Meso-mammal behavior and resource use in central Texas caves

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Meso-mammals serve an important function in a cave's oligotrophic ecosystem through the introduction of nutrients via their scat (Gary 2009). Previous studies have noted the frequency and type of meso-mammal cave visitation (Montalvo 2017), but there is still relatively little research describing meso-mammal behavioral activities within caves. Determining typical behaviors of meso-mammals in caves is essential for management decisions because different behaviors can be associated with different risks to cave-obligate species.

Management of meso-mammal cave use is especially important at Joint Base San Antonio–Camp Bullis (hereafter Camp Bullis), where many of the caves are actively managed for three United States federally-listed endangered invertebrates *(Cicurina madla* Gertsch, 1992; *Rhadine exilis* Barr & Lawrence, 1960; *Rhadine infernalis* Barr & Lawrence, 1960) as well as cave crickets (*Ceuthophilus* spp.), whose eggs serve as an important food source for cave-obligate species. Generally, Raccoons (*Procyon lotor* Linnaeus, 1758*;* Reddell 1994) and Virginia Opossums *(Didelphis virginiana* Kerr, 1792) are suspected to use caves for denning and feeding on arthropods (Winkler and Adams 1972; Allen et al. 1985; Martin et al. 2003; Elliott and Ashley 2005; Elbroch and Rinehart 2011; Moseley et al. 2013). North American Porcupines (*Erethizon dorsatum* Linnaeus, 1758) are suspected to use caves for resting and denning (Woods 1973; Morin et al. 2005; Roze 2009). This prolonged behavior in caves equates to a greater abundance of scat deposits. The geographic range of North American Porcupines is expanding and the species is now naturalized in central Texas (Ilse and Hellgren 2001; Schmidly and Bradley 2016). Whereas Raccoons (Reddell 1994), and likely Virginia Opossums, historically used caves in central Texas, North American Porcupines were first seen at Camp Bullis

in 2003 (C. Thibodeaux, unpublished data), so their scat represents a novel, and often abundant, energy input. This surplus of nutrients may help support cave-obligate species, but they also may facilitate the invasion of less-specialized, facultative species (Gary 2009).

Furthermore, management based on an incomplete understanding in the ecosystem dynamics of a cave can affect areas beyond the cave itself. For instance, a recent highway project in San Antonio, Texas, USA was delayed following the discovery of a cave containing the federally endangered Bracken Bat Cave Meshweaver (*Cicurina venii* Gertsch, 1992; Davila 2012). The highway building plan had to be changed to reduce the impact on the endangered species and increased the final project cost from $15 million USD to $44 million USD (Degollado 2014).

Current literature on the behaviors of meso-mammals in caves generally focuses on single caves, seasons, or consists of observations made secondary to a primary research questions (Elder and Gunier 1981; Pape 2014). Because of this, we can only speculate as to why mammal cave use in central Texas occurs or what constitutes typical or atypical use. The goal of this study was to determine the behaviors and resource use of meso-mammals in central Texas caves. Our objectives were to (1) determine which meso-mammal species use caves for feeding or hunting, resting, and grooming behaviors, and (2) determine if any behaviors are associated with particular seasons or time of day.

We performed this study on Camp Bullis (11,286 ha) just north of San Antonio, Texas, USA at the intersection of the Edward's Plateau, South Texas Plains, and the Blackland Prairie ecoregions (**Figure 1**; Gould 1975). For our purposes, caves were defined as naturally formed, human-accessible cavities that are at least 5m in depth and/or length, where no dimension of the entrance exceeded the length or depth (Gary 2009). Approximately 88% of meso-mammal cave use in this area consists of use by North American Porcupines, Raccoons, and Virginia Opossums (Montalvo 2017).

