown that North American porcupines use caves and rocky outcrops for denning. Raccoons are known to use caves for hunting (Winkler and Adams 1972, Elliott and Ashley 2005, Moseley et al. 2013) and as a year-round dens (Moseley et al. 2013). Less information is available on the behaviors of Virginia opossums *Didelphis virginiana* in caves though they are known to feed on bats (Winkler and Adams 1972, Martin et al. 2003) and likely use caves as dens (Elbroch and Rinehart 2011). Unfortunately, the available information on meso-mammal cave use generally focuses on single caves or seasons, or consists of observations made secondarily to other research questions. Focusing only on single caves or unexpected observations draws an incomplete picture of the ecosystem, and basing management decisions on these results can lead to speculative and potentially misleading conclusions.

Determining typical levels of meso-mammal cave use is especially critical because scat left by meso-mammals such as North American porcupines (Calder and Bleakney 1965, Peck 1988) and raccoons (Elliott and Ashley 2005, Moseley et al. 2013) represents significant nutrient inputs into the oligotrophic cave environment. If a cave's total nutrient input is too small, cave-obligate species have no resources; too much, and the cave-adapted species are replaced by more competitive or predatory terrestrial species (Gary 2009). Monitoring meso-mammal nutrient inputs is especially significant for Texas caves because of the recent range expansion and naturalization of North American porcupines in Texas (Bailey 1905, Ilse and Hellgren 2001). North American porcupine scat, previously absent from the

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ecosystem, is now abundant in many of Camp Bullis' caves (C. Thibodeaux pers. comm.).

A more complete understanding of caves also is essential because of their potential to impact the growth and development of neighboring human communities. In San Antonio, Texas, for example, a 15 million USD highway expansion project was recently delayed during construction of a highway underpass after the federally endangered Bracken Bat Cave meshweaver *Cicurina venii* was detected for the first time in more than three decades (Davila 2012). After the species was confirmed, construction plans for the underpass had to be modified to an overpass, nearly tripling the cost to 44 million USD (Degollado 2014).

Our goal with this study was to determine meso-mammal cave use across a variety of caves and over the course of a year. Specifically, our objectives were to: 1) identify meso-mammal species that use central Texas caves, and 2) analyze visitation according to temporal variation, weather, and cave characteristics.

Study area

We performed this study on Camp Bullis military base (11 286 ha) just north of San Antonio at the intersection of the Edward's Plateau, south Texas Plains and the Blackland Prairie ecoregions of Texas (Gould 1975). We randomly selected 30 caves from 100 available (Supplementary material Appendix 1 Fig. A1, Table A1). We defined a cave as any naturally-formed, humanly-accessible cavity that was at least 5 m in depth and/or length, and where no dimension of the entrance exceeds the length or depth (Gary 2009). The selected caves varied in length from 3 – 235 m ($\bar{x}=44$ m) and in depth from 1.2 – 46 m ($\bar{x}=13$ m). Twenty-three percent of caves had steel gates. Gates were constructed for particular Camp Bullis caves to prevent unauthorized use and protect resources (Gary 2009). Forty three percent of caves had at least one federally endangered invertebrate species, 60% were in the Edwards aquifer recharge zone, and 13% had permanent water features. Cannonball Cave contained a sump (a cave passage that descends below flowing or standing water), Darling's Pumpkin Hole and Stealth caves had streams, and Vera Cruz Shaft cave had a small seep (a trickle of spring water moving towards the surface). Eighty three percent of caves had structural modifications including excavated or enlarged entrances, excavated passages, or removed debris. Forty three percent of caves had previous records of meso-mammal signs (e.g. tracks, feces, skeletons) or direct sightings (Gary 2009). Eighty three percent of caves were in forested cover where trees form at least 25% of the canopy cover. Ten percent of caves were in natural herbaceous cover where the majority of ground cover was native or naturalized herbaceous vegetation. The remaining 7% of caves were in mixed shrub cover where vegetative cover was dominated by both trees and shrubs, but neither had more than 75% of the canopy cover (Supplementary material Appendix 1 Table A1, USGS 2001, Gary 2009).

