2021

Spatial and Temporal Patterns of Sympatric Bobcats *(Lynx Rufus)* and Coyotes *(Canis Latrans)* in an Agricultural Landscape

Marlin M. Dart
South Dakota State University

SPATIAL AND TEMPORAL PATTERNS OF SYMPATRIC BOBCATS (*LYNX RUFUS*) AND COYOTES (*CANIS LATRANS*) IN AN AGRICULTURAL LANDSCAPE

BY

MARLIN M. DART

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Wildlife and Fisheries Science

Specialization in Wildlife Sciences

South Dakota State University

2021

THESIS ACCEPTANCE PAGE

Marlin M. Dart

This thesis is approved as a creditable and independent investigation by a candidate for the master's degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Robert C. Lonsinger
Advisor Date

Michele R. Dudash
Department Head Date

Nicole Lounsbery, PhD
Director, Graduate School Date

ACKNOWLEDGEMENTS

I would like to thank my academic advisor, Dr. Robert Lonsinger, for entrusting me with this opportunity and for his guidance throughout this process. His commitment to mentoring graduate students has undoubtedly propelled my education and professional development. His unwavering support was essential to the success of this project and to me as a graduate student. I would also like to thank Dr. Lora Perkins for accepting me into her lab, allowing me to complete my research, and for sharing her knowledge of habitat sampling and plant species identification. I would also like to thank my graduate committee, Dr. Jonathan Jenks and Dr. Gary Hatfield, for their assistance in the development of my research. Thank you to Dr. Michele Dudash and the front office staff, Beth Byre, Katie Tvedt, and Ji Young Kim, for all their assistance. They were always willing to help. I want to thank my previous mentors, Dr. Amber Wright from the University of Hawaii at Manoa and Dr. John Hoogland from the University of Maryland, for their guidance and support.

I want to thank the graduate student community for making my time at South Dakota State University so enjoyable and memorable. I am glad to have made great friends along the way. Thank you to Cindy Anchor, Skyler Arent, Abby Blanchard, Jacob Comer, Mandy Ensrud, Sam Fino, Katelin Frerichs, Will Gallman, Cade Lyon, Trenton Rohrer, and Austin Wieseler for your friendships and fun times. I would like to thank my amazing lab mates Stuart Fetherston, Kara White, Brandon Snavely, Sprih Harsh, and Hilary Kauth for the great times and for sharing their knowledge. I need to thank my dedicated technicians Ellie Burken, Penelope Murphy, and Daniel Meyers for their hard work, contributions to my research, the fun times we spent together, and always having

good attitudes despite having to deal with me, swarming mosquitos and ticks, and having to crawl through cedar thickets.

I want to thank the South Dakota State University Department of Natural Resource Management, the United States Department of Agriculture Hatch, McIntire-Stennis Funds, the South Dakota Agriculture Experiment Station, and South Dakota Game, Fish, and Parks (SDGFP) for funding my research. Thank you SDGFP for logistical and in-kind support. Collaborative relationships with Chad Lehman (SDGFP), Keith Fisk (SDGFP), and Justin Thede (SDGFP) have been integral to the development and coordination of this research. Thank you to the 98 landowners that granted me land access. Without you, none of this is possible.

I want to thank my family for their encouragement and support. I want to thank my mother, Carla, I would not be here without her support. Lastly, but most importantly, I want to thank my wife, Ali, and my daughter, Emma. Their love, support, and sacrifice through this journey are unmatched. I do not know many people that would leave friends and family to follow their husband or father as he pursues his dreams. I owe everything to you.