Four caves with the most meso-mammal activity (Montalvo 2017) were monitored for one month per season. We monitored Constant Sorrow Cave and Well Done Cave for all seasons across a year, and Chigger Cave and Horse Tooth Cave during the summer and fall only, as high levels of CO_2 made placing cameras in them unsafe during the winter and spring (**Table 1**). We monitored caves with Cuddeback Attack IR (Cuddeback Digital, De Pere, WI, USA) and Browning Range Ops (Browning Trail Cameras, Birmingham, AL, USA) infrared game cameras between June 2015 and May 2016. Cameras were placed throughout the caves' passages and set to record 10-second video with a 30-second delay. We positioned cameras to cover as much of the cave as possible, especially where there were animal signs (e.g., scat, scratches, tracks, hair), and kept placement consistent for each sampling season. Well Done Cave was covered with six cameras, while Chigger Cave, Horse Tooth Cave, and Constant Sorrow Cave were all covered by two cameras. We examined the videos for the presence of meso-mammals, defined for this study as any mammal at least as large as a Cottontail Rabbit (*Sylvilagus* spp.; Hoffman et al. 2010) up to the size of a North American Porcupine.

Figure 1. Location of caves (white dots) monitored for one year on Camp Bullis (white outline) near San Antonio, Texas, USA, 2015–2016.

For each video with a meso-mammal, we noted the location, date, season, species, number present, and time of day. We then categorized each meso-mammal's behavior as being either 'feeding or hunting', 'grooming', 'resting', 'other', or 'unknown'. Behaviors

were assigned only when at least 70% of the video (seven seconds) could be attributed to a single behavior. We defined 'feeding or hunting' as when a meso-mammal was trailing, reaching towards, or eating a known prey species. We defined 'grooming' as when the video showed a meso-mammal scratching, cleaning, or shaking their fur. We defined 'resting' as when a meso-mammal was shown sitting or lounging in at least two successive videos with little additional movement. This included no signs of feeding, hunting, or grooming. We defined a behavior as 'other' when a less common action could confidently be identified (e.g., fighting or defecating). We classified remaining behavior as 'unknown' when the angle, clarity, depth, or timing of a video prevented any single behavior from being identified. Data were compiled according to behavior, season, and time of day, and were summarized with descriptive statistics. For this study we defined winter as December, January, and February; spring as March, April, and May; summer as June, July, and August; fall as September, October, and November.

Table 1. Caves monitored by seasons of data collection and corresponding cave length, cave depth, and the number of mammal videos with identifiable behaviors at Camp Bullis near San Antonio, Texas, USA, 2015–2016.

	Seasons				Length (m)	Depth (m)	North American Porcupine	Raccoon	Virginia Opossum
	W	Sp	Su	F					
Chigger †			X	X	20	5.0	15	0	0
Constant Sorrow	X	X	X	X	6.0	1.5	17	1.0	1.0
Horse Tooth †			X	X	6.3	2.8	2.0	0	0
Well Done	X	X	X	X	34	3.0	58	0	33

† Caves that could not be entered in winter and spring because of dangerously high levels of CO_2

Behaviors

During this study, we recorded 569, 10-second videos (totaling 94.8 minutes of video) of three meso-mammal species and were able to assign behaviors for 127 videos (totaling 21 minutes of video). North American Porcupines (72%) were the most commonly recorded species with a majority of videos showing individuals resting followed by grooming (**Table 2**). Additionally, five videos were categorized as other behaviors and included three videos of an individual hiding during initial camera set-up, a video of an individual defecating, and a video of two individuals aggressively posturing (**Table 2**). Virginia Opossums (27%) were the second most commonly captured species with all 34 videos showing feeding or hunting (**Figure 2**), and Raccoons had a single video of a known behavior showing feeding or hunting (**Table 2**).

The species recorded in this study match the three most common species found using the caves at this study site: North American Porcupines, Raccoons, and Virginia Opossums (Montalvo 2017). We expected to have recorded a greater number of Raccoon videos as compared to Virginia Opossum videos based on previous surveys of local meso-mammal cave visitation (Montalvo 2017). This may be because Raccoons

performed behaviors out of sight, were wary of cameras, or were using different caves, though previous research showed that both Chigger Cave and Constant Sorrow Cave have regular Raccoon visitation (Montalvo 2017). It is also possible that Raccoons, or other meso-mammal species, are using inaccessible passages. Camp Bullis caves often have portions that are too small for humans but show signs of animal use (e.g., scat). This likely negatively effects the collection of all behavior videos, especially resting videos. Finally, it is possible that the numerous North American Porcupines are excluding Raccoons from caves. Previous research at this site has shown Chigger and Constant Sorrow caves with interspecific sharing, while Well Done and Horse Tooth caves showed almost exclusive use by North American Porcupines (Montalvo 2017). The paucity of Raccoon videos makes any ecological interpretation speculative.

Table 2. An annual distribution of grooming, resting, feeding or hunting, and other behavior videos for North American Porcupine, Raccoon, and Virginia Opossum on Camp Bullis near San Antonio, Texas, USA, 2015–2016.

	Grooming	Resting	Feeding/Hunting	Other	Total
North American Porcupine	35 (38%)	52 (57%)	–	5 (5%)	92 (100%)
Raccoon	–	–	1.0 (100%)	–	1.0 (100%)
Virginia Opossum	–	–	34 (100%)	–	34 (100%)

Behaviors recorded for meso-mammals varied by species and agrees with previous studies that suggest North American Porcupines generally use caves for resting (Woods 1973; Morin et al. 2005; Roze 2009) while Virginia Opossums and Raccoons use caves for feeding on small mammals and insects (Winkler and Adams 1972; Martin et al. 2003; Elliott and Ashley 2005; Moseley et al. 2013). Other studies have suggested Raccoons and Virginia Opossums also use caves for resting. We did not see this behavior during the course of this study, but Raccoon and Virginia Opossum populations may use other sites for these activities. Our videos also show both species hunting arthropods though we were unable to identify the species. The consumption of arthropods is an especially significant behavior because it represents a direct risk to the cave system's endangered species and cave crickets.

Defecation by North American Porcupines into the caves is an understudied phenomenon that could have considerable impact on cave ecosystems. Scat left by meso-mammals, such as North American Porcupines (Calder and Bleakney 1965; Peck 1988; Moseley 2007), represents an important source of nutrient inputs into the otherwise oligotrophic cave environment. Cave fauna require external nutrient inputs but if a cave's total nutrient input is too large, the cave-adapted species can be replaced by more competitive or predatory species (Gary 2009). Camp Bullis caves were historically supported with nutrient inputs from both cave crickets (*Ceuthophilus* spp.; Reddell 1994) and Raccoons (Veni et al. 2002) but nutrient inputs are now often dominated by newly naturalized North American Porcupines (Montalvo 2017). North American Porcupine scat is therefore a new and often abundant nutrient source that needs continued research and

monitoring to prevent extirpation of cave-adapted species. This is especially true for caves with multiple meso-mammal species where North American Porcupine scat is additive to native meso-mammal deposits.

Figure 2. Virginia Opossum reaching for an arthropod on the ceiling of Well Done Cave on Camp Bullis near San Antonio, Texas, USA, 2015–2016.

Timing

We recorded meso-mammal videos in all four seasons but none of the videos recorded in the winter or spring had identifiable behaviors. Ninety-three percent of summer videos consisted of resting, and feeding or hunting videos while 90% of fall videos were resting, and grooming. No identifiable behaviors occurred in the winter or spring. This is likely because both North American Porcupines and Virginia Opossums restrict their movement during cold weather (Elbroch and Rinehart 2011).

The hourly distribution of behavior videos had bimodal distributions. As expected, most recorded behaviors occurred around dawn and dusk when meso-mammals are most active in caves (Montalvo 2017). Feeding or hunting peaked at approximately 03:00 and 19:00 ($\overline{x}$ = 10:00), grooming videos peaked at approximately 06:00 and 17:00 ($\overline{x}$ = 08:00), and resting videos peaked at 05:00 and 18:00 ($\overline{x}$ = 11:00; **Figure 3**). Additionally, grooming videos were most often recorded during the day, when North American Porcupines are in caves resting, while feeding or hunting behaviors often occurred during the night, when Virginia Opossums are typically active and looking for food.

Conclusion

Our data support previous studies that suggest herbivorous North American

Porcupines largely use caves for resting and grooming, while omnivorous Virginia Opossums and Raccoons use caves to feed on arthropods. Oligotrophic caves require external nutrient subsidies to support cave-obligate species, often provided in the form of meso-mammal scat. However, the over-abundance of meso-mammals could potentially lower overall diversity through direct consumption of cave-obligate species, through consumption of their food source, or by supporting the invasion of competitors or predators. Alterations to cave ecosystem dynamics is especially relevant for central Texas with the extensive cave use by newly naturalization of North American Porcupines and presence of multiple U.S. federally endangered species.

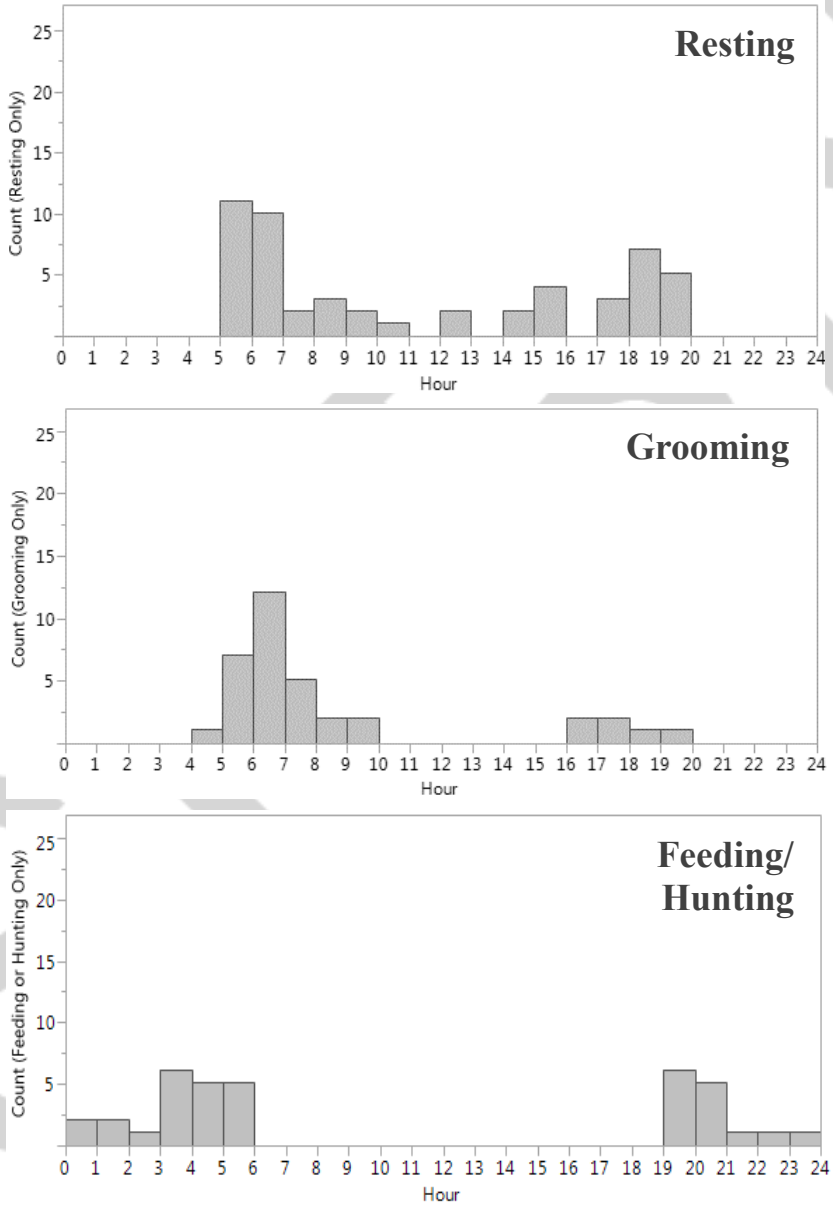

Figure 3. Annual frequency of detected meso-mammal behaviors according to hour for resting videos, grooming videos, and feeding or hunting videos on Camp Bullis, Texas, USA, 2015–2016.

We suggest future research begin to determine typical diets of meso-mammals that regularly visit caves, how they compare to non-cave using populations, and if diets differ if caves contain endangered species or cave crickets. Additionally, it is critical to investigate the typical timing, volume, and nutrient load of North American Porcupine, Raccoon, and Virginia Opossum scat left in caves. We suggest cave managers continue monitoring meso-mammal cave use and define acceptable levels of meso-mammal visitation, arthropod consumption, and scat deposits. If this threshold is reached, additional management (e.g., North American Porcupine exclusion or harvesting) may be considered.

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