Methods

We monitored caves with Cuddeback Attack IR (Cuddeback Digital, De Pere, WI) and Browning Range Ops (Browning Trail Cameras, Birmingham, AL) infrared game cameras which we placed at cave entrances and set with a 30-s delay. We split caves into two groups of 15 (group A and group B). We monitored group A for two weeks after which we retrieved cameras, downloaded data, checked batteries, and then re-deployed cameras for two weeks at the caves of group B. We continued this schedule so that at least four weeks of data were collected at each cave for each season. Seasons were defined according to the month: winter included December, January, and February; spring included March, April and May; summer included June, July and August; fall included September, October and November. We mounted cameras near the cave entrance in a manner that allowed the photograph to capture the entirety of the cave entrance while tilted slightly up to minimize the triggers from mice *Mus* spp. and rats *Rattus* spp.

We examined the photographs for the presence of meso-mammals, defined for this study as any mammal at least as large as a cottontail rabbit *Sylvilagus* spp. (approximately 1.0 kg) to the size of a North American porcupine (approximatley 15.0 kg; Hoffman et al. 2010). For each photograph with a meso-mammal, we noted the location, date, season, species, time of day, hourly temperature and hourly percent humidity. We collected weather data from weather stations located on Camp Bullis using Onset Hobo U30 data loggers and Onset temperature and humidity sensors (Onset Computer Corp., Bourne, MA).

We analyzed data by first reporting descriptive statistics for the total number of photographs taken, as well as the number of each meso-mammal species at each cave. We grouped photographs by species: North American porcupines, raccoons, Virginia opossums (the three most common meso-mammals), and other meso-mammals (all other species; e.g. ringtail, bobcat *Lynx rufus*, striped skunk *Mephitis mephitis*, eastern cottontail *Sylvilagus floridanus*, gray fox *Urocyon cinereoargenteus*, nine-banded armadillo *Dasypus novemcinctus*). We summarized each group's cave use according to season, hour, temperature, relative humidity, and cave characteristics (i.e. presence of endangered species, water source, gates, entrance type, US Geological Survey designated cover type) and then tested for significant differences with χ^2 goodness of fit test or Kruskal–Wallis χ^2-tests.

Results

Species assemblage

We deployed cameras from February 2014 – March 2015 capturing a total of 27 852 photographs ($\bar{x}=928.4$/cave, CI = 594.1–1262.7) including 4516 photographs of meso-mammals (16.2%). North American porcupines were the most common meso-mammal at 64% ($\bar{x}=96.9$/cave, n = 2906, CI = 27.1–166.7 / cave), followed by raccoons at 14% ($\bar{x}=20.6$ / cave, n = 619, CI = 7.5–33.7), and Virginia opossums at 10% ($\bar{x}=14.4$/cave, N = 431, CI = 1.0–27.7). Less commonly photographed meso-mammals included nine-banded armadillos (n = 95), ringtails (n = 174), bobcats (n = 43), eastern cottontails (n = 27), striped skunks (n = 19) and gray foxes (n = 2; Supplementary material Appendix 1 Table A1). Though not specifically investigated for this