CONTENTS

LIST OF FIGURES

Chapter 1:

Chapter 2:

LIST OF TABLES

Chapter 1:

Chapter 2:

ABSTRACT

SPATIAL AND TEMPORAL PATTERNS OF SYMPATRIC BOBCATS (*LYNX RUFUS*) AND COYOTES (*CANIS LATRANS*) IN AN AGRICULTURAL LANDSCAPE

MARLIN M. DART

2021

Bobcat (*Lynx rufus*) populations experienced declines in the Midwest during the 20th century due to land conversion for agriculture and overexploitation and were practically nonexistent in areas by the 1970-80s. Populations have been recovering following changes in land-use practices and habitat improvement. Eastern South Dakota was closed to bobcat harvest in 1977 but reopened in 2012 to select counties. Bobcats are elusive, have large home ranges, and occur at low densities, making monitoring their populations difficult. Camera trapping is an effective tool for monitoring elusive carnivores but can be burdened by low detection rates. Researchers often employ attractants to increase detection, but attractants can unequally influence detection of species among different trophic levels. We ran a pilot season in 2019 to evaluate the efficacy of an olfactory lure, a non-consumable attractant, as a means of increasing detection of bobcats. We expanded our species of interest to include additional species (coyote [*Canis latrans*], raccoon [*Procyon lotor*], and eastern cottontail [*Sylvilagus floridanus*]) that represented a range of foraging guilds. We evaluated the influence of the lure at three temporal scales (i.e., daily probability of detection, sequences per detection, and triggers per sequence). The influence of the lure varied between the two most-carnivorous species, bobcat and coyote. The lure positively influenced detection of coyote and raccoon, an intermediate omnivore, and negatively influenced detection of

bobcat and eastern cottontail, an herbivorous prey. Bobcats are of management interest in South Dakota that are potentially vulnerable to land conversion and may be influenced by coyotes. We used occupancy modeling to evaluate the influences of landscape features on space use of bobcats and coyotes and generated activity curves to quantify temporal overlap between species using remote camera data collected in the summers of 2019 and 2020. Coyote space use was positively associated with slope, small-scale percent agriculture, and edge density. Bobcat space use was limited and positively associated with coyote activity, distance to roads, and large-scale percent woodland/shrubland. Our results indicate that bobcats are using smaller, less-disturbed woodland/shrubland patches, which are associated with higher coyote activity levels. Bobcat and coyote temporal activity had high overlap.

CHAPTER 1: THE IMPACT OF SCENT LURES ON DETECTION IS NOT EQUITABLE AMONG SYMPATRIC SPECIES

Abstract

Camera trapping is an effective tool for cost-effective monitoring of rare and elusive species over large temporal and spatial scales and is becoming an increasingly popular method for investigating wildlife communities or species across trophic levels. Camera trapping research targeting rare and elusive species can still be hampered by low detection rates. Consequently, researchers often employ attractants in an effort to increase detection without accounting for how attractants may differentially influence detection of species across trophic levels. Therefore, we evaluated the influence of a non-species-specific olfactory lure (i.e., a non-consumable attractant; sardines) and sampling design on detection of four species (i.e., bobcat [*Lynx rufus*], coyote [*Canis latrans*], raccoon [*Procyon lotor*], and eastern cottontail [*Sylvilagus floridanus*]) that represented a range of foraging guilds in an agricultural landscape in southcentral South Dakota. We evaluated the influence of the lure at three temporal scales of detection (i.e., daily probability of detection, independent sequences per detection, and triggers per sequence). The influence of the lure on detection varied among trophic levels, including between the two most carnivorous species. The lure generally positively influenced detection of coyotes and negatively influenced detection of bobcats. The lure also generally positively influenced detection of raccoon, an intermediate omnivore, and negatively influenced detection of eastern cottontail, an herbivorous prey. We also demonstrated that the influence of the lure can vary across temporal scales.

Introduction

Early efforts to use camera traps for mammal research largely centered on documenting the presence and distribution of rare and elusive carnivores (Kucera and Barrett 1993, Zielinski and Kucera 1995). Advancements in analytical techniques employing detection data expanded the role of camera trapping, which has been used to evaluate patterns of occurrence (MacKenzie et al. 2002, 2018), quantify patterns of reproduction (Fisher et al. 2014), estimate abundance with (Karanth 1995, Heilbrun et al. 2006, Rich et al. 2019) and without (Moeller et al. 2018) individual identification, and evaluate temporal activity patterns (Ridout and Linkie 2009, Wang et al. 2015). Recent advancements in approaches for jointly analyzing data from multiple species (Richmond et al. 2010, Rota et al. 2016) and the ability to non-invasively monitor a wide range of species over large spatial and temporal scales at reduced costs compared to traditional monitoring methods (Lesmeister et al. 2015) has made camera trapping an effective tool for evaluating communities or species across trophic levels.

