BOBCAT RESPONSE TO DROUGHT IN A SEMI-ARID ECOSYSTEM AND THE INFLUENCE OF MICROHABITAT STRUCTURE ON DETECTION

A Thesis

by

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ABSTRACT

Bobcat Response to Drought in a Semi-Arid Ecosystem and the Influence of Microhabitat Structure on Detection (May 2015) Gordon Wesley Watts III, B.B.A., University of Georgia

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The large area requirements and trophic level position of large mammalian carnivores allow them to serve as indicators of community health and function as umbrella species for the habitat they occupy. The bobcat (*Lynx rufus*) is a resilient species that is able to adapt to a variety of ecosystems. My first objective was to determine the influence of environmental conditions, habitat, and coyotes (*Canis latrans*) on bobcat population density. I examined bobcat populations over time using remote cameras and spatially explicit capture-recapture methods at 3 study sites in South Texas, a highly dynamic ecoregion. Bobcat densities were similar over time at each study site but varied somewhat among the study sites. The differences in environmental productivity, habitat, and coyote occupancy rates may each partially explain the variation in bobcat density among the sites.

Second, I examined the influence of woody micro-scale habitat structure and commercial trapping lure on the encounter rate of bobcats at 3 study sites in South Texas. I found a positive association between bobcat encounter rate and 3 habitat variables: screening cover 0.5–1 m, canopy cover >1 m high, and opening width. Lure and study site were not important variables in the final model. However, lure did elicit a behavioral response for some individuals, which aided in their identification. My study was unique in that it examined the simultaneous effects of

iii

lure and micro-scale habitat variables on bobcat travel routes. This information can be used to increase detection of bobcats and improve the precision and reliability of population estimates. These structural habitat variables may also be used to identify travel corridors for bobcats and other wildlife that share similar habitat.

DEDICATION

I would like to dedicate this thesis to all my friends and family far and wide and in Kingsville whom I have not been able to spend as much time with as I would have liked during this graduate school endeavor. I'll make up for it, promise!

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vi

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TABLE OF CONTENTS

ABSTRACT	iii
DEDICATION	v
ACKNOWLEDGMENTS	vi
TABLE OF CONTENTS	viii
LIST OF TABLES	x
LIST OF FIGURES	xii
CHAPTER I. BOBCAT POPULATION RESPONSE TO DROUGHT IN A SEM	I-ARID

ECOSYSTEM	1
1.1. Introduction	1
1.2. Study Area	5
1.3. Methods	7
1.4. Results	21
1.5. Discussion	33
1.6. Management Implications	37
1.7. Literature Cited	37
CHAPTER II. INFLUENCE OF MICROHABITAT STRUCTURE AND LURE ON	
ENCOUNTER RATES ALONG BOBCAT TRAVEL ROUTES	46
2.1. Introduction	46
2.2. Study Area	48
2.3. Methods	50

	2.4. Results	55
	2.5. Discussion	60
	2.6. Management Implications	64
	2.7. Literature Cited	64
VITA		69

LIST OF TABLES

Table 1. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the San Antonio Viejo study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a Table 2. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the Buena Vista study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a hyphen (-) between them represent sessions grouped together for each parameter......14 Table 3. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the Santa Rosa study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a hyphen (-) between them represent sessions grouped together for each parameter......16 Table 4. Multi-season occupancy models and occupancy estimates ($\hat{\Psi}$) for covotes at 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul Table 5. Summary of parameters estimated for San Antonio Viejo, Buena Vista, and Santa Rosa, South Texas, Feb 2012–Jul 2014......25 Table 6. Model-averaged estimates of bobcat detection (g_0) and decay rate in detection (σ) for 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul

Table 7. Probability of detection (p) for coyote multi-season occupancy models at 3 study sitesin South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul 2014......32

Fable 8. Mean, range, and parameter estimates for all variables included in the global and final
negative binomial mixed models with repeated measures. Data were collected on 3 study
sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa from 17 Oct 2013-14
May 2014

LIST OF FIGURES

Figure 1. Location of 3 study sites where camera trapping was conducted in South Texas: San
Antonio Viejo, Buena Vista, and Santa Rosa. Sites were sampled continuously from Feb
2012–Jul 2014
Figure 2. Bobcat density estimates (bobcats/100 km ²) and standard error bars at San Antonio
Viejo for sessions 1-5, Feb 2012–Jul 201422
Figure 3. Bobcat density estimates (bobcats/100 km ²) and standard error bars at Buena Vista for
sessions 1-5, Feb 2012–Jul 201423
Figure 4. Bobcat density estimates (bobcats/100 km ²) and standard error bars at Santa Rosa for
sessions 1-5, Feb 2012–Jul 201424
Figure 5. Bobcat density estimates (bobcats/100 km ²) and standard error bars for San Antonio
Viejo, Santa Rosa, and Buena Vista for sessions 1-5, Feb 2012–Jul 2014. Density estimates
were extracted from the top models for each study site that held density constant
Figure 6. Palmer Modified Drought Index (PMDI) for Texas Climate Region 9 and Normalized
Difference Vegetation Index (NDVI×10) for San Antonio Viejo (SAV), Buena Vista (BV),
and Santa Rosa (SR), South Texas, Jun 2010 – Aug 2014. Negative PMDI values indicate
drought conditions and positive values indicate wet conditions. Session start dates are
indicated on the x-axis. Number of different juvenile bobcats photographed is indicated by a
"+" above the NDVI values

CHAPTER I

BOBCAT POPULATION RESPONSE TO DROUGHT IN A SEMI-ARID ECOSYSTEM

The large area requirements, slow population growth rates, relatively stationary home ranges, and trophic level position of large mammalian carnivores allow them to serve as indicators of community health. They may also function as umbrella species for the habitat they occupy. Habitat that supports stable carnivore populations may also support high diversity and resiliency in small mammal, bird, herpetofauna, and arthropod communities. Specialists near the top of the trophic pyramid may function as indicator species because they are the most sensitive to changes in habitat (Odum 1971). However, use of specialist species as indicators is limited to the narrow range of resources they exploit (Landres et al. 1988). In contrast, generalists tend to use a variety of habitat types and food items.

Bobcats (*Lynx rufus*) are the most common native felid in North America. They are found from southern Canada to central Mexico (Anderson and Lovallo 2003). Bobcats occupy a plethora of habitat types, absent only from areas of intense agriculture and urban development (Crooks 2002, Hansen 2012), and although strictly carnivorous, they exploit a variety of prey species (Larivière and Walton 1997).

This plasticity in habitat use and prey selection makes the bobcat a remarkably resilient species that is able to adapt to a variety of ecosystems. The bobcat still occupies most of its historic range despite major previous exploitation (Anderson and Lovallo 2003, Hansen 2012). It is able to persist in residential areas (Harrison 1998, Riley et al. 2003), the Mojave and Sonoran deserts (Zezulak and Schwab 1980, Lawhead 1984), and persistent cold winters (-30°C)

This thesis chapter follows the style of the Journal of Wildlife Management.

of the Kootenay Mountains (Hansen 2012). The bobcat also thrives in the erratic climate of the South Texas brush country. The climate of South Texas resembles a tropical desert (Norwine and Bingham 1986, Fulbright and Bryant 2004) characterized by fluctuations between large, infrequent precipitation events and drought conditions. This climatic variability creates boom-and-bust population dynamics for many lower trophic level species (Hernández et al. 2002, Bradley et al. 2006). My main objective was to examine the stability of bobcat populations in this dynamic ecosystem.

The thornshrub of South Texas is a semi-arid, subtropical ecoregion with a mean temperature >20°C, and a mean frost-free period of 330 days (Haines et al. 2005). These warm temperatures enable many species to breed through the year when conditions are favorable (Davis and Schmidly 1997, Taylor et al. 1998, Tewes and Hornocker 2008). However, when rainfall is sparse, drought conditions can have a rapid negative effect on wildlife populations. Fluctuations between intense drought and periods of higher than average precipitation can produce highly dynamic prey populations (Tewes and Hornocker 2008).

Rainfall patterns also vary spatially. Average precipitation decreases as one moves from east to west across the region (Norwine et al. 2007). Localized precipitation events further contribute to spatial variability in drought conditions (Korn 2013).

Precipitation has a strong effect on bobcat prey abundance. Ernest et al. (2000) found a positive relationship among precipitation, primary productivity, and rodent abundance. Precipitation has also been linked to lagomorph reproductive activity (Portales et al. 2004). Semi-arid ecosystems are particularly sensitive to rainfall events. Previous researchers have documented a 3-month lag period between the response of rodent populations and either

significant rainfall or the onset of drought conditions (Windberg 1998, Bradley et al. 2006, Korn 2013).

Bobcat populations may respond to fluctuations in prey populations in two ways. Because rodents and lagomorphs are the two main prey for bobcats in the southern United States (Chamberlain and Leopold 1999, Fedriani et al. 2000, Thornton et al. 2004), precipitation and productivity should have a strong effect on bobcat population density, particularly in the semi-arid, subtropical ecosystems of South Texas. Conversely, bobcats can exploit a variety of prey, switching to more abundant species when populations of preferred prey decline (Beasom and Moore 1977, Leopold and Krausman 1986, Maehr and Brady 1986, Knick 1990, Blankenship 2000). High prey density and diversity associated with southern temperate areas such as South Texas may further enable prey switching by bobcats (Tewes and Hornocker 2008). This prey switching may buffer against the effects of environmental stress allowing bobcat populations to remain stable over time.

The spatial and temporal variation in precipitation and productivity of this study served as a natural experiment to test the resiliency of bobcat populations to environmental fluctuations. If bobcat populations were strongly affected by environmental conditions, then I would predict bobcat density to be lower during periods of lower productivity and in less productive areas. If bobcat populations were not strongly affected by environmental conditions, then I would predict densities to be similar over time and space.

I expected bobcat populations to be affected by environmental conditions on two time scales. I expected a shift in space use 3–4 months after a major change in environmental conditions, corresponding to the response of prey populations (Litvaitis et al. 1986, Knick 1990, Blankenship 2000). I also expected an 18-month lag between rain pulses and kitten recruitment.

This predicted lag would encompass a 3-month lag for initial increase of prey populations, 1 month for bobcat breeding, 2 months for bobcat gestation, and bobcat dispersal after 1 year of age.

Habitat structure and diversity at the landscape scale may also affect bobcat density. Although bobcats are generalist in habitat selection, one common feature among bobcat habitat types is understory cover, which provides screening cover to ambush or pursue prey from a short distance and for protection from larger predators (Anderson and Lovallo 2003, Horne et al. 2009, Hansen 2012). Also, the main prey of bobcats, lagomorphs and rodents, are associated with dense understory cover (Knowles 1985, Litvaitis et al. 1986). In South Texas, bobcats have been shown to have a positive relationship with moderate levels of woody understory structure (Horne et al. 2009). The different structural vegetation characteristics present in my study area allowed me to examine the influence of woody understory on bobcat populations, which was the second objective of my study. I predicted that bobcat density would be greater at study sites that had greater woody understory structure compared to sites that had more open understories.

Coyotes (*Canis latrans*) are a third major factor that influence bobcat populations, either through predation (Toweill 1986, Fedriani et al. 2000) or competition for prey resources. Although several studies identified diet overlap (Leopold and Krausman 1986, Major and Sherburne 1987, Fedriani et al. 2000), exploitative competition may not occur in areas where prey is abundant (Chamberlain and Leopold 1999, Neale and Sacks 2001, Thornton et al. 2004). However, when prey is scarce, spatial overlap between bobcats and coyotes can be high (Wilson et al. 2010), thereby increasing predation risk and competition for limited food resources. A third objective was to examine the effect of coyote occupancy on bobcat populations. I predicted

that time periods and study sites with a higher coyote occupancy rate would result in lower bobcat density.

STUDY AREA

I conducted camera trapping on 3 ranches in South Texas owned and operated by the East Wildlife Foundation. Eighty-four percent of the land area in Texas is represented by privately owned farms and ranches (Kjelland et al. 2007), and many of these properties are used for hunting. The study sites were unusual in that there was no hunting or predator control for the past several decades. Study sites were located on an east-west gradient (Fig. 1) and were composed of 3 distinct habitat types.

San Antonio Viejo Ranch (SAV) was the western-most study site located in Jim Hogg and Starr counties. The majority of this site was in the South Texas Brush Country Ecoregion, and it also contained the western border of the Coastal Sand Plains Ecoregion. The vegetation community was dominated by Tamaulipan thornshrub with few grassland communities. Shrub diversity at SAV was high. Dominant species included blackbrush (*Acacia rigidula*), cenizo (*Leucophyllum frutescens*), hogplum (*Colubrina texensis*), and granjeno (*Celtis pallida*). Dominant soil types included Brennan soils, Copita fine sandy loam, and Copita soils (McLendon et al. 2013a, KS2 Ecological Field Services, LLC, unpublished report).



Fig. 1. Location of 3 study sites where camera trapping was conducted in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa. Sites were sampled continuously from Feb 2012–Jul 2014.

Buena Vista Ranch (BV) was located about 13 km east of SAV and was also located in Jim Hogg County and the South Texas Brush Country and Coastal Sand Plains Ecoregions. This study site was dominated by grasslands interspersed with small patches of dense thornshrub. Mesquite (*Prosopis glandulosa*) dominated the woodland and shrubland areas. Other dominant shrub species included hogplum and catclaw (*Acacia greggii*). Dominant soil types were the Nueces-Sarita association and Delmita soils (McLendon et al. 2013b, KS2 Ecological Field Services, LLC, unpublished report).

Santa Rosa Ranch (SR) was located 50 km east of BV in Kenedy County and occurred within the Coastal Sand Plains Ecoregion. Vegetation consisted of mesquite shrublands and woodlands dominated by mature live oak (*Quercus virginiana*) and mesquite trees. This study site also contained a few wetland and grassland communities. Dominant soil types included Palobia loamy fine sand, Falfurrias fine sand, Falfurrias-Cayo complex, and Sarita fine sand (McLendon et al. 2012, KS2 Ecological Field Services, LLC, unpublished report). This site was closer to the Gulf of Mexico and typically received more rainfall than SAV and BV.

METHODS

Data Collection

I used infrared-triggered Cuddeback® Capture Flash digital cameras (Non Typical, Inc., Green Bay, WI, USA) to conduct the study. I overlaid a grid consisting of 1 km² cells on each study site and placed one camera station in each cell. Camera location within each grid cell was based on habitat features that would maximize detection of carnivores, which is a typical protocol for camera trapping studies (Karanth and Nichols 1998, Gardner et al. 2010, Sunarto et al. 2013). Therefore, I placed cameras adjacent to thornshrub corridors, trails, roads, and water. I separated cameras by ≥ 600 m, which resulted in 26–29 (SAV = 29; BV = 26; SR = 29) camera stations per study site spaced 600–1,800 m apart. Camera stations consisted of 1 or 2 cameras attached to a stake, tree, or fence post 40–50 cm above the ground and cameras operated for 24-hr each day with a 30-sec delay between photographs. I operated camera grids continuously from February 2012 to July 2014 and downloaded photograph data and replaced camera batteries every 3 months. To obtain photographs of both sides of individual bobcats, I added a second camera to each single camera station that photographed bobcats during previous sessions. These additional cameras were added during the last sampling periods or 'sessions' (sessions 4–5).

Lure increased precision of population estimates for Malagasy civets (Fossa fossana) without introducing bias (Gerber et al. 2012). Consequently, I added several types of trapping lure to all camera stations during the last sampling period (session 5) to increase detection rates and therefore precision of my density estimates. I used two types of lures: call lures and local lures. Call lures had a strong odor and were designed to attract animals from a distance whereas local lures consisted of gland, food, or "curiosity" lures designed to attract nearby animals to a specific point. The call lures I used were Gusto (Minnesota Trapline Products, Inc., Pennock, MN) and Snow Cat Bobcat #2 Lure (Grawe's Lures, Wahpeton, ND). The local lures I used were Feline Fix (Minnesota Trapline Products, Inc., Pennock, MN), Badlands Bob Gland Lure (Fur Country Lures, Jordan, MT), Cat-Man-Do (Milligan Brand, Chama, NM), and Finicky Feline #801 (Hoosier Trapper Supply, Greenwood, IN). I systematically implemented a one-time lure application in which I placed 1 of 2 call lures and 1 of 4 local lures at each camera station. This resulted in 8 lure combinations, which were replicated >3 times at each study site. I placed call lures 1.5–1.8 m high within view of the camera and on an object and aspect that would maximize scent dispersal by wind. Local lures were placed on the ground in front of the camera.

Drought and Productivity Analysis

I used the Palmer Modified Drought Index (PMDI) and the Normalized Difference Vegetation Index (NDVI) to assess regional drought conditions and productivity at each camera grid, respectively. The PMDI is a cumulative meteorological drought index that incorporates precipitation, temperature, and available water content of the soil. The index generally ranges between –6 and +6 with negative values indicating drought conditions and positive values indicating wet conditions. I obtained monthly PMDI values for Texas Climate Region 9 (NOAA 2014).

Because the 3 camera grids were located on the east-west extremes of the same PMDI climate region, I used NDVI to compare conditions among study sites. The NDVI is created from spectral reflectance data and can be used to determine the availability and condition of green vegetation (Andreo et al. 2009, Ferguson et al. 2009). This index has been correlated with aboveground net primary productivity and biomass (Burke et al. 1991, Paruelo et al. 2000). It has also been used as an estimate of herbivorous prey availability for bobcats and was found to be negatively correlated with female bobcat home range size (Ferguson et al. 2009). Therefore, I used NDVI as an index of prey abundance and compared values among study sites and among sessions within each study site. I downloaded 1-km resolution monthly NDVI values that were collected by the Moderate Resolution Imaging Spectrometer (MODIS) (NASA 2014). I buffered each camera grid by 3 km and calculated the mean NDVI value at each study site for each month from June 2010 to August 2014 to account for lag effects between environmental productivity and bobcat population responses. To provide a comparison with NDVI values, I downloaded long-term (1981–2010) and study period (Dec 2011–Jun 2014) precipitation values for each

study site (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 29 Mar 2015).

Individual Identification

I discarded bobcat photographs that were distorted, overexposed, or taken at extreme angles. Spotting patterns on the inside and outside of each bobcat leg were the most conspicuous markings and showed considerable variation among individuals (Heilbrun et al. 2003). Therefore, I mainly used these markings to distinguish among individuals. Photographs needed to contain \geq 3 clearly visible legs to be classified as "initial captures." I also used tail striping patterns, body spots, and facial markings for individual identification. I zoomed in on spotting patterns and made comparisons among individuals using 2 adjacent computer monitors. The 2 monitors measured 51 x 29 cm (width x height) and 47 x 30 cm.

I used 3 steps to ensure individual identification was correct. First, I classified photographs as a "recapture" if I was 100% confident that the markings were the same as a previously captured individual. Second, for photographs that I believed were a recapture, I compared every previously obtained photograph of that individual with the new photograph. Third, I compared each new bobcat photograph to previously obtained photographs. These comparisons were made even if I matched the photograph to a previously identified individual to ensure that the new photograph did not match >1 individual.

Bobcat Density Analysis

I used spatially explicit capture-recapture within a maximum likelihood framework to estimate bobcat densities for each session and study site. I used the secr package in program R to conduct the analysis (secr Version 2.9.2,

http://cran.r-project.org/web/packages/secr/index.html, accessed 30 Nov 2014; R Version 3.1.0, www.r-project.org, accessed 5 May 2014). I defined a sampling occasion as 7 days and divided capture data evenly into 5 sessions of 24 weeks each. Dates for the 5 sessions were as follows: Session 1 (Feb–Aug 2012), session 2 (Aug 2012–Jan 2013), session 3 (Jan–Jul 2013), session 4 (Jul–Dec 2013), and session 5 (Dec 2013–Jul 2014).

A session length of 5.5 months may seem lengthy in regards to the assumption of demographic closure; however, I believe this concern is not warranted for several reasons. Survival estimates for resident bobcats in South Texas were high ($\hat{S} = 0.95$) for a period of 24 weeks excluding road mortality (calculated from Blankenship et al. 2006). I excluded road mortality because there were no major roads within 3 km of the camera grids, whereas the Blankenship et al. (2006) study area bordered a major highway. Similar to other studies, I did not include juveniles in my analysis because they were captured infrequently (Karanth and Nichols 1998, Karanth et al. 2006, Rodgers et al. 2014). One of the main objectives of the bobcat capture-recapture analysis was to examine density over time and among the 3 study sites. I partitioned the study period into sampling periods of equal length. This was done to make density estimates comparable even if the assumption of closure was violated. If closure was violated, density estimates would still be comparable, but they would pertain to the superpopulation, which is the total number of individual bobcats at the study site that were alive at some point during the session (Schwarz and Arnason 1996, Royle and Gardner 2011).

To ensure independence in my analysis, I excluded photographs that were of the same individual at the same station within a 24-h period (Royle et al. 2009). Opposing cameras set at selected stations yielded simultaneous photographs of both sides for many individuals, but some individuals were only photographed on one side. Bobcat pelage patterns are bilaterally asymmetrical (Heilbrun et al. 2003); therefore, I analyzed left and right side datasets separately (Alonso 2012). If both sides of an individual were photographed, I included it in both left and right side analyses. I fit several initial models for each side separately and obtained the same results for top-ranked models and parameter estimates. Consequently, I only used the right side dataset for more in-depth analyses because it contained more samples for all 3 study sites.

I analyzed each study site separately using the multi-session population model in program secr. This model is considered a simplified open population model in which recruitment and survival are not modeled explicitly and sampling is assumed to be independent within each session (Efford 2012, Royle et al. 2014). I fit initial models holding density (\hat{D}) constant and models allowing \hat{D} to vary among sessions (Tables 1–3). Because data were sparse, I used peaks in the PMDI to determine how to group additional session-specific density estimates in the multisession model (Tables 1–3). To determine whether the 2-point spike in PMDI near the beginning of the study affected the bobcat density in session 1, I fit models varying density estimates for session 1 using the best fit model(s) for detection.

Table 1. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the San Antonio Viejo study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a hyphen (-) between them represent sessions grouped together for each parameter.

D^1	g_0^2	σ^3	NPar ⁴	logLik ⁵	AIC^{6}	ΔAIC^7	w^8
1-3,4-5	1-3,4,5	1-5	6	-446.80	905.59	0.00	0.26
1-3,4,5	1-3,4,5	1-5	7	-446.22	906.44	0.85	0.17
1-5	1-3,4,5	1-5	5	-448.53	907.07	1.48	0.13
1,2-3,4-5	1-3,4,5	1-5	7	-446.79	907.57	1.98	0.10
1,2-3,4,5	1-3,4,5	1-5	8	-446.21	908.42	2.83	0.06
1-3,4,5	1-3,4-5	1-5	6	-448.30	908.61	3.01	0.06
1,2-5	1-3,4,5	1-5	6	-448.43	908.86	3.26	0.05
1-4,5	1-3,4,5	1-5	6	-448.53	909.07	3.47	0.05
1,2,3,4,5	1-3,4,5	1-5	9	-446.14	910.28	4.69	0.03
1-3,4-5	1-3,4-5	1-5	5	-450.34	910.69	5.09	0.02
1,2-4,5	1-3,4,5	1-5	7	-448.43	910.85	5.26	0.02
1-5	1-4,5	1-5	4	-451.56	911.11	5.52	0.02
1,2,3,4,5	1-3,4-5	1-5	8	-448.22	912.45	6.85	0.01
1-3,4-5	1-4,5	1-5	5	-451.49	912.97	7.38	0.01
1-4,5	1-4,5	1-5	5	-451.54	913.08	7.49	0.01
1-5	1-3,4-5	1-5	4	-452.65	913.30	7.71	0.01
1-4,5	1-3,4-5	1-5	5	-452.14	914.28	8.68	0.00
1-3,4,5	1-4,5	1-5	6	-451.48	914.97	9.38	0.00
1,2,3,4,5	1-4,5	1-5	8	-451.40	918.81	13.21	0.00
1-4,5	1-5	1-5	4	-464.76	937.52	31.93	0.00
1-3,4,5	1-5	1-5	5	-464.68	939.36	33.77	0.00
1-3,4-5	1-5	1-5	4	-466.88	941.76	36.16	0.00
1,2,3,4,5	1-5	1-5	7	-464.60	943.20	37.60	0.00
1-5	1-5	1-5	3	-469.24	944.48	38.88	0.00

¹Density

²Probability of detecting an animal with a home range center located at the camera station

³Decay rate of the capture probability over distance from the home range center

⁴Number of parameters in the model

⁵Log likelihood

⁶Akaike's Information Criterion (AIC)

⁷Difference in AIC between model and the highest-ranked model

⁸AIC model weight

Table 2. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the Buena Vista study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a hyphen (-) between them represent sessions grouped together for each parameter.

D^1	g_0^2	σ^3	NPar ⁴	logLik ⁵	AIC^{6}	ΔAIC^7	w ⁸
1-3,4-5	1-4,5	1-5	5	-545.20	1100.40	0.00	0.13
1-3,4,5	1-3,4,5	1-5	5	-545.30	1100.60	0.20	0.12
1-5	1-3,4-5	1-5	4	-546.58	1101.15	0.35	0.11
1-3,4-5	1-3,4,5	1-5	6	-544.58	1101.17	1.26	0.07
1-3,4-5	1-3,4-5	1-5	5	-545.90	1101.80	1.40	0.06
1-3,4,5	1-4,5	1-5	6	-544.77	1101.54	1.63	0.06
1,2-5	1-3,4,5	1-5	6	-545.04	1102.08	2.17	0.04
1,2-5	1-3,4-5	1-5	5	-546.32	1102.65	2.24	0.04
1,2-3,4-5	1-4,5	1-5	6	-545.17	1102.34	2.43	0.04
1-5	1-4,5	1-5	4	-547.63	1103.25	2.45	0.04
1-3,4-5	1-3,4-5	1-5	5	-546.54	1103.07	2.67	0.03
1-4,5	1-3,4,5	1-5	6	-545.30	1102.59	2.68	0.03
1-3,4,5	1-3,4,5	1-5	7	-544.31	1102.61	3.30	0.03
1-3,4-5	1-5	1-5	4	-548.07	1104.13	3.33	0.02
1,2-5	1-4,5	1-5	5	-546.89	1103.77	3.37	0.02
1,2-3,4-5	1-3,4,5	1-5	7	-544.54	1103.09	3.77	0.02
1,2-3,4-5	1-3,4-5	1-5	6	-545.86	1103.72	3.81	0.02
1-3,4,5	1-3,4-5	1-5	6	-545.87	1103.75	3.84	0.02
1,2-3,4,5	1-4,5	1-5	7	-544.74	1103.47	4.16	0.02
1-4,5	1-4,5	1-5	5	-547.54	1105.08	4.67	0.01
1,2-4,5	1-3,4-5	1-5	6	-546.31	1104.62	4.71	0.01
1,2-4,5	1-3,4,5	1-5	7	-545.01	1104.03	4.71	0.01
1-3,4,5	1-5	1-5	5	-548.04	1106.08	5.68	0.01
1,2-4,5	1-4,5	1-5	6	-546.88	1105.76	5.85	0.01
1,2-3,4,5	1-3,4,5	1-5	8	-544.27	1104.53	5.92	0.01
1,2-3,4,5	1-3,4-5	1-5	7	-545.83	1105.67	6.35	0.01
1,2,3,4,5	1-4,5	1-5	8	-544.65	1105.30	6.68	0.00
1,2,3,4,5	1-3,4,5	1-5	9	-544.17	1106.34	8.54	0.00
1,2,3,4,5	1-3,4-5	1-5	8	-545.74	1107.48	8.86	0.00
1-5	1-5	1-5	3	-552.10	1110.20	9.09	0.00
1-4,5	1-5	1-5	4	-551.09	1110.18	9.38	0.00
1,2,3,4,5	1-5	1-5	7	-547.94	1109.88	10.56	0.00

¹Density ²Probability of detecting an animal with a home range center located at the camera station

³Decay rate of the capture probability over distance from the home range center
⁴Number of parameters in the model
⁵Log likelihood
⁶Akaike's Information Criterion (AIC)
⁷Difference in AIC between model and the highest-ranked model
⁸AIC model weight

Table 3. Spatially explicit capture-recapture models fit using program secr to estimate bobcat densities at the Santa Rosa study site in South Texas from Feb 2012–Jul 2014. Numbers in columns labeled D^1 and g_0^2 represent sampling sessions and numbers with a hyphen (-) between them represent sessions grouped together for each parameter.