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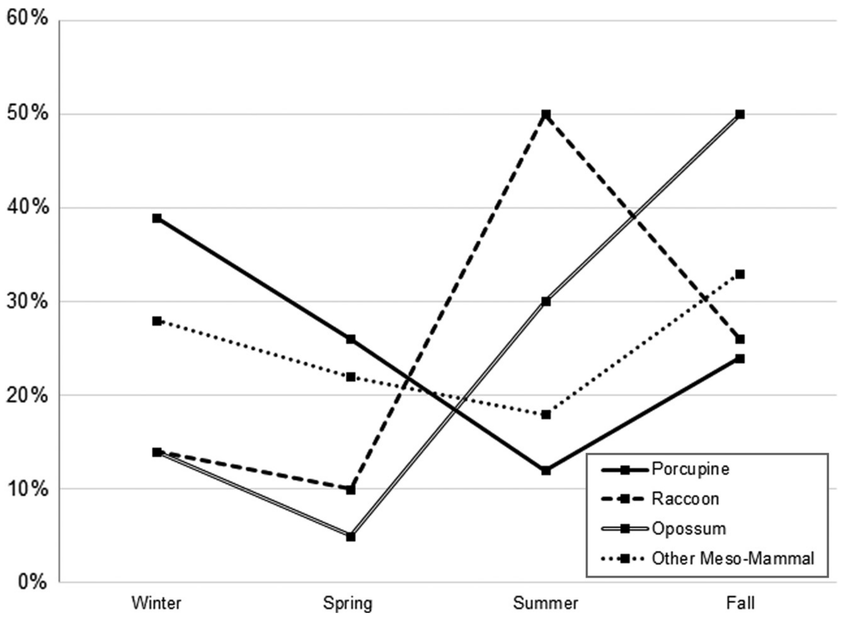

Figure 1. Annual percent use of Camp Bullis caves by North American porcupines, raccoons, Virginia opossums, and all other meso-mammals according to season on Camp Bullis, near San Antonio, Texas for the period of 01 February 2014 – 31 March 2015.

project, cave entrance photographs most frequently captured mice and rats (n = 8409) and vultures (n = 2668).

Temporal variation

North American porcupines were most photographed in winter, raccoons in summer, Virginia opossums in fall, and all other meso-mammal species in fall (Fig. 1). There was a significant difference ($\chi^2 = 703.0$, $p < 0.01$) between meso-mammal species and cave use by season.

The distribution of meso-mammal hourly cave entrance activity showed a bimodal distribution peaking at approximately 06:00 and 20:00 with the least movement during daylight between 07:00 and 17:00. North American porcupines and raccoons were crepuscular displaying most activity from 06:00 to 08:00 and 18:00 to 22:00 whereas Virginia opossums were most active during the night from 03:00 to 06:00 and 19:00 to 23:00 (Fig. 2). There was a significant difference ($\chi^2 = 104.2$, $p < 0.01$) between meso-mammal species and the hour on which they enter or leave the caves.

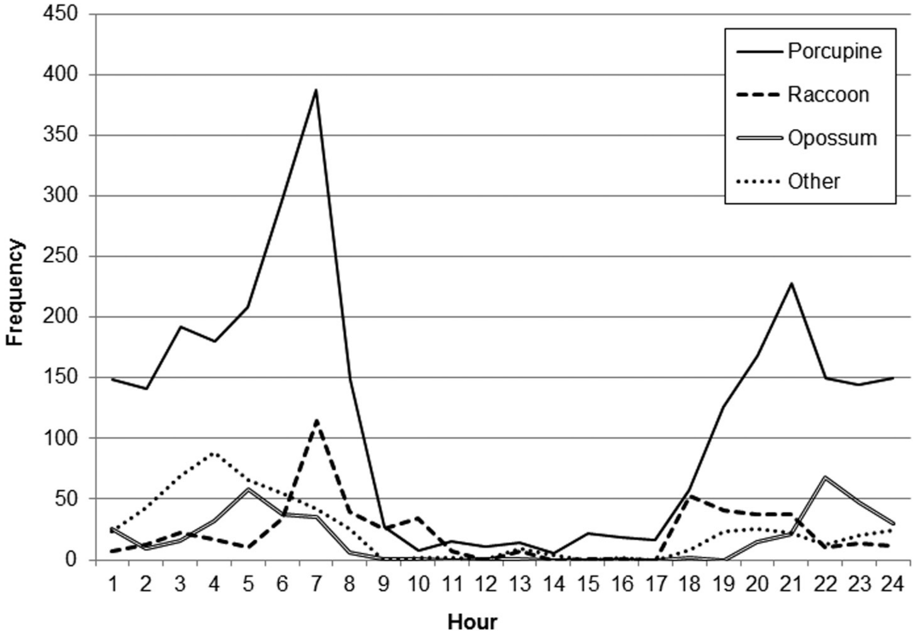

Figure 2. Hourly frequency of entrance photographs of North American porcupines, raccoons, Virginia opossums, and all other meso-mammal photographs at Camp Bullis caves in Camp Bullis, near San Antonio, Texas for the period of 01 February 2014 – 31 March 2015.

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Cave characteristics

North American porcupines, raccoons, Virginia opossums and all other meso-mammals showed greater use of caves without permanent water sources (Supplementary material Appendix 1 Table A2) which appears to correspond to availability. Statistical testing shows there was a significant difference ($\chi^2 = 29.22$, $p < 0.01$) between meso-mammal species and their use of caves with and without a permanent water source.

Raccoons, Virginia opossums and other meso-mammals showed a greater use of caves containing endangered invertebrate species while North American porcupines showed a greater use of caves not containing endangered species (Supplementary material Appendix 1 Table A2). Accordingly, we found a significant difference ($\chi^2 = 775.47$, $p < 0.01$) between meso-mammal categories and their use of caves according to presence or absence of endangered species.

North American porcupines, raccoons, Virginia opossums and all other meso-mammals showed a greater use of caves without gates ($\chi^2 = 880.12$, $p < 0.01$; Supplementary material Appendix 1 Table A2). Raccoons and Virginia opossums had a greater use of caves with pit entrances while North American porcupines and all other meso-mammals had a greater use of caves with walk-up entrances (Supplementary material Appendix 1 Table A2). There was a significant difference ($\chi^2 = 512.6$, $p < 0.01$) between cave entrance type and meso-mammal use. Interestingly, one of the most unique cave entrances on Camp Bullis was the highly modified pit entrance of Cement Cave. The cave starts with a gate and drops straight down with the walls of the first 1–2 m consisting completely of steel culvert. This was the only cave to show no animal activity.

The majority of North American porcupines, raccoons, Virginia opossums and all other meso-mammals were photographed at forested cave entrances (Supplementary material Appendix 1 Table A2). Accordingly, we found a significant difference ($\chi^2 = 161.7$, $p < 0.01$) between meso-mammal category and vegetative cover type.

Weather

North American porcupines visited caves during a greater range of temperatures while Virginia possums, raccoons and all other meso-mammals visited when ambient temperatures reached approximately 40°C (Fig. 3; Supplementary material Appendix 1 Table A3). We found a significant difference ($\chi^2 = 380.53$, $p < 0.01$) between meso-mammal categories in terms of the mean external temperature when they entered caves. Cave use according to percent relative humidity showed North American porcupines, Virginia opossums and raccoons entering caves

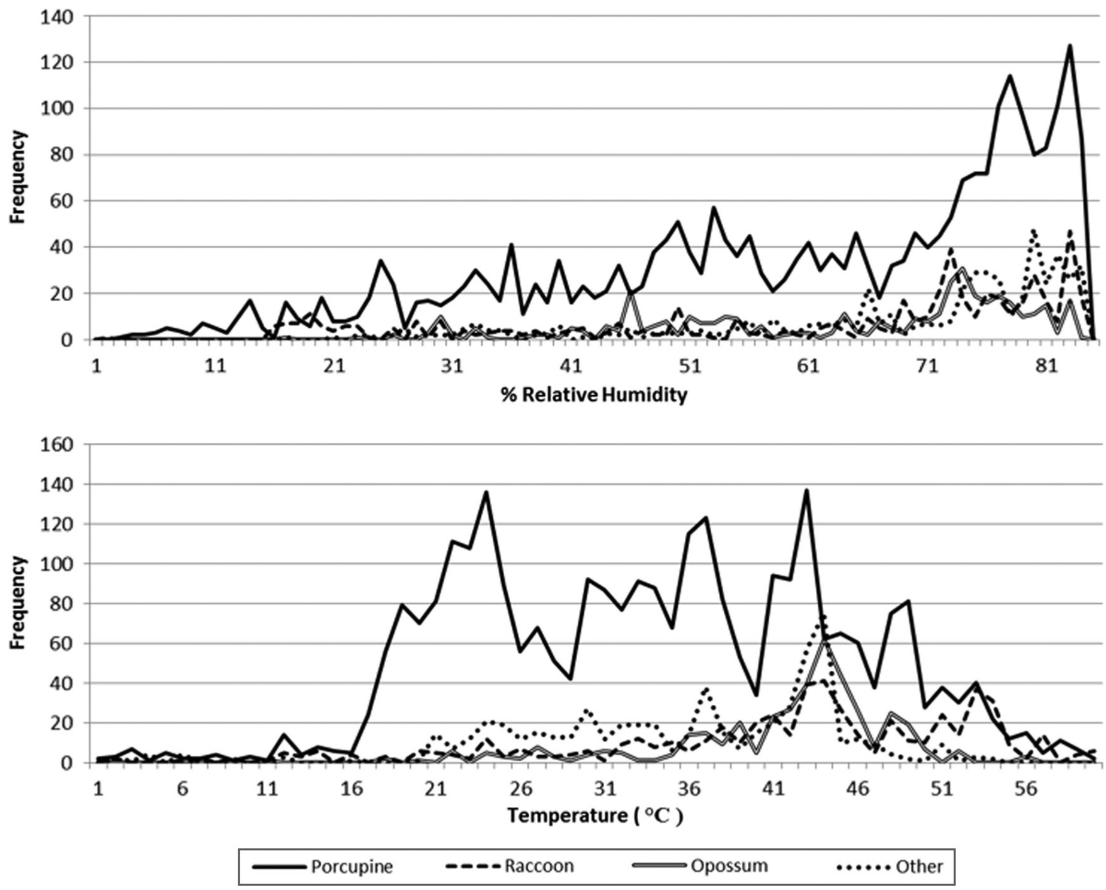

Figure 3. Photograph frequency by temperature (upper) and relative hmidity (lower) taken at cave entrances of North American porcupines, raccoons, Virginia opossums, and all other meso-mammals in Camp Bullis caves near San Antonio, Texas for the period of 01 February 2014 – 31 March 2015.

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with humidity levels near the annual average (75%) while the all other meso-mammal group used caves at higher humidity levels (Supplementary material Appendix 1 Table A3, Fig. 3). We did not find a significant difference ($\chi^2 = 1.47$, $p = 0.48$) between meso-mammal categories in terms of the mean external relative humidity when they entered caves.

Discussion

Our objective was to enumerate meso-mammal use of a variety of caves on Camp Bullis according to season, time of day, weather, and cave characteristics. Our results show regular cave use by meso-mammals including North American porcupines, raccoons, and Virginia opossums consistent with previous observations (Reddell 1994, Gary 2009).

Species assemblage

Our data suggested that North American porcupines, raccoons, and Virginia opossums were using Camp Bullis caves for denning, entering at sunrise and leaving at sundown. This is similar to what has been found by others (Allen et al. 1985, Roze 1987, 2009, Griesemer et al. 1998, Morin et al. 2005, Moseley 2012, Moseley et al. 2013). One picture shows a Virginia opossum entering a cave with its tail wrapped around dried grass, which is a known behavior of Virginia opossum den preparation (Pray 1921, Layne 1951).

In addition to denning, raccoons and Virginia opossum may have been using a cave's bat, rodent, and invertebrate populations as a food source (Lay 1942, Wiseman and Hendrickson 1950, Sandidge 1953, Wood 1954, Shirer and Fitch 1970, Winkler and Adams 1972, Kasparian et al. 2002, Moseley et al. 2013). Only four of Camp Bullis' caves were home to small resident bat populations (i.e. cave myotis *Myotis velifer* and tricolor bat *Perimyotis subflavus*; Gary 2009), but a majority of the caves provided ample food resources through established rodent and invertebrate populations (Baker et al. 1945, Wood 1954, Shirer and Fitch 1970, Gary 2009). North American porcupines are primarily herbivorous and unlikely to find edible plant material in caves. North American porcupine carnivory on local invertebrates also is unlikely and unsupported by the literature (Taylor 1935). North American porcupines do have a high salt drive (Dodge 1967, Roze 2009) and may be using a cave's cache of bones as a source of sodium (Roze 2009, Elbroch and Rinehart 2011).

Though less common in Camp Bullis, ringtails are also known to use caves for feeding, as a water source, and for denning (Clark 1951, Wynne 2013, Pape 2014). Nine-banded armadillo cave use was particularly interesting because they were exclusively photographed at Up the Creek Cave. Their timing leads us to believe it was used as a den (Newman 1913, Taber 1945, Clark 1951). This is supported by photographs of a nine-banded armadillo carrying dried grass under its body, which is characteristic of den preparation (Taber 1945).

Temporal variation

Previous studies in northern climes have described North American porcupines using caves largely in the winter (approximatley October or November through March or April; Dodge and Barnes 1975, Roze 1987, 2009, Griesemer et al. 1996, 1998), but our North American porcupine population used caves consistently, regardless of season. Rotational use of the Camp Bullis caves by raccoons and Virginia opossums was consistent with previous research that found both species used multiple dens (Lay 1942, Shirer and Fitch 1970, Juen 1981, Allen et al. 1985, Endres and Smith 1993). Interestingly, turkey vultures *Cathartes aura* and black vultures *Coragyps atratus* often nested in the cave entrances in the spring. Once a vulture began nesting, there was an abrupt and sustained drop in meso-mammal cave use that persisted until the vulture fledglings dispersed.

Cave characteristics

All meso-mammal groups appeared to favor particular cave characteristics. Caves with gates had fewer North American porcupines, probably due to limited access. All groups except the North American porcupines showed a greater use of caves containing endangered invertebrates. Though there was no observable difference in cave structure and conditions, caves with endangered species were more intensely managed, which included more frequent visitation by cave biologists as well as bi-annual treatment of red imported fire ant *Solenopsis invicta* mounds using boiling water (more information can be found at Veni et al. 2002). We suspect the rigorous management of fire ants makes these caves more desirable to raccoons and Virginia opossum since cave crickets *Ceuthophilus* spp., a food source for both species (Elbroch and Rinehart 2011), are not competing with or being preyed on by fire ants (Gary 2009). The North American porcupine's greater use of non-endangered species caves may be because they do not eat cave crickets (Taylor 1935) and the majority of endangered species caves had pit entrances, which were avoided by North American porcupines.

Our vegetative cover data showed all mammal groups used forested caves most, which was unsurprising since the three most common meso-mammal species, North American porcupines (Sweitzer and Berger 1992, Sweitzer 1996), raccoons (Shirer and Fitch 1970, Juen 1981, Henner et al. 2004), and Virginia opossums (Lay 1942, Sandidge 1953, Shirer and Fitch 1970, Hossler et al. 1994) all den and spend most of their lives in dense, wooded vegetation. Banzai Mud Dauber Cave had the most unique cover type in the middle of a firing range. This area is a large, mowed field with very few trees, little cover, and commonly disturbed by live fire shooting. We were interested to see what animals would risk using this cave, but the only mammals photographed were mice, rats, and squirrels *Sciurus* spp.

Five caves in our study are known to have periods of high CO_2 (Supplementary material Appendix 1 Table A1; Gary 2009) though this did not appear to influence meso-mammal use. Interestingly, North American porcupines have an increased breathing rate when exposed to rising levels of carbon dioxide (CO_2), more similar to humans than to adapted burrowing or fossorial mammals (e.g. woodchuck *Marmota*

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monax; Boggs et al. 1984, Boggs and Birchard 1989). In spite of this, many North American porcupines spent their days in caves known to have seasonal CO_2 levels high enough to make entering dangerous for people (Supplementary material Appendix 1 Table A1; Gary 2009).

The presence of a permanent water source was the only cave characteristic that did not have a statistically significant influence on how meso-mammals used caves. It is possible that the small number of caves with permanent water sources used in this study site masked any patterns. Instead, we believe it is more likely that meso-mammals were able to satisfy their water needs elsewhere on Camp Bullis including at the site's numerous creeks, wildlife guzzlers, and springs. Additionally, it has been shown that North American porcupine, in particular, are able to subsist solely on the water content of their food (Roze 2009).

Weather

Caves are often used by animals for refuge from temperature extremes (Roze 1987, Wolfe 1990, Griesemer et al. 1996, Elbroch and Rinehart 2011). Camp Bullis caves maintain temperatures near the annual average (20 ± 3°C; Gary 2009) therefore offering meso-mammals a permanent mesic temperature microclimate. External temperature was the most distinct weather variable in our study with North American porcupines entering caves in a considerably larger range of external temperatures than the all other species. This suggests North American porcupines are using the caves more consistently throughout the year, as compared to all other meso-mammal groups that typically used caves as thermal refuges when external air temperatures exceeded 40°C. This could be a result of Virginia opossum and raccoon entering torpor with cold temperature (Elbroch and Rinehart 2011) therefore limiting their movements to and from caves. North American porcupines do not hibernate or enter torpor (Coltrane et al. 2011) and are thus more sensitive to temperature drops. The steady temperature of caves may therefore serve an essential role in their survival in the winter.

Unlike temperature, external humidity levels had no significant influence on meso-mammal cave use. The small differences we did see was likely a covariate of the crepuscular timing of cave visitation rather than directly influencing cave visitation. It is possible meso-mammal cave use during periods of high humidity is associated with animals escaping rain, but this is a dangerous strategy because as water run-off enters caves, the rapidly rising water level can drown cave occupants (USFWS 2011).

Caves in central Texas were historically associated with raccoons (Reddell 1994, Veni et al. 2002), but the naturalization of North American porcupines now represents a novel, and dominant organic input. Additionally, the lack of historical data makes it difficult to determine if current meso-mammal cave use and nutrient inputs are comparable to historic levels. Slight increases in organic inputs may provide a more desirable environment for obligate cave fauna (Sket 1999), but can also support the invasion of terrestrial predators and more competitive, less specialized species (Veni et al. 2002). Additionally, the threshold at which nutrient inputs are beneficial is unknown and may be fluctuating. For example, a cave system in the United Kingdom experienced two similar organic nutrient input events (Wood et al. 2008). One resulted in the elimination of most of the endemic cave taxa while the second a couple of years later brought an increase in the cave community's abundance (Wood et al. 2008). At our study site, North American porcupine appear not to select for cave with endangered invertebrates but if a cave's organic inputs should exceed acceptable levels, managers should first consider North American porcupine control through brush removal, trapping, or installation of exclosures.

The results from our study will represent an initial step in understanding meso-mammal cave use but further studies are crucial to establish acceptable levels of meso-mammal nutrient inputs into caves. Future studies should also investigate the intensity with which raccoons and Virginia opossum prey upon endangered cave invertebrates, and if it is likely to affect the arthropods' long-term survival. If predation of endangered species is negligible, as suspected, researchers should then investigate raccoon and opossum take of cave crickets since their scat is an essential food source to the endangered invertebrates (Gary 2009). Also, it is still unclear how vultures affect the visitation patterns of meso-mammals, and how corresponding periods of no nutrient input from meso-mammals could affect survival of cave-obligate species.

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Supplementary material (available as Appendix wlb-00320 at <www.wildlifebiology.org/appendix/wlb-00320>). Appendix 1.

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