One challenge associated with camera trapping, particularly with rare and elusive species, is obtaining a sufficient number of detections; the accuracy and precision of estimates from occupancy and capture-recapture methods require a sufficient number of detections (White et al. 1982, MacKenzie et al. 2002). The accuracy of occupancy estimates is influenced by the number of detections (MacKenzie et al. 2002) and capture-recapture methods require a sufficient sample size (White et al. 1982). Studies targeting species that are rare or occur in low densities often employ baits (i.e., a consumable attractant) or lures (i.e., a non-consumable attractant) to increase their probability of detection (*p*; Burton et al. 2015). Some capture-recapture methods also require recaptures

of some known individuals (Karanth 1995, du Preez et al. 2014, Braczkowski et al. 2016). Attractants can entice the animal to remain in front of the camera longer and increase the potential for identifying individuals through unique physical features (e.g., pelage patterns; du Preez et al. 2014) or applied marks (e.g., ear tags; Jordan et al. 2011). Commonly used carnivore attractants include canned fish (Cove et al. 2013, Lesmeister et al. 2015, Rocha et al. 2016), carcasses (du Preez et al. 2014, Robinson et al. 2017), predator gland or musk scent lures (Holinda et al. 2020), and fatty acid tablets (Lesmeister et al. 2015). Studies evaluating the effect of attractants on carnivore detection have yielded mixed results, with some finding positive effects (e.g., Thorn et al. 2009, du Preez et al. 2014, Mills et al. 2019), whereas others found no effect (Braczkowski et al. 2016, Rocha et al. 2016). Studies evaluating the influence of attractants on the detection of species within and among different trophic levels are limited. For example, olfactory attractants specific to carnivores (e.g., scent lures) increased detection of some carnivores without impacting prey detection (Holinda et al. 2020). Conversely, a more general olfactory attractant (e.g., sardines and egg mixture) did not increase carnivore detections, but decreased detection of prey (Rocha et al. 2016). The influence of olfactory attractants may change over time as well (Mills et al. 2019).

The influence of an attractant in an agricultural landscape has not been formally assessed and may differ from other systems due to differences in human disturbance and pressure from harvest. We evaluated the influence of sardines, a commonly used non-species-specific attractant, as a non-consumable olfactory attractant (i.e., a lure) on the detection of four sympatric mammals including bobcat (*Lynx rufus*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), and eastern cottontail (*Sylvilagus floridanus*) in an

agricultural landscape. We selected species that represented a range of foraging guilds in southcentral South Dakota. Bobcats are strictly carnivorous (Nomsen 1982, Anderson and Lovallo 2003) and a species of management interest due to their value as a furbearer. Coyotes are more omnivorous (Kamler et al. 2002, Cepek 2004), are potentially dominant to bobcats (Henke and Bryant 1999, Wilson et al. 2010), and are often managed through lethal control (Knowlton et al. 1999). Raccoons are mesocarnivores and intermediate omnivores with broad and opportunistic diets (Greenwood 1982). Eastern cottontails are herbivorous (Chapman and Litvaitis 2003) and are important prey for bobcats (Nomsen 1982, Rolley and Warde 1985) and coyotes (Kamler et al. 2002, Cepek 2004).

Detection data from camera trapping can be used at multiple scales. For instance, studies have used the number of independent photos of a prey species as an index of prey availability (Díaz-Ruiz et al. 2016, Santos et al. 2019), however, camera trapping data could be used at other temporal scales, such as daily (e.g., days with detection per days surveyed). The influence of an attractant could potentially vary across scales. For example, an attractant may entice an animal to stay in front of a camera longer, increasing the number of photos captured within a 24-hour period, without influencing detection at a daily level. Understanding whether or not the influence of an attractant varies across different temporal scales would be an important step towards understanding how to properly apply or collect camera trapping detection data, particularly for studies using cameras to simultaneously survey predators and their prey.