D^1	g_0^2	σ^3	NPar ⁴	logLik ⁵	AIC ⁶	ΔAIC^7	w^8
1-4,5	1-4,5	1-5	5	-479.08	968.15	0.00	0.18
1-3,4-5	1-3,4,5	1-5	6	-478.33	968.65	0.50	0.11
1-4,5	1-3,4,5	1-5	6	-478.44	968.88	0.73	0.10
1-5	1-4,5	1-5	4	-480.52	969.05	0.89	0.14
1-5	1-3,4,5	1-5	5	-479.92	969.83	1.68	0.08
1-3,4,5	1-4,5	1-5	6	-479.00	970.01	1.85	0.06
1-3,4,5	1-3,4,5	1-5	7	-478.04	970.08	1.93	0.04
1,2-4,5	1-4,5	1-5	6	-479.05	970.11	1.95	0.05
1-3,4-5	1-4,5	1-5	5	-480.29	970.59	2.44	0.05
1,2-3,4-5	1-3,4,5	1-5	7	-478.32	970.65	2.49	0.03
1,2-4,5	1-3,4,5	1-5	7	-478.43	970.86	2.71	0.03
1,2-5	1-4,5	1-5	5	-480.50	970.99	2.84	0.04
1,2-5	1-3,4,5	1-5	6	-479.77	971.53	3.38	0.03
1,2-3,4,5	1-4,5	1-5	7	-479.00	972.00	3.85	0.02
1,2-3,4,5	1-3,4,5	1-5	8	-478.04	972.07	3.92	0.01
1,2-3,4-5	1-4,5	1-5	6	-480.29	972.58	4.43	0.02
1,2,3,4,5	1-4,5	1-5	8	-478.94	973.89	5.74	0.00
1,2,3,4,5	1-3,4,5	1-5	9	-477.99	973.97	5.82	0.00
1-3,4-5	1-3,4-5	1-5	5	-482.45	974.91	6.75	0.01
1-3,4,5	1-3,4-5	1-5	6	-482.25	976.49	8.34	0.00
1-5	1-3,4-5	1-5	4	-484.68	977.36	9.20	0.00
1-4,5	1-3,4-5	1-5	5	-484.63	979.26	11.10	0.00
1,2,3,4,5	1-3,4-5	1-5	8	-482.19	980.38	12.23	0.00
1-5	1-5	1-5	3	-494.02	994.04	25.89	0.00
1-4,5	1-5	1-5	4	-493.31	994.62	26.47	0.00
1-3,4-5	1-5	1-5	4	-493.41	994.83	26.68	0.00
1-3,4,5	1-5	1-5	5	-494.20	996.39	28.24	0.00
1,2,3,4,5	1-5	1-5	7	-493.11	1000.22	32.07	0.00

¹Density

²Probability of detecting an animal with a home range center located at the camera station

³Decay rate of the capture probability over distance from the home range center

⁴Number of parameters in the model

⁵Log likelihood

⁶Akaike's Information Criterion (AIC) ⁷Difference in AIC between model and the highest-ranked model ⁸AIC model weight I used a half-normal detection model for g_0 (the probability of detecting an animal with a home range center located at the camera station) and shared g_0 across the first 3 sessions of each study area because the data were sparse. I modeled detection separately for the 4th session when an additional camera was added to each of several single camera stations and the 5th session when lure was added and several stations had two opposing cameras (Tables 1–3). I held σ (the decay rate of the capture probability over distance from the home range center) constant across all sessions.

I applied a 3-km rectangular buffer to the camera grids because the true sampling area included individuals that spent time outside the camera grids. The secr package accounts for varying sampling effort using a linear adjustment or offset on g_0 (Efford et al. 2013). I used this adjustment to account for camera failure and the doubling of camera stations, which varied from neither camera working during an occasion (0) to both cameras working for the entire week-long occasion (14). I used Akaike's Information Criterion (AIC) to evaluate parsimony for each capture-recapture model and considered models with Δ AIC values <2 equally as likely to be supported by the data. I used model-averaging to obtain estimates of \hat{D} , g_0 , and σ because several models were within Δ AIC of 2, and I was primarily interested in the resulting parameter estimates, specifically density.

I averaged all models with an AIC weight (w_i) >0.01 using the delta-method (Seber 1982). The secr package calculates density estimates using a log link function; thus, I compared the model-averaged log density estimates within each site to each other to examine trend in relation to NDVI. The density estimates for the last 2 sessions were more precise; thus, I compared them among study sites. Following Gerber et al. (2012), when the 95% confidence intervals for the density estimates overlapped <half (50%) the average margin of error of the means, I considered

them statistically different ($\alpha = 0.05$) (Cumming and Finch 2005). This test is considered conservative because it is possible for estimates with >50% overlap to be significantly different (Cumming and Finch 2005).

Coyote Occupancy

I fit multi-season occupancy models in program PRESENCE (Version 7.8, www.mbrpwrc.usgs.gov/software/presence.html, accessed 23 Dec 2014) to estimate coyote occupancy for each session and study site. Similar to the bobcat capture-recapture analysis, I partitioned the capture histories for each study site into 5, 24-week sessions with 7-day sampling occasions. I defined the effective sample size as the number of camera stations (n=26-29) and estimated 3 parameters: seasonal occupancy (ψ), seasonal colonization (γ), and occasion-specific detection (p). I held colonization constant and fit 4 combinations of this model, parameterizing occupancy and detection as constant or varying by session (Table 4). To obtain parameter estimates, I selected the most parsimonious model from the models that had a Δ AICc <2. Table 4. Multi-season occupancy models and occupancy estimates ($\widehat{\Psi}$) for coyotes at 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul 2014.

San Antonio Viejo						
Model ^{1,2}	ΔAIC_{c}^{3}	w^4	Likelihood ⁵	NPar ⁶	$\widehat{\psi}$	$\mathrm{SE}(\widehat{\psi})$
$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.00	1.00	1.00	7	0.83	0.041
$\psi(\text{session})\gamma(\cdot)p(\text{session})$	13.94	0.00	0.00	11		
$\psi(\cdot)\gamma(\cdot)p(\cdot)$	16.53	0.00	0.00	3		
$\psi(\text{session})\gamma(\boldsymbol{\cdot})p(\boldsymbol{\cdot})$	22.58	0.00	0.00	7		

Buena Vista

Model ^{1,2}	ΔAIC_{c}^{3}	w^4	Likelihood ⁵	NPar ⁶	$\hat{\psi}$	$\mathrm{SE}(\widehat{\psi})$
$\psi(\cdot)\gamma(\cdot)p(\cdot)$	0.00	0.56	1.00	3	0.92	0.030
$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.47	0.44	0.79	7		
$\psi(\text{session})\gamma(\cdot)p(\cdot)$	21.03	0.00	0.00	7		
ψ (session) γ (•) p (session)	52.95	0.00	0.00	11		

Santa Rosa

Model ^{1,2}	ΔAIC_{c}^{3}	w^4	Likelihood ⁵	NPar ⁶	$\widehat{\psi}$	$\mathrm{SE}(\widehat{\psi})$
$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.00	0.99	1.00	7	0.91	0.027
$\psi(\text{session})\gamma(\cdot)p(\text{session})$	10.78	0.00	0.00	11		
$\psi(\boldsymbol{\cdot})\gamma(\boldsymbol{\cdot})p(\boldsymbol{\cdot})$	14.23	0.00	0.00	3		
$\psi(\text{session})\gamma(\cdot)p(\cdot)$	20.37	0.00	0.00	7		

 ψ Seasonal occupancy

 γ Seasonal colonization

p Seasonal detection
¹(•) Parameter held constant among sessions
²(session) Parameter allowed to vary among each session
³Akaike's Information Criterion adjusted for small sample size (AICc)

⁴AICc model weight

⁵Log likelihood

⁶Number of parameters in the model

RESULTS

The 28-month study period yielded 48,166 (SAV = 15,710; BV = 13,811; SR = 18,645) functional camera station nights that produced 730 (SAV = 243; BV = 216; SR = 271) bobcat photographs and 4,008 (SAV = 1,022; BV = 1,467; SR = 1,519) coyote photographs. I identified 149 (SAV = 49; BV = 42; SR = 58) individual bobcats from 636 (SAV = 201; BV = 203; SR = 232) usable photographs. Ninety (SAV = 32; BV = 27; SR = 31) of these individual bobcats and 334 (SAV = 107; BV = 122; SR = 105) photographs were used in the right-side analysis.

Model-averaged bobcat density estimates ranged from 21–82 bobcats/100 km² (Figs. 2–4). For the 3 study sites, there was substantial support (Δ AIC <2) for models holding density constant across all sessions and models that varied density by sessions grouped into mild drought and severe drought periods. All of the models that allowed density to vary by each individual session had low support (Δ AIC >4) (Tables 1–3).

Model-averaged estimates of density were similar among sessions for all study sites (Figs. 2– 4). Although not statistically significant (overlap of the average margin of error = 67%), bobcat density estimates that were obtained from the highest-ranked constant density models were 37% greater for SAV than for BV (Table 5). Bobcat density for SR was in between the estimates for the other 2 study sites (Fig. 5). Density estimates were similar among sites for the last 2 sessions (Figs. 2-4).

Model-averaged detection (g_0) ranged from 0.0024–0.0320 (Table 6). Detection increased for all study sites after some camera stations received 2 cameras (session 4) and increased further after lure was added (session 5) (Table 6). Detection was about 3 times greater at SAV and about 4 times greater at SR for the session in which lure was added, but only 0.5 times greater at BV (Table 6). The model-averaged decay rate in detection (σ) varied from 445–804 m (Table 6).



Fig. 2. Bobcat density estimates (bobcats/100 km²) and standard error bars at San Antonio Viejo for sessions 1-5, Feb 2012–Jul 2014.



Fig. 3. Bobcat density estimates (bobcats/100 km²) and standard error bars at Buena Vista for sessions 1-5, Feb 2012–Jul 2014.


Fig. 4. Bobcat density estimates (bobcats/100 km²) and standard error bars at Santa Rosa for sessions 1-5, Feb 2012–Jul 2014.

Table 5. Summary of parameters estimated for San Antonio Viejo, Buena Vista, and Santa Rosa, South Texas, Feb 2012–Jul 2014.

Variable ¹⁻⁴	San Antonio Viejo	Buena Vista	Santa Rosa
Bobcat density (bobcats/100 km ²) from top constant density model	44.7	28.1	32.9
Coyote occupancy $(\widehat{\psi})$ from top model(s)	0.83	0.92	0.91
Average NDVI (Dec 2011–Jul 2014) ¹	0.42	0.37	0.45
Average annual precipitation (1981-2010) (mm)	532	557	678
Average monthly precipitation (Dec 2011–Jun 2014) (mm)	27.9	30.7	38.4
Average percent understory cover ²	21.6	19.7	8.5
Average bobcat detection (g_0) from top constant density model ³	0.011	0.006	0.008
Decay rate in bobcat detection (σ) (m) from top constant density model ⁴	447.0	801.9	620.5
Average coyote detection (<i>p</i>) from top occupancy model(s)	0.25	0.32	0.27

¹NDVI (Normalized Difference Vegetation Index) ²Average percent understory cover for each camera station calculated from Watts (2015) by averaging screening cover from 0–0.5 m, screening cover 0.5–1 m, and canopy cover 0–1 m

³Probability of detecting an animal with a home range center located at the camera station (g_0) ⁴Decay rate of the capture probability over distance from the home range center (σ)



Fig. 5. Bobcat density estimates (bobcats/100 km²) and standard error bars for San Antonio Viejo, Santa Rosa, and Buena Vista for sessions 1-5, Feb 2012–Jul 2014. Density estimates were extracted from the top models for each study site that held density constant.

Parameter ^{1,2}	San Antonio Viejo	Buena Vista	Santa Rosa
Detection $(g_0)^1$			
Session 1	0.0024	0.0054	0.0028
Session 2	0.0024	0.0054	0.0028
Session 3	0.0024	0.0054	0.0028
Session 4	0.0110	0.0087	0.0039
Session 5	0.0320	0.0134	0.0150
Decay rate in detection (σ) (m) ²	445.0	804.5	619.8

Table 6. Model-averaged estimates of bobcat detection (g_0) and decay rate in detection (σ) for 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul 2014.

¹Probability of detecting an animal with a home range center located at the camera station (g_0) ²Decay rate of the capture probability over distance from the home range center (σ) The PMDI values were classified as drought for the entire study, ranging from incipient drought to severe drought (-0.69 to -4.33). I identified a severe drought period (sessions 1–3) and a mild drought period (sessions 4–5) using PMDI. The PMDI and mean NDVI paralleled each other for most of the study period, but there were a few peaks in NDVI that did not correspond with a peak in PMDI, likely the result of localized rain events (Fig. 6). The peak in both indices at the beginning of the study period in 2012 was of short duration compared to the peak that was sustained from late 2013 to early 2014. These peaks corresponded with sessions 1, 4, and 5; thus, I parameterized the bobcat density models accordingly (Fig. 6, Tables 1–3). The SR had the highest NDVI values during the majority of the study, and BV had the lowest values (Table 5, Fig. 6). The SAV values varied between BV and SR with the exception of 2 spikes that exceeded the other study sites, one occurring 6 months prior to the beginning of the study and one occurring near the end of the study period (Fig. 6).

Coyotes were detected at every station but not in every sampling period. There was strong support for constant occupancy across all sessions for all 3 study sites (Table 4). Occupancy estimates were high for all sites, ranging from 0.83 (SE = 0.04) to 0.92 (SE = 0.03) (Table 4). Coyote occupancy was 8% lower at SAV than the other 2 study sites, but the differences were not significant (Fig. 7). Detection probability for coyotes ranged from 0.16 (SE = 0.02) to 0.40 (SE = 0.03) among the sessions and study sites (Table 7). Average detection for coyotes was lowest at SAV (Table 7).

Fig. 6. Palmer Modified Drought Index (PMDI) for Texas Climate Region 9 and Normalized Difference Vegetation Index (NDVI×10) for San Antonio Viejo (SAV), Buena Vista (BV), and Santa Rosa (SR), South Texas, Jun 2010 – Aug 2014. Negative PMDI values indicate drought conditions and positive values indicate wet conditions. Session start dates are indicated on the x-axis. Number of different juvenile bobcats photographed is indicated by a "+" above the NDVI values.





Fig. 7. Multi-season occupancy estimates ($\hat{\psi}$) and standard error bars for coyotes at 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul 2014.

Table 7. Probability of detection (*p*) for coyote multi-season occupancy models at 3 study sites in South Texas:

		Detection probability (<i>p</i>)					
Study site	Model ^{1,2}	Session 1	Session 2	Session 3	Session 4	Session 5	Average
San Antonio Viejo	$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.28	0.24	0.27	0.16	0.32	0.25
Buena Vista	$\psi(\cdot)\gamma(\cdot)p(\cdot)$	0.32	0.32	0.32	0.32	0.32	0.32
	$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.31	0.40	0.32	0.29	0.29	-
Santa Rosa	$\psi(\cdot)\gamma(\cdot)p(\text{session})$	0.29	0.26	0.25	0.22	0.35	0.27

San Antonio Viejo, Buena Vista, and Santa Rosa, Feb 2012–Jul 2014.

 ψ Seasonal occupancy

y Seasonal colonization

p Seasonal detection
¹ (•) Parameter held constant among sessions
² (session) Parameter allowed to vary among each session

Juvenile bobcats were not included in the capture-recapture analysis because of infrequent detection. Eight photograph events of juveniles were recorded during the study. Six of these events were at SR, the most productive study site. These photographs were recorded about a year after a peak in NDVI and immediately before PMDI dipped into moderate drought. The other 2 juvenile photographs were recorded on BV and SAV also about a year after a peak in NDVI (Fig. 6).

DISCUSSION

Bobcat population density seemed to remain stable over time for the range of conditions sampled during this study. None of the study sites ranked highest for all 3 individual factors (i.e., environmental conditions, woody understory structure, and coyote occupancy) that I predicted would affect bobcat populations, which may explain the lack of significant differences in bobcat density among the 3 ranches. However, SAV did rank the highest overall and BV the lowest for the 3 factors combined, which may explain the difference in the point estimates of bobcat density among the sites.

The greater bobcat density at SAV compared to BV may be partly explained by differences in productivity (i.e., NDVI) at each of the study sites. This result showed some support for my prediction that productivity would have a positive effect on bobcat density. However, if prey abundance, which was assumed to be correlated with NDVI, was the sole driver of bobcat density, then SR should have produced the highest bobcat density estimates. Other factors such as habitat structure may have also affected bobcat densities.

Whereas areas with higher NDVI may have greater prey abundance, bobcats can only pursue prey for a short distance (Kleiman and Eisenberg 1973) and require understory cover to ambush

their prey (Knowles 1985). The SR study site contained little woody understory structure compared to the other study sites (Watts 2015). The foraging strategies of "sitting and waiting" and "stalking and ambushing" both require understory cover and would be facilitated by the extensive woody understory structure at SAV (Watts 2015).

My prediction that bobcat density would be greater at the study sites with more woody understory structure was supported when comparing density estimates between SAV and SR. However, BV also had high estimates of woody understory where cameras were placed (Watts 2015), but I do not believe that the understory cover measurements were as representative of this site at the landscape scale as they were for the other sites. These dense patches were sparse across the landscape and interspersed among more extensive grassland communities.

The slightly lower coyote occupancy rate at SAV may have also contributed to this site having the greatest point estimate of bobcat density. This provided some support for my prediction that bobcat density would have an inverse relationship with coyote populations. Coyote occupancy estimates were slightly lower on SAV, but detection was also lower, suggesting a lower abundance of coyotes (Royle and Nichols 2003). Previous research has shown that coyotes limit bobcat populations. Litvaitis and Harrison (1989) found a negative correlation between coyote and bobcat harvest over a 10-year period in Maine. In a manipulative study, Henke and Bryant (1999) found an increase in the relative abundance of bobcats after reducing the coyote population by 50%.

I expected high coyote occupancy rates at the 3 study sites for several reasons. South Texas supports some of the highest coyote densities in the United States (Bekoff and Gese 2003), and no large carnivores (e.g., mountain lions, *Puma concolor*) that kill coyotes were detected at any

of the sites. Also, coyotes are plastic in their habitat and diet preferences and considered more generalist in their niche than bobcats, even persisting in urban areas (Gehrt et al. 2011).

The stability of bobcat density over time in this study suggested that bobcat populations are resilient to some fluctuations in environmental conditions, which provided some support for my prediction that bobcat populations would not be strongly affected by environmental conditions. Bobcat populations may be adapted to the swings in precipitation and environmental conditions that are characteristic of South Texas. In addition, prey switching may have occurred during periods of low prey productivity, which allowed bobcat populations to remain stable (Blankenship 2000, Tewes and Hornocker 2008).

There may not have been enough variation in environmental conditions at the 3 study sites, and I may not have had sufficient statistical power to detect an effect of environmental conditions on bobcat density estimates. However, conditions may have exceeded a threshold that forced bobcats to delay reproduction until conditions became more favorable. Although there were too few juvenile detections to statistically analyze, the timing and location of juvenile bobcats provided anecdotal evidence of a reproductive response to productivity and drought. The timing of the appearance of juvenile bobcat observations is supported by research that documented a direct relationship between prey abundance and bobcat fecundity (Blankenship 2000). Kitten survival has also been correlated with prey availability (Rolley 1985). The high reproductive potential of bobcats and ability to breed through the year in South Texas (Emmons 1988, Hansen 2012) may encourage a "bet-hedging" strategy to maintain territories during periods of low prey abundance and forego reproduction during unfavorable environmental conditions.

The bobcat density estimates of this study $(21-82 \text{ individuals}/100 \text{ km}^2)$ were similar to previous estimates of bobcat density in the southern United States and higher than densities found in more northern areas (Anderson and Lovallo 2003). Density estimates using remote cameras were $43-53/100 \text{ km}^2$ in southern Texas (Heilbrun et al. 2006) and $29-58/100 \text{ km}^2$ in eastern Texas (Symmank et al. 2008). Ruell et al. (2009) used scat samples to estimate bobcat density at 25-42 individuals/100 km² in southern California.

The moderate to high bobcat density estimates for the severe drought period (sessions 1-3) suggested that bobcat population densities were not negatively affected by these conditions. However, bobcat detection was low, which negatively affected the precision of the density estimates and compromised my ability to examine trends in bobcat density over time. Low detection may have been related to low sampling effort and wide-ranging bobcat movements in response to low prey availability. Several studies have documented nomadic movements and extraterritorial forays in bobcat and Canada lynx (*Lynx canadensis*) during long-term prey declines, suggesting a breakdown of home ranges to meet energy requirements (Ward and Krebs 1985, Knick 1990, Mowat et al. 2000, Anderson and Lovallo 2003). This phenomenon may have occurred to some extent at my study sites, thereby decreasing detection.

A strength of this study was that it examined bobcat density simultaneously in 3 distinct habitat types: the Tamaulipan thornshrub woodlands and shrublands at SAV that contained few grasslands, the grassland-dominated mesquite woodlands and shrublands at BV, and the mesquite and live oak woodlands at SR that contained few shrublands. Another strength was the 2.5-yr timeframe of the study and the variability among the study sites, which allowed development of inferences about bobcat population dynamics by examining variation in 3 main

drivers of bobcat populations: environmental conditions (i.e., drought and productivity), habitat (i.e., woody cover), and coyotes.

MANAGEMENT IMPLICATIONS

Bobcat population stability during low to moderate environmental fluctuations suggested that bobcat populations are resilient to the dynamic conditions of South Texas. Also, bobcat density estimates during drought were high. Both of these results imply that actions to either reduce or increase bobcat populations can be implemented by managers regardless of conditions.

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CHAPTER II

INFLUENCE OF MICROHABITAT STRUCTURE AND LURE ON ENCOUNTER RATES ALONG BOBCAT TRAVEL ROUTES

Carnivores play a key role in ecosystems through their influence on community structure and their ability to transfer energy and nutrients (Zielinski et al. 2013). However, large carnivores can be difficult to survey. Researchers typically sample carnivore populations using a systematic sampling scheme at the landscape scale, but the exact placement of sampling devices is usually based on microsite or fine-scale features that are expected to maximize encounter rates. Researchers also use attractants to increase encounter rates. The effectiveness of these strategies may vary depending on species, study area characteristics, or other factors.

Carnivores can be challenging to survey because of their low density, large home range size, and secretive behavior. Many felid species use understory cover to stalk and ambush their prey, making them particularly difficult to detect compared to other taxa such as canids, which employ an open pursuit hunting strategy (Kleiman and Eisenberg 1973). This challenge, combined with advances in molecular techniques that allow both species and individual identification to be more cost-effective has led to the rapid development of non-invasive carnivore sampling methods.

Several techniques exist to determine species presence and individual identification. Common non-invasive methods used for felids include scent stations, track surveys, scat detection dogs, hair snares, and remote cameras (Long et al. 2008). Scent stations and track surveys are an easy, inexpensive way to determine presence of a species; however, individuals are not identifiable in most sampling situations. Scat dogs are efficient but costly (Harrison 2006, Long et al. 2007, Adams 2009). In addition, in areas where dung beetles (*Scarabaeoidea*

This thesis chapter follows the style of the Journal of Wildlife Management.

spp.) are prevalent, such as parts of South Texas, they can remove a scat shortly after it is deposited (E. Rulison, personal communication).

Hair snares can be used to determine individual identification, but require a behavioral response from the target species and can become cross-contaminated from multiple species and individuals (Stricker et al. 2012). Researchers have had limited success with collecting hair from bobcats (*Lynx rufus*) (Harrison 2006, Long et al. 2007, Adams 2009, Comer et al. 2011, but see Stricker et al. 2012).

Motion-triggered cameras are commonly used for species in which individuals have unique natural marks, including many felid species. Cameras overcome many of the shortcomings of other techniques because they can "capture" multiple individuals, require minimal effort and skill to collect and analyze the data, and are relatively inexpensive after the initial equipment is purchased. To increase encounter rates, cameras are typically placed along perceived travel routes such as trails, roads, and other features that "funnel" the target species in front of the camera (Karanth and Nichols 1998, Gardner et al. 2010, Sunarto et al. 2013).

Even with strategic camera placement, carnivore surveys are hindered by low encounter rates, which make it difficult to obtain precise or even reliable estimates of population parameters (e.g., occupancy, abundance, density). Researchers commonly rearrange data to increase precision of parameter estimates. Sampling occasions can be extended to increase detection probability (i.e., the frequency of detection). However, as the length of each sampling occasion increases, the frequency of independent captures may be reduced. Sampling periods can also be extended to increase the total number of captures and recaptures. This can be achieved through data collection or *post hoc* data partitioning. However, increasing sampling period duration increases the likelihood of violating the assumption of population closure (Foster and Harmsen 2012). By

identifying and characterizing the vegetation structure of travel and foraging habitats for bobcats, cameras can be placed at microsites that will maximize encounter rates, which will increase sampling efficiency and the precision and reliability of population parameter estimates. Also, bobcats show a reduced tolerance to human development. Consequently, travel habitat preferences can be used to identify habitat characteristics of travel corridors and ensure connectivity among bobcat populations and possibly other species (Crooks 2002, Poessel et al. 2014). My objective was to examine the influence of microhabitat structure and lure on bobcat encounter rates at remote camera stations.

Bobcats range from southern Mexico to southern Canada and occupy a plethora of habitat types, absent only from areas of intense agriculture and urban development (Crooks 2002, Hansen 2012). One common habitat feature is dense understory cover, which provides screening cover to ambush or pursue prey from a short distance and for protection from larger predators (Anderson and Lovallo 2003, Horne et al. 2009, Hansen 2012). Also, the main prey of bobcats, lagomorphs and rodents, are associated with dense understory (Knowles 1985, Litvaitis et al. 1986). In South Texas, bobcats have shown a positive relationship with moderate levels of woody understory structure (Horne et al. 2009). Therefore, I predicted that bobcat encounter rate would show a positive relationship with the lower stratum (i.e., ≤ 1 m) of woody screening cover and canopy cover. I also predicted that the application of lure would increase encounter rates.

STUDY AREA

I conducted camera trapping on 3 ranches in South Texas owned and operated by the East Wildlife Foundation. Eighty-four percent of the land area in Texas is represented by privately owned farms and ranches (Kjelland et al. 2007), and many of these properties are used for

hunting. The study sites were unusual in that there was no hunting or predator control for the past several decades. Study sites were located on an east-west gradient (Fig. 1) and were composed of 3 distinct habitat types.

San Antonio Viejo Ranch (SAV) was the western-most study site located in Jim Hogg and Starr counties. The majority of this site was in the South Texas Brush Country Ecoregion, and it also contained the western border of the Coastal Sand Plains Ecoregion. The vegetation community was dominated by Tamaulipan thornshrub with few grassland communities. Shrub diversity at SAV was high. Dominant species included blackbrush (*Acacia rigidula*), cenizo (*Leucophyllum frutescens*), hogplum (*Colubrina texensis*), and granjeno (*Celtis pallida*). Dominant soil types included Brennan soils, Copita fine sandy loam, and Copita soils (McLendon et al. 2013a, KS2 Ecological Field Services, LLC, unpublished report).

Buena Vista Ranch (BV) was located about 13 km east of SAV and was also located in Jim Hogg County and the South Texas Brush Country and Coastal Sand Plains Ecoregions. This study site was dominated by grasslands interspersed with small patches of dense thornshrub. Mesquite (*Prosopis glandulosa*) dominated the woodland and shrubland areas. Other dominant shrub species included hogplum and catclaw (*Acacia greggii*). Dominant soil types were the Nueces-Sarita association and Delmita soils (McLendon et al. 2013b, KS2 Ecological Field Services, LLC, unpublished report).

Santa Rosa Ranch (SR) was located 50 km east of BV in Kenedy County and occurred within the Coastal Sand Plains Ecoregion. Vegetation consisted of mesquite shrublands and woodlands dominated by mature live oak (*Quercus virginiana*) and mesquite trees. This study site also contained a few wetland and grassland communities. Dominant soil types included Palobia loamy fine sand, Falfurrias fine sand, Falfurrias-Cayo complex, and Sarita fine sand (McLendon et al. 2012, KS2 Ecological Field Services, LLC, unpublished report). This site was closer to the Gulf of Mexico and typically received more rainfall than SAV and BV.

METHODS

Data Collection

I used infrared-triggered Cuddeback® Capture Flash digital cameras (Non Typical, Inc., Green Bay, WI, USA) to conduct the study. I overlaid a grid consisting of 1 km² cells on each study site and placed one camera station in each cell. Camera location within each grid cell was based on habitat features that would maximize detection of carnivores, which is a typical protocol for camera trapping studies (Karanth and Nichols 1998, Gardner et al. 2010, Sunarto et al. 2013). Therefore, I placed cameras adjacent to thornshrub corridors, trails, roads, and water. I separated camera stations by >600 m, which resulted in 26–29 (SAV = 29; BV = 26; SR = 29) stations per study site spaced 600–1,800 m apart. Camera stations consisted of 1 or 2 cameras attached to a stake, tree, or fence post 40–50 cm above the ground, and cameras operated for 24hr each day with a 30-sec delay between photographs.

I used a protocol similar to Horne et al. (2009). I measured 7 microhabitat variables at each camera station to describe woody vegetation structure for bobcat travel corridors and to determine which microsite characteristics affected encounter rate. The 7 microhabitat variables measured were sampling or opening width, canopy cover at 2 heights (0–1 and >1 m), vertical vegetation structure (i.e., screening cover) at 3 heights (0–0.5, >0.5–1, and >1–2 m), and canopy height. I measured woody vegetation because I expected it to experience less seasonal variability than herbaceous vegetation over the 7-month study period. Also, woody vegetation provides consistent cover for bobcats compared to herbaceous cover. All measurements were

taken along 5-m transects radiating in the 4 cardinal directions from the center of the opening width of each camera station. A 10-m diameter sampling area was used because the cameras could not reliably photograph bobcats beyond a distance of 10 m, and I could not be certain that bobcats were using habitat outside the photographed area.

The opening width for each camera station was defined as the width of the area that the camera could reliably sample. For single camera stations, this was the width between the camera and dense vegetation beyond which bobcats were not photographed. For stations with two cameras, opening width was the distance between opposing cameras on opposite sides of the sampling area.

I used the point-intercept method at 1-m intervals to obtain percent canopy cover along each transect and at the center of the sampling unit for a total of 21 observations. I measured canopy intercepts at heights of 0-1 m and >1 m and averaged the 21 intercept measurements to calculate percent canopy cover for each height profile.

I measured vertical vegetation structure or screening cover at 3 heights (0-0.5, >0.5-1, and >1-2 m) using a Nudds Density Board that was 30.48 cm wide (Nudds 1977). I placed the board at the camera capture point and visually estimated the percentage of the board that was obscured by woody vegetation from a squatting position 0.7 m high (to simulate bobcat height) at a distance of 5 m in each cardinal direction. I averaged these 4 measurements for each of the 3 heights.

To obtain canopy height for each camera station, I averaged 5 measurements of canopy height, 1 at each end of the 5-m transects and 1 at the center. Canopy height was not measurable at points where there was no vegetation, so I used the maximum canopy height measurement for that study site to calculate a corrected mean canopy height for the station.

Lure increased precision of population estimates for Malagasy civets (*Fossa fossana*) without introducing bias (Gerber et al. 2012). Consequently, I added several types of commercial trapping lure to all camera stations at the mid-point of the study. Call lures had a strong odor and were designed to attract animals from a distance whereas local lures consisted of gland, food, or "curiosity" lures designed to attract nearby animals to a specific point. The call lures I used were Gusto (Minnesota Trapline Products, Inc., Pennock, MN) and Snow Cat Bobcat #2 Lure (Grawe's Lures, Wahpeton, ND). The local lures I used were Feline Fix (Minnesota Trapline Products, Inc., Pennock, MN) and Snow Cat Bobcat , MT), Cat-Man-Do (Milligan Brand, Chama, NM), and Finicky Feline #801 (Hoosier Trapper Supply, Greenwood, IN). I systematically implemented a one-time lure application in which I placed 1 of 2 call lures at each study site. I placed call lures 1.5–1.8 m high within view of the camera and on an object and aspect that would maximize scent dispersal by wind. Local lures were placed on the ground in front of the camera.

Analysis

I defined each camera station as a sample unit. I used Camera Base (M. Tobler, Camera Base Version 1.6.1, http://www.atrium-biodiversity.org/tools/camerabase/, accessed 1 Nov 2014) to manage photograph data and SAS to analyze it (SAS Version 9.2, SAS Institute, Inc., Cary, NC). At stations with 2 cameras, I analyzed data from the camera that was functioning for the longest amount of time so that counts and effort were comparable to single-camera stations. To ensure independence, I defined photograph events as the number of bobcat photographs separated by >30 min (Silver et al. 2004). I recorded photograph events and functional trap nights for each

camera station from 17 October 2013 to 14 May 2014 and partitioned the photograph count data into 2 sampling periods or 'sessions' for each study site, one session before lure was applied and one session after.

I organized the data so that total site effort (i.e., number of functional camera trap nights) was similar before and after lure was applied. Session length varied from 86–100 days. I fit a generalized linear model in a repeated measure framework to examine the response of bobcats to habitat and lure at each camera station. The encounter rate data were skewed with many low values, typical for count data, so I assumed a negative binomial distribution (Sileshi 2008, Davis et al. 2011). I used backwards stepwise multiple regression, beginning with a global model that included study site as a random effect, lure as a fixed effect, a site×lure interaction, and 7 continuous habitat variables: opening width, screening cover at 3 heights, canopy cover at 2 heights, and canopy height. I also added 3, 2-way interactions for the 3 variables that were included in the final model (Table 8). I fit several regression models, removing the variable with the highest *P*-value from the model each time it was fit. At each step, I re-fit the model with the remaining habitat variables until all variables in the model were significant ($P \le 0.10$). Because lure was a design effect, I included this variable in every model, regardless of its statistical significance. I included the log number of camera trap nights as an offset variable to account for variable effort among cameras and sessions. To test if the offset was necessary, I included the log number of camera trap nights as a covariate in the final model but did not use it as an offset for that model. To examine the behavioral response to the lure, I calculated the percentage of photographs that were not considered independent in each session.

Table 8. Mean, range, and parameter estimates for all variables included in the global and final negative binomial mixed models with repeated measures. Data were collected on 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa from 17 Oct 2013–14 May 2014.

			Parameter coefficients (SE)		
	Mean value (SE)				
Parameter	per station	Range	Global model	Final model	Interactions
Intercept	NA	NA	-6.103 (1.130)	-5.961 (0.753)	
Lure	NA	NA	-0.328 (0.265)	-0.337 (0.287)	
Opening width (m)	4.3 (0.15)	2.0 - 8.8	0.181 (0.090)**	0.200 (0.091)**	
Canopy height corrected (m)	2.0 (0.05)	1.0-3.2	0.204 (0.328)		
Screening cover (%)					
<0.5 m	19.7 (1.72)	0-75	-0.012 (0.019)		
0.5–1 m	18.6 (1.71)	0-78	0.021 (0.026)	0.012 (0.007)*	
1–2 m	24.2 (1.98)	0-92	0.007 (0.014)		
Canopy cover (%)					
<u><</u> 1 m	10.5 (1.12)	0-52	-0.013 (0.013)		
>1 m	70.1 (2.48)	5-100	0.015 (0.006)**	0.017 (0.006)***	
HorCov 0.5-1 \times Opwidth					0.00070 (0.007)
HorCov 0.5-1 \times VertCov >1					0.00006 (0.0005)
Opwidth \times VertCov >1					-0.00152 (0.003)

P* < 0.10, *P* < 0.05, ****P* < 0.01

RESULTS

I recorded 121 bobcat photograph events (2.0 events/camera/100 trap nights) before lure was applied and 154 (2.6 events/camera/100 trap nights) after lure was applied for a total of 275 events (2.3 events/camera/100 trap nights) (Fig. 8). I surveyed for 11,345 functional camera trap nights with an average of 86 trap nights for each camera.

I did not find any significant 2-way interactions in the final model. Although more bobcat photographs were recorded during the time period after lure was applied, I found no effect of lure on encounter rate, despite similar effort (P = 0.36). I did not find an effect of study site on bobcat encounter rate. However, screening cover at 0–0.5 m and 0.5–1 m and canopy cover at 0–1 m varied among the sites. Values for these 3 measurements were particularly low for SR (Fig. 9).

Three of the 7 habitat variables were included in the final model: screening cover 0.5-1 m, canopy cover >1 m high, and opening width (Table 8). Canopy cover >1 m high showed a positive association and was the best predictor of bobcat encounter rate ($t_{123} = 2.85$, P = 0.005). The width of the opening where cameras were placed also showed a strong positive relationship with bobcat photographs ($t_{123} = 2.19$, P = 0.030). Screening cover 0.5-1 m high had a positive association with bobcat photographs, although the effect was not as strong as the other 2 habitat variables ($t_{123} = 1.66$, P = 0.099). The log number of camera trap nights had a positive relationship ($t_{123} = 2.94$, P = 0.004) with bobcat encounter rate and was as strong of a predictor of encounter rate as canopy cover >1 m high ($t_{123} = 2.92$, P = 0.004) when both were included in the model.



Fig. 8. Average number of bobcat photograph events per station for 100 trap nights before and after lure was applied to camera stations. Data displayed for all study sites combined, San Antonio Viejo, Buena Vista, and Santa Rosa, South Texas, 17 Oct 2013–14 May 2014.



Fig. 9. Average woody cover (%) per camera station for 3 vegetation measurements: screening cover 0–0.5 m and 0.5–1 m and canopy cover 0–1 m. Vegetation was measured at 3 study sites in South Texas: San Antonio Viejo, Buena Vista, and Santa Rosa, South Texas, 17 Oct 2013–14 May 2014.

Ten percent (n = 34) of photographs were excluded from the analysis because they were not considered independent (i.e., taken within 30 min of a previous photograph). Two percent (n = 3) of the excluded photographs were taken during the session before lure was applied and 16% (n = 31) after it was applied, implying a behavioral response (Fig. 10). This behavioral response was present at all 3 study sites (Fig. 10).



Fig. 10. Bobcat photographs (%) representing a behavioral response (i.e., a sequence of photographs taken within 30 min) for all study sites combined, San Antonio Viejo, Buena Vista, and Santa Rosa, South Texas, 17 Oct 2013–14 May 2014.
DISCUSSION

Generally, I expected bobcat encounter rate to show a positive association with woody understory cover and specifically, with screening and canopy cover ≤ 1 m high. Bobcat encounter rate was positively associated with 1 of the 3 vegetation measurements (screening cover 0.5–1 m) that I predicted. Bobcat encounter rate was also positively associated with canopy cover >1 m. Bobcat prey may be associated with lower-level understory cover, but it may be difficult for bobcats to pursue and catch their prey when vegetation close to the ground is dense. I expected bobcats to be associated with understory cover ≤ 1 m high because cover at this level would support bobcat foraging strategies as well as habitat for their main prey, rodents and lagomorphs. However, the vegetation characteristics that were positively associated with bobcat photograph events may only be related to habitat bobcats use for travel and not necessarily for foraging.

Habitat with denser canopy cover at a height >1 m could be used by bobcats for easy travel while providing escape from predators such as coyotes (*Canis latrans*). Anderson (1990) documented bobcats climbing trees to escape researchers on 6 occasions and to avoid a coyote on 1 occasion. Also, overhead cover casts shadows during the day and nights with high lunar illumination, which would help conceal bobcats from both predators and prey during these time periods. The similarly-sized ocelot (*Leopardus pardalis*) switched to areas of dense cover during nights of high lunar illumination (Emmons 1989). In addition, South Texas is characterized by high temperatures for most of the year, and even animals that forage in more open areas may seek cover for thermal or predatory reasons (Guthery et al. 2001, Wiemers et al. 2014, H. N. Kline, Caesar Kleberg Wildlife Research Institute, personal communication). Canopy cover may provide some thermal relief for bobcats while they are traveling.

Similar to habitat with dense canopy cover, travel habitat with more screening cover may also provide some thermal protection, particularly from wind during colder periods. In addition, screening cover may contribute to camouflage during crepuscular periods when the sun is positioned at a low angle and bobcats are particularly active (Anderson and Lovallo 2003) as well as when the moon is at a low angle. The association of bobcats with mid-level screening cover (0.5-1 m) and no relationship with the lowest level of screening cover (0-0.5 m) and canopy cover ≤ 1 m may be a compromise between habitat that provides screening cover from prey and predators, but is open enough at the lowest level to allow bobcats to travel.

The positive association of bobcat photographs with opening width is also consistent with the conclusion that bobcats prefer overhead and lateral cover, but need openings in the vegetation to facilitate travel. Lovallo and Anderson (1996) found that bobcats selected home ranges with high densities of trails, which included snowmobile trails and railroad grades. These types of trails are wider than a typical game trail, so it is possible that bobcats may be selecting for wide trails in my study area as well. Also, wider openings may provide edge habitat where prey availability and vulnerability is greater (Davis et al. 2011). It should be noted that aiming cameras across a wider opening increases the sampling area and reduces the probability of "missing" a bobcat as it passes by the camera (Kelly et al. 2013). Thus, this association may be a factor of sampling area and not necessarily a characteristic of bobcat travel habitat. Microsite evaluation of trail characteristics used by felids wearing Global Positioning System (GPS) collars may provide a better understanding of selection. An additional advantage of sampling across wider openings was that photographs of the entire bobcat were more likely to be obtained, which aided in individual identification.

Although I did obtain more total photographs of bobcats after lure was applied, the mean rate of photographs per camera station was similar. These results were consistent with other studies that found that deer (*Odocoileus* spp.) urine or bobcat urine (Gabor et al. 1994), and fatty acid tablets or bobcat urine (Chamberlain et al. 1999) did not affect bobcat visitation rates at scent stations. It has been suggested that low bobcat visitation rates, characteristic of low population densities, may limit the ability of researchers to detect differences in lure effects on bobcat visitation rates (Conner et al. 1983, Gabor et al. 1994, Chamberlain et al. 1999). Although this study recorded 275 bobcat photograph events and moderate to high bobcat densities were estimated at each study site (Watts 2015), I still did not detect an effect of lure, which did not support my prediction. However, the variation in bobcat encounter rate may have limited my ability to detect a lure effect.

The increase in total photographs and average number of photographs at 2 of the study sites could be a result of numerous other factors such as change in space use, population dynamics, and prey abundance or availability. Whereas this study could have benefited from having control stations in which no lure was applied during the entire study period, the main objective of the lure application was to increase detection rates to aid in estimating bobcat densities (Watts 2015); thus, I applied lure to every station halfway through the study.

An additional advantage of using lure was that it elicited a behavioral response in some individual bobcats. These individuals remained in front of the camera for longer periods, which allowed me to obtain more photographs and photographs of different angles of the same individual. This behavioral response aided in identifying both sides of individuals based on their pelage patterns, particularly at stations with a single functioning camera, and ultimately increased the precision of my density estimates (Watts 2015).

The 3 study sites consisted of vegetation communities that were distinct in composition and structure, but I found no difference in bobcat encounter rate among them. This result is supported by previous research that categorizes bobcats as habitat generalists (Anderson and Lovallo 2003). Overall, the results of this study suggest that for travel habitat, bobcats are generalists at the macro-scale, but are associated with certain variables related to woody cover and structure at the micro-scale.

This study is important because it examined fine-scale habitat relationships along bobcat travel routes, information that is challenging to obtain using radio collars. This information can also be challenging to obtain using GPS collars in forested areas or areas with topographic variation where locations would not be accurate enough to identify exact travel routes. Also, this study examined the effect of commercial lures and woody habitat structure simultaneously in an area of high bobcat density. These habitat characteristics may be important for traveling, but caution should be used when making inferences about foraging or other activities occurring in relation to these habitat variables. Bobcats may just be passing through the areas where the cameras were located and not using the surrounding habitat (Scognamillo et al. 2003, Davis et al. 2011). Lastly, the strong positive association of bobcat encounter rate with survey effort (i.e., the log number of camera trap nights) suggested that survey effort was as important as the fine-scale woody vegetation variables that I measured. Both sampling intensity and duration as well as the selection of habitat patches that bobcats use for travel are important to increase sampling efficiency and the resulting precision of population parameters.

MANAGEMENT IMPLICATIONS

Habitat alterations that reduce woody vegetation structure may have a negative effect on finescale bobcat habitat. This negative effect could also "scale up" to affect bobcats at the landscape scale. In addition, reducing woody vegetation structure along bobcat travel routes could reduce connectivity among habitat patches.

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