MESO-MAMMAL CAVE USE AND NORTH AMERICAN PORCUPINE HABITAT USE IN CENTRAL TEXAS

A Dissertation

by

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DOCTOR OF PHILOSOPHY

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ABSTRACT

Meso-mammals are frequent cave visitors whose role in cave ecology is poorly understood. Understanding meso-mammal cave use is essential because caves are often managed for United States federally endangered, cave-obligate arthropods. My objectives for this study were to quantify annual meso-mammal cave visitation, determine behaviors of meso-mammals while in the caves, to develop multinomial regression to determine which variables best differentiate caves use by each species, and to determine how North American porcupines incorporate caves into their home range and habitat use.

North American porcupines (*Erethizon dorsatum*) were the most common cave visitor (64%), followed by raccoons (*Procyon lotor*; 14%) and Virginia opossums (*Didelphis virginiana*; 10%). These results are noteworthy because central Texas caves were historically associated with raccoons and the additional nutrient inputs of North American porcupines could facilitate replacement of cave-obligate species by more competitive, or predatory, terrestrial species. Videos recorded in cave passages showed North American porcupines used caves for denning and grooming, while Virginia opossums used caves for feeding. The strongest multinomial model showed that, compared to North American porcupine, raccoons and Virginia opossums had greater odds of using caves with gates (2.36, 4.10, respectively) and pit entrances (6.11, 2.23, respectively). Conversely, raccoons and Virginia opossums, compared to North American porcupine, had lower odds of using caves that were constructed or excavated

(0.42, 0.14, respectively), and visiting during the spring (0.46, 0.28, respectively) and winter (0.43, 0.37, respectively). These variables all likely relate to either Virginia opossums' and raccoons' greater dexterity or restricted movements after entering torpor during low temperatures. North American porcupine home range estimates (46–421 ha) and overlap indices (42% and 93%) were larger than expected with females spending a majority of their time near a cave entrance. All individuals selected forested cover at the landscape and point scales. Bare ground was selected at the home range scale likely to be used as trails.

The results from my study represent an initial step in understanding meso-mammal cave use in central Texas. Should cave nutrient levels need to be managed, my data can be used to manipulate habitats to make caves less desirable to North American porcupine.

DEDICATION

Dedicado a mi familia.

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Contributors

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All work for the dissertation was completed by the student, under the advisement of Roel R. Lopez [advisor], Nova J. Silvy, and Susan M. Cooper of the Department of Wildlife and Fisheries Sciences, Professor Rusty A. Feagin of the Department of Ecosystem Science and Management, and Cave and Karst Specialist Christopher Thibodaux of Joint Base San Antonio.

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CHAPTER I

INTRODUCTION

Meso-mammal cave use is an important, but relatively little-studied aspect of cave ecology. Current literature on meso-mammals in caves generally focuses on singular caves, seasons, or consists of observations made secondary to a primary research questions (Elder and Gunier 1981; Pape 2014). Studies (Woods 1973, Roze 1987, Griesemer et al. 1998, Morin et al. 2005, Roze 2009) have shown that North American porcupines use caves and rocky outcrops for denning. Raccoons (*Procyon lotor*) 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). Cave biologists on Camp Bullis have long noted extensive cave use by meso-mammals including North American porcupines (*Erethizon dorsatum*), raccoons, and ringtails (*Bassariscus asstutus*), but little is known about the abundance or motivations of their visitations.

Determining typical levels of meso-mammal cave use is 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).

This information is especially critical for caves located on the Joint Base San Antonio-Camp Bullis military base (hereafter Camp Bullis) because approximately 20% are inhabited by 3 federally-listed endangered, cave-obligate invertebrates *(Cicurina madla*, *Rhadine exilis*, *Rhadine infernalis*). Additionally, Camp Bullis caves were historically associated with raccoon use (Reddell 1994) with the first cave sighting of a North American porcupine not occurring until 2003 (C. Thibodeaux, Natural Resources Joint Base San Antonio, unpublished data). North American porcupines are now naturalized in central Texas (Ilse and Hellgren 2001) and their scat, previously absent from the cave ecosystem, is now abundant in many of Camp Bullis' caves.

A more complete understanding of caves also is essential because of their potential to dramatically 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 3 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 (Degollado 2014).

Similarly, little is known about North American porcupines' habitat use in central Texas. The North American porcupines have large ranges, from Alaska to northern Mexico and much of the southwest, and therefore are able to exploit a large variety of habitats. In Nevada, North American porcupines had home range that averaged 15.3 ha for males, 8.2 ha for females, and preferred riparian habitats with buffalo-berry (*Shepardia argentia*) and willow (*Salix* sp.; Sweitzer 2003). In contrast, North American porcupines in Quebec had home ranges averaging at 20.9 ha for males, and 15.4 ha for females, and selected for trembling aspen (*Populus tremuloides*) dominated deciduous and mixed forests (Morin et al. 2005). Understanding North American porcupine habitat use would allow for more informed management decisions especially should their cave use becomes excessive.

My goals for this dissertation were to better understand meso-mammal use of caves and the land use of naturalized North American porcupines in central Texas. Specifically, my objectives were to: identify meso-mammal species that use central caves and quantify their visitation according to temporal variation, weather, and cave characteristics (Chapter II); determine which meso-mammal species use caves for denning, feeding, hunting, and grooming behaviors, and if any behaviors are associated with particular seasons or time of day (Chapter III); develop a model to determine which variables best predict meso-mammal species cave visitation (Chapter IV); determine the influence of caves on North American porcupine home range, overlap, and multi-scale habitat use (Chapter V).

CHAPTER II

QUANTIFYING MESO-MAMMAL CAVE USE IN CENTRAL TEXAS

Introduction

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 3 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 abundance or motivations of their visitations.

Studies (Woods 1973, Roze 1987, Griesemer et al. 1998, Morin et al. 2005, Roze 2009) 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 singular caves, seasons, or consists of observations made secondarily to other research questions. Focusing only on singular 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, absent from the ecosystem until approximately 2003 (C. Thibodeaux, Natural Resources Joint Base San Antonio, unpublished data), is now abundant in many of Camp Bullis' caves.

A more complete understanding of caves also is essential because of their potential to dramatically 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 3 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 (Degollado 2014).

My goal with this study was to determine meso-mammal cave use across a variety of caves and over the course of a year. Specifically, my 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

I 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). I randomly selected 30 caves from 100 available (Fig. 1, Table 1). I 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 1 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 descend 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

Figure 1. Map of Camp Bullis near San Antonio, Texas, USA (inset) with aerial imagery showing the installation's boundary (white outline) and the cave locations (white dots).

Table 1. Thirty caves and their corresponding length, depth, presence of entrance gate, entrance type (i.e., walk-up [W] or pit [P]), presence of seasonally elevated CO_2 level, cover type (i.e., forested [F], natural vegetation [N], mixed shrub [M]), prior construction or excavation (C/E), presence of endangered species, if located within the Edward's aquifer recharge zone, presence of a permanent water source, and the count of photographs for each animal group or species at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

Cave	Length (m)	Depth (m)	Gate	Entrance Type	CO_2	Cover Type	C/E	End. Spp.	Aquifer	Water	Meso-mammal	Porcupine	Raccoon	Virginia Opossum	Ringtail	Bobcat	Skunk	Rabbit	Fox	Armadillo
Accident Sink	18.3	15		P	x	F	x				38	5	2	0	31	0	0	0	0	0
Banzai Mud Dauber	25	37.2		P		N		x	x		0	0	0	0	0	0	0	0	0	0
Camp Bullis Bad Air	113	21		W	x	F					130	65	31[†]	2	14	18	0[†]	0	0	0
Cannonball	139	17.3	x	P	x	F	x			x	121	38	52	30[†]	1	0	0	0	0	0
Caribbean Cruise	7	2.5		P		F	x		x		7	4	3	0	0	0	0	0	0	0
Cement	9.2	19	x	P		F	x		x		0	0	0	0	0	0	0	0	0	0
Chigger	20	5		P		F	x		x		699	626	36	34	0	3	0	0	0	0
Constant Sorrow	6	1.5		P		F		x			428	92	149	181	0	4	2	0	0	0
Cross the Creek	9	8		P		F	x	x	x		17	15[†]	0[†]	1[†]	0	1	0	0	0	0
Darling's Pumpkin Hole	156	20		P	x	F	x			x	107	3	1	0	103	0	0	0	0	0
Dos Viboras	11.3	13.5		P		F	x	x	x		39	32	6[†]	0	1	0	0	0	0	0
Eagles Nest	235	33.5		W		F		x	x		187	113[†]	2	72	0	0	0	0	0	0
Flying Buzzworm	16	13	x	P		F	x	x	x		111	0[†]	111	0	0	0	0	0	0	0
Hanging Rock	8	8		P		F	x		x		0	0	0	0	0	0	0	0	0	0

Table 1, Continued.

Cave	Length (m)	Depth (m)	Gate	Entrance Type	CO_2	Cover Type	C/E	End. Spp.	Aquifer	Water	Meso-mammal	Porcupine	Raccoon	Virginia Opossum	Ringtail	Bobcat	Skunk	Rabbit	Fox	Armadillo
Haz Mat Pit	3	7.2		P		F	x				78	4	51	6	12	4	0	1	0	0
Headquarters	142	13	x	W		F	x	x	x		29	$8^{\dagger}$	$9^{\dagger}$	12	0	0	0	0	0	0
Horse Tooth	6.3	2.8		P		F	x		x		165	155	9	0	0	1	0	0	0	0
Low Priority	15	4.3	x	P		F	x	x			91	0	$90^{\dagger}$	1	0	$0^{\dagger}$	0	0	0	0
MARS	11	5		P		F	x		x		132	$123^{\dagger}$	1	8	0	0	0	0	0	0
NBC	15	3.4		P		M	x		x		76	70	4	0	0	2	0	0	0	0
Peace Pipe	34	12		P		F	x	x			3	0	0	0	3	0	0	0	0	0
Platypus Pit	55	31		P		F	x	x	x		13	$7^{\dagger}$	$4^{\dagger}$	0	0	2	0	0	0	0
Poor Boy Baculum	36	46		P		F	x	x	x		0	0	$0^{\dagger}$	0	0	0	0	0	0	0
Record Fire 1	6	1.2		W		N			x		20	0	7	0	0	1	0	10	2	0
Root Toupee	13	11		P		F	x	x	x		0	0	0	0	0	0	0	0	0	0
Stahl	18	14.5		P	x	F	x				49	0	27	5	5	6	3	3	0	0
Stealth	138	7.7	x	W		N	x			x	331	316	0	1	0	0	14	0	0	0
Up the Creek	18	4		W		M	x	x	x		830	$435^{\dagger}$	$21^{\dagger}$	78	0	1	$0^{\dagger}$	0	0	295
Vera Cruz Shaft	9	8	x	P		F	x			x	0	0	0	0	0	0	0	0	0	0
Well Done	34	3		W		F	x				815	$795^{\dagger}$	3	0	4	0	0	13	0	0

†Coordinating animal group previously noted at cave 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 (Table 1; USGS 2001, Gary 2009).

Method

I monitored caves with Cuddeback Attack IR (Cuddeback Digital, De Pere, WI) and Browning Range Ops (Browning Trail Cameras, Birmingham, AL) infrared game cameras which I placed at cave entrances and set with a 30-second delay. I split caves into 2 groups of 15 (Group A and Group B). I monitored Group A for 2 weeks after which I retrieved cameras, data downloaded, checked batteries, and then re-deployed cameras for 2 weeks at the caves of Group B. I continued this schedule so that at least 4 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. I 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 and rats (Muridae).

I 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, I noted the location, date, season, species, time of day, hourly temperature, and hourly percent humidity. I collected weather data from weather stations located on Camp Bullis using Onset Hobo U30 data loggers (Onset Computer Corporation, Bourne, MA), and Onset temperature and humidity sensor (S-THB-M002).

I 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. I grouped photographs by species: North American porcupines, raccoons, Virginia opossums (the 3 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*]). I 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, U.S. Geological Survey designated cover type) and then tested for significant differences with Chi-squared goodness of fit test (χ^2) or Wilcoxon signed-rank (SR) tests.

Results

Species assemblage

I deployed cameras from February 2014 – March 2015 capturing a total of 27,852 photographs ($\bar{x}$ = 928.4/cave, CI = 594.1 – 1,262.7) including 4,516 photographs of meso-mammals (16.2%). North American porcupines were the most common meso-mammal at 64% ($\bar{x}$ = 96.9/cave, *n* = 2,906, 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; Table 1). Though not specifically investigated for this project, cave entrance photographs most frequently captured mice and rats (*n* = 8,409), and vultures (*n* = 2,668).

Temporal variation

Considering each species independently, North American porcupines were most photographed in winter, raccoons in summer, Virginia opossums in fall, and all other meso-mammal species in fall (Fig. 2). There was a significant difference (χ^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 0600 hours and 2000 hours with the least movement during daylight between 0700 hours and 1700 hours. North American porcupines and raccoons were crepuscular displaying most activity from 0600 hours to 0800 hours and 1800 hours to 2200 hours whereas Virginia opossums were most active

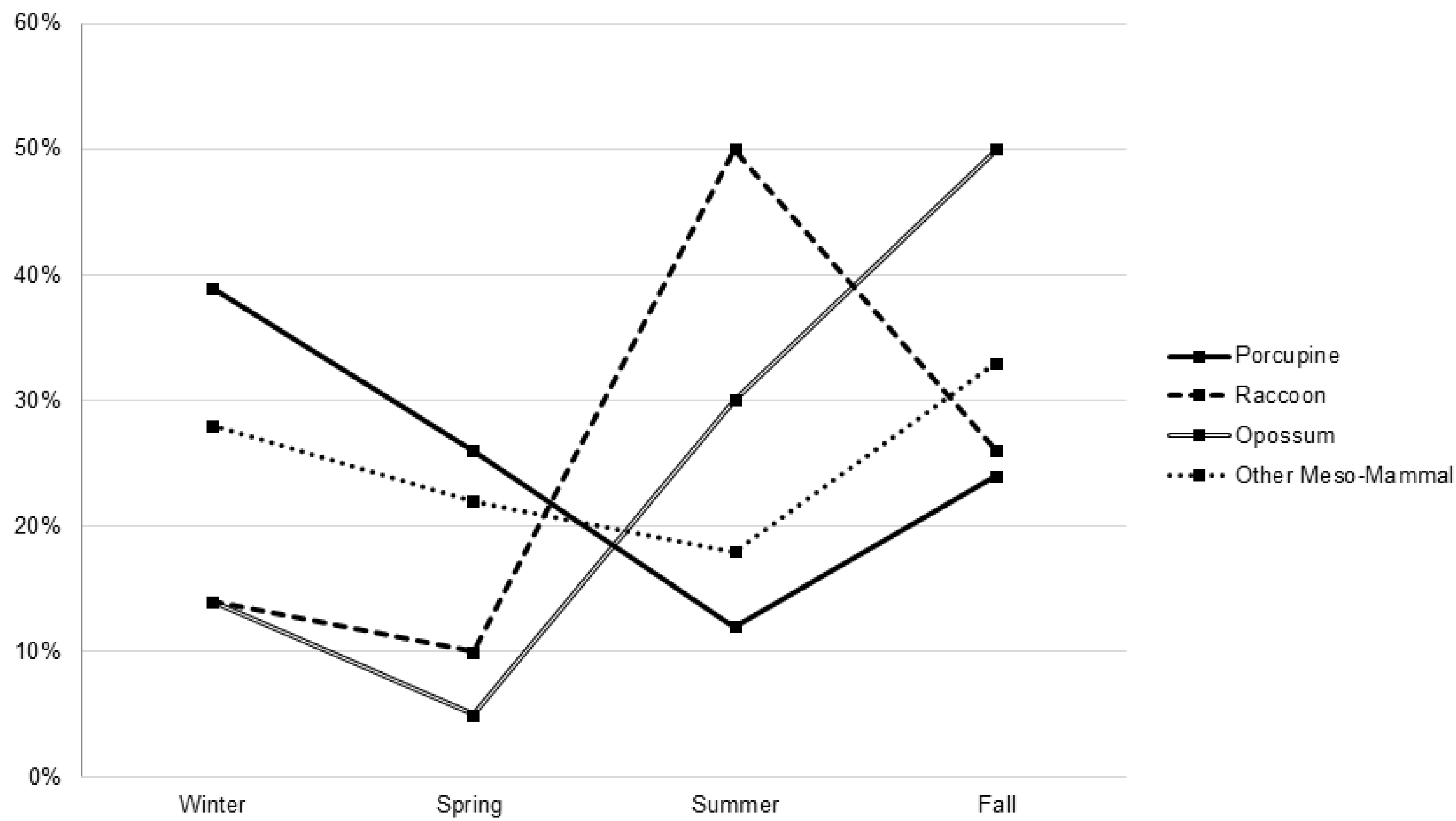

Figure 2. Annual percent use of Camp Bullis caves by North American porcupines, raccoons, Virginia opossums, and all other meso-mammals according to season on Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

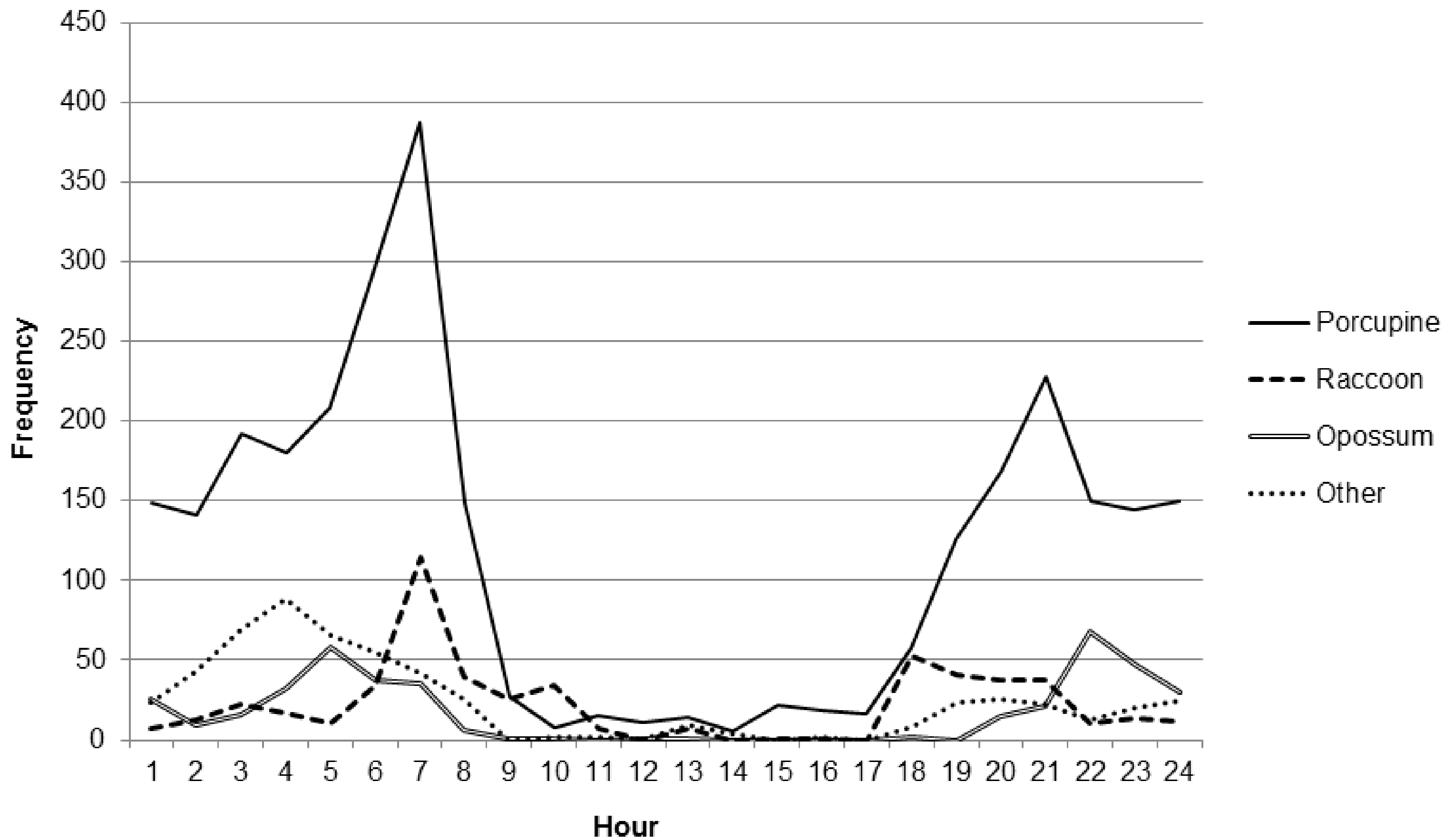

Figure 3. Hourly frequency of entrance photographs of North American porcupines, raccoons, Virginia opossums, and all other meso-mammal photographs at caves in Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

during the night from 0300 hours to 0600 hours and 1900 hours to 2300 hours (Fig. 3). 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.

Cave characteristics

North American porcupines, raccoons, Virginia opossums, and all other meso-mammals all showed an overwhelmingly greater use of caves without permanent water sources (Table 2). Significant differences were observed ($\chi^2 = 29.22$, $P < 0.01$) between meso-mammal species and their use of caves with and without permanent water sources.

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 (Table 2). Accordingly, I 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 ($\chi^2 = 880.12$, $P < 0.01$; Table 2). 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 (Table 2). 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

Table 2. The count and percent of North American porcupine, raccoon, Virginia opossum, and all other species cave entrance photographs according to cave characteristic (i.e., permanent water source, presence of endangered species, entrance type, cover type, and entrance gates) at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

Species	Water		Endangered Species		Entrance		Cover Type			Gates	
	Present (n = 4)	Absent (n = 26)	Present (n = 13)	Absent (n = 17)	Pit (n = 13)	Walk-Up (n = 17)	Forested (n = 25)	Mixed Forest/Shrub (n = 32)	Natural Herbaceous (n = 3)	Present (n = 6)	Absent (n = 24)
Porcupine	349 (12%)	2514 (88%)	671 (23%)	2192 (77%)	1169 (41%)	1694 (59%)	2482 (87%)	69 (2%)	312 (11%)	42 (1%)	2821 (99%)
Raccoon	53 (10%)	482 (90%)	312 (58%)	223 (42%)	462 (86%)	73 (14%)	524 (98%)	4 (1%)	7 (1%)	182 (34%)	353 (66%)
Opossum	31 (8%)	375 (92%)	320 (79%)	86 (21%)	265 (65%)	141 (35%)	405 (100%)	0	1 (0%)	43 (11%)	363 (89%)
Other	103 (18%)	464 (82%)	350 (62%)	217 (38%)	159 (28%)	408 (72%)	554 (98%)	0	13 (2%)	1 (0%)	566 (100%)

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 (Table 2). Accordingly, I 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 opossums, raccoons, and all other meso-mammals visited when ambient temperatures reached approximately 40° C (Fig. 4; Table 3). I found a significant difference ($\chi^2 = 384.63$, $P < 0.01$) between meso-mammal category and external temperature. Cave use according to percent relative humidity showed North American porcupines, Virginia opossums, and raccoons entering caves with humidity levels near the annual average (75%) while the all other meso-mammal group used caves at higher humidity levels (Table 3; Fig. 4). Accordingly, I found a significant difference ($\chi^2 = 85.88$, $P < 0.01$) between meso-mammal category and external relative humidity.

Discussion

My 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. My results show regular cave use by meso-mammals including North American porcupines, raccoons, and Virginia opossums consistent with previous observations (Reddell 1994, Gary 2009).

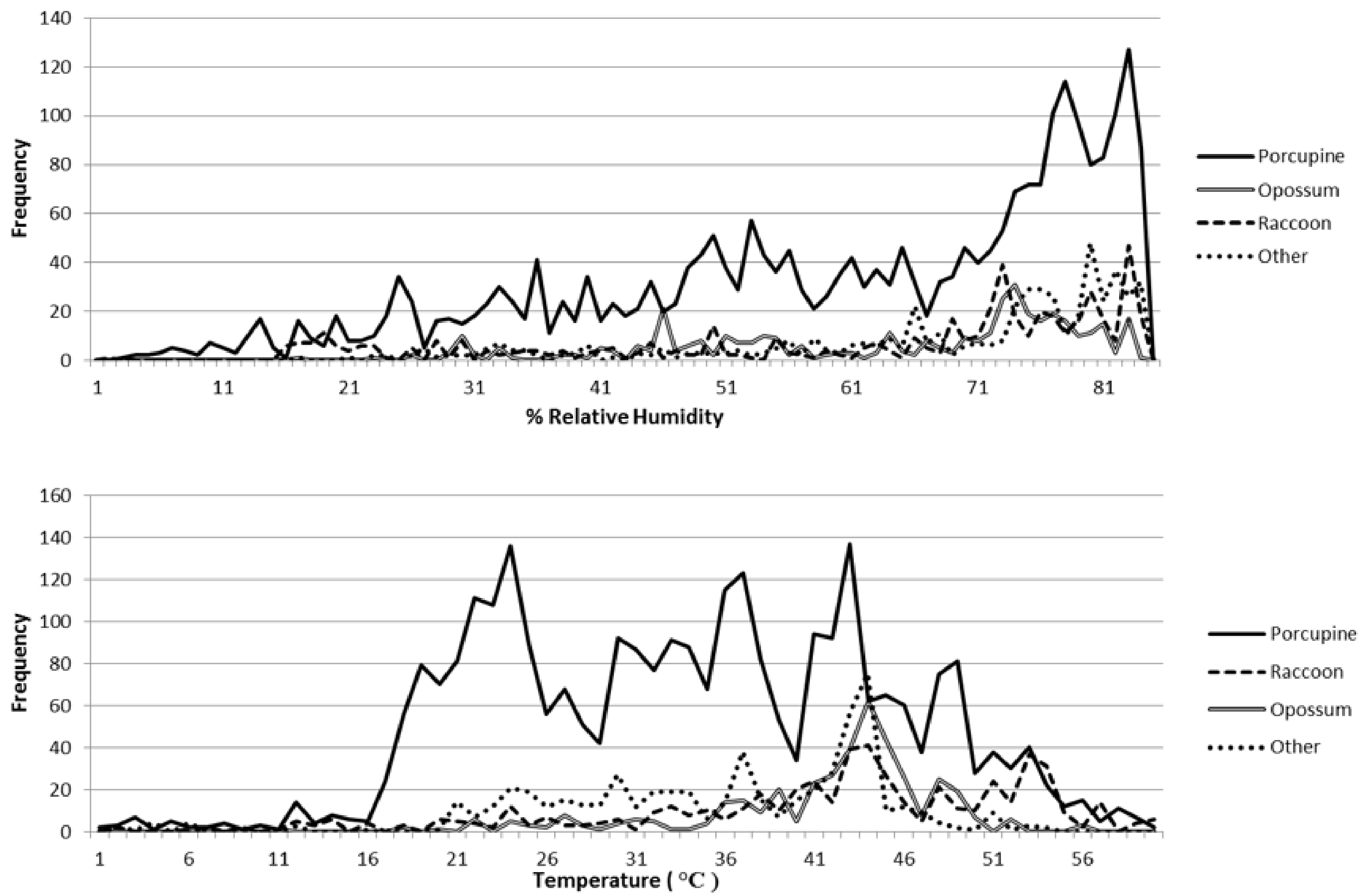

Figure 4. Photograph frequency by temperature (above) and relative hmidity (below) taken at cave entrances of North American porcupines, raccoons, Virginia opossums, and all other meso-mammals in Camp Bullis caves near San Antonio, Texas, 1 February 2014–31 March 2015.

Table 3. The mean and 95% confidence interval of external temperature and relative humidity for cave entrance photographs of North American porcupines, Virginia opossums, raccoons, all other meso-mammal species at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

Species	Temperature Mean (CI)	% Relative Humidity Mean (CI)
Porcupine	13.92 (13.52, 14.32)	77.26 (76.52, 78.00)
Opossum	21.45 (20.77, 22.14)	79.30 (77.79, 80.82)
Raccoon	21.74 (20.77, 22.70)	78.03 (76.21, 79.86)
Other	15.65 (14.89, 16.42)	85.16 (83.86, 86.46)
Annual	19.18 (19.10, 19.27)	74.66 (74.46, 74.86)

Species assemblage

My 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, Griesemer et al. 1998, Morin et al. 2005, Roze 2009, Moseley 2007, Moseley et al. 2013). One picture in particular 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 opossums were likely 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 4 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 caves' 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 lends us to believe it was used as a den (Newman 1913, Taber 1945, Clark 1951) which was confirmed by photographs of a nine-banded armadillo carrying dried grass under its body which is characteristic for 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, Griesemer et al. 1996, Griesemer et al. 1998, Roze 2009), but my 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-mammals 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, endangered species caves were more intensely managed including 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). The rigorous management of fire ants is intended to support greater cave crickets (*Ceuthophilus* spp.) numbers since cave cricket are generally associated with a greater abundance of cave-obligate species, including endangered species (Gary 2009). This management practices makes the endangered species caves more desirable to raccoons and Virginia opossums since cave crickets are a food source for both species (Elbroch and Rinehart 2011). The North American porcupine's greater use of non-endangered species caves may be because they do not feed on cave crickets (Taylor 1935). Additionally, the majority of endangered species caves had pit entrances, which were avoided by North American porcupines.

My vegetative cover data showed all mammal groups used forested caves most which was unsurprising since the 3 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. I was 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 my study are known to have periods of high CO_2 (Table 1; Gary 2009) though this did not appear to influence meso-mammal use positively or negatively. 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 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 (Table 1; Gary 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). Cave 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 my 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 opossums and raccoons 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 less influence on meso-mammal cave use. It is likely this weather variable was 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. Also the absence of meso-mammal monitoring 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 nutrients inputs are beneficial is unknown and may be fluctuating. For example, a cave system in the United Kingdom experienced 2 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 my study site, North American porcupines 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 my 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 which raccoons and Virginia opossums prey upon endangered cave invertebrates and if it is likely to affects the arthropods' long-term survival. If the levels of endangered species take is negligible, as suspected, researchers should then investigate raccoons and Virginia opossums 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 no meso-mammal nutrient inputs could affect cave-obligate species' survival.

CHAPTER III

MESO-MAMMAL BEHAVIOR AND RESOURCE USE IN CENTRAL TEXAS CAVES

Introduction

Mammals serve an important function in a cave's ecosystem through the introduction of nutrients into the oligotrophic caves via their scat (Gary 2009). If there are too few nutrients, cave obligate species have no nutritional resources; too much and they are out-competed by less specialized, facultative species (Gary 2009). Previous studies have noted the frequency and type of meso-mammal cave visitation (Table 1), but there is still relatively little research confirming meso-mammal behavioral activities within caves.

Determining typical behaviors and motivations of meso-mammals in caves is essential for management decisions related to cave natural resources. The management of meso-mammal use and behavior is especially important at Joint Base San Antonio – Camp Bullis (hereafter Camp Bullis) where many of the caves are actively managed for 3 United States federally listed endangered invertebrates *(Cicurina madla*, *Rhadine exilis*, *Rhadine infernalis*) as well as cave crickets (*Ceuthophilus* spp.) whose eggs serve as an important food source for many cave-obligate species. For example, a biologist might manage a denning, non-insectivore meso-mammal differently than an insectivore if the target cave is home to an endangered arthropod. A denning meso-mammal would likely cause little stress to endangered species as it added nutrients to the cave system through scat deposition. On the other hand, an insectivorous meso-mammal would bring in nutrients through their scat, but also potentially prey on the endangered arthropod.

Furthermore, management based on an incomplete understanding in the ecosystem dynamics of a cave can affects 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*; 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 to $44 million (Degollado 2014).

Current literature on the behaviors of meso-mammals in caves generally focuses on singular caves, seasons, or consists of observations made secondary to a primary research questions (Elder and Gunier 1981, Pape 2014). Because of this, I can only speculate as to why mammal cave use in central Texas occurs or what constitutes typical or atypical use. Researchers have documented the extensive use of Camp Bullis caves by North American porcupines (*Erethizon dorsatum*), raccoons (*Procyon lotor*), and Virginia opossums *(Didelphis virginiana*; Gary 2009, Table 1). Studies have suggested that raccoons and Virginia opossums hunt and den in caves (Winkler and Adams 1972, Allen et al. 1985, Martin et al. 2003, Elliott and Ashley 2005, Elbroch and Rinehart 2011, Moseley et al. 2013), whereas North American porcupines solely use caves as den sites (Woods 1973, Morin et al. 2005, Roze, 2009).

The goal of this study was to determine the behaviors and resource use of meso-mammals in central Texas caves. My objectives were to (1) determine which meso-mammal species use caves for denning, feeding, hunting, and grooming behaviors, and (2) determine if any behaviors are associated with particular seasons or time of day.

Study Area

I performed this study on the Camp Bullis (11,286 ha) just north of San Antonio, Texas, USA at the cross-section of the Edward's Plateau, South Texas Plains, and the Blackland Prairie ecoregions (Fig. 5; Gould 1975). For my 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). I monitored 4 caves with the most meso-mammal activity (Table 1) for 1 month per season. I 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 4). Only 4 caves were studied because I wanted to ensure all cave rooms and passages could be simultaneously monitored with cameras.

Methods

I monitored caves with the 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. Cameras were positioned to cover as much of the cave as possible, especially where there were animal signs (e.g., scat, scratches, tracks, hair). I examined the videos for the presence of meso-mammals, defined for this study as any mammal at least as at

Figure 5. Location of 4 caves monitored for 1 year on Camp Bullis near San Antonio, Texas, USA, 2015–2016.

Table 4. Caves monitored by seasons of data collection and corresponding cave length, cave depth, and known meso-mammal visitors at Camp Bullis near San Antonio, Texas, USA, 2015–2016.

	Seasons				Length (m)	Depth (m)	CO_2	North American Porcupine	Raccoon	Virginia Opossum
	W	Sp	Su	F						
Chigger			X	X	20	5	X	X	X	X
Constant Sorrow	X	X	X	X	6	1.5		X	X	X
Horse Tooth			X	X	6.3	2.8	X	X	X	
Well Done	X	X	X	X	34	3		X	X	X

least large as a cottontail rabbit (*Sylvilagus* spp.; Hoffman 2010) up to the size of a North American porcupine.

For each video with a meso-mammal, I noted the location, date, season, species, number present, and time of day. I 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 (7 seconds) could be attributed to a single behavior. I defined 'feeding or hunting' as when a meso-mammal was trailing, reaching towards, or eating a known prey species. I defined 'grooming' as when the video showed a meso-mammal scratching, cleaning, or shaking their fur. I defined 'resting' as when a meso-mammal was shown sitting or lounging in at least 2 successive videos with little additional movement. This included no signs of feeding, hunting, or grooming. I defined a behavior as 'other' when a less common action could confidently be identified (e.g., fighting or defecating). I 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.

Results

Behaviors

During the course of this study, I recorded 569, 10-second videos (totaling 94.8 minutes of video) of 3 meso-mammal species and were able to assign behaviors for 126 videos (totaling 21 minutes of video). North American Porcupines (72%) were the most commonly captured species with a majority of videos showing individuals resting,

Table 5. An annual distribution of grooming, resting, hunting/feeding, and other behavior videos for North American porcupine, raccoon, and Virginia opossum on Camp Bullis near San Antonio, Texas, USA, 2015–2016.

	Grooming	Resting	Hunting/ Feeding	Other
North American Porcupine	35 (38%)	52 (57%)	–	5 (5%)
Raccoon	–	–	1 (100%)	–
Virginia Opossum	–	–	34 (100%)	–

followed by grooming (Table 5). Additionally, 5 videos were categorized as other behaviors and included 3 videos of an individual hiding during initial camera set-up, a video of an individual defecating, and a video of 2 individuals aggressively posturing (Table 5). Virginia opossums (27%) were the second most commonly captured species with all videos showing feeding or hunting, and raccoons had a single video of a known behavior showing feeding or hunting (Table 5).

Timing

I recorded meso-mammal videos in all 4 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 hunting or feeding videos while 90% of fall videos were resting, and grooming (Fig. 6). The hourly distribution of behavior videos had bimodal distributions. Feeding or hunting peaked at 0500 hours and 2000 hours ($\bar{x}$ = 1000 hours), grooming videos peaked at 0500 hours and 1500 hours ($\bar{x}$ = 0800 hours), and resting videos peaked at 0500 hours and 2000 hours ($\bar{x}$ = 1100 hours; Fig. 7).

Discussion

The species recorded in this study match the 3 most common species found using the caves at this study site: North American porcupines, raccoons, and Virginia opossums (Table 1). I expected to have recorded a greater number of raccoon videos as compared to Virginia opossum videos based off previous surveys of local meso-mammal cave visitation (Table 1). The relative paucity of raccoon videos 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

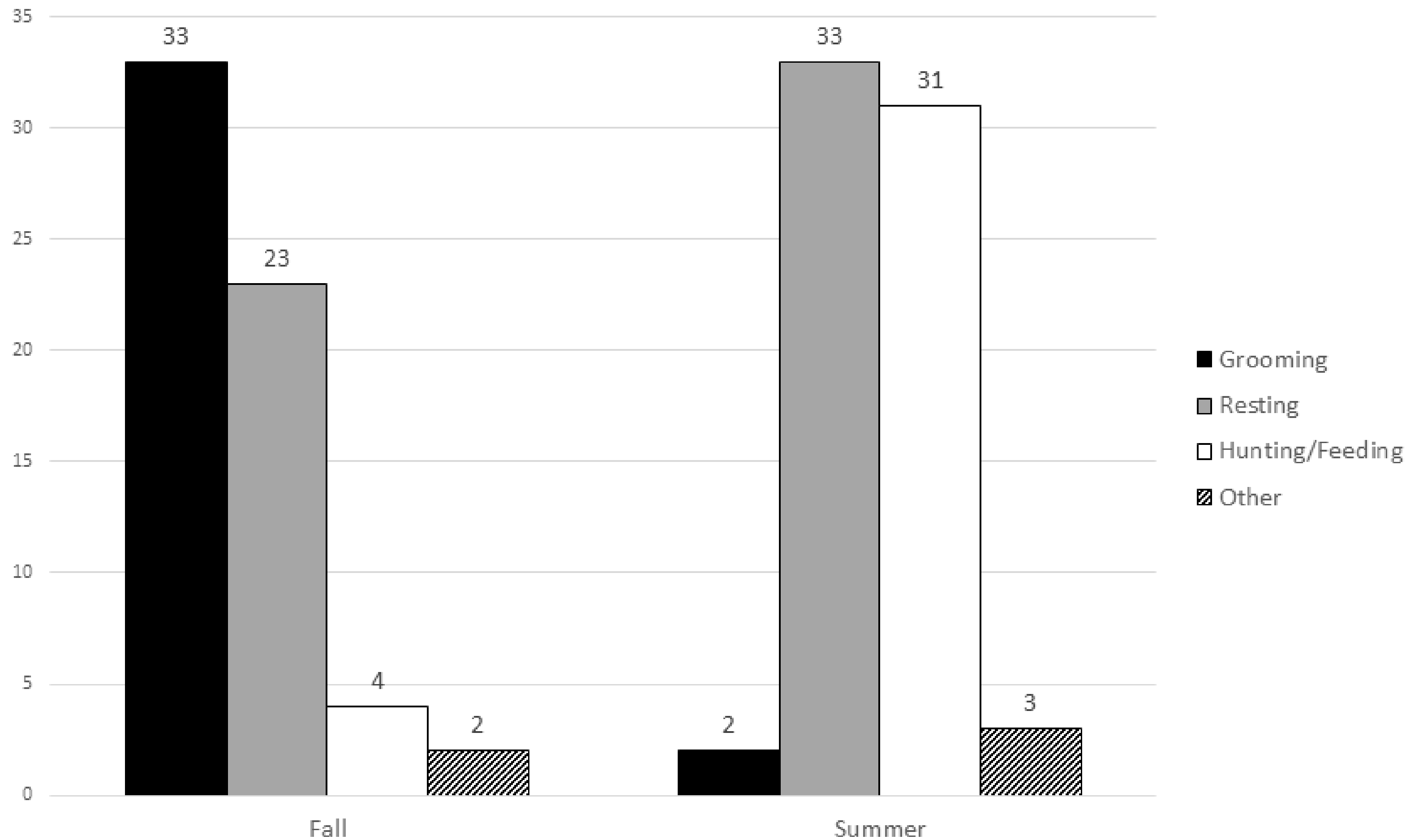

Figure 6. An annual count of grooming, resting, hunting/feeding, and other behavior videos during the fall and summer seasons on Camp Bullis near San Antonio, Texas, USA, 2015–2016.

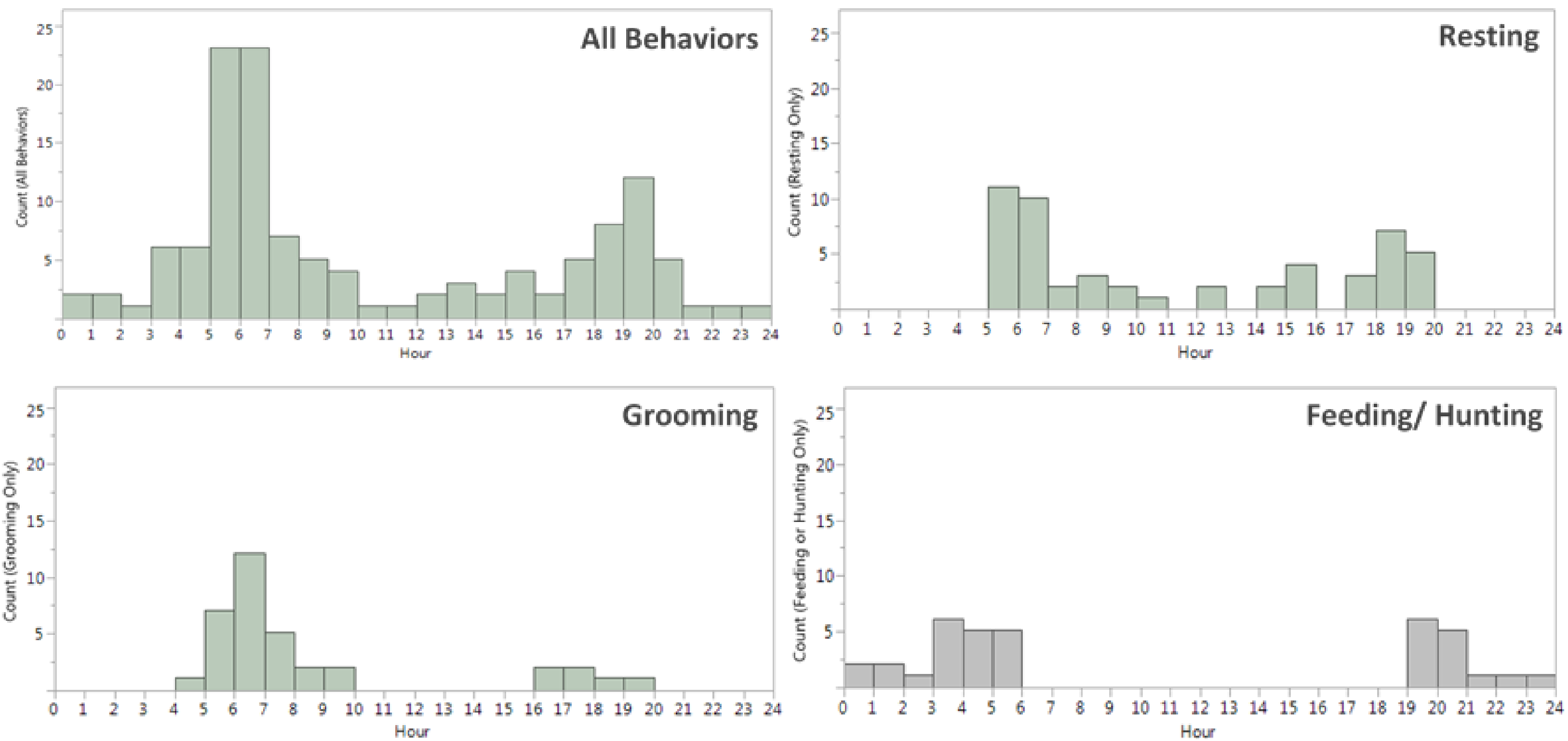

Figure 7. Annual frequency of behaviors according to hour for all behavior videos, resting videos, grooming videos, and feeding or hunting videos on Camp Bullis, Texas, USA, 2015–2016.

Constant Sorrow Cave historically had regular raccoon visitation (Table 1). 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 denning 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 (Table 1).

Behaviors

My data showed a clear separation of cave behaviors according to species and agrees with previous studies that suggest North American porcupines generally use caves for resting and denning (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 denning. I did not see this behavior during the course of this study, but since both species characteristically rotate use of several den sites, this population may use other den sites preferentially for these activities. My videos also show both species hunting arthropods though I was unable to identify the species. The consumption of arthropods is an important aspect of cave ecology in the area, because of the presence of 3 United States, federally listed endangered arthropods (*Cicurina madla, Rhadine exilis, Rhadine* *infernalis*) and cave crickets (*Ceuthophilus* spp.). These endangered species are only found in select caves in central Texas and the cave crickets eggs are an important food source for the *Rhadine* spp. beetles, in particular (Gary 2009).

North American Porcupine research has found varying degrees of territoriality depending on the population (Roze 2009, Sweitzer 2003, Elbroch and Rinehart 2011). My data included video of aggressive posturing by 2 North American porcupines confirming that there is some degree of territoriality in this population, though multiple Camp Bullis caves are known to be simultaneously used by several individuals.

Defecation by North American porcupines into the caves is perhaps the most ecologically important behavior recorded by the cameras. 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 meso-mammal nutrient input of both cave crickets (*Ceuthophilus* spp.; Reddell 1994) and raccoons (Veni et al. 2002) but are now dominated by North American porcupines (Table 1). 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.

Timing

Meso-mammal behavior was highly seasonal. 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). As expected, most behaviors occurred around dawn and dusk when meso-mammals are most active in caves (Fig. 3). Additionally, grooming videos were most often recorded during the day, when North American porcupines are in caves denning. Feeding or hunting activities often occurred during the night, when Virginia opossums typically active and looking for food.

I 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 they 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. I 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) should be considered.

Conclusions

This study confirms the use of caves by meso-mammals largely for hunting and denning. These activities, performed in central Texas caves, have the potential for to alter the diversity of cave-obligate species. Oligotrophic caves require external nutrient subsidies to support these 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. The alteration of cave ecosystem dynamics is especially relevant for central Texas caves with multiple United States, federally endangered species. Further research is needed to confirm the behaviors of raccoons in central Texas caves as well as if meso-mammal behaviors are maintained elsewhere in their range.

CHAPTER IV

MODELING MESO-MAMMAL CAVE USE IN CENTRAL TEXAS

Introduction

Meso-mammals are an important part of a cave's ecosystem. Historic records suggest central Texas caves were historically associated with use by raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*; Veni et al. 2002) but are now used extensively by newly naturalized North American porcupines (*Erethizon dorsatum*; Table 1). The first record of North American porcupines in Joint Base San Antonio – Camp Bullis (hereafter Camp Bullis) caves did not occur until 2003 (C. Thibodeaux, Natural Resources Joint Base San Antonio, unpublished data). North American porcupines use caves for denning (Woods 1973, Morin et al. 2005, Roze 2009) and their scat deposits, previously absent from the ecosystem, represents a new and abundant nutrient input into the cave environment. The scat deposited by meso-mammals, such as North American porcupines, raccoons, and Virginia opossum, is an essential source of nutrition for cave-obligate species in the oligotrophic cave environment (Gary 2009) but too much and it may support the invasion of more competitive or predatory terrestrial species (Gary 2009). Understanding how meso-mammals interact with the cave ecosystem is especially critical for Camp Bullis because these caves are habitat for 3 federally endangered species (*Cicurina madla*, *Rhadine exilis*, *Rhadine infernalis*) and many rare species (Reddell 1994, Gary 2009).

Specifically, it is not well understood what variables influence cave use for multiple meso-mammal species and the magnitude of their influence. Knowing which climactic and cave characteristics encourage or dissuade meso-mammal cave use will allow cave managers to better anticipate and manage a specific cave's nutrient needs. This information is especially important because risks to federally endangered cave species can impact the growth of surrounding communities. For example, in San Antonio, Texas the federally endangered Bracken Bat Cave meshweaver (*Cicurina venii*) was detected for the first time in 3 decades during the construction of a $15 million (USD) highway expansion project (Davila 2012). As a result, the project was modified, nearly tripling the cost to $44 million (USD; Degollado 2014).

My goal with this study was to determine why meso-mammals choose to use particular caves. Specifically, my objective was to construct a model using cave characteristics and climate parameters to accurately predict cave use by North American porcupine, raccoon, and Virginia opossum.

Method

I performed this study on Joint Base San Antonio – Camp Bullis (11,286 ha) just north of San Antonio, Texas at the cross-section of the Edward's Plateau, South Texas Plains, and Blackland Prairie ecoregions (Gould 1975). I randomly selected 30 caves (Fig. 1), defined as any naturally-formed, humanly-accessible cavity at least 5m deep and/or long where none of the entrance dimensions exceeds the length or depth (Gary 2009). The 30 caves varied in length from 3 – 235 m ($\bar{x}$ = 44) and in depth from 1.2 – 46 m ($\bar{x}$ = 13; Table 1). Forty three percent had at least 1 endangered species, 60% were in the Edward’s aquifer recharge zone, 13% had a permanent water source, 83% had structural modifications (e.g., enlarged entrances or passages, excavated entrances or passages, debris removal), and 23% had gates to prevent unauthorized use and protect cave resources (Table 1). Eighty-three percent of caves had entrances in forest cover (trees form at least 25% of the canopy cover), 10% had entrances in herbaceous cover (majority of ground cover was native or naturalized herbaceous vegetation), and 7% had entrances in mixed shrub (vegetative cover was dominated by both trees and shrubs buth neither was more than 75% of the canopy cover; USGS 2001; Table 1).

I monitored caves with Cuddeback Attack IR (Cuddeback Digital, De Pere, WI) and Browning Range Ops (Browning Trail Cameras, Birmingham, AL) infrared game cameras placed at cave entrances for a minimum of 4 weeks in every season. Seasons were defined according to month: summer (June–August); fall (September–November); winter (December–February); spring (March–May). I placed cameras at an angle that allowed the camera to monitor the entire cave entrance while tilted slightly up to minimize triggers from mice and rats.

I examined pictures for the presence of North American porcupines, raccoons, and Virginia opossums. I focused on these 3 species because they compromise the large majority (87%) of all meso-mammal cave visitors in this area (Table 1). For all photos with 1 of these 3 species, I noted the date, time, season, hourly temperature, hourly percent humidity, and hourly barometric pressure. My weather data was collected with on-site weather stations using Onset Hobo U30 data loggers (Onset Computer

Corporation, Bourne, MA), Onset temperature and humidity sensor (S-THB-M002), and Onset Barometric Pressure Smart Sensor (S-BPB-CM50).

I used this data to develop a multinomial logistic regression model designating North American porcupine (1), raccoon (2), and Virginia opossum (3) as the response variables. For the explanatory variables I included the continuous variables of temperature (°C), percent relative humidity, barometric pressure (mbar), and hour of the meso-mammal photo (24h). I also included the variables of distance to major road (m) and distance to minor road (m) measured using the distance tool in ArcMap 10.3 (Environmental System Research Institute [ESRI], Redlands, CA). I define major roads as paved roads accessible by any vehicle while minor roads were either dirt or caliche and only accessible by truck or all-terrain vehicle (ATV). I included categorical variables for each season (winter [1 = present, 0 = absent], spring [1 = present, 0 = absent], summer [1 = present, 0 = absent], fall [1 = present, 0 = absent]), as well presence of a permanent water source (1 = present, 0 = absent), entrance gate (1 = present, 0 = absent), endangered species (1 = present, 0 = absent), seasonally high levels of carbon dioxide (CO_2; 1 = present, 0 = absent), constructed or excavated areas (1 = present, 0 = absent) and cave entrance type (1 = pit, 2 = horizontal). With the horizon designated at 0°, I defined a horizontal entrance as those measuring from ± 0 – 45° while a pit cave's entrance angle measured from ± 46 – 90°. I also included if caves were in the Edward's aquifer recharge zone (1 = present, 0 = absent), and if they were located in forested cover (1 = present, 0 = absent), herbaceous cover (1 = present, 0 = absent), or mixed shrub cover (1 = present, 0 = absent).

Before model selection I examined each variable for collinearity by calculating their variance inflation factors (VIF). If at least 1 variable had a VIF of 5 or greater (i.e., 80% of the variable can be represented by other independent variables), I removed the largest from the dataset (Rogerson 2001, Vu et al. 2015) and recalculated VIFs. I repeated this until all parameters in the dataset had a VIF less than 5. I began model selection by randomly selecting 80% of the total dataset, therefore creating the training dataset (Table 6), and designated North American porcupine (1) as the base response variable. I analyzed full, reduced, and constant only models and the strongest model was selected using the goodness-of-fit, lack of fit, Akaike information criterion (AIC_c), effects likelihood ratios, and the area under the receiver operating curve (AUC). An AUC value (range = 0 – 1) demonstrates a logistic model's ability to differentiate between groups (i.e., North American porcupine, raccoon, Virginia opossum cave use). A model where the AUC = 1 indicates the model perfectly distinguishes between the groups while an AUC = 0.5 indicates the model predicts the group no better than random.

After a model was selected, I also calculated the odds ratio for each model parameter keeping 'North American porcupine' as the base response variable. I validated the model with the validation dataset (remaining 20%; Table 6) reporting the results for the whole-model test, goodness-of-fit test, AIC_c, and AUC.

Results

I collected a total of 3,804 cave entrance photographs of North American porcupines, raccoons, and Virginia opossums. The large majority of photographs

Table 6. Sample size and percent North American porcupine, raccoon, and Virginia opossum photographs for the total dataset, and the resulting training dataset (80%), and validation dataset (20%) collected at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

	n =	Porcupine	Raccoon	Opossum
Total dataset	3804	2863 (75.3%)	535 (14.1%)	406 (10.7%)
Training dataset	3043	2307 (75.8%)	420 (13.8%)	316 (10.4%)
Validation dataset	761	556 (73.1%)	115 (15.1%)	90 (11.8%)

captured North American porcupines, followed by raccoons and Virginia opossums (Table 6). I calculated the VIF for each the variables and first removed the variables of mixed shrub cover and the fall season. Testing of these two variables showed ‘zeroed’ parameters indicating both showed very strong linear dependencies. I re-calculated VIFs and, in order, I removed the parameters of caves with permanent water source (VIF = 9.95), distance to major road (VIF = 8.56), and caves with endangered species (VIF = 6.64) before model selection. This left distance to nearest road (VIF = 2.20), the winter season (VIF = 1.92), spring season (VIF = 1.60), summer season (VIF = 1.83), temperature (VIF = 2.97), percent relative humidity (VIF = 1.34), barometric pressure (VIF = 1.72), hour of photograph (VIF = 1.28), caves in the aquifer recharge zone (VIF = 2.04), caves with seasonally high levels of CO_2 (VIF = 1.68), caves with construction or excavation (VIF = 1.51), caves with a gate (VIF = 1.92), entrance type (VIF = 2.73), caves with forested cover (VIF = 2.67), and caves with herbaceous cover (VIF = 2.20) as parameters available during model selection.

I first calculated the ‘full model’ using the training dataset (Table 6). The whole model test was significant, lack of fit was non-significant, and all parameters were significant (Table 7). In hopes of finding a simpler model, I removed the parameter barometric pressure and calculated the statistics for the model ‘reduced A’. With ‘reduced A’, the whole model test remained was significant, lack of fit was non-significant, all parameters were significant, AUC was consistent, and the AIC_c increased from 2424.9 to 2430.2 (ΔAIC_c = 5.3; Table 7). I further simplified the potential model removing the parameter of hour of photograph, calculating the model ‘reduced B’. The

Table 7. The potential full and reduced multinomial regression models (including ‘reduced C’, the selected model) and their corresponding whole model statistics, lack of fit statistics, Akaike Information Criterion (AIC_c), parameter effects likelihood ratios (construction and excavation [Const./Excav.], entrance type, spring season, distance to nearest road [Dist. Nearest Rd], summer season, winter season, forested cover, herbaceous [Herb.] cover, temperature, relative humidity [R. Humidity], gated entrances, aquifer recharge zone, seasonally high CO_2 [CO_2], hour of photograph, and barometric [Baro] pressure), and area under the receiver operating curve (AUC; 1 = North American porcupine, 2 = raccoon, 3 = Virginia opossum) for data collected at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

	Whole Model	Lack of Fit	AIC_c	Effects Likelihood Ratio	AUC
Full Model	$\chi^2 = 2012.78$; $P < 0.01$	$\chi^2 = 2339.58$; $P = 1.00$	2424.90	Const./Excav. ($\chi^2 = 309.17$; $P < 0.01$) Entrance ($\chi^2 = 211.95$; $P < 0.01$) Spring ($\chi^2 = 116.58$; $P < 0.01$) Dist. Nearest Rd ($\chi^2 = 95.97$; $P < 0.01$) Summer ($\chi^2 = 86.76$; $P < 0.01$) Winter ($\chi^2 = 85.43$; $P < 0.01$) Forested Cover ($\chi^2 = 76.27$; $P < 0.01$) Herb. Cover ($\chi^2 = 70.08$; $P < 0.01$) Temperature ($\chi^2 = 35.06$; $P < 0.01$) R. Humidity ($\chi^2 = 34.78$; $P < 0.01$) Gate ($\chi^2 = 31.20$; $P < 0.01$) Aquifer ($\chi^2 = 18.94$; $P < 0.01$) CO_2 ($\chi^2 = 15.00$; $P < 0.01$) Hour ($\chi^2 = 10.69$; $P < 0.01$) Baro Pressure ($\chi^2 = 9.42$; $P = 0.01$)[a]	1 = 0.93 2 = 0.89 3 = 0.91
Reduced A	$\chi^2 = 2002.86$; $P < 0.01$	$\chi^2 = 2338.58$; $P = 1.00$	2430.24	Const./Excav. ($\chi^2 = 334.42$; P < 0.01) Entrance ($\chi^2 = 259.97$; P < 0.01) Spring ($\chi^2 = 110.52$; P < 0.01) Dist. Nearest Rd ($\chi^2 = 99.76$; P < 0.01) Summer ($\chi^2 = 90.51$; P < 0.01)	1 = 0.93 2 = 0.89 3 = 0.90

Table 7, Continued.

	Whole Model	Lack of Fit	AIC_c	Effects Likelihood Ratio	AUC
				Winter ($\chi^2 = 81.45$; P < 0.01) Forested Cover ($\chi^2 = 74.18$; P < 0.01) Herb. Cover ($\chi^2 = 62.99$; P < 0.01) Temp. ($\chi^2 = 26.95$; P < 0.01) R. Humidity ($\chi^2 = 29.75$; P < 0.01) Gate ($\chi^2 = 39.12$; P < 0.01) Aquifer ($\chi^2 = 19.99$; P < 0.01) CO_2 ($\chi^2 = 9.37$; P = 0.01) Hour ($\chi^2 = 9.76$; P = 0.01)[a]	
Reduced B	$\chi^2 = 1993.10$; $P < 0.01$	$\chi^2 = 2284.42$; $P = 1.00$	2435.92	Const./Excav. ($\chi^2 = 333.25$; P < 0.01) Entrance ($\chi^2 = 260.80$; P < 0.01) Spring ($\chi^2 = 112.21$; P < 0.01) Dist. Nearest Rd ($\chi^2 = 100.12$; P < 0.01) Summer ($\chi^2 = 93.81$; P < 0.01) Winter ($\chi^2 = 78.64$; P < 0.01) Forested Cover ($\chi^2 = 76.02$; P < 0.01) Herb. Cover ($\chi^2 = 63.83$; P < 0.01) Temperature ($\chi^2 = 31.88$; P < 0.01) R. Humidity ($\chi^2 = 20.39$; P < 0.01) Gate ($\chi^2 = 39.38$; P < 0.01) Aquifer ($\chi^2 = 19.69$; P < 0.01) CO_2 ($\chi^2 = 10.72$; P < 0.01)[a]	1 = 0.93 2 = 0.89 3 = 0.90
Reduced C	$\chi^2 = 1982.38$; $P < 0.01$	$\chi^2 = 2295.13$; $P = 1.00$	2442.57	Const./Excav. ($\chi2 = 330.48$; P < 0.01) Ent. ($\chi2 = 277.33$; P < 0.01) Spring ($\chi2 = 111.43$; P < 0.01) Dist. Nearest Rd ($\chi2 = 109.18$; P < 0.01) Summer ($\chi2 = 95.14$; P < 0.01)	1 = 0.93 2 = 0.89 3 = 0.90

Table 7, Continued.

	Whole Model	Lack of Fit	AIC$_c$	Effects Likelihood Ratio	AUC
				Winter (χ^2 = 94.96; P < 0.01) Forested Cover (χ^2 = 75.65; P < 0.01) Herb. Cover (χ^2 = 73.42; P < 0.01) Temperature (χ^2 = 28.98; P < 0.01) Gate (χ^2 = 60.40; P < 0.01) Aquifer (χ^2 = 38.48; P < 0.01) R. Humidity (χ^2 = 19.70; P < 0.01)[a]	
Reduced D	χ^2 = 1962.68; *P* < 0.01	χ^2 = 939.60; *P* < 0.01	2458.19	Const./Excav. (χ^2 = 321.62; P < 0.01) Entrance (χ^2 = 283.19; P < 0.01) Spring (χ^2 = 128.35; P < 0.01) Dist. Nearest Rd (χ^2 = 115.79; P < 0.01) Summer (χ^2 = 100.16; P < 0.01) Winter (χ^2 = 97.40; P < 0.01) Forested Cover (χ^2 = 75.38; P < 0.01) Herb. Cover (χ^2 = 73.28; P < 0.01) Temp. (χ^2 = 23.75; P < 0.01 Gate (χ^2 = 62.83; P < 0.01) Aquifer (χ^2 = 41.08; P < 0.01)	1 = 0.93 2 = 0.89 3 = 0.90

[a] Parameter removed in subsequent model

whole model test remained significant, there was no lack of fit, all parameters were significant, AUC remained the same, and the AIC_c again increased from the whole model's 2424.9 to 2435.9 (ΔAIC_c = 11.0; Table 7). We, again, further simplified the model with the removal of the seasonally high CO_2 parameter calculating the model 'reduced C'. The whole model test remained significant, there was no lack of fit, all parameters were significant, AUC remained the same, and the AIC_c also increased from the whole model's 2424.9 to 2442.6 (ΔAIC_c = 17.7; Table 7). The final model simplification was the model 'reduced D' with the removal of the parameter percent relative humidity. The whole model test remained significant, there was now a lack of fit, all parameters were significant, AUC remained the same, and the AIC_c increased from the whole model's 2424.9 to 2458.2 (ΔAIC_c = 33.3; Table 7).

I considered the full model, 'reduced A', 'reduced B', and 'reduced C' as potential models since all had significant whole model tests, no lack of fit, significant parameters, and similar AUCs (Table 7). Ultimately I chose 'reduced C' as the best model because it maintained similar predictive power, despite the elimination of parameters, and showed an acceptable increase in the AIC_c (ΔAIC_c = 33.3; Table 7). Application of the model correctly classified 97% of North American porcupine entrance photos, 57% of raccoon photos, and 59% of Virginia opossum photos (Table 8).

I calculated the odds ratios (OR; Table 9) and found that compared to North American porcupines, raccoons and Virginia opossums had greater odds of using caves with gates, and pit entrances. Raccoons and Virginia opossums also had lower odds than North American of visiting caves in the spring and winter, using caves with herbaceous

Table 8. The chosen model's ('Reduced C') ability to correctly predict North American porcupine, raccoon, and Virginia opossum cave visitation at Camp Bullis, near San Antonio, Texas, 1 February 2014 –31 March 2015.

		Model Predicted ID		
		North American porcupine	Raccoon	Virginia opossum
Photo ID	North American Porcupine	2242 (97.18%)	54 (2.34%)	11 (0.48%)
	Raccoon	157 (37.38%)	240 (57.14%)	23 (5.48%)
	Virginia opossum	106 (33.54%)	23 (7.28%)	187 (59.18%)

Table 9. The chosen model's ('Reduced C') parameter estimates, χ^2 test of significance, and odds ratios for Virginia opossum vs. North American porcupine (3/1) and raccoon vs. North American porcupine (2/1) at Camp Bullis, near San Antonio, Texas, 1 February 2014–31 March 2015.

	Parameter	Estimate	χ^2; P-value	Odds Ratio
Log odds 3/1	Intercept	−4.91	45.23; <0.01	0.01
	C/E [1]	−2.00	197.12; <0.01	0.14
	Entrance [1]	0.80	30.72; <0.01	2.23
	Season			
	Spring [1]	−1.27	72.13; <0.01	0.28
	Summer [1]	−0.01	0.01; 0.92	0.99
	Winter [1]	−0.99	68.31; <0.01	0.37
	Cover			
	Herbaceous [1]	−2.13	15.52; <0.01	0.12
	Forested [1]	−1.22	63.75; <0.01	0.30
	Gate [1]	1.41	44.48; <0.01	4.10
	Dist. To Nearest Rd	−0.002	1.33; 0.25	1.00
	Aquifer [1]	0.10	0.84; 0.36	1.11
	Temp	0.05	25.15; <0.01	1.05
	%RH	0.02	18.19; <0.01	1.02
Log odds 2/1	Intercept	−1.89	14.15; <0.01	0.15
	C/E [1]	−0.87	69.35; <0.01	0.42
	Entrance [1]	1.81	205.22; <0.01	6.11
	Season			
	Spring [1]	−0.78	41.70; <0.01	0.46
	Summer [1]	−0.97	65.16; <0.01	0.38
	Winter [1]	−0.85	47.29; <0.01	0.43
	Cover			
	Herbaceous [1]	−1.53	30.06; <0.01	0.22
	Forested [1]	−0.74	24.11; <0.01	0.48
	Gate [1]	0.86	32.90; <0.01	2.36
	Dist. To Nearest Rd	−0.01	95.04; <0.01	0.99
	Aquifer [1]	−0.54	30.41; <0.01	0.58
	Temp	0.002	0.04; 0.84	1.00
	%RH	0.01	5.43; 0.02	1.01

or forested cover, and using caves that had been constructed or excavated. Said another way, North American porcupines were more likely to use caves in the spring and winter, use non-gated, constructed or excavated caves, as well as caves with herbaceous or forested cover (Fig. 8).

I validated the model using the validation dataset model (Table 6) maintained a significant whole model test (χ^2 = 5558.99; P < 0.01), no lack of fit (χ^2 = 606.16; P = 1.00), an even lower AIC_c (662.84), and AUC of 0.94 for North American porcupines, 0.91 for raccoons, and 0.92 for Virginia opossums.

Discussion

This model gives us an effective means of predicting meso-mammal cave use and also enumerates how variables influence their visitation. My dataset consisted largely of North American porcupine data and unsurprisingly the model best predicts their use of caves. Though the AUC for each of the species is similarly high, caution should be taken when using it to predict raccoon and Virginia opossum cave use since application of the model correctly assigned less than 60% of their cave visit photos.

The number of parameters in this model demonstrate the complexity of meso-mammal cave use and how these 3 species balance their preferences of multiple climactic and cave characteristics. The parameter with the strongest effect likelihood ratio differentiated if caves had constructed or excavated areas which included reinforced, excavated, or enlarged entrances, excavated passages, or debris removal. This was done to either confirm the cave designation, determine the extent and areas relevant to endangered species and groundwater, or allow for safer conditions (Gary

Figure 8. A North American porcupine using a cave with a horizontal entrance, forested cover, and no gate on Camp Bullis, near San Antonio, Texas, USA, 2015–2016.

2009). All 3 species are very nimble and are known to use portions of caves inaccessible to humans but my data showed raccoons and Virginia opossums less likely than North American porcupines to use caves with constructed or excavated areas. I suspect the added bulk of the North American porcupine's quills and their reduced dexterity made non-excavated caves more difficult to access.

Entrance type was the parameter with the second strongest effect likelihood ratio. All 3 species are known to use both pit and horizontal cave entrances at Camp Bullis (Table 1), but the model demonstrated that North American porcupines are more likely than both raccoons and Virginia opossums to use horizontal entrances. This might be a result of the North American porcupine's more limited dexterity and the potential of fatal injury from falling in a pit entranced cave. Similarly, my data also shows Raccoons and Virginia opossums to have greater use of gated caves compared to North American porcupine. Gates are used on selected Camp Bullis caves to prevent injury or vandalism from trespassers and are designed to allow the passage of full-sized raccoons. Though raccoons and North American porcupines often overlap in weight (Burt 1998), again I suspect the added bulk of the North American porcupine's quills and reduced dexterity made gated cave entrances less ideal.

Surprisingly, my data also shows that compared to North American porcupines, both raccoons and Virginia opossums were less likely to use caves with forested cover. This was surprising since all 3 species are associated with dense, wooded habitats (Shirer and Fitch 1970, Juen 1981, Sweitzer 1996). This may be a result of the raccoons and Virginia opossums' habitat flexibility and ability to thrive in even urban environments.

Caves often serve as refuge for animals during temperature extremes (Roze 1987, Wolfe 1990, Griesemer et al. 1996, Elbroch and Rinehart 2011) so it was not surprising that temperature was a significant parameter in this model. Camp Bullis caves maintain steady temperatures at 20 ± 3°C (Gary 2009). This microclimate is a considerable resource for North American porcupines which, unlike raccoons and Virginia opossums (Elbroch and Rinehart 2011), cannot conserve energy during winter by entering torpor (Coltrane and Sinnott 2013). Accordingly, this model shows North American porcupine cave use associated with lower temperatures. I speculate the winter, spring and summer season parameters were found to be a significant for similar reasons.

Percent relative humidity was a surprising parameter since Camp Bullis caves typically maintain high year-round humidity (Gary 2009). My data shows North American porcupines using caves when relative humidity is low while Virginia opossums used caves when relative humidity was high. I do not believe caves are being used for relief from terrestrial humidity. Instead, surface humidity may signal meso-mammals to seek shelter from impending rain or storms. This strategy is unlikely to be useful in all circumstances. Many caves on Camp Bullis are natural sinks for surface water runoff and apt to flooding (Gary 2009) therefore drowning cave occupants (USFWS 2011). This is also relevant for the Aquifer parameter which categorized caves located in or out of the Edward's Aquifer recharge zone. My data shows Virginia opossums more likely to use caves in the aquifer recharge zone while raccoons used more caves that were not in the aquifer recharge zone. Despite the danger of flooding, this parameter also does not appear to deter regular meso-mammal use of caves (Table 1).

Management Implications

My model has clarified how North American porcupines, raccoons, and Virginia opossums chose caves and has estimated the magnitude of each variables influence. Additionally, the model can be applied to manage a cave's nutrient inputs through the manipulation of the parameters. This can be especially critical in managing an endangered species cave's nutrient levels. For example, if cave managers wanted to decrease nutrient inputs by limiting North American porcupines' use of a horizontal cave, managers might consider building-up the entrance into a pit or adding an entrance gate, therefore lowering the odds of North American porcupine visitation. In applying this research it is important to remember that all 3 of these meso-mammal species have large ranges and their cave preferences likely vary according to changes in habitats. For example, North American porcupine cave use in Alaska may be more strongly associated with temperature since, compared to central Texas, cold temperatures begin earlier, last longer, and are more severe. Accordingly, I suggest future research explore how meso-mammals select caves outside of central Texas.

CHAPTER V

NORTH AMERICAN PORCUPINE (*Erethizon dorsatum*) HOME RANGE, HABITAT SELECTION, AND CAVE USE IN CENTRAL TEXAS

Introduction

North American porcupines (*Erethizon dorsatum*) are an extremely adaptable species with populations found from the Alaska to the southwest (Taylor 1935, Elbroch and Rinehart 2011, Coltrane and Sinnott 2013). Accordingly, home range and habitat use varies considerably across their range. In Nevada North American porcupines had home range that averaged 15.3 ha for males and 8.2 ha for females, and preferred riparian habitats with buffalo-berry (*Shepardia argentia*) and willow (*Salix* sp.; Sweitzer 2003). In contrast, North American porcupines in Quebec had home ranges averaging at 20.9 ha for males and 15.4 ha for females, and selected for trembling aspen (*Populus tremuloides*) dominated deciduous and mixed forests (Morin et al. 2005).

The North American porcupine's adaptability has helped them expand their range and naturalize in 69% (n = 177) of Texas counties (Schmidly and Bradley 2016). The North American porcupine populations in central Texas are especially troubling because of their use of caves as den sites (Taylor 1935, Dodge and Barnes 1975, Griesemer et al. 1996). Central Texas caves are habitat for cave-obligate species who are adapted to a cave's oligotrophic conditions. The nutrients these species rely on comes from external sources, particularly the scat of meso-mammals such as the raccoons or North American porcupines (Calder and Bleakney 1965, Peck 1988, Elliott and Ashley

2005, Moseley et al. 2013). The caves on Joint Base San Antonio – Camp Bullis (hereafter Camp Bullis) include 3 endangered arthropod species (*Cicurina madla*, *Rhadine exilis*, *Rhadine infernalis*) that were historically associated with raccoon nutrient inputs (Reddell 1994). North American porcupine were first recorded in Camp Bullis caves in 2003 (C. Thibodeaux, Natural Resources Joint Base San Antonio, unpublished data). Therefore, North American porcupine scat represents a novel, and often abundant, nutrient source. This is alarming because while small additions to cave's nutrient input can help cave-adapted species, too much and cave-adapted species become vulnerable to more competitive or predatory terrestrial species (Gary 2009).

Currently, resource managers in central Texas do not have enough information to make informed management decisions regarding North American porcupine. This includes knowing what draws North American porcupines to particular habitat and how changes in the habitat might affect their numbers. The goal of this study was to determine how North American porcupines incorporate caves into their habitat use in central Texas. Specifically, my objectives were to (1) calculate North American porcupine home and home range overlap using data from GPS collars, and (2) determine significant habitat features using habitat selection ratios.

Method

I performed this study on Joint Base San Antonio - Camp Bullis (hereafter Camp Bullis; 11,286 ha) just north of San Antonio at the cross-section of the Edward's Plateau, South Texas Plains, and the Blackland Prairie ecoregions of Texas (Gould 1975). Typical vegetation includes pockets of mixed grass prairie, and mowed landscapes, and dense stands of Ashe juniper (*Juniperus ashei*), live oak (*Quercus virginiana*), and Texas oak (*Quercus fusiformis*). Camp Bullis has areas of both plains and rolling hills. This site has a limestone, karst geology that contains approximately 100 caves. For this study, caves were defined as naturally formed, humanly accessible cavities that are at least 5m in depth and/or length where no dimension of the entrance exceeds the length or depth (Gary 2009).

Caves known to have frequent North American porcupine use (Table 1) were first monitored with Cuddeback Attack IR trail camera (Cuddeback Digital, De Pere, WI). When the camera data showed a North American porcupine had entered a cave for daytime denning, I baited a large Tomahawk box trap (Tomahawk Live Trap, Hazelhurt, WI) with apples and salt and placed it in the cave entrance (Fig. 9 & 10). Traps were checked the next day at sunrise. Once a North American porcupine was trapped they were weighed and immobilized with Telazol (Zoetis Inc., Kalamazoo, MI) at a dosage of 9-11 mg/kg from a 100mg/ml solution (Hale et al. 1994). They were then sexed, and fitted with a GPS collar. I used 2 styles of collars including Telonics TGW-4200-2 GPS/SOB (location every 90 minutes) and Lotek G2C 171C WGPS (location every 2 hours, and every 6 hours between 06:00-18:00). These collar configurations were selected because they maximized the number of locations that could be collected while maintaining a battery-life of at least 6 months. North American porcupines were then returned to the trap to recover, and then were released at the trap site before dark. All procedures were performed under Texas Parks and Wildlife Research Permit SPR-0914-168 and Texas A&M Institutional Animal Care and Use Committee (IACUC) permit

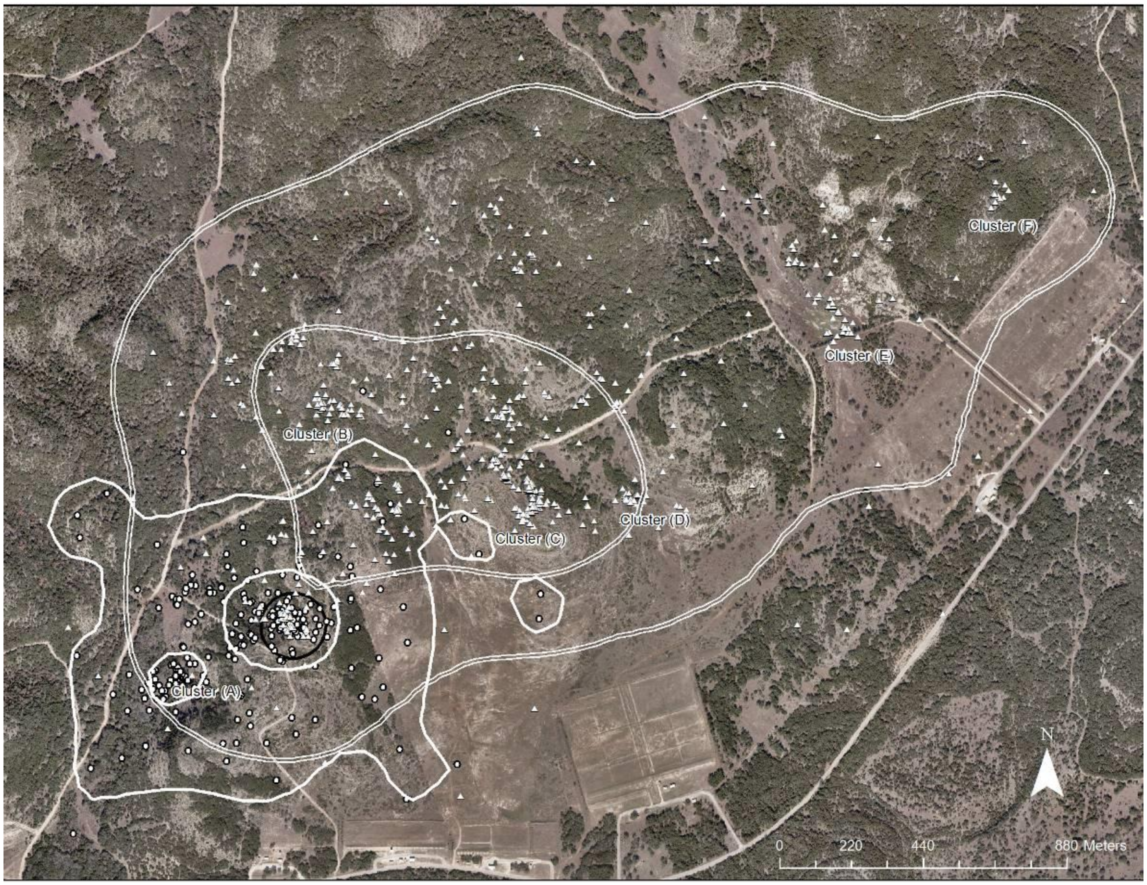

Figure 9. Ninety-five percent KDE home range and 50% core estimates (single, white line), and individual locations (white circles) for PorcA, 95% KDE home range and 50% core estimates (double, white line), and individual locations (white triangles) for PorcB, and 100m buffer around trap site cave (single, black line) at Camp Bullis, Bexar Co., Texas, USA.

Figure 10. Ninety-five percent KDE home range and 50% core estimates (single, white line), and individual locations (white circles) for PorcC, 95% KDE home range and 50% core estimates (double, white line), and individual locations (white triangles) for PorcD, and 100m buffer around trap site cave (single, black line) at Camp Bullis, Bexar Co., Texas, USA.

2014-0233.

I calculated kernel density estimator's (KDE) 95% home range and 50% core utilization distribution isopleths using Home Range Tools for ArcGIS (Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystems, Thunder Bay, Canada) after removing points known or suspected to be error. Calculations were performed using a fixed-kernel estimator and least-squares cross-validation to estimate the smoothing parameter. I found the areas of KDE overlap using ArcMap 10.3 (Environmental Systems Resource Institute, Redland, CA) intersect tool and calculated overlap indices with the formula

$$OI = [(n_1 + n_2) / (N_1 + N_2)] \text{ x } 100.$$

The variables n_1 and n_2 correspond to the number of the adjacent individual North American porcupines' locations within the overlap polygon, and N_1 and N_2 correspond to the number of locations for the 2 North American porcupines used in the calculation of the home-range overlap (Chamberlain and Leopold 2002, Brunjes et al. 2009, Kelley et al. 2011, Montalvo et al. 2014). I did not include overlap indices with a value of zero.

I calculated second- (landscape), third- (home range), and fourth-order (point locations) spatial scales of resource selection ratios (Johnson 1980). I calculated second-order selection ratios by comparing the proportion of locations in each mapped variable to their proportion in the study area. I calculated third-order selection ratios by dividing the proportion of each mapped variable in each home range by the proportion in the study area. I calculated fourth-order selection ratios by comparing the proportion of locations in each mapped variable to those present in their individual 95% KDE home-range estimate. Selection ratios equal to 1.0 indicated resource use proportional to availability, >1.0 indicates preference, and <1.0 indicated avoidance (Manly et al. 2002).

Selection ratios were calculated from a map created using ArcMap's supervised classification. This map assigned the study site 1 of 3 land cover variables: woody vegetation, grassland, and bare ground. Woody vegetation included dense mottes of shrubs and trees with heavy canopy cover, grassland included areas dominated by grass and forb species with minimal canopy cover, and bare ground included paved and non-paved roads, rock, buildings, and rock.

Results

I trapped and tracked a total of 4 North American porcupines for this study. Only 4 individuals were used for this study because I was focused on obtaining an initial understanding of how caves are incorporated into an individual's habitat use. One female (PorcA) and 1 male (PorcB) were trapped at near Well Done cave and were followed from, the end of July 2015 through November 2015 (Table 10; Fig. 9). I also trapped 2 female (PorcC and PorcD) at Peace Pipe cave and were followed from August 2016 – January 2017 (Table 10; Fig. 10). The 4 North American porcupines averaged 500.3 GPS points (σ = 137.9; Table 10). North American porcupine GPS locations clumped into clusters. Clusters A–D, and F–L were closed canopy, mixed forested areas with established oaks (*Quercus* spp.). Cluster E was a grassland with mottes of trees and shrubs (Fig. 9 & 10).

I calculated PorcA 95% home range KDE at 103.6 ha and 50% core KDE at 10.6

Table 10. Individual North American porcupine home range data including sex, dates of data collection, number of GPS locations (*n*), 95% KDE home range estimate (ha), 50% KDE core estimate (ha) at Camp Bullis, Bexar County, Texas, USA.

	Sex	Dates	*n*	95% KDE	50% KDE
PorcA	F	07/28/2015 – 11/11/2015	314	103.6	10.6
PorcB	M	07/24/2015 – 11/23/2015	645	420.6	7.39
PorcC	F	08/10/2016 – 01/11/2017	538	46.35	4.04
PorcD	F	08/10/2016-01/03/2017	504	64.0	5.4

hectares (Table 10). Both the home range and core KDE were centralized around the Well Done cave where this individual was trapped though a number of points were collected around 'cluster A' (Fig. 9). I calculated PorcB 95% home range KDE at 420.6 ha and 50% core KDE at 7.4 hectares (Table 10). The core KDE included points collected around 'cluster B', 'cluster C', and 'cluster D'. The home range KDE also included points collected around 'cluster E', and 'cluster F', and original cave trap site (Well Done cave; Fig. 9). Overlap index for PorcA and PorcB was calculated at 42.44% though they only spent a total of 5/100 days simultaneously collared within 100 m of each other. These probable interactions all occurred around Well Done cave where both were trapped, and collared.

I calculated PorcC 95% home range KDE at 46.4 ha and 50% core KDE at 4.0 ha (Table 10). The core KDE centered on the cave trap site (Peace Pipe cave) and closely mimics a 100 m buffer around the cave entrance. The home range KDE further included points collected around 'cluster J', 'cluster, H, cluster I, and cluster G. I calculated PorcD 95% home range KDE at 64.0 ha and 50% core KDE at 5.4 ha (Table 10; Fig. 10). The core KDE also centered on the cave trap site (Peace Pipe Cave) and closely mimics a 100 m buffer around the cave entrance. The home range KDE includes points collected around 'cluster G', 'cluster I', and 'cluster K' (Fig. 10). Overlap index for PorcC and PorcD was calculated at 92.7% and spent a total of 69/147 days within 100m of each other. Almost all of these probably interactions occurred around Peace Pipe cave where both were trapped, and collared.

At the landscape scale (2nd order), PorcA and PorcB both selected forested cover and selected against bare ground and herbaceous cover. PorcC and PorcD also avoided herbaceous cover and bare ground but used forested cover proportionally to what was available (Table 11). At the home range scale (3rd order), PorcA, PorcB, PorcC, and PorcD all selected for bare ground. PorcC and PorcD also selected for herbaceous cover and avoided forested cover (Table 11). At the point scale (4th order), PorcA, PorcB, PorcC, and PorcD all selected for forested cover and selected against bare ground and herbaceous cover (Table 11).

Discussion

Across their range, North American porcupine populations have an average home range of 25 ha for females and 78 ha for males (Elbroch and Rinehart 2011). All of my females had home range estimates that were larger than this average, 1 being 4 times as large, and the male's home range estimate was more than 5 times as large as the male average. This may be because much of Camp Bullis is a patchwork of closed canopy forest and open grasslands. Open grasslands are a known to be high risk areas for predation (Sweitzer and Berger 1992, Sweitzer 1996). This population's home ranges may have circumvent these risky patches by expanded into fringe forested patches. I can see this avoidance behavior in the aerial image of PorcA and PorcB GPS locations where points follow, but do not surpass, the brush line (Fig. 9). This can also be seen in the locations of PorcC and PorcD though to a lesser extent since there is less of the open risky patches in this area (Fig. 10).

My data demonstrate the importance of caves as den sites. All of my female

Table 11. Individual North American porcupine multi-level, habitat selection ratios for forested (F), herbaceous (H), and bare ground, road, or buildings (BG) cover types at Camp Bullis, Bexar Co., Texas, USA.

	2nd Order (Landscape)	3rd Order (HR)	4th Order (Point)
PorcA			
F	1.26	1.06	1.22
H	0.74	0.86	0.88
BG	0.53	1.20	0.45
PorcB			
F	1.20	0.98	1.27
H	0.76	0.98	0.80
BG	0.57	1.20	0.49
PorcC			
F	1.09	0.72	1.52
H	0.86	2.55	0.34
BG	0.38	1.37	0.28
PorcD			
F	1.11	0.70	1.63
H	0.74	3.80	0.20
BG	0.25	1.21	0.21

North American porcupines' core habitats, in particular, centered on caves. Additionally, they did not appear to rotate den sites as seen in other populations (Roze 1987, Morin et al. 2005, Roze 2009). My population's use of various 'clusters' indicate some resource is not being met in the cave or its immediate surroundings. Many of the cave entrances at Camp Bullis are surrounded by mottes dominated by Ashe juniper, while clusters typically had more diverse vegetation that often includes large, mature oak trees. Given the North American porcupines' known use more diverse vegetation (Morin et al. 2005, Coltrane and Sinnott 2013) and acorns (Griesemer et al. 1998, Ilse and Hellgren 2007, Roze 2009), I suspect these clusters are an important microhabitat.

My North American porcupines, especially PorcC and PorcD, show a large amount of home range overlap suggesting that this study site's population is not markedly territorial; especially female to female. The cave used by PorcA and PorcB, in particular, has been known to be used by a minimum of 3 individuals, concurrently. Interesting, New York populations showed territoriality between females while (Roze 2009) while Nevada populations showed territoriality between males. Furthermore, female overlap of the Nevada population averaged only 20% (Sweitzer 2003); much lower than my female-female pair overlap of 92.7%. This pair may be suspected as an outlier but, instead, I believe that this overlap calculation further demonstrates the importance of caves, that a typically solitary species (Morin et al. 2005, Roze 2009) would tolerate such an intense degree of interaction.

The North American porcupines in this study selected for landscapes with ample forested cover and little bare ground or roads. Their home ranges, by contrast, contained more regions of bare ground or roads. At the point scale, North American porcupines used forested cover rather than herbaceous cover, bare ground or roads. I suspect bare ground and roads were crucial at the home range level because they are used as corridors between the cave dens and feeding sites (e.g., clusters). Other habitat studies also showed that North American porcupines selected for diverse, forest cover though they did not select for bare ground or roads (Morin et al. 2005, Coltrane and Sinnott 2013).

My study demonstrates the variability of North American porcupine home range and habitat use. This population had a male with an exceptionally large home range, while all individuals demonstrated the importance of forest cover as well as cleared paths. All 4 individuals also demonstrate the importance of caves as a fixed den site around which all the females centered their core habitat. This results of this study are also critical for North American porcupine management on Camp Bullis where their extensive cave use could jeopardize the federally endangered cave-obligate arthropods. Should cave managers need to limit North American porcupine cave use, my data indicates that replacement of forested landscapes with grasslands would make the landscape and habitat surrounding caves less desirable den sites.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Summary

This project began as a means to better understand the role of meso-mammals in the cave ecosystem. Cave-obligate species are adapted to oligotrophic cave conditions and require the introduction of nutrients since caves lack primary producers. The caves on Joint Base San Antonio – Camp Bullis (hereafter Camp Bullis) were historically associated with the introduction of nutrients through raccoon scat but in the proceeding decades, cave biologists had noticed a rise in cave use by recently naturalized North American porcupine.

This shift in meso-mammal cave visitation raised basic questions exploring what constitutes typical meso-mammal visitation patterns and behaviors in the caves. This information is especially critical to the caves on Camp Bullis because many are habitat to 3 federally endangered, cave-obligate arthropods (*Rhadine infernalis*, *Rhadine exilis*, *Cicurina madla*). Cave obligate species, such as these, are sensitive to changes in the nutrient balance within the cave: too small, cave-obligate species have no resources; too much, and the cave-adapted species are replaced by more competitive or predatory terrestrial species. A more complete understanding of endangered species cave ecology is also important because of its ability to directly impact the development of surrounding communities. In San Antonio, Texas, federally endangered Bracken Bat Cave meshweaver spider (*Cicurina venii*) was discovered for the first time in thirty years after a cave was uncovered during the construction of a highway underpass. As a result, construction was delay and plans were changed to an overpass nearly tripling the overall costs from $15 million to $44 million.

I first quantified meso-mammal cave visitation on Camp Bullis according to species, season, time of day, weather, and cave characteristics (Chapter 2). Using trail cameras at 30 cave entrances for a year, my results showed North American porcupines, raccoons, and Virginia opossums constitute greater than 87% of meso-mammal visitors. These 3 species used caves differently according to season, weather, and cave characteristics. My data most meso-mammals were using caves for denning while raccoons and Virginia opossums, in particular, were using caves for feeding on either resident arthropod or small mammal populations. This is especially noteworthy because both raccoons and Virginia opossums also showed greater use of caves containing endangered species.

I then investigated typical meso-mammal behaviors in caves according to species, season, and time of day using trail cameras throughout the passages of the 4 busiest caves (Chapter 3). My results confirmed that North American porcupines used caves for denning and grooming while Virginia opossums and raccoons used largely used caves to feed on arthropods.

I then used a multinomial regression to determine which variables best predict North American porcupine, raccoon, and Virginia opossum cave use, and to what magnitude. The model showed if caves were constructed or excavated, entrance type, season, ground cover, climate, if the caves were gated, or in the aquifer recharge zone as significant parameters to predict which meso-mammal visited a particular cave. Odds ratios showed raccoons and Virginia opossums had greater odds of using gated caves and pit entrances while North American porcupines had greater odds of using caves in the spring and winter, constructed or excavated caves, and caves with herbaceous or forested cover.

Finally, I placed GPS collars on North American porcupines in order to better understand North American porcupine habitat use in relation to caves and local vegetation. My results showed that North American porcupine home range size varies but often center around a cave. At the landscape and point levels, individuals selected for forested cover and avoided areas without cover. At the home range level, bare ground and roads were selected for, likely for use as trails to get from the cave den site to feed at the mixed forest patches.

Conclusions

Caves are a complex ecosystem including poorly studied direct and indirect interactions between meso-mammals and cave-obligate species. My research shows the meso-mammal cave selection is a balance of accessibility and resource availability. Raccoons and Virginia opossums were able to access a wider variety of caves because of their greater mobility though their cave use was only a fraction of North American porcupine cave use. This may be because of raccoon and Virginia opossum adaptability to a greater variety of habitats and resources as it is not uncommon to see these 2 species in urban or developed areas while North American porcupines are generally confined to undeveloped, forested areas. Given the North American porcupine's intensity of cave use, especially during winter, I believe caves to be a critical resource for North American porcupines in this area.

Future Research

This study represents an initial step meso-mammals role in the cave ecosystem and future studies are needed to determine if the results found in this study are consistent of meso-mammal cave use in other parts of these species' ranges. For example, the intensity of North American porcupines cave use is likely lower in areas were have not, or only recently, established. It would also be useful determine the typical nutrient inputs of each meso-mammal species' scat and use this information to hypothesize acceptable or unacceptable levels. During the course of this study I noted that vultures nesting in the entrances of caves halted almost all meso-mammal visitation. It would be interesting to determine if this interruption of meso-mammal nutrient inputs affect cave-obligate species. Conversely, I noted that despite seasonally elevated CO_2 levels, there appeared to be no cessation of meso-mammal cave use. Further research is needed to determine if, and how, elevated CO_2 affects meso-mammal visitation, behavior, and nutrient inputs.

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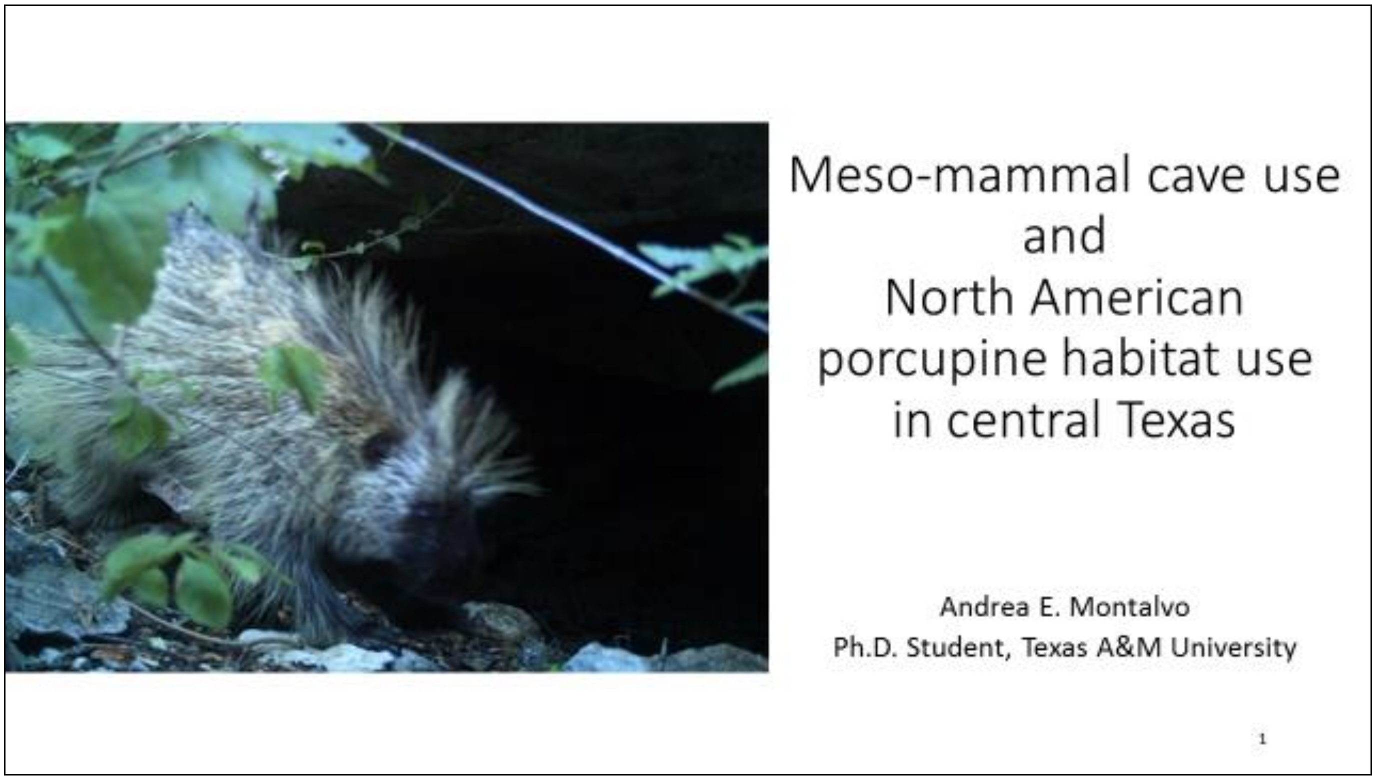
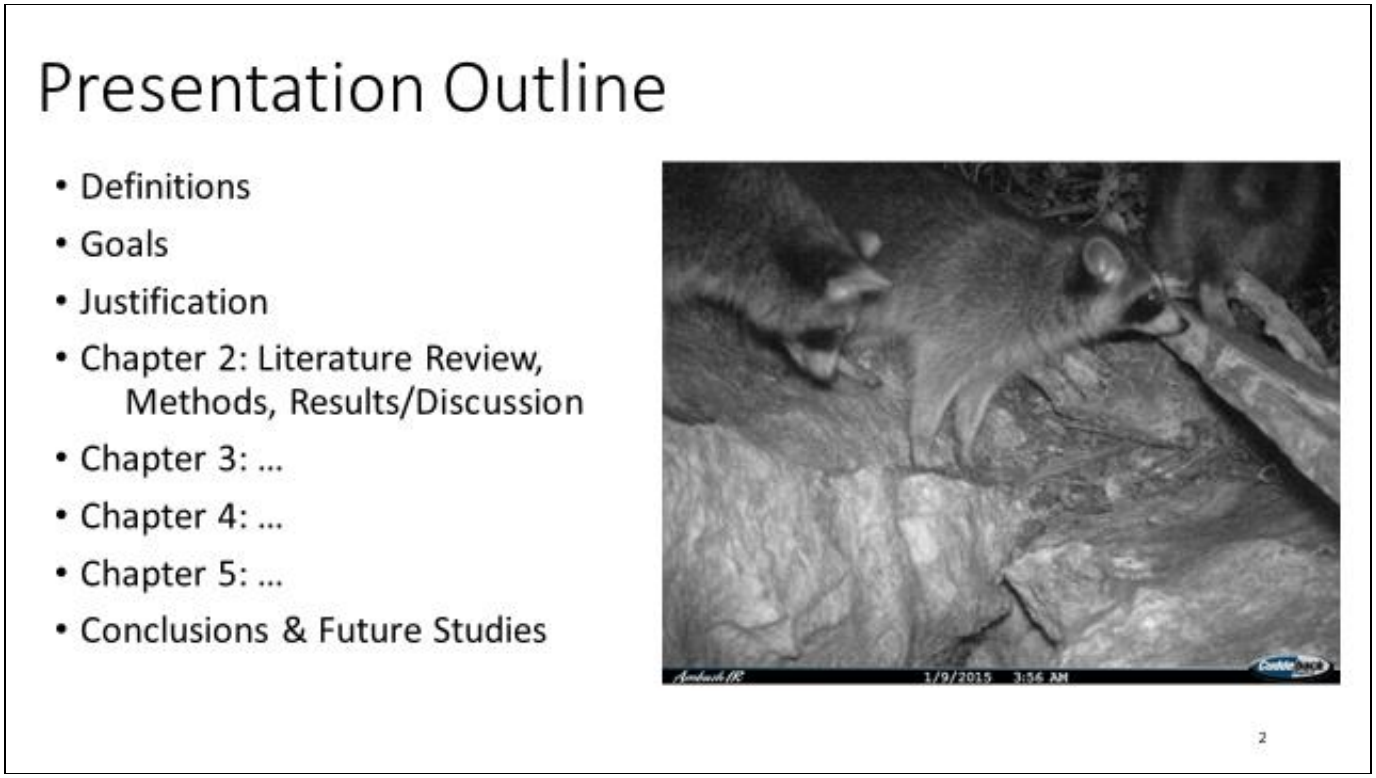
APPENDIX A

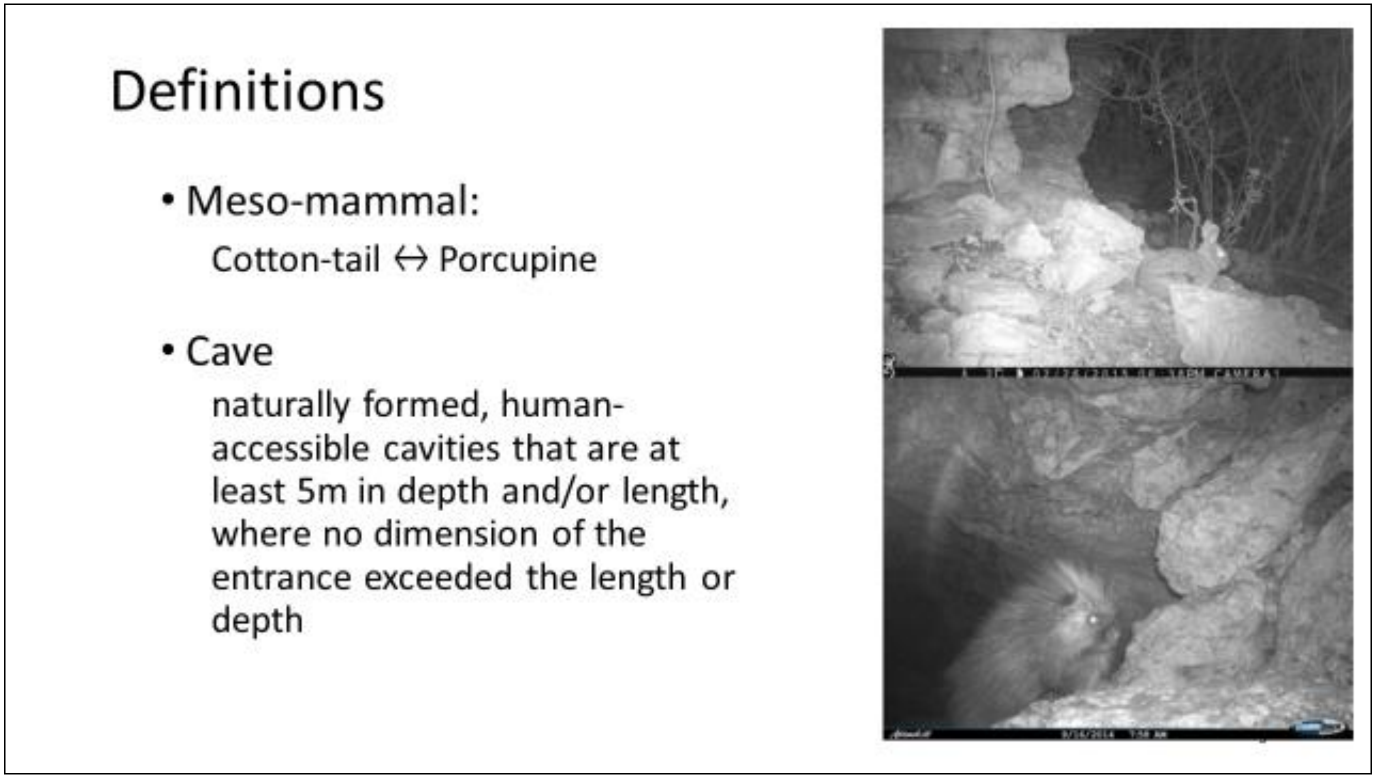
ANNOTATED DEFENSE PRESENTATION



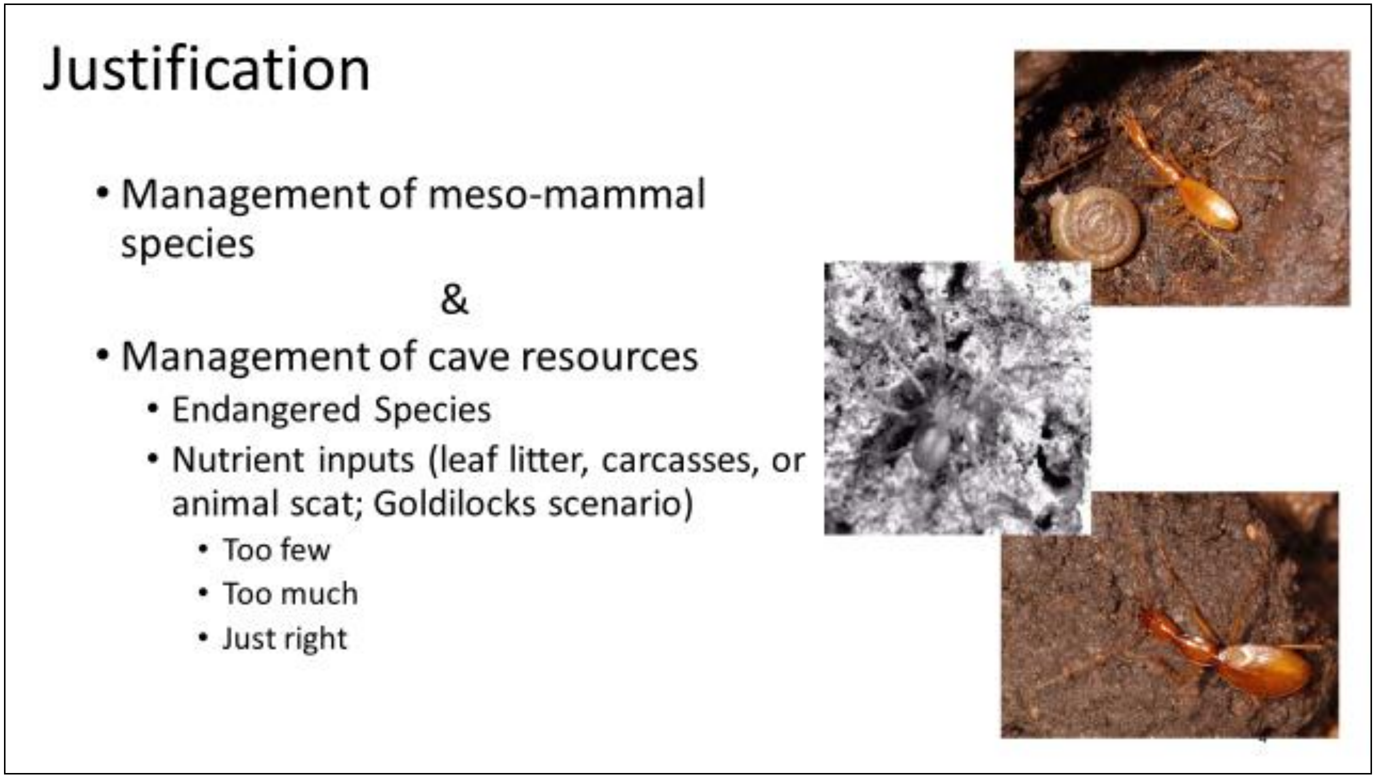
A-1. I have included the slides from my dissertation defense in this appendix as a means to summarize the results of my project and include some of the more interesting photos collected during the study. This presentation was given 03/09/2017 at the San Antonio office of the Institute of Renewable Natural Resources.



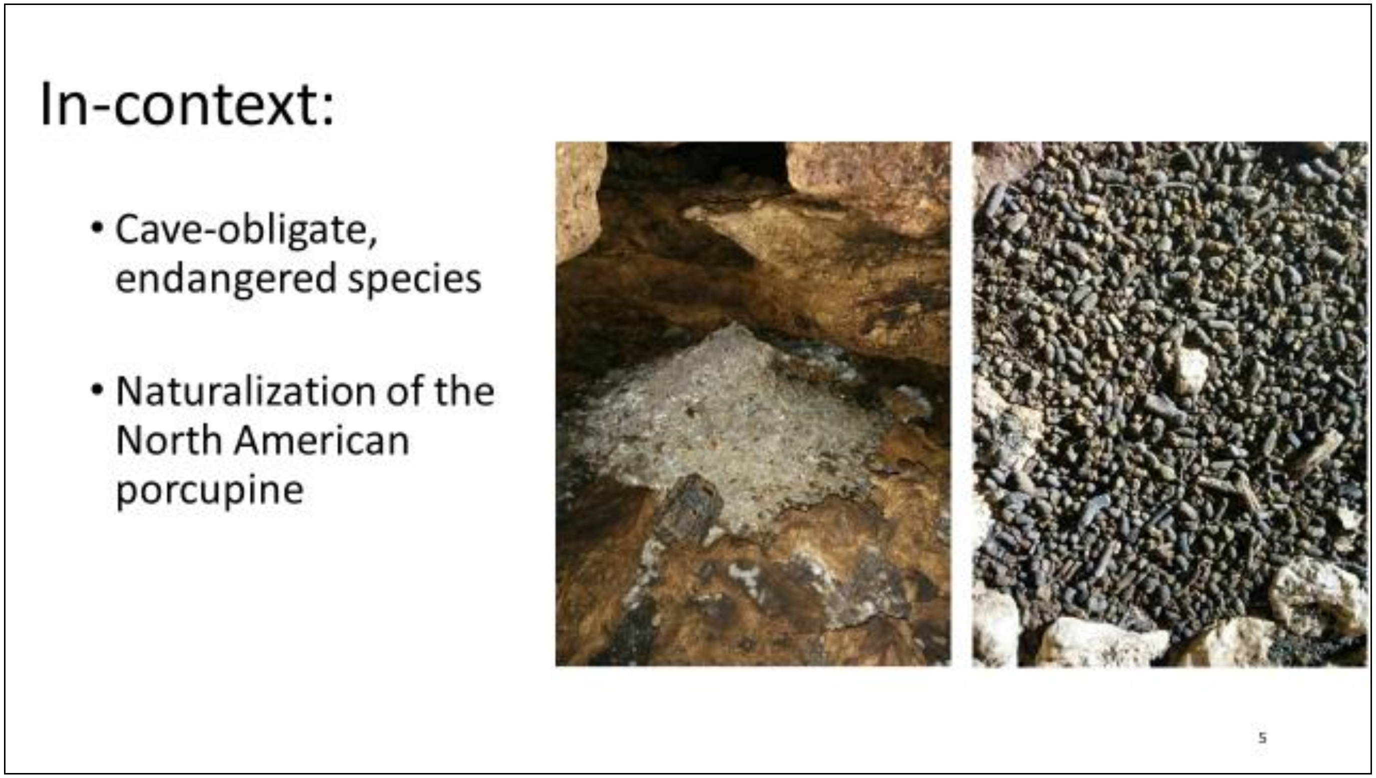
A-2. My presentation included common definitions, the goals of the study, justification, 4 chapters of my research, overall conclusions, and potential future studies. The photo shows three raccoons at the entrance of a pit entrance cave.



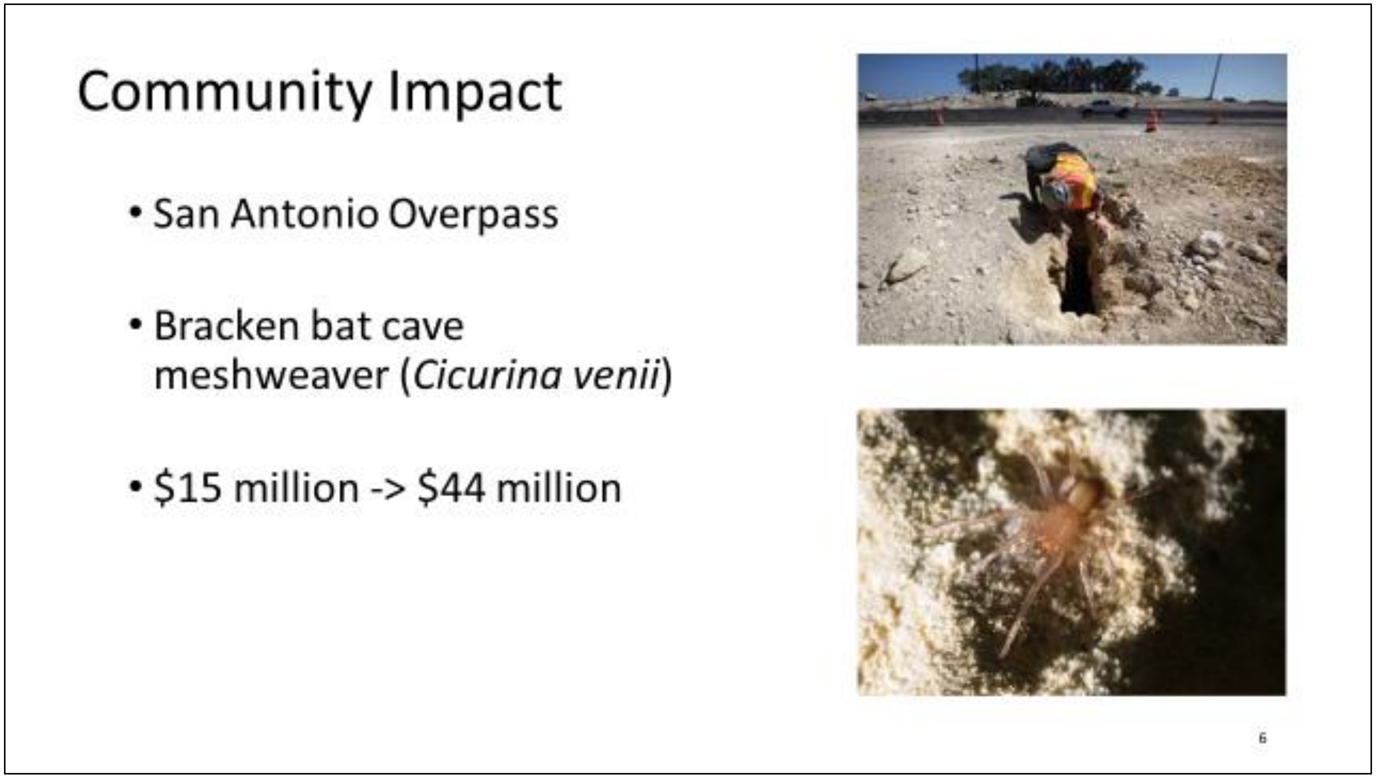
A-3. For my purposes, ‘meso-mammal’ was any mammal at least as large as a cottontail (*Sylvilagus* spp.; pictured) but no larger than a North American porcupine (*Erethizon dorsatum*; pictured). The term ‘cave’ was also defined therefore excluding karst features, also found extensively on Camp Bullis, from this study.



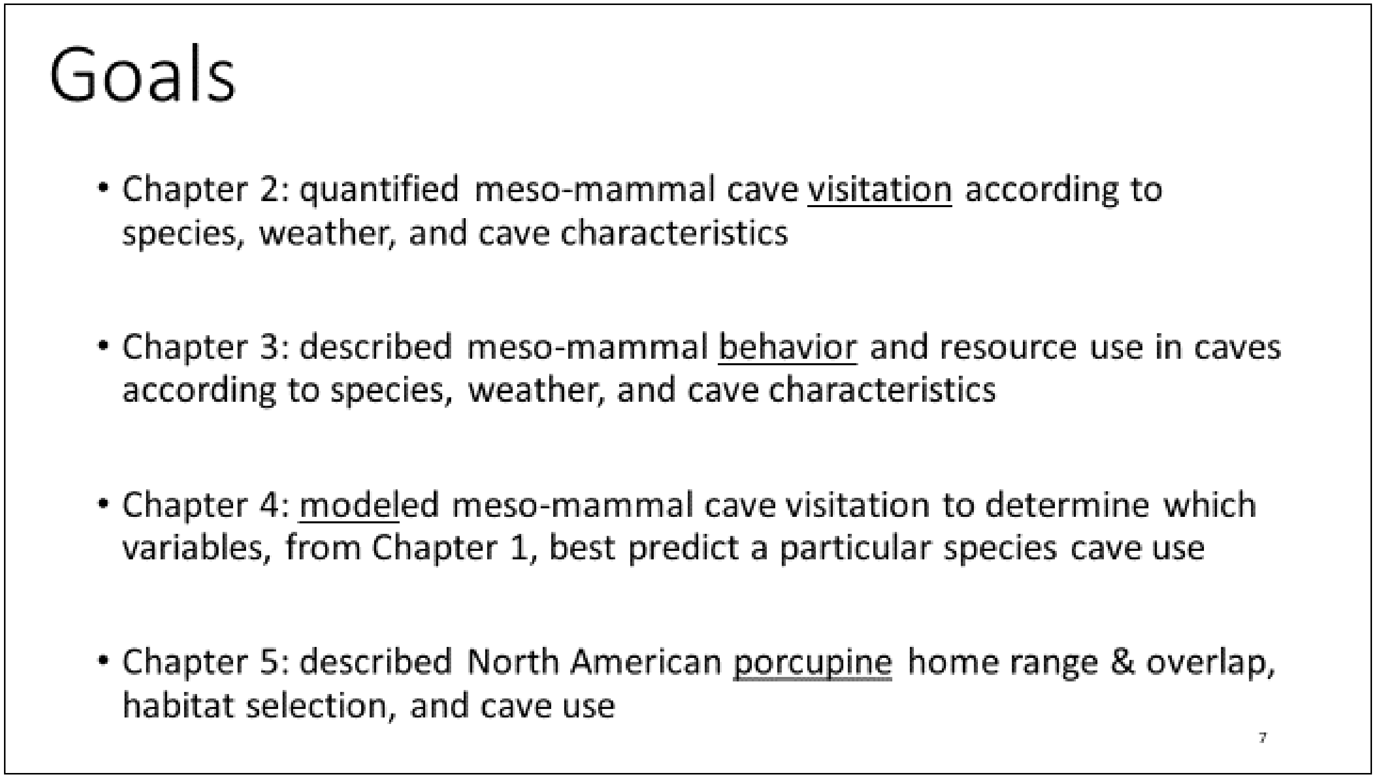
A-4. Why study meso-mammal cave use? This study further details meso-mammal ecology and also helps in the management of cave resources, including cave-obligate endangered species. Cave-obligate species are adapted to oligotrophic cave environments and, because of the absence of primary producers, depend on external nutrient inputs. These nutrient inputs can be from washed-in leaf litter, animal carcasses, or meso-mammal scat. The amount of nutrient inputs into caves is important; too little and the cave-obligate species have no resources, too much and cave-obligate species are replaced by more competitive or predatory terrestrial species. This all equates to an overall decrease in cave diversity. These three photos show the three cave-obligate, endangered species found on my study site: *Cicurina madla*, *Rhadine infernalis*, *Rhadine exilis*. Cave-obligate species, arthropod or otherwise, can generally be identified by their loss of eyesight, loss of pigmentation, and elongated appendages.



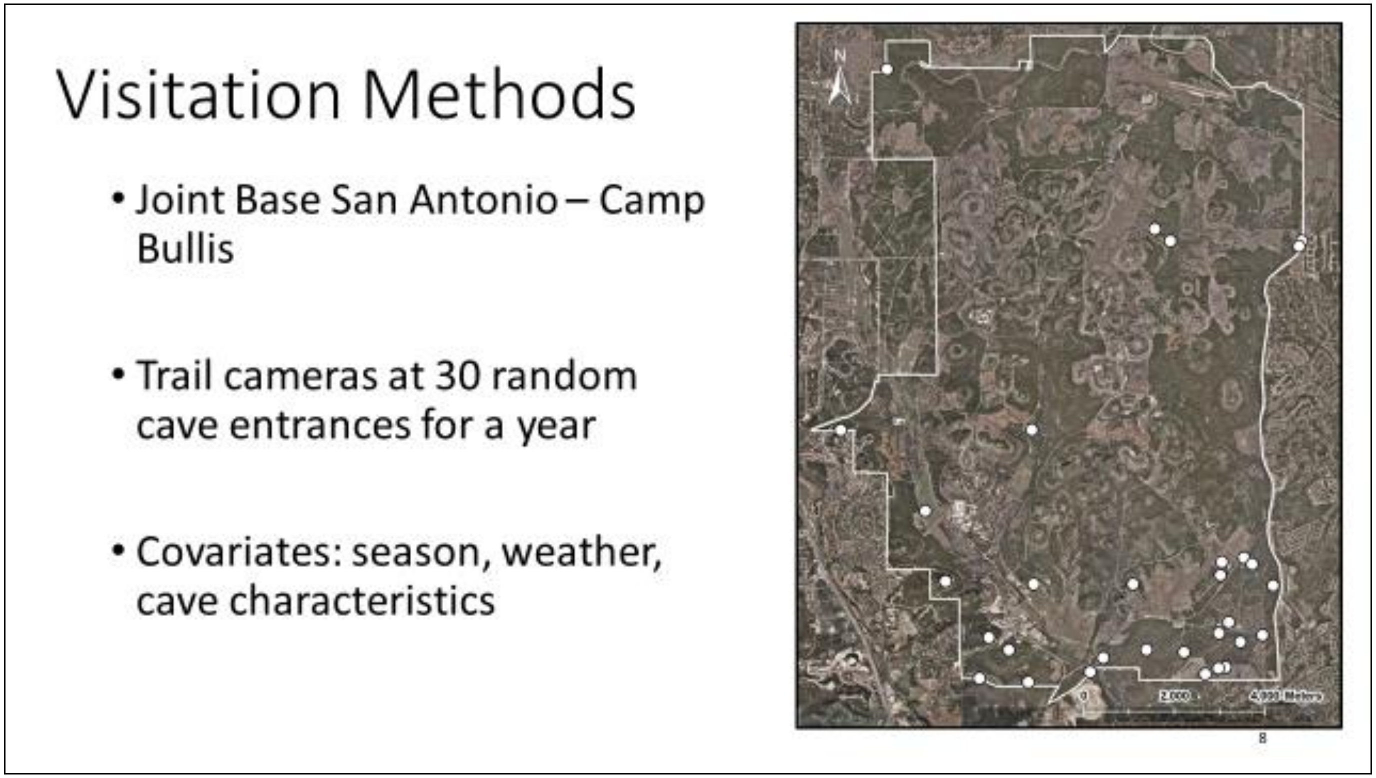
A-5. Putting this all in-context, cave managers are trying to protect cave-obligate and endangered species but also have noticed changes to the cave systems that may put them in danger. Historically, caves in central Texas were primarily supported by raccoon scat but now caves are also frequently used by porcupines. Porcupines leave lots of scat in caves and these added nutrients could lead to a loss in cave diversity. These two photos show the amount of porcupine scat that can be found in caves. The photo on the left shows a particularly large pile with a Browning trail camera in the foreground for scale. The photo on the right shows a cave floor covered in porcupine scat. Everything in this photo that is not a rock, is scat.



A-6. Additionally, a better understanding and better management of caves also benefits the community. For example, San Antonio, Texas recently halted construction on a highway underpass after a cave entrance was uncovered (top photo). Surveys of the cave discovered the bracken bat cave meshweaver (*Cicurina venii*; bottom photo), a federally endangered cave-obligate spider seen for the first time in 3 decades. Construction plans had to be altered from a highway underpass to and overpass and the cost nearly tripled from $15 million USD to $44 million USD.

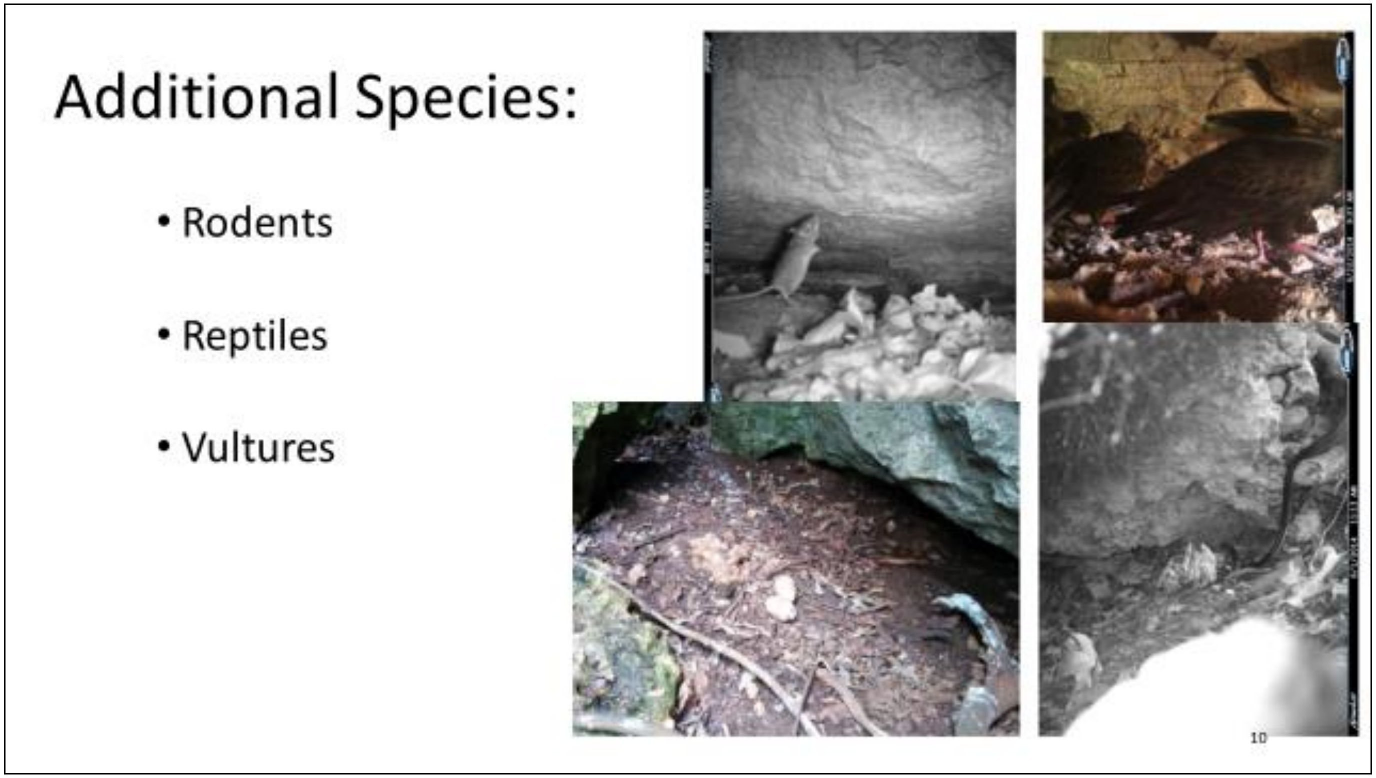


A-7. Here are the specific goals for each chapter of my dissertation. You will notice the numbering starts with Chapter 2 because Texas A&M University requires the introduction and literature review to be Chapter 1. For Chapter 2 I first approach the most basic question of which meso-mammals are using which caves, and how often. I build on this knowledge in Chapter 3 where I explore meso-mammals behaviors and resource use in the caves. In Chapter 4 I returned to the entrance data and build a statistical model to better understand which combination of variables best predicts a particular species' cave use. Finally, in Chapter 5 I looked at the porcupines' habitat use in central Texas and how caves are incorporated into their home ranges.

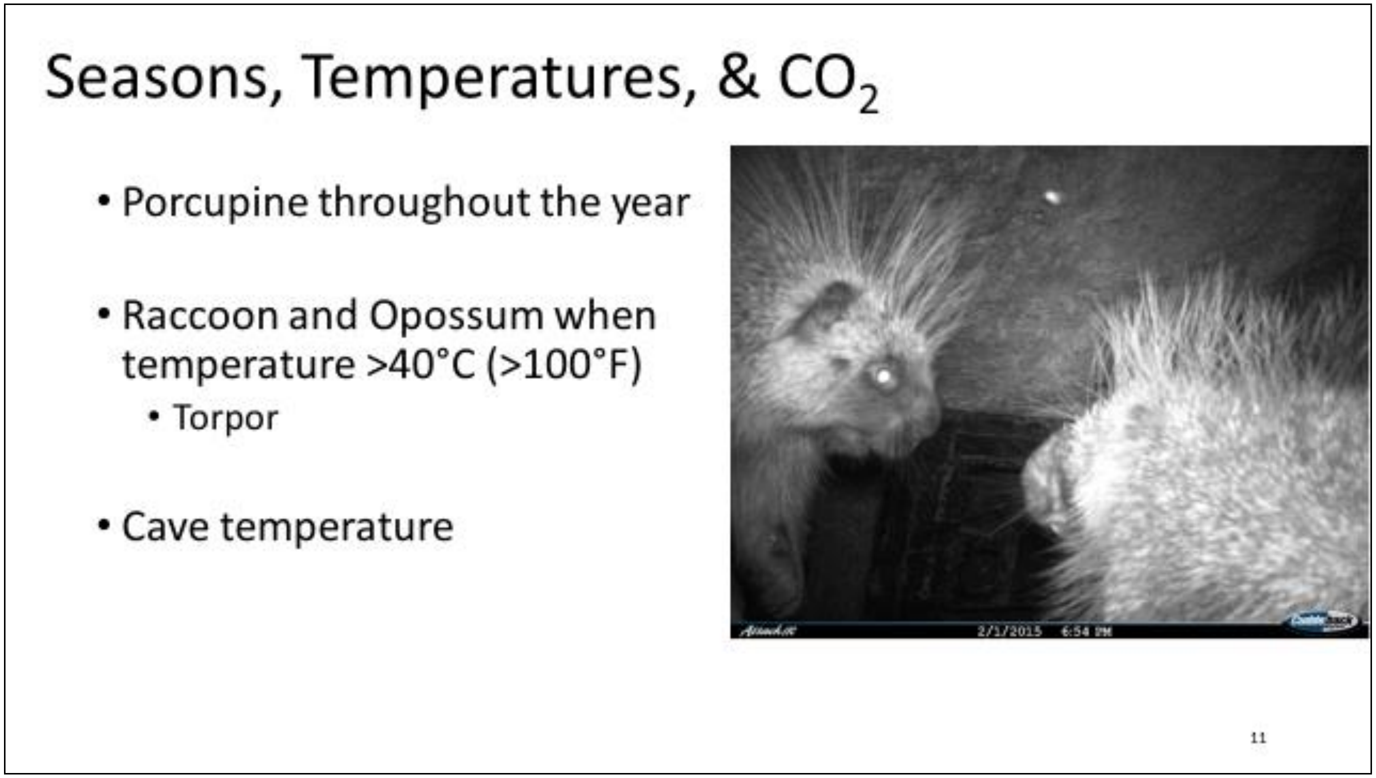


A-8. All the data for this project was collected on Joint Base San Antonio – Camp Bullis (hereafter Camp Bullis). Camp Bullis is an 11,000 ha military instillation just north of San Antonio, Texas. For Chapter 2 (quantifying meso-mammal cave use), I randomly selected 30 caves and placed infrared trail cameras in their entrances for a year. I then compared each meso-mammal species cave use with the covariates of season, weather, and a variety of cave characteristics. This photo is an aerial image of the study site where the white line is the installation's boundary line and the white dots mark each of the 30 cave entrances.

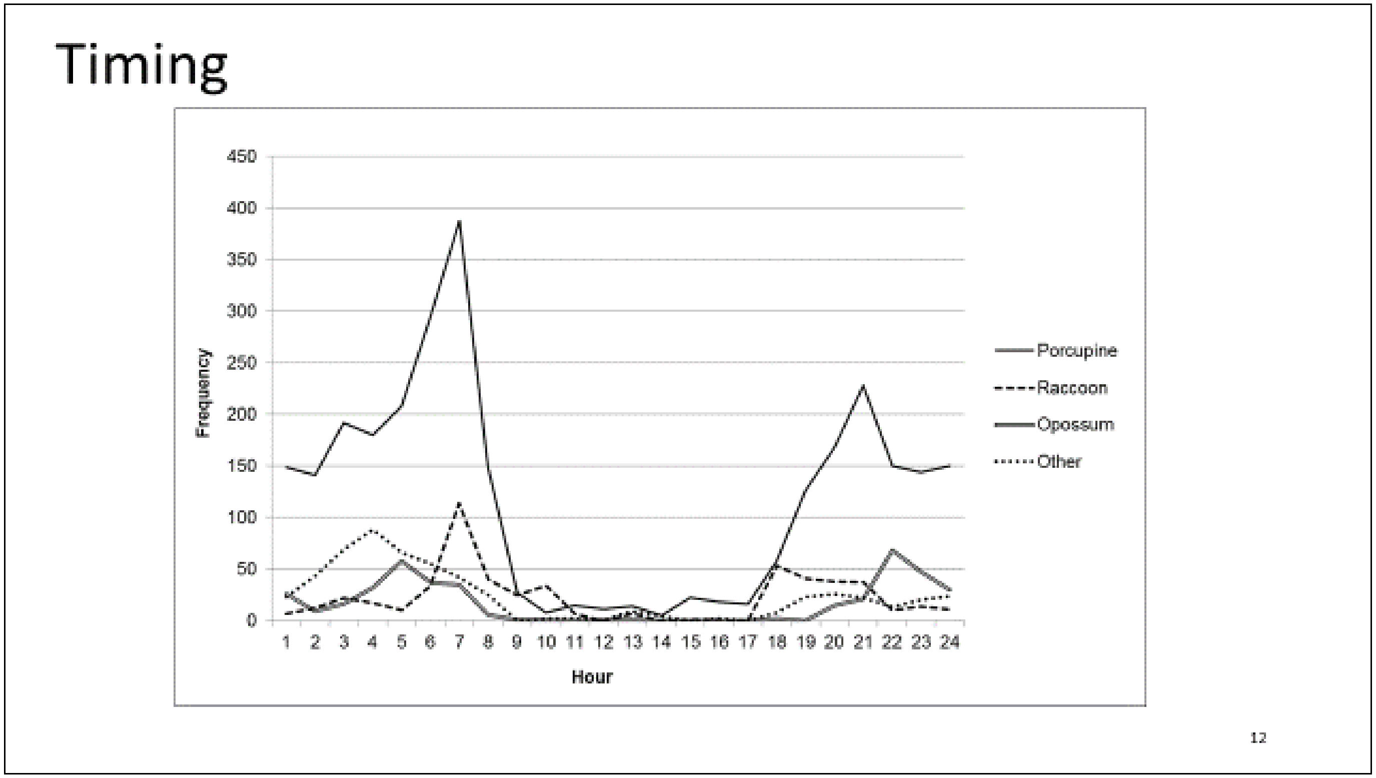
A-9.My results showed that 88% of all meso-mammal visitation was from either porcupines, raccoons (*Procyon lotor*), or opossums (*Didelphis virginiana*) with the large majority of photos coming from porcupines. Less common species include ringtails (*Bassariscus astutus*; top photo) and armadillos (*Dasypus novemcinctus*) which were only found at select caves. Bobcats (*Lynx rufus*; bottom photo) also used caves but were infrequent, regardless of cave.



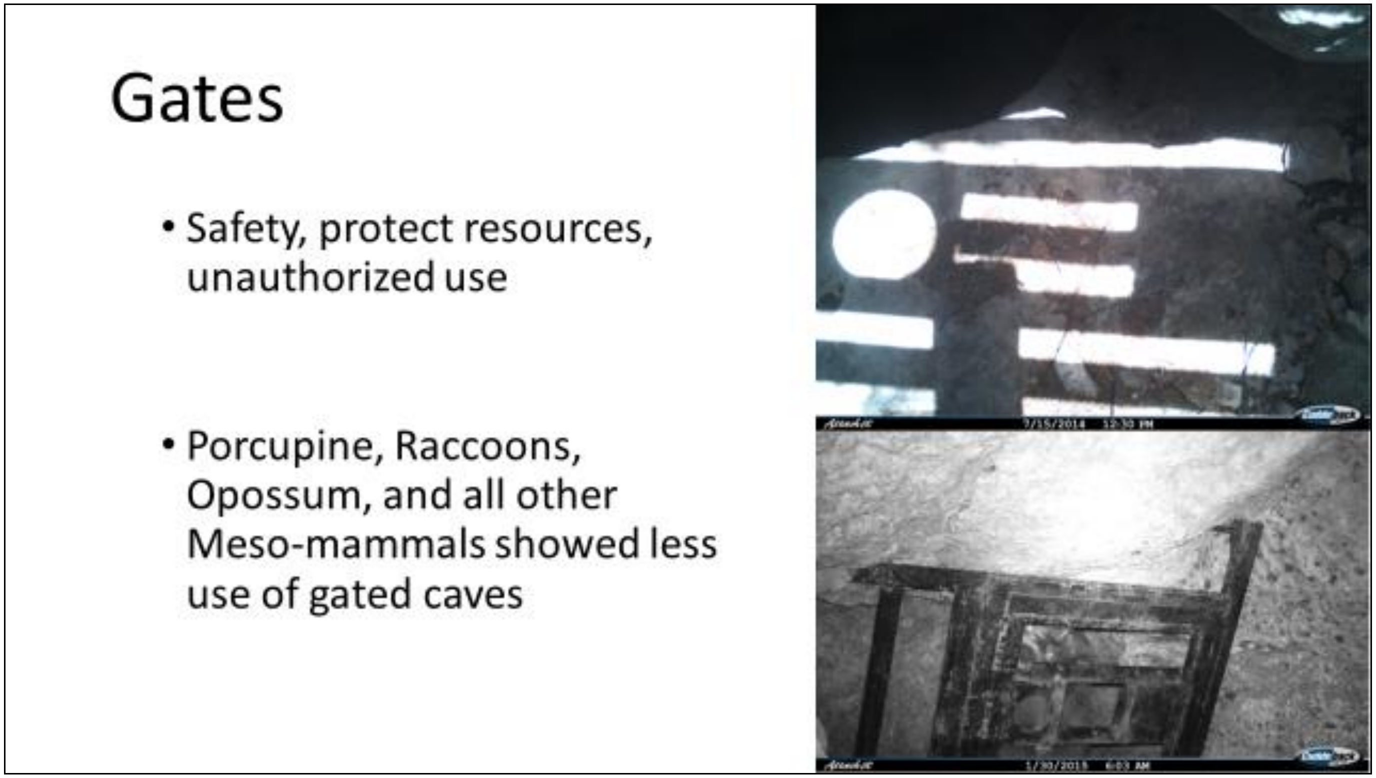
A-10. Other species seen at cave entrances includes small rodents (Muridae; top left photo) which were the most common camera trigger. Reptiles (bottom right photo) were not commonly captured by the infrared cameras but are common in cave entrances. They use the caves for warmth and to hunt small mammal populations. Vultures (Cathartidae; top right photo) also commonly used caves and built nests (bottom left photo) near the entrances. Once a vulture nest was established, all meso-mammal cave use stopped until nesting season ended and the young fledged.



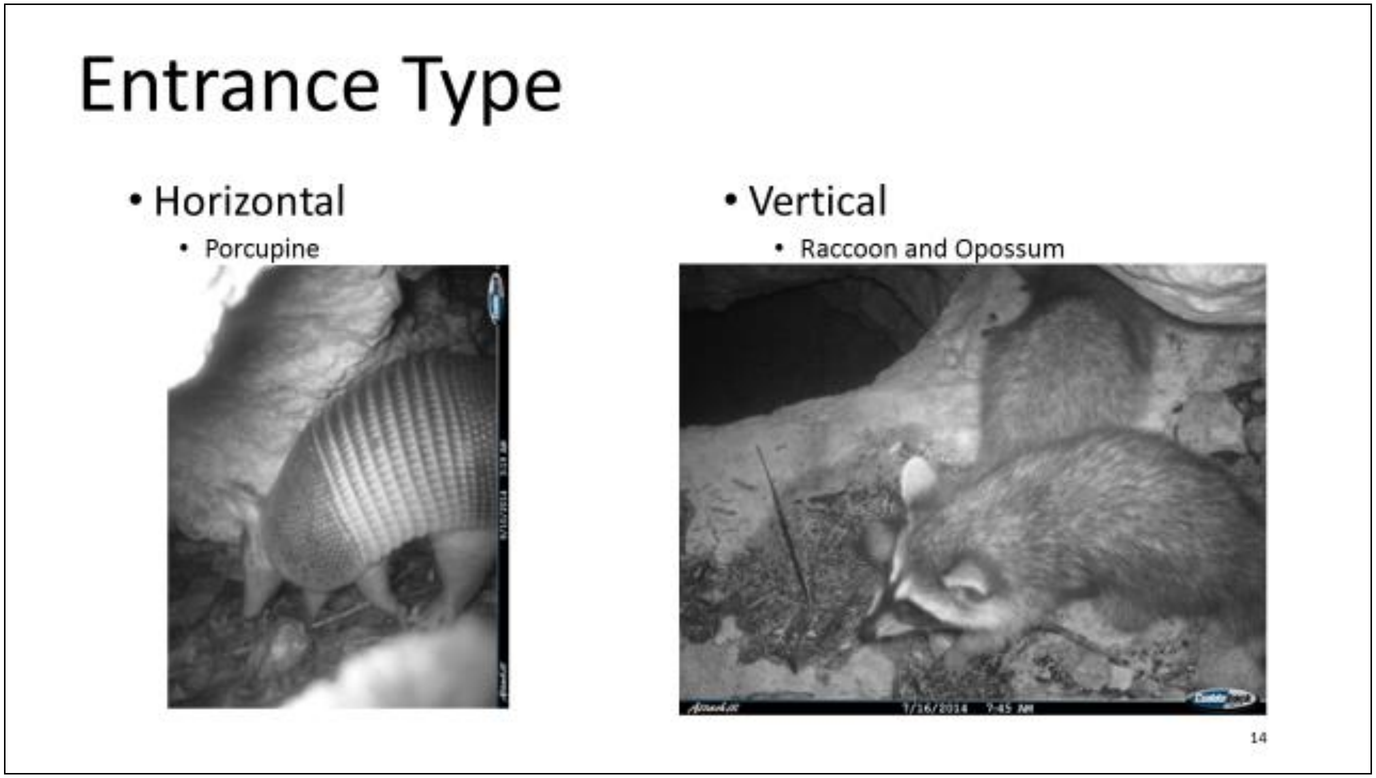
A-11. My data also showed that porcupines were using caves throughout the year while raccoons and opossum were typically using caves when temperatures were greater than 40°C. This is likely because raccoons and opossums both enter torpor during cold weather and therefore are not moving in and out of caves. On the other hand, porcupines do not enter torpor during cold weather and are exposed except when in caves. Caves at Camp Bullis maintain a year-round temperature of approximately 18°C so caves are likely an important microhabitat for porcupines during weather extremes. It is also worth noting that caves with high CO_2 levels did not appear to affect meso-mammal cave use. In humans, high levels of CO_2 can cause increased respiration, nausea, headache, sweating, and, with sufficient exposure, death. Fossorial mammals, like groundhogs (*Marmota monax*), are adapted to these conditions, but neither porcupines, raccoons, nor opossums are known to possess these adaptations.



A-12.The timing of the cave entrance photos showed a bimodal distribution for all species. This is consistent with the nocturnal habits of porcupines, raccoons, and opossums which likely leave the caves at night to feed and re-entering in the mornings to rest.

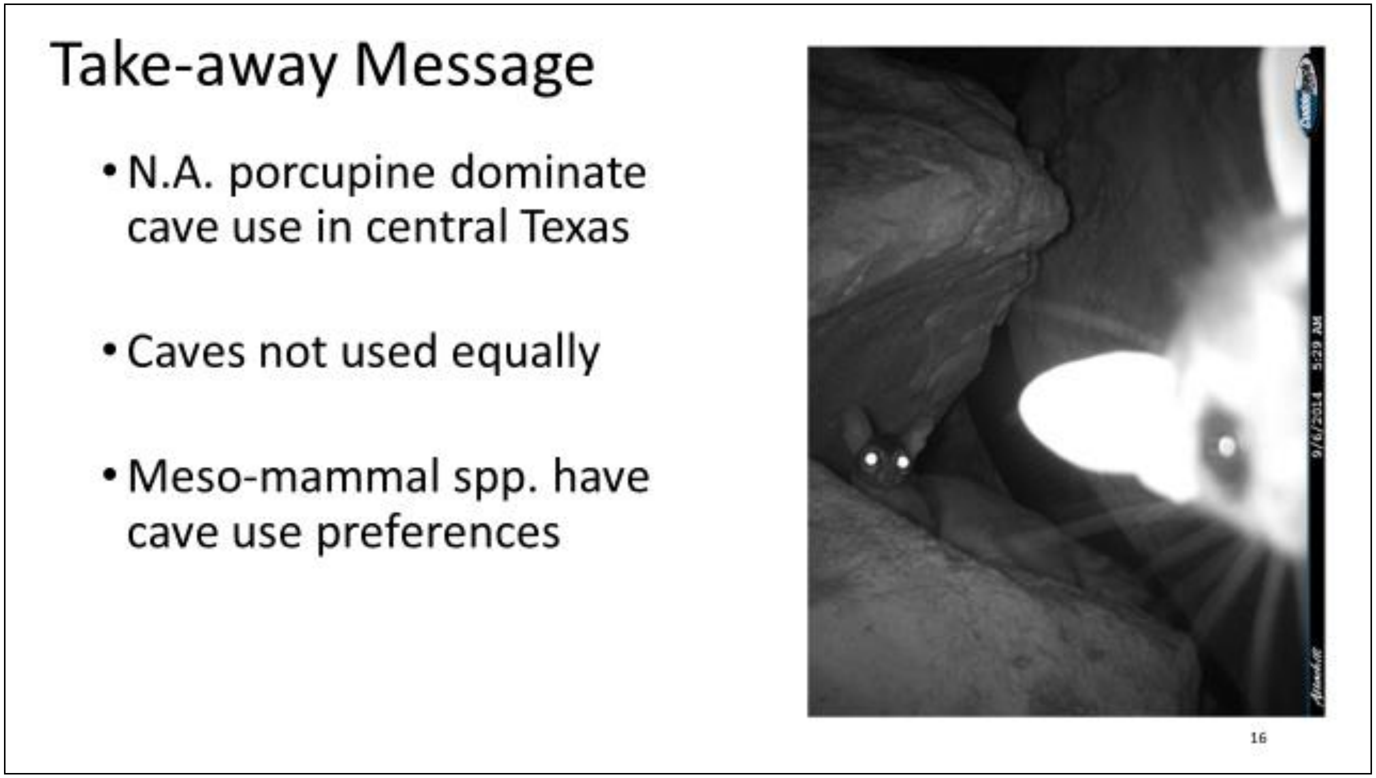


A-13.One of the cave characteristics I looked at were caves with, and without, entrance gates. Cave gates are installed for safety, to protect resources, and prevent unauthorized use. Porcupines, raccoons, and opossums all showed less use of gated caves. You can see in the bottom photo you can see a porcupine exiting a cave through the gate.

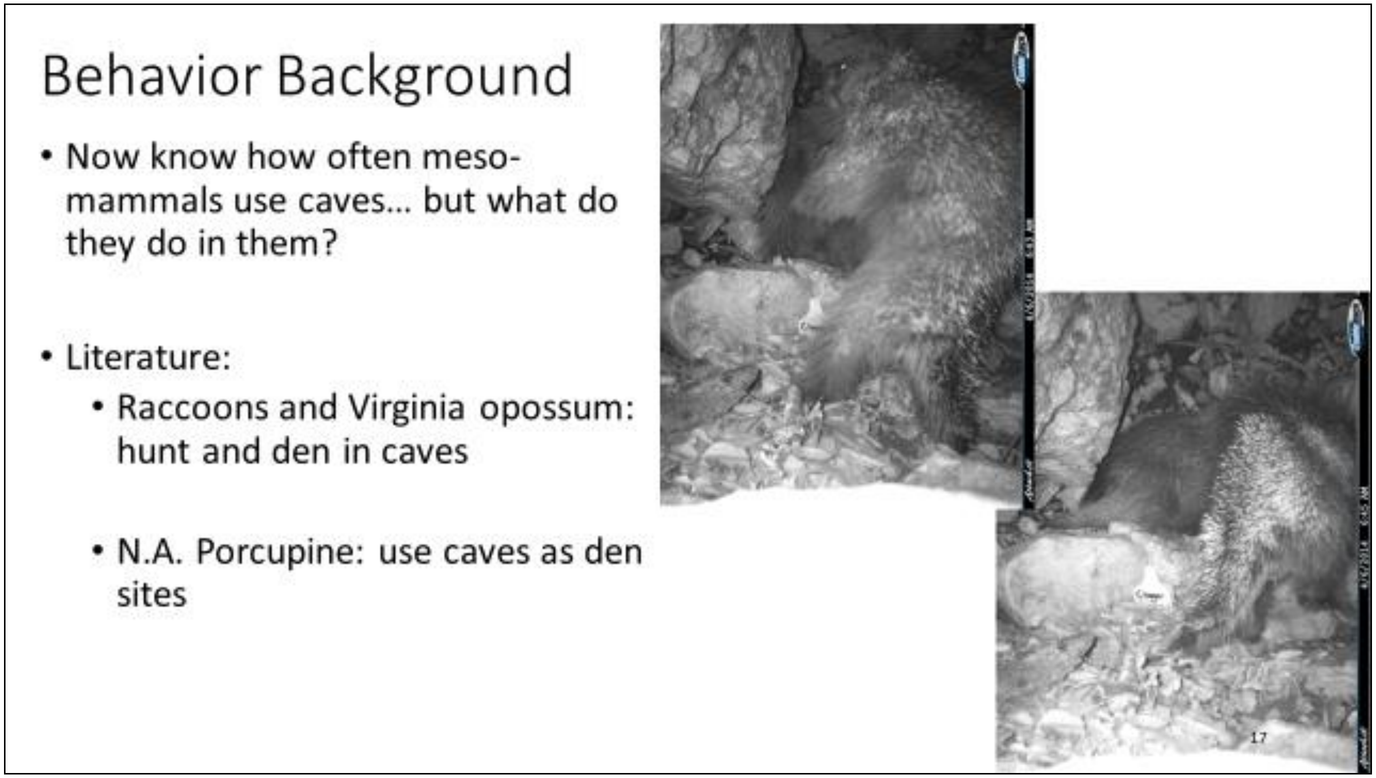


A-14. I also compared cave use by entrance type. Horizontal caves are those you would crawl into and were used largely by porcupines. Vertical caves are those you climb down and were mostly used by raccoons and opossums. I suspect porcupines used fewer vertical caves because they require more mobility and agility and therefore represent an increased risk for falls. The picture on the left shows an armadillo also using a horizontal cave. This cave was also the only cave used by armadillos.

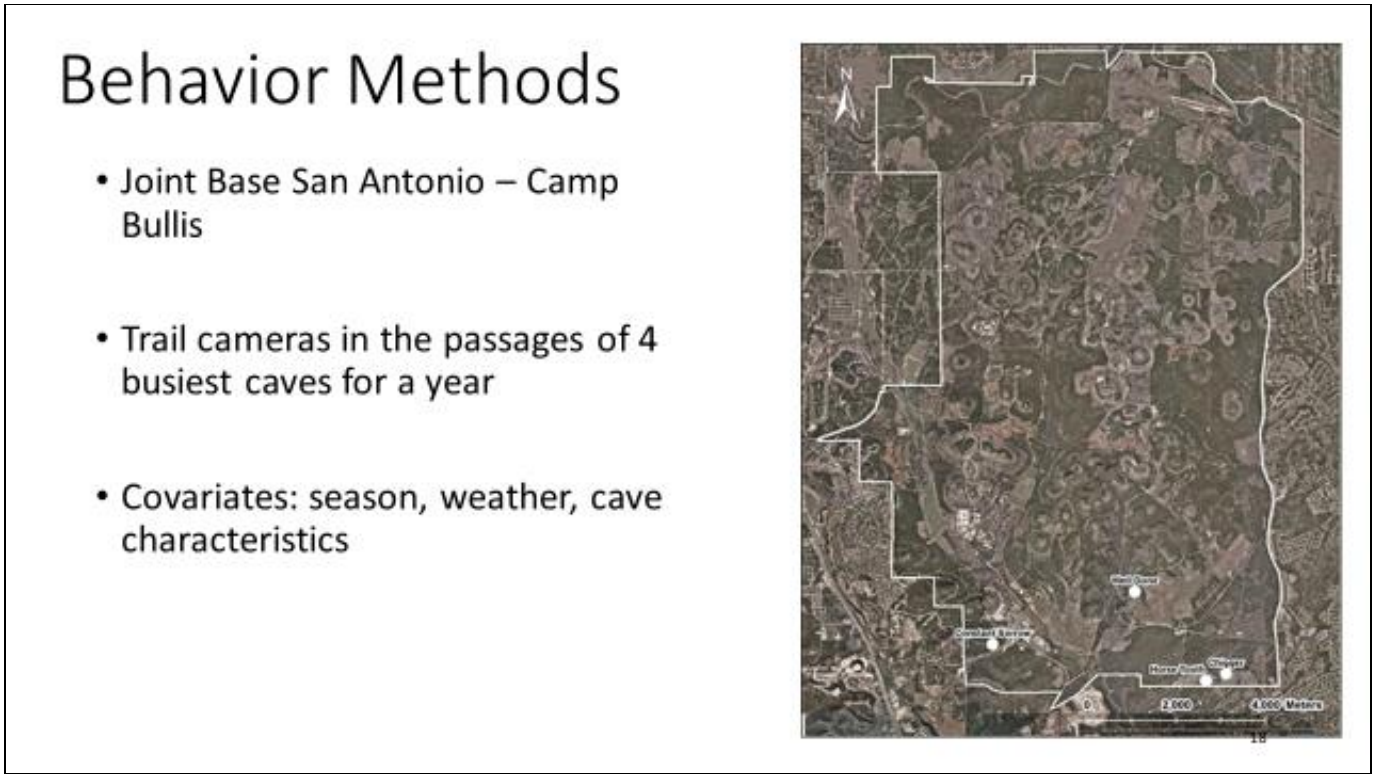
A-15. I also compared meso-mammal cave use according to presence or absence of endangered arthropods. Endangered species caves are managed for red imported fire ants which compete and may directly prey upon cave crickets (photo; *Ceuthophilus* spp.). Cave crickets are an indicator of cave health and also provide nutrients (e.g. scat) into portions that are inaccessible to meso-mammals. Cave crickets are also hunted by raccoons and opossums. Unsurprisingly, endangered species caves were used more by raccoons and opossums than by strictly herbivorous porcupines.



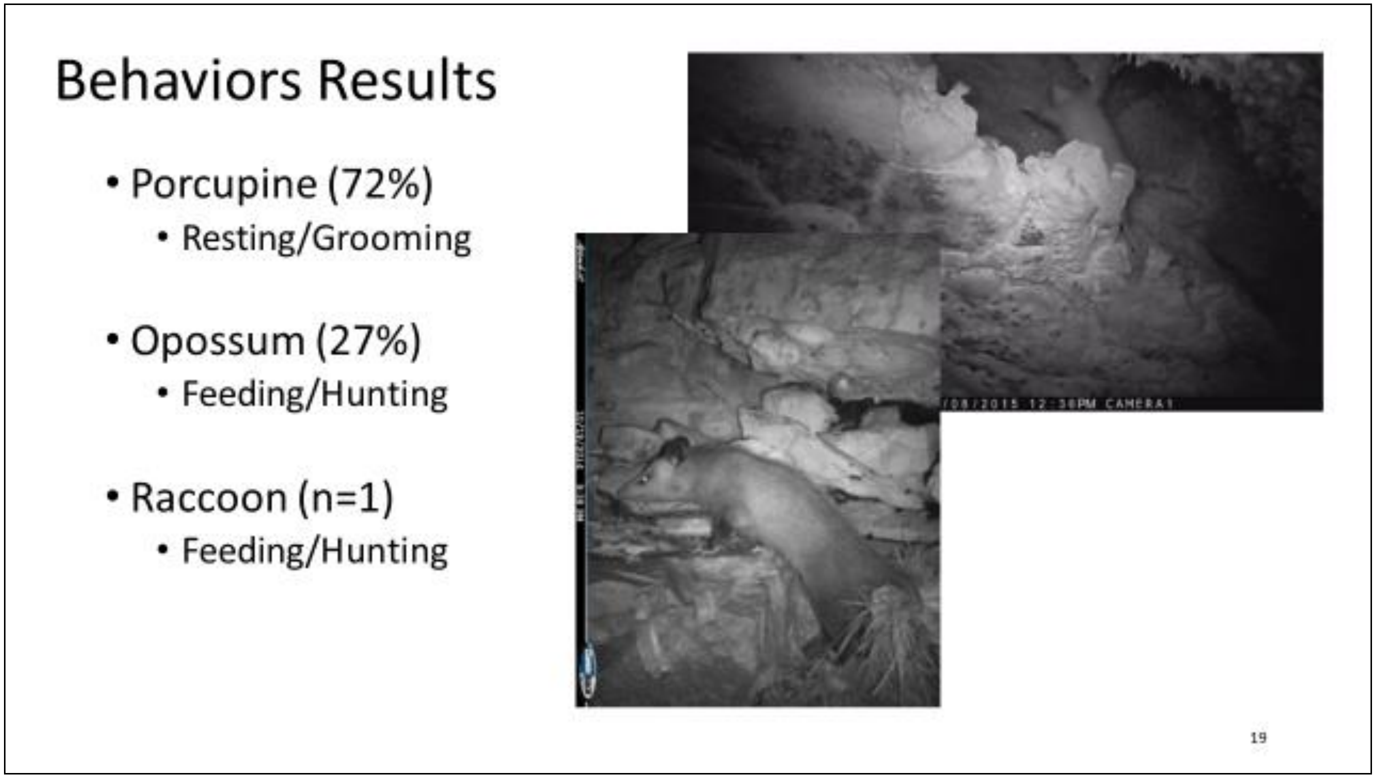
A-16. The take-away message from this chapter is that porcupines dominate cave use in central Texas. My data shows that caves are not used equally and that species have preferences according to weather conditions and cave characteristics. This photo shows two ringtails in one of the caves they frequented.



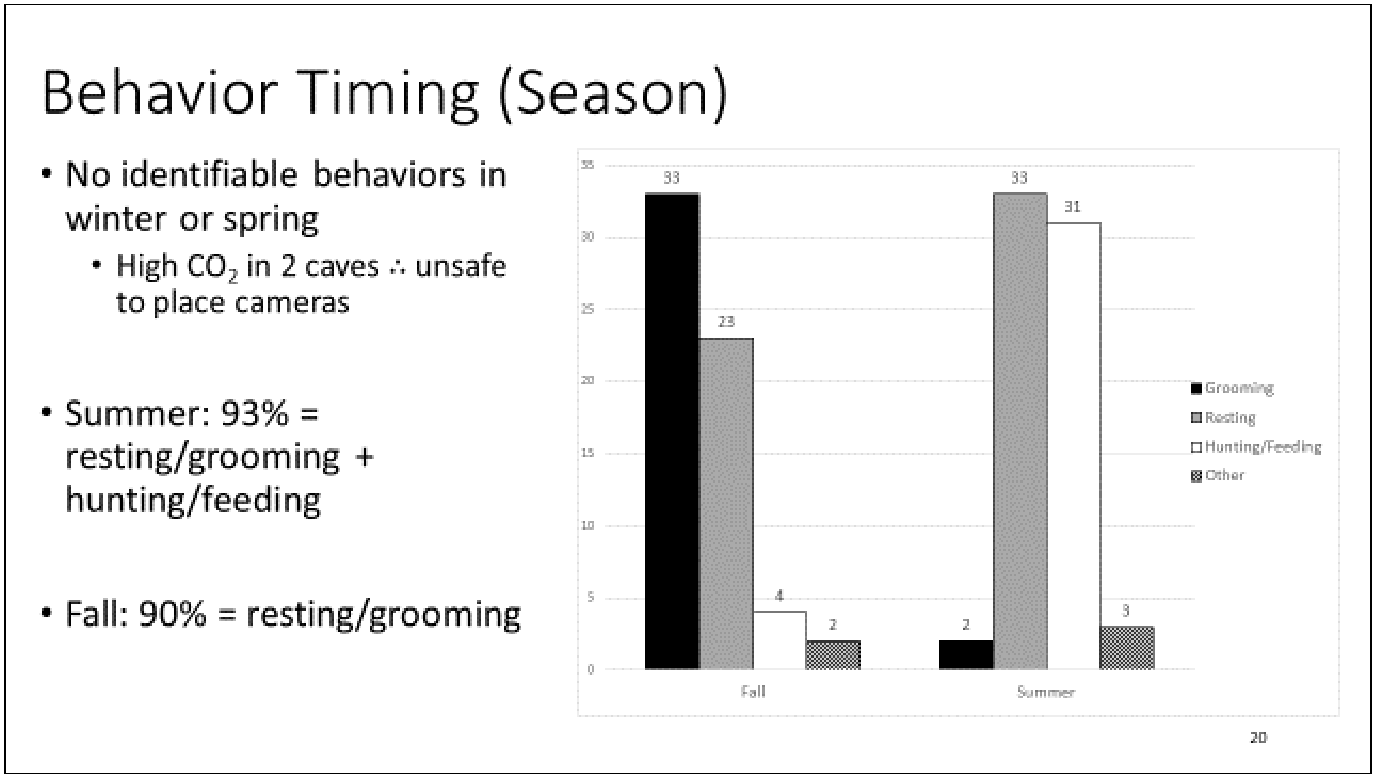
A-17. Moving on to Chapter 3, I now know which meso-mammals visit caves, and I next looked at what meso-mammals were doing in caves. Literature has hypothesized that raccoons and opossums use caves for hunting and denning while porcupines only use caves for denning. These two photos are consecutive shots of two porcupines fighting. In the top left photo, you can just see the hind legs and stomach of the second porcupine standing on the large rock.



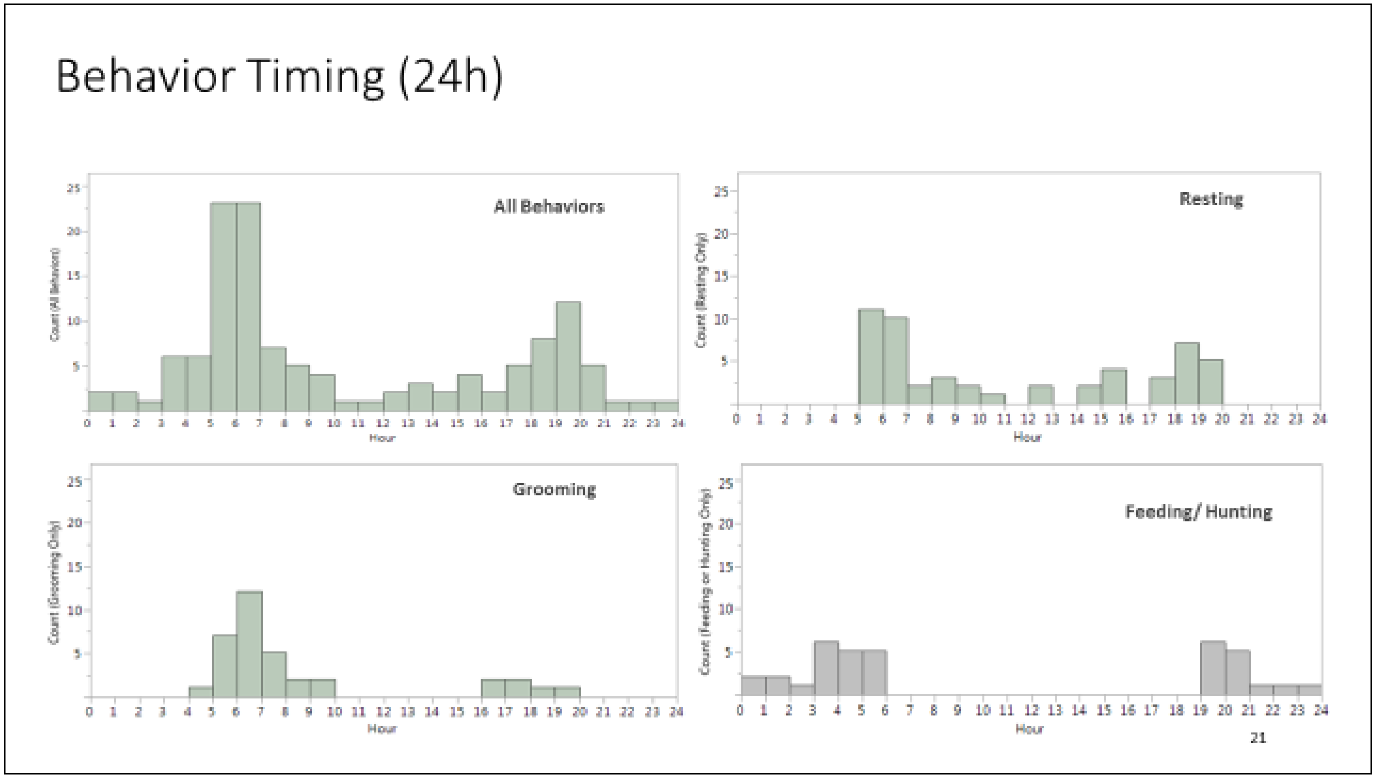
A-18. For this portion of my study, I selected the 4 caves most visited by meso-mammals. In each cave I placed infrared cameras, set to record videos, throughout all the passages for a year. I then compared these videos to the covariates of season, weather, and a variety of cave characteristics. This photo is an aerial image of Camp Bullis with a white line around the installation's boundary and white dots for each of the caves.



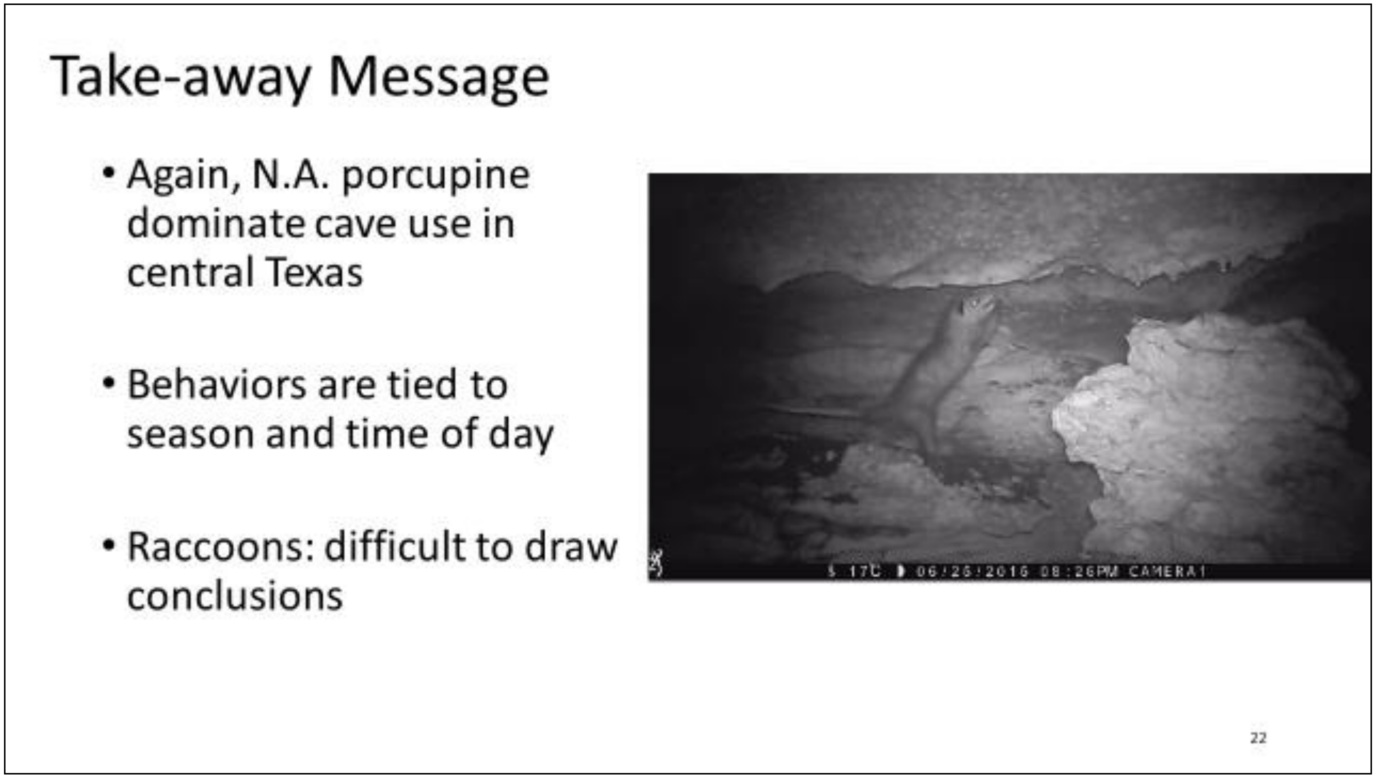
A-19. Porcupines were again the most frequently captured species with all the videos showing them resting or grooming. Opossums were the second most frequently captured species with all videos showing them hunting of feeding. The top video freeze-frame shows the belly of an opossum as it reaches for arthropods on the cave ceiling. I have evidence that opossum are using Camp Bullis caves for denning (bottom photo) but this was only seen in the preceding year's entrance photo dataset rather than in the passage behavior videos. There was only one video of a raccoon with an identifiable behavior therefore making any analysis unreliable.



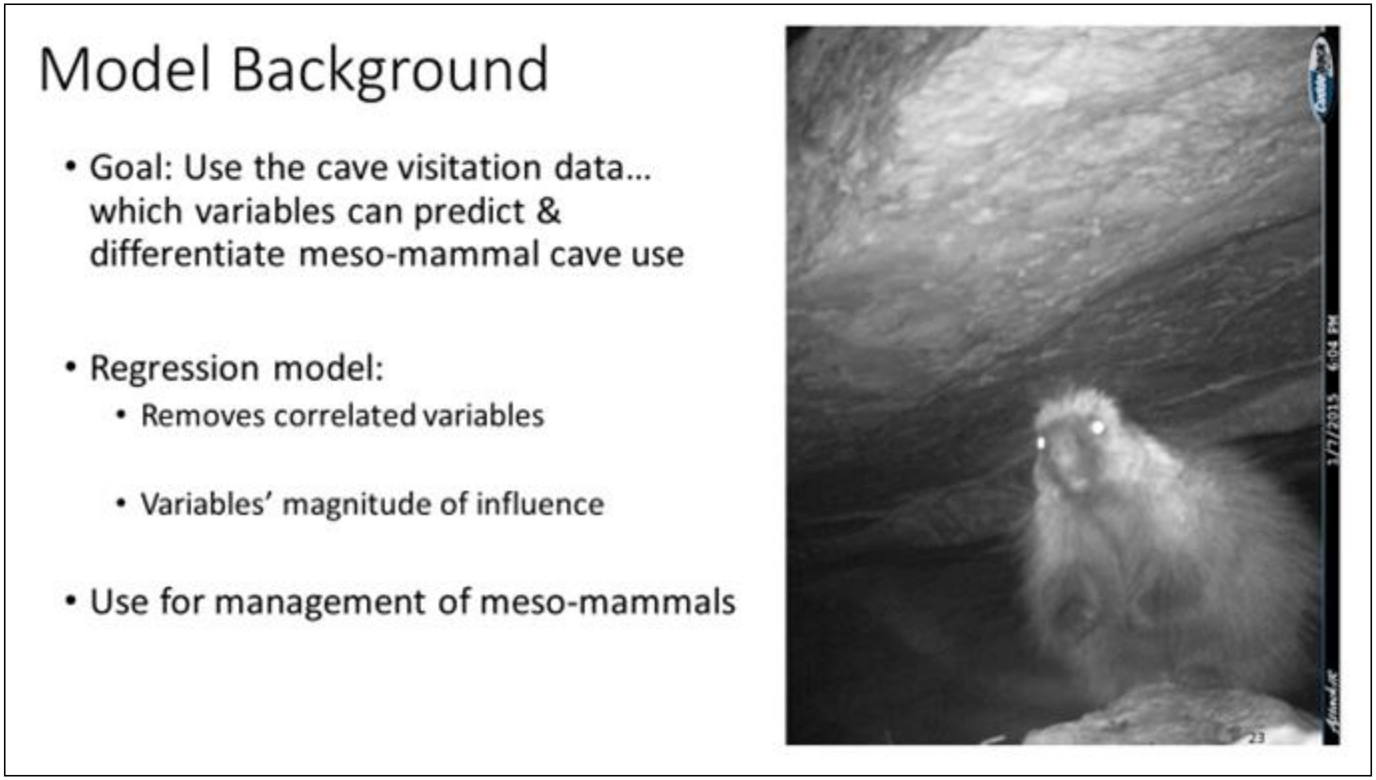
A-20. No videos with identifiable behaviors were recorded in the winter or spring. Two caves were not followed during these seasons because high CO_2 levels made placing cameras unsafe. Summer behavior videos were equally split between resting/grooming and hunting/feeding videos. On the other hand, almost all fall videos showed only resting/grooming behaviors.



A-21. Overall, behaviors videos maintained a bimodal distribution with peaks at dawn and dusk (see A-12). Only the resting behavior videos deviated from this pattern with videos occurring during daylight hours. This was expected since nocturnal animals (e.g. porcupines, raccoons, opossums) are most likely to be resting during daylight hours.



A-22. The take-away message for Chapter 3 is that, again, porcupine dominate cave use in central Texas. My data shows that behaviors are tied to season and time of day. Finally, because I had very little data for raccoons, further studies are needed to understand raccoon behaviors in caves. This photo shows another opossum hunting for arthropods on a cave ceiling.



A-23. In Chapter 4 my goal was to use Chapter 2's dataset to build a model that explained the differences in meso-mammal cave use by species. Modeling this data allowed me to remove correlated variables and quantify the influence of only the most influential variables. The results from this chapter can be used to influence meso-mammal visitation.

Model Methods

- Used the entrance camera visitation data
- Multinomial logistic regression
  - Response variables: N.A. porcupine, raccoon, Virginia opossum
  - Explanatory variables: cave characteristics, weather, season, time of day

A-24. I used the entrance photo data for all 30 caves (Chapter 2) for this multinomial logistic regression model. The response variables were either porcupine, raccoon, or opossum, and the explanatory variables were the weather data, cave characteristics, and temporal data.

Model Methods

- Training dataset (80%) & validation dataset (20%)
- Removed correlated variables (VIF > 5)
- Chose model based on low AIC_c, high AUC, Whole model test, & lack of fit

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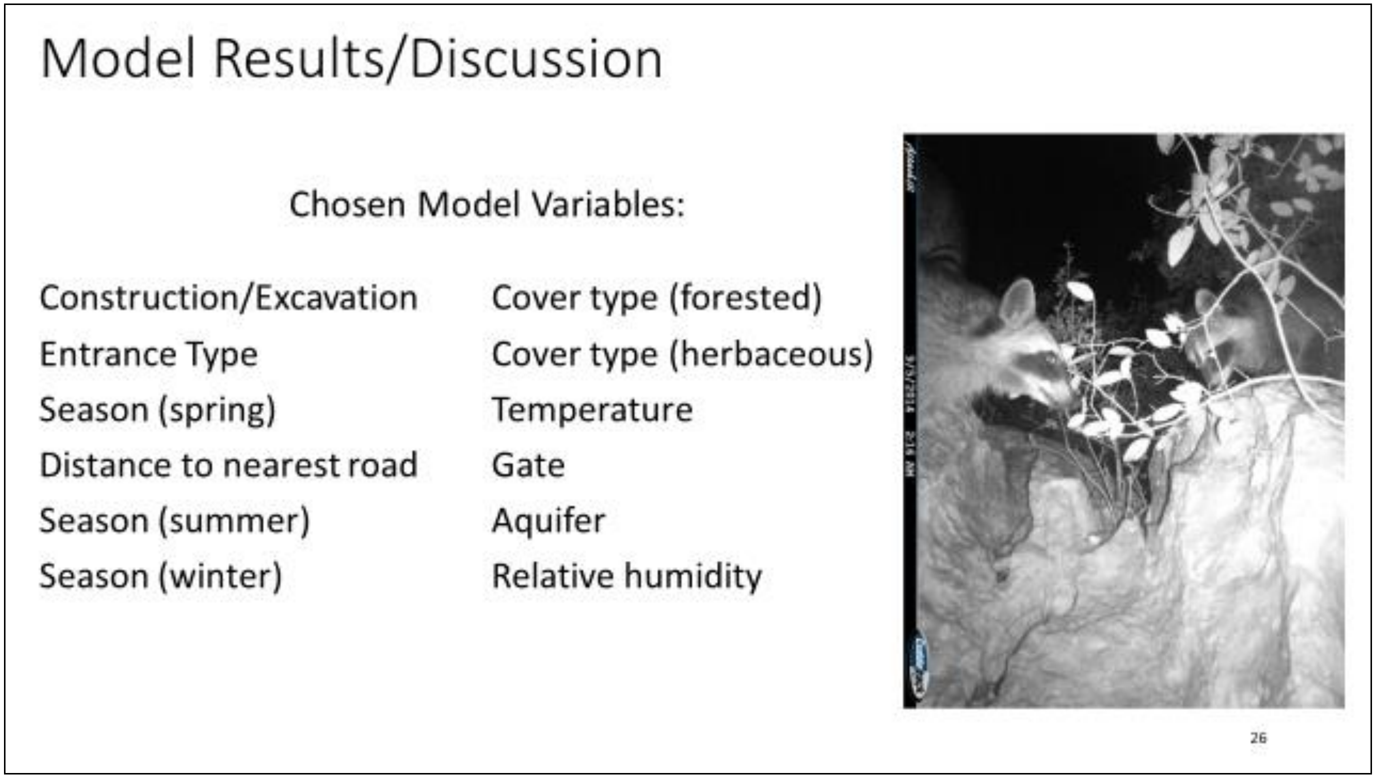
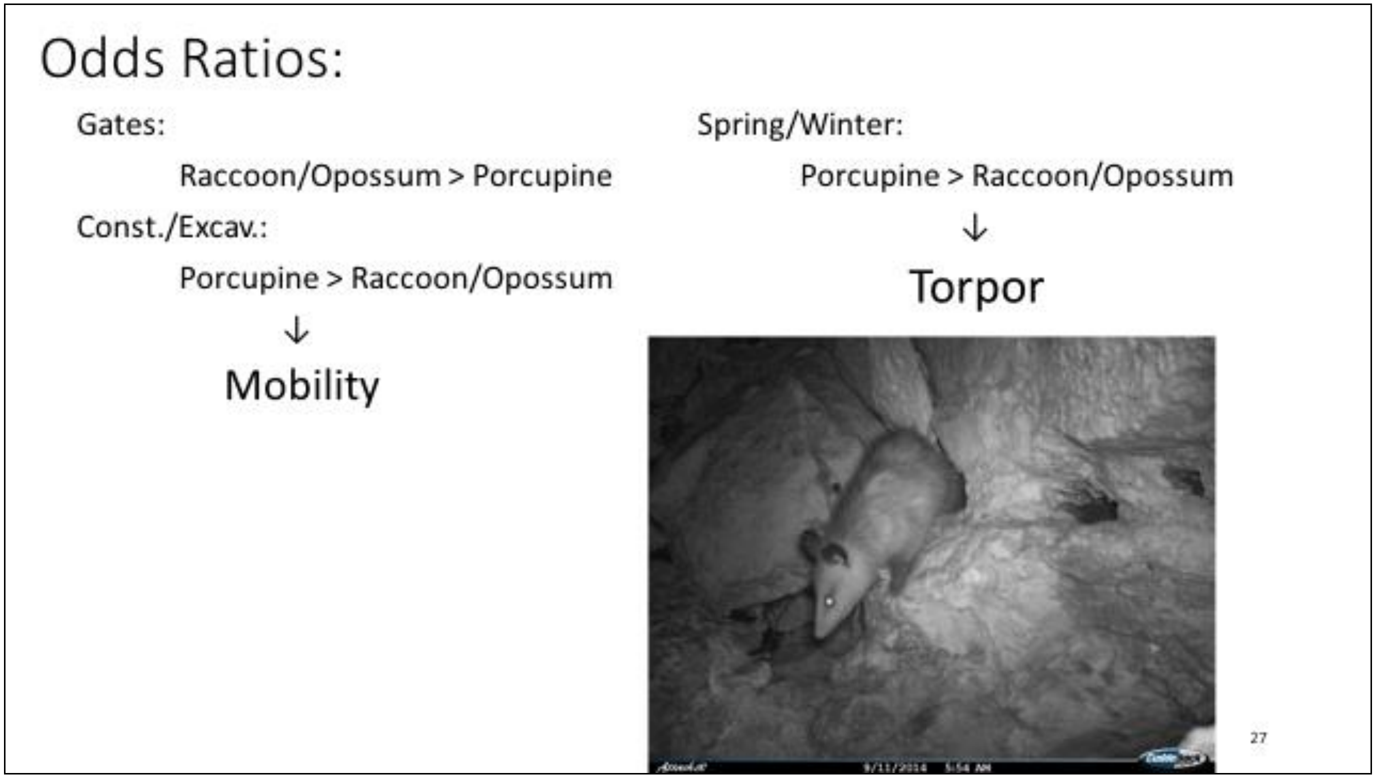
A-25. Before beginning model selection, I split the dataset in two. Eighty percent of the data was used as a training dataset to build the model. The remaining 20% was the validation dataset used to confirm the utility of the model. I also removed any correlated variables by calculating their variance inflation factors (VIF). Any variables with a VIF of 5 or greater was removed because it suggested that approximately 80% of the variance could be explained by linear correlation. The final model was chosen based on a low AIC_C, high area under the receiver operating curve (AUC), significant whole model test, and non-significant lack of fit test.



A-26. The chosen model included these 12 variables and are ordered from greatest to least effect (top to bottom, then left to right) so construction/excavation had the greatest effect and relative humidity had the least effect.



A-27. I then focused on those variables with significant odds ratios. My calculations showed that raccoons and opossums had greater odds than porcupines of using gated caves while porcupines had greater odds than raccoons or opossums of using constructed or excavated caves. I believe both of these calculations are a result of differences in species mobility and agility. Porcupines are not as agile as raccoons and opossums and therefore are more likely to use caves that do not require them to navigate through a gate, restricted entrance, or narrow passage. Also, my calculations show that porcupines had greater odds than raccoons and opossums of visiting caves during the spring and winter. I believe this is a result of raccoons and opossums entering torpor during cold periods and therefore visiting caves less frequently.

Model Results/Discussion

Photo ID	Model Predicted ID: North American porcupine	Raccoon	Virginia opossum
North American Porcupine	2242 (97.18%)	54 (2.34%)	11 (0.48%)
Raccoon	157 (37.38%)	240 (57.14%)	23 (5.48%)
Virginia opossum	106 (33.54%)	23 (7.28%)	187 (59.18%)

Validation:

- Model still signification
- No lack of fit
- Even lower AIC_C
- AUC > 0.90

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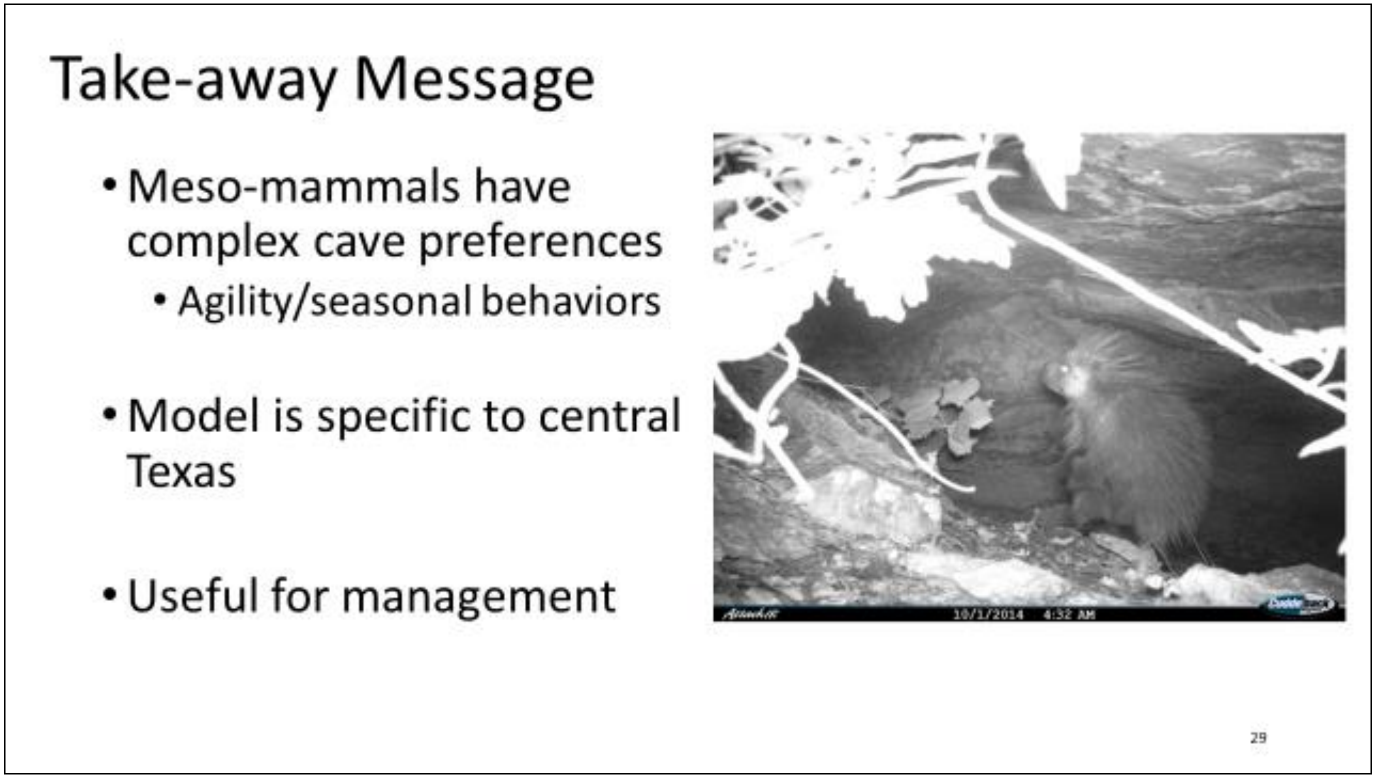
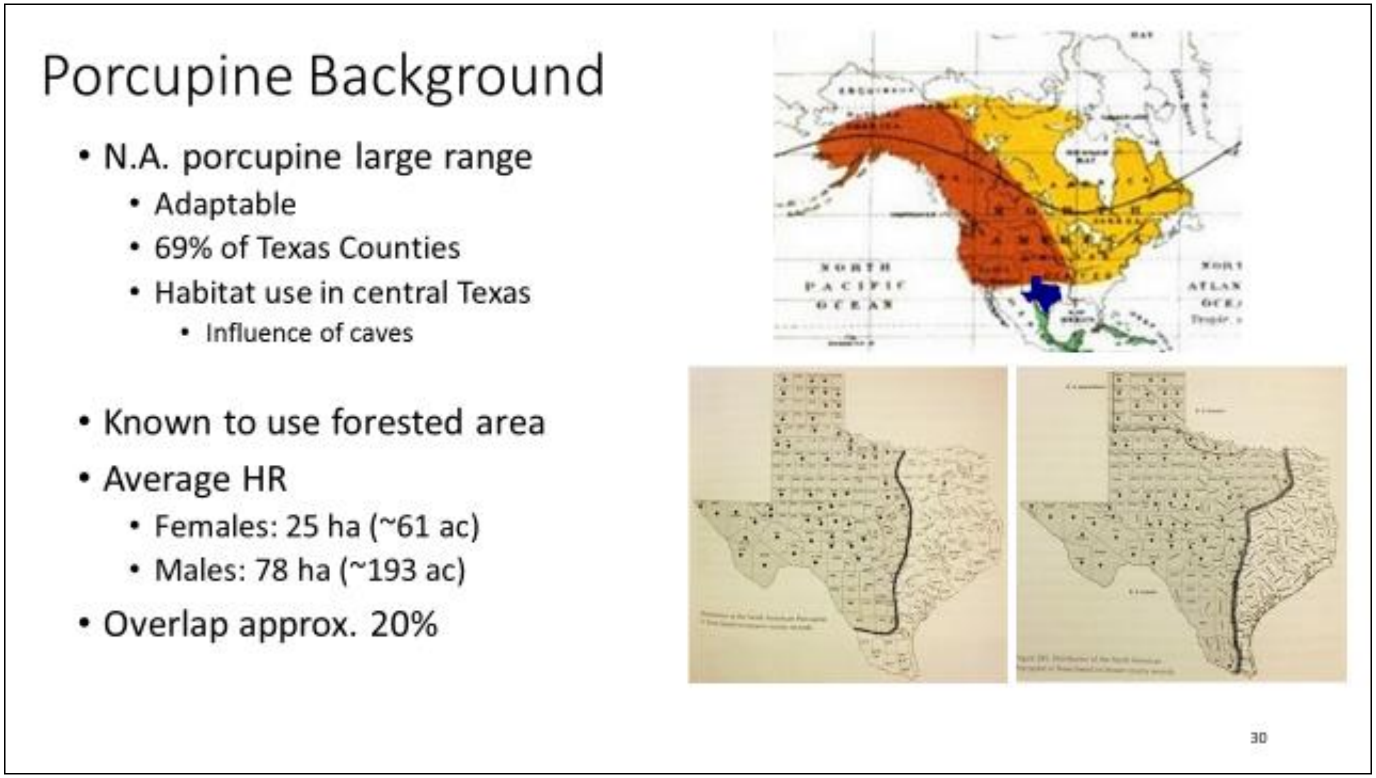
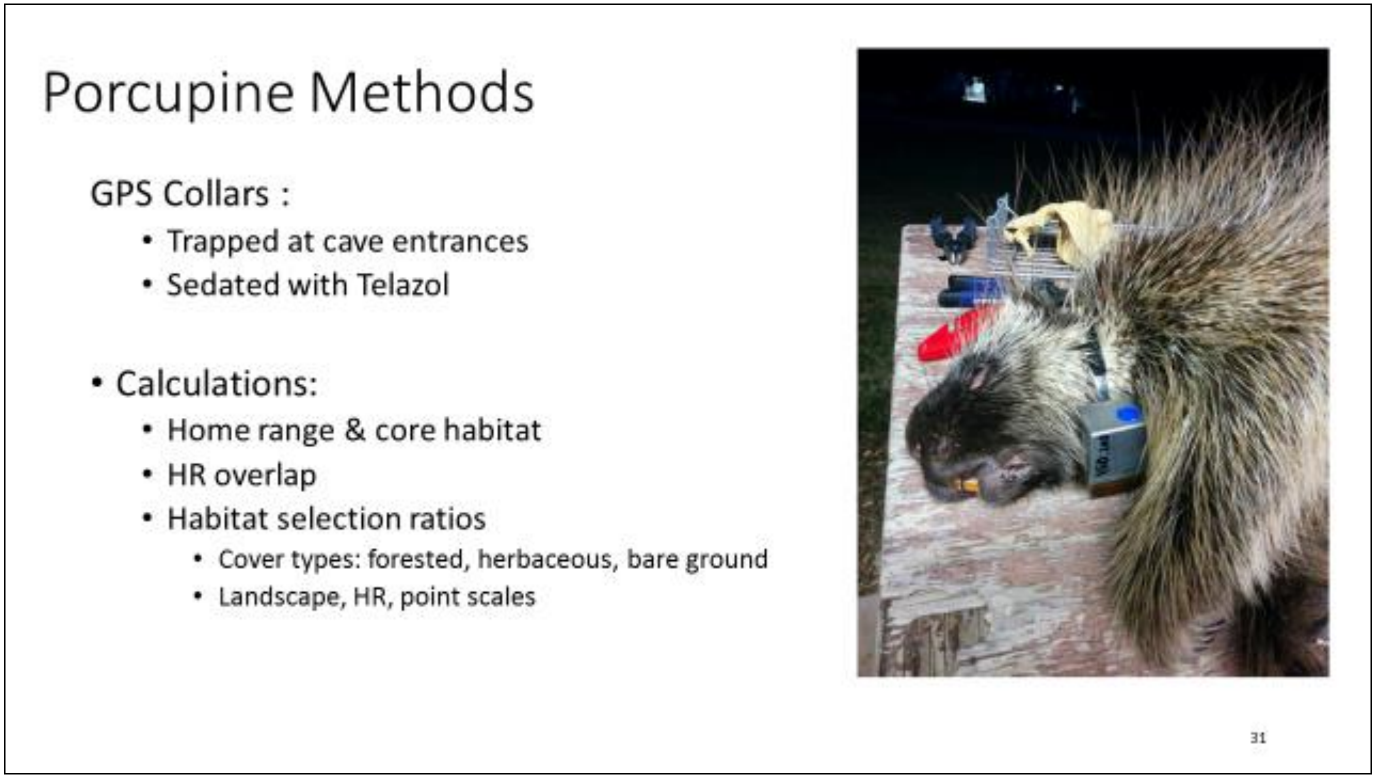
A-28. Applying the model to the data correctly classified 97% of porcupine photos but only 57% of raccoon photos, and 59% of opossum photos. Applying the model to the validation dataset still returned a significant whole model test, showed no lack of fit, a lower AIC_C, and an AUC > 0.90.



A-29. The take-away message from this chapter is that meso-mammal cave use in central Texas is complex (as demonstrated by the number of significant variables in this model). It is worth emphasizing that this model is best applied to managing porcupines, in particular, and is specific to meso-mammal cave use in central Texas. Meso-mammal cave use, and the variables that influence their decisions, are is likely different for other cave systems. For example, I suspect that porcupine cave use in Alaska is likely much more strongly tied to temperature. Should cave managers need to decrease porcupine use of a particular cave in central Texas, my data suggests they should consider adding a cave gate and constricting entrances and passageways.



A-30. The final portion of my project (Chapter 5) looked into the habitat use of porcupines in central Texas and how caves are incorporated into their home ranges. Porcupines are extremely adaptable and have expanded their range into Texas. The top photo is a porcupine range map from 1866 and shows porcupines just in the northern portion of the Texas panhandle. The bottom left photo shows their range in 2004, and finally the photo on the bottom right shows their range as of 2016. As of 2016 porcupines were found in 69% of Texas counties and are now naturalized in central Texas. Porcupines are known to use forested areas throughout their range but it is unknown what specific habitat porcupines use in central Texas. Previous studies have shown that porcupines have an average home range size of 25 ha for females, 78 ha for males, and an approximate 20% home range overlap.



A-31. For this study I trapped porcupines at cave entrances, sedated them with Telazol, and fitted them with GPS telemetry collars. From this data I calculated their 95% kernel density estimate home range, 50% kernel density estimate core habitat, and home range overlap. I also calculated habitat selection ratios for the landscape, home range, and point scales for the 3 cover type variables of forested, herbaceous, or bare ground.

Porcupine Results/Discussion

	Sex	Dates	*n*	95% KDE	50% KDE
PorcA	F	07/28/2015 – 11/11/2015	314	103.6	10.6
PorcB	M	07/24/2015 – 11/23/2015	645	420.6	7.39
PorcC	F	08/10/2016 – 01/11/2017	538	46.35	4.04
PorcD	F	08/10/2016-01/03/2017	504	64.0	5.4

PorcA/PorcB
- Well Done cave
- Overlap index: 42.4%
  - 5/100 days

PorcC/PorcD
- Peace Pipe cave
- Overlap index: 92.7%
  - 69/147 days

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A-32. I trapped a total of 4 individual porcupines; 3 females and 1 male. PorcA and PorcB were both trapped at Well Done Cave and were followed for approximately 4 months. PorcC and PorcD were both trapped at Peace Pipe Cave and were followed for approximately 6 months. Home ranges ranged from 46 to 421 ha and core areas ranged from 4 to 10 ha. PorcA and PorcB had an overlap index of 43% and spent 5/100 days within 100m of each other. PorcC and PorcD had an overlap index of 93% and spend 69/147 days within 100m of each other. All individuals had home ranges and overlap calculations that were larger than the range average.

A-33. This is an aerial image of PorcA (single white line) and PorcB's (double white line) home range and core areas. PorcA's core area closely mimics the 100m buffer around the cave trap site (single black line) while PorcB, the male, had a much larger home range and a core adjacent to the cave. Both individuals had clusters of points away from the cave and were shown to be forested habitat with greater tree diversity. These clusters also typically had mature oak trees and an abundance of acorns.

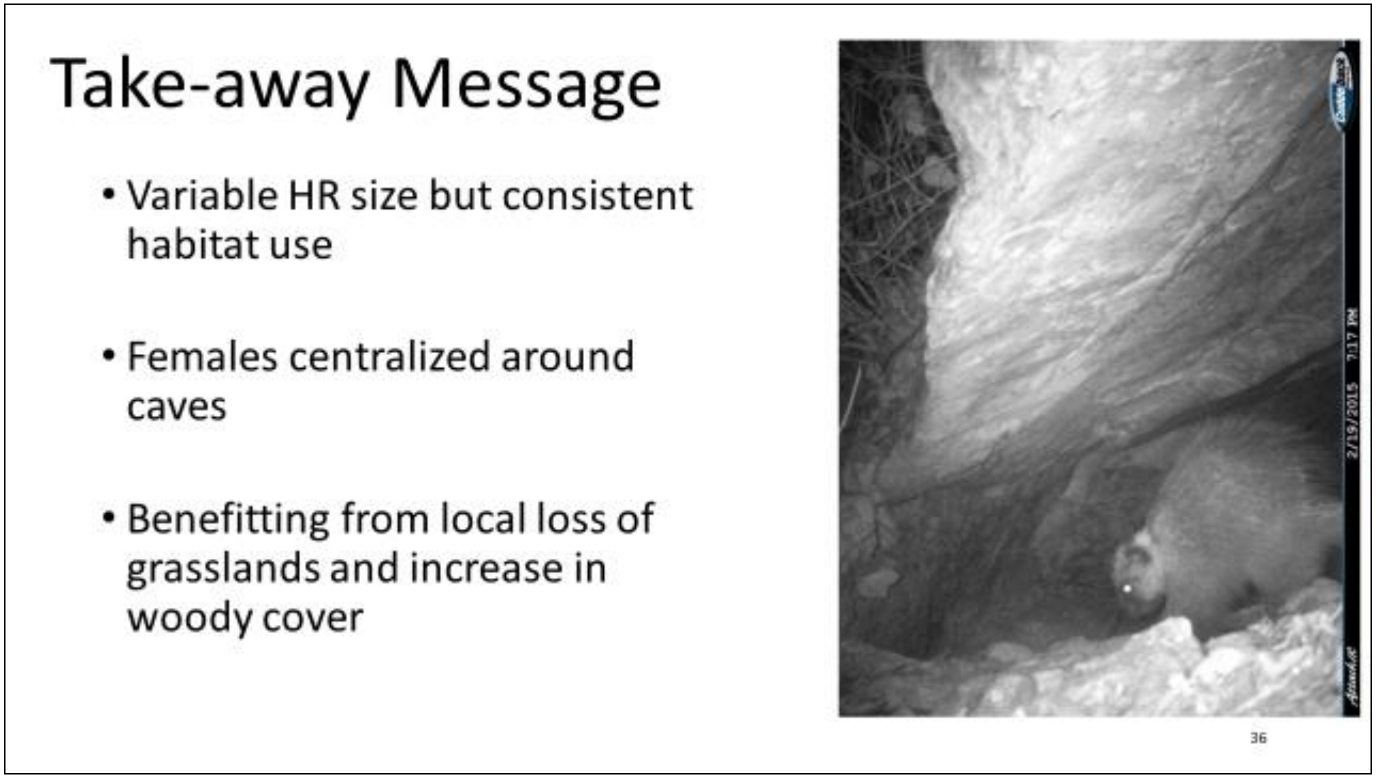
A-34. This is an aerial image of PorcC (single white line) and PorcD's (double white line) home range and core areas. PorcC and PorcD's core areas both closely mimics the 100m buffer around the cave trap site (single black line). Both individuals also had clusters of points away from the cave that were shown to be forested habitat with greater tree diversity. The clusters also typically had mature oak trees and an abundance of acorns.

Selection Ratios

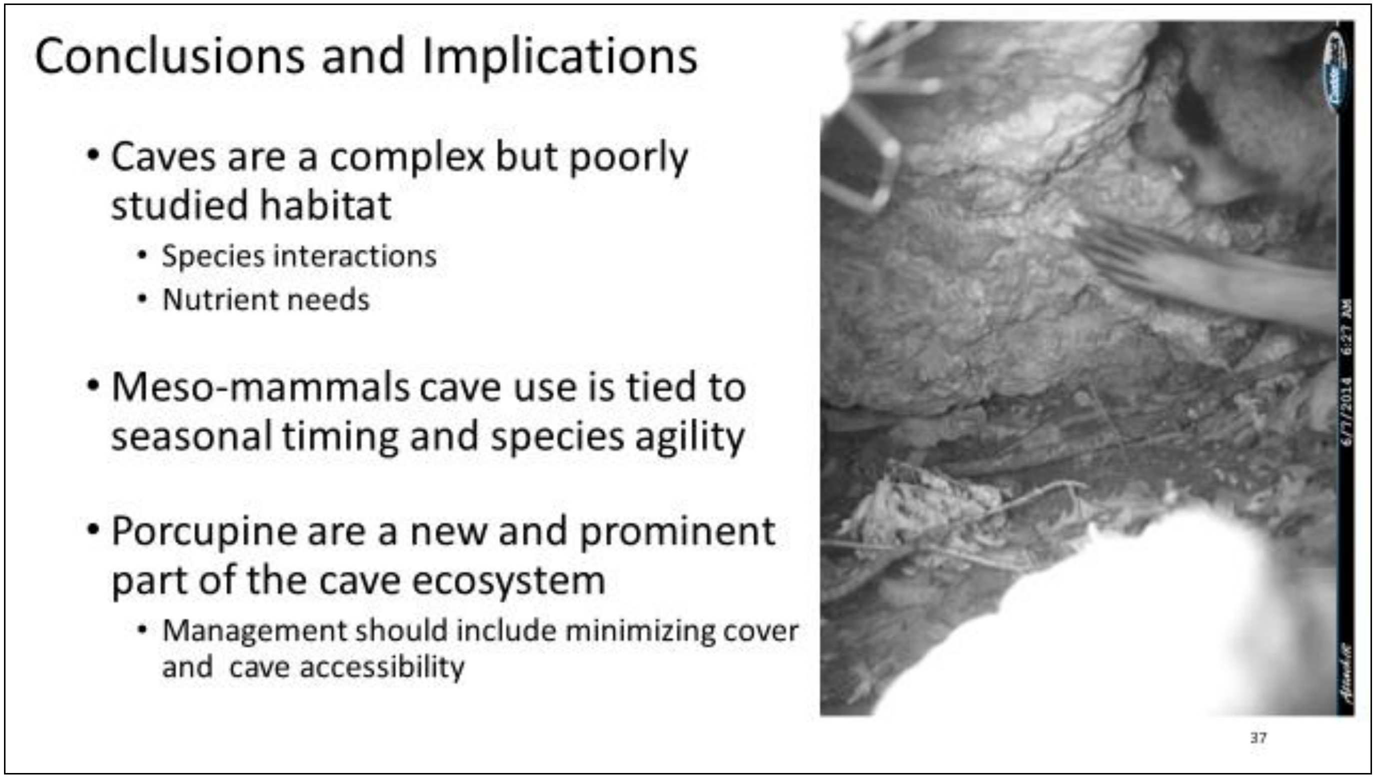
- Landscape scale
  - Selected for forested/closed cover
- Home range scale
  - Selected for bare ground/open cover
- Point location scale
  - Selected for forested/closed cover

35

A-35. Porcupines selected for forested or closed cover at both the landscape and point scale, but selected for bare ground and open cover at the home range scale. This means that as porcupine expanded their range into central Texas, they stopped at Camp Bullis because it was forested (landscape scale). Within Camp Bullis, the chose home ranges that had sufficient bare ground (home range scale). I suspect this was used for trails or corridors, perhaps to different clusters to feed on acorns. Finally, though their home range had bare ground, the points they actually used were forested.



A-36. The take-away message from this chapter is that individual porcupines have variable home range sizes, typically larger than average, but all showed consistent habitat use. Females, in particular, centralized their core areas around the cave which they were trapped. My data also suggests that porcupine in the area have benefited from the local loss of grasslands and increase in woody cover.



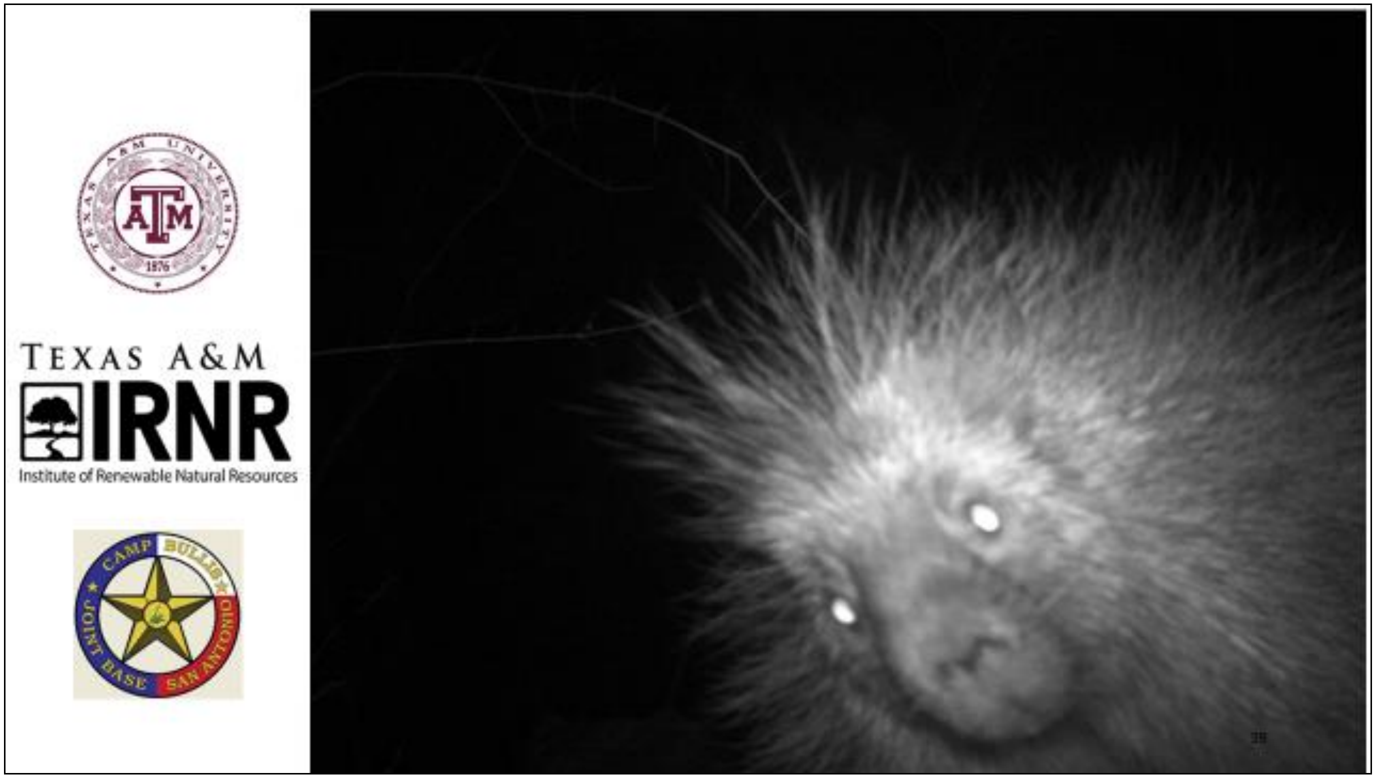
A-37. This study has demonstrated the complexity of caves including species interactions and nutrient needs. My study also showed meso-mammal cave use is likely tied to seasonal timing and species agility. Also, porcupine are a new and prominent part of the cave ecosystem and should management be needed to decrease their cave use, strategies ought to include minimizing vegetative cover and cave accessibility. This photo shows a raccoon hunting for arthropods on a cave wall.

Future Studies

- Determining acceptable/unacceptable nutrient levels
- Describe direct and indirect interactions between meso-mammals and cave-obligate species (including ES)
- Determine role of vultures in annual cave nutrient cycles
- Explore implications of meso-mammal & porcupine cave use for disease
  - Chagas
  - Relapsing fever

38

A-38. Finally, potential future studies might include determining acceptable or unacceptable cave nutrient levels, describing direct and indirect interactions between meso-mammals and cave-obligate species, determining the role of vultures in annual cave nutrient cycles, and exploring implications of meso-mammal and porcupine cave use in the transmission of diseases like Chagas and Relapsing Fever.



A-39. Acknowledgements