We quantified the rates of camera-based detections using three approaches: (i) daily *p* given an area is used; (ii) number of independent photo sequences per daily

detection (hereafter, sequences), and (iii) number of triggers per sequence (hereafter, triggers). Fidino et al. (2020) found that attractants can decrease daily *p* and the number of triggers of eastern cottontail, so we predicted that the attractant would decrease eastern cottontail daily *p*, sequences, and triggers. Attractants have been shown to positively influence detection of carnivores at multiple scales (Holinda et al. 2020, Fidino et al. 2020), so we predicted that the attractant would increase daily *p*, sequences, and triggers for bobcat, coyote, and raccoon.

Methods

Study Area

The study area was located along the Missouri River in Charles Mix and Brule counties in southcentral South Dakota. The study area was ~4,275 km^2 and was bound by the borders of Charles Mix and Brule counties and by Interstate 90 to the north. The majority of the area was dominated by flat, privately-owned rangelands used for domestic cattle (*Bos taurus*) grazing and croplands (primarily corn [*Zea mays*] and soybean [*Glycine max*]) interspersed with woodland shelterbelts. Conversely, the western extent of the study area along the river was characterized by rugged drainages that had been impacted by eastern red cedar (*Juniperus virginiana*) encroachment. Dominant plant species included smooth bromegrass (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), big bluestem (*Andropogon gerardii*), porcupine grass (*Hesperostipa spartea*), eastern red cedar, and green ash (*Fraxinus pennsylvanica*). The study area experienced cold winters and moderate summers with the coldest month being January (average = -

6.5°C) and the warmest month being July (average = 23.8°C). Average monthly precipitation, defined as the liquid equivalent of precipitation not including snowfall (Arguez et al. 2012), ranged from 12.7 mm (December) to 98.8 mm (June). Average annual precipitation and snowfall of 609 mm and 1054 mm, respectively (National Oceanic and Atmospheric Administration [NOAA] 2020).

Camera Trapping Design

Our sampling design was intended for evaluating occupancy of bobcats. We divided our study area into 25 km^2 sites (5 km x 5 km), which approximated the home range size of female bobcats in South Dakota (Mosby 2011). We randomly selected 60 sites for surveying, excluding sites where land-access permissions could not be obtained. Single cameras within a site can fail to produce reliable assessments of occupancy and spatial replication within sites has been recommended (O'Connor et al. 2017, Kolowski et al. 2021). We used three cameras (hereafter, stations) to survey each site, which ensured that we surveyed a range of conditions within each site. We set stations ≥1.2 km from one another (both within and among sites), which represented the approximate home range diameter of eastern spotted skunks (*Spilogale putorius*) reported in the Midwest (Lesmeister et al. 2015). Eastern spotted skunks were of management interest in South Dakota and were a secondary target species of our initial survey efforts. We developed the sampling design to evaluate patterns of occupancy of species with larger home ranges (e.g., bobcats, coyote) at the site level and smaller home ranges (e.g., eastern spotted skunk, eastern cottontail) at the station level. We surveyed selected sites

during a single summer season from May to September 2019. Each station within a site was surveyed concurrently.

We set stations near habitat features frequented by carnivores (e.g., edge habitat, fence lines). We set all stations within a site with one of three passive infrared game camera models (Browning model BTC-6HDP, Bushnell Trophy Cam No Glow, or Moultrie model M-880), keeping models consistent within a site. We set cameras ~1 m high with a slight downward angle. We trimmed vegetation within 4 meters in front of each camera to increase species detectability, maximize visibility of smaller species, and minimize false triggers (Si et al. 2014, Moll et al. 2020). We hung a quarter of an aluminum pie tin ~1 m high and ~4 m in front of each camera as a visual lure. Within each site, we randomly assigned one of three olfactory lure treatments to each station without replacement. Treatments included (i) an olfactory lure, (ii) no olfactory lure, or (iii) an olfactory lure only during the latter half of the survey. For treatments including an olfactory lure, we used 3.75 ounces of sardines in soybean oil enclosed in a perforated polyvinyl chloride pipe (5” length x 2” diameter) to prevent consumption and secured to the ground with a rebar stake ~4 m in front of the camera. We set cameras to operate 24 hours a day and capture 3 photos per trigger with a one-minute delay between triggers. Stations were set for ~28 nights. We checked cameras after ~14 nights to replace memory cards and batteries (if necessary) and replace or add attractants for sites receiving an attractant during the entire survey or the latter half of the survey, respectively.

Data Analysis

To characterize how an olfactory lure influenced the detection of sympatric species with disparate life-history strategies, we identified four target species. Bobcats represented a hypercarnivorous predator. Coyotes represented an omnivorous predator with more carnivorous tendencies. Raccoons represented an omnivore and eastern cottontails represented an herbivorous prey species. For each species, we generated daily encounter histories for each camera station with detection (1) or non-detection (0) being coded as a binary response. We analyzed encounter histories within an occupancy modeling framework to estimate species-specific daily *p* and evaluate factors influencing detection (MacKenzie et al. 2002). We used two covariates to evaluate the influence of an olfactory lure on detection: (i) lure, which indicated if the olfactory lure was present at the time of the survey; and (ii) lure age, which indicated the number of days since the lure was applied or refreshed.

Cameras set near game trails may influence detection (Tobler et al. 2015, Kolowski and Forrester 2017). To account for the influence of game trails, we included a covariate for game trail (hereafter, trail) that characterized if the camera was set adjacent to a game trail or not. Precipitation and temperature may also influence *p* (Lesmeister et al. 2015). We obtained daily precipitation totals (mm) and maximum temperatures (ºC) for 5 NOAA weather stations near the study area (NOAA 2021a) and characterized each camera station with data from the nearest reporting weather station. Both predator and prey species may alter their nocturnal movement patterns with changes in lunar illumination (Rockhill et al. 2013, Prugh and Golden 2014, Melville et al. 2020). We generated a daily illumination covariate from recorded moon phase data (NOAA 2021b)

by scaling illumination from a range of 0 (new moon) to 100 (full moon). To account for unmodeled heterogeneity in detection that resulted from temporal variation, we included a covariate for time based on Julian day.

We tested for correlation (Kendall's $\tau \geq 0.7$; Dormann et al. 2013) between all covariate combinations using a Kendall's rank correlation test (Robinson et al. 2014, Lonsinger et al. 2017). We hypothesized that the effect of time may change over the season (i.e., detection increases, then decreases), so we also considered time with a quadratic effect (i.e., time + time^2). To identify which characterization of time was most supported by the data, we fit two global detection models (i.e., including all detection covariates) while holding the occupancy submodel as the null model. Each model varied only by how time was characterized: time versus quadratic effect of time. We retained the most parsimonious characterization of time for each species for subsequent analyses.

For each species, we developed a candidate model set for detection that included all possible additive combinations of detection covariates (Doherty et al. 2012), while holding the occupancy model constant at the null (Mills et al. 2019). Relative support for competing models was ranked by Akaike's Information Criterion (AIC) values (Burnham and Anderson 2002). We evaluated the importance of covariates on detection by considering the structure of the most-supported models, beta coefficients of predictors, and cumulative model weights (a measure of relative predictor importance; Burnham and Anderson 2002, Arnold 2010, Lonsinger et al. 2017). Covariates with cumulative model weights >0.5 were considered significant predictors (Erb et al. 2012). All analyses were completed in program MARK (White and Burnham 1999).

We estimated the daily *p* in the presence and absence of the lure from the most-supported detection model containing the lure covariate for each species; this was the most-supported model for all species but coyote (*see* Results). Daily *p* was estimated at the mean value for continuous covariates and the mode for categorical covariates (trail = set adjacent to trail; camera type = Browning). We used daily *p* estimates to generate daily p^* curves ($p^* = 1 - [1 - p]^K$), where p^* was defined as the cumulative probability of detecting the species at least once during *K* surveys given the station was used (MacKenzie and Royle 2005).

For each target species, we defined a trigger as an event leading to the photo capture (i.e., observation) of the species in at least one of the three photos taken per trigger. We defined an independent photo sequence as ≥1 trigger that captured the presence of a specific species and was separated from the next trigger capturing the same species by ≥30 minutes (Wang et al. 2015, Iannarilli et al. 2021). A photo containing multiple individuals of the same species was recorded as a single observation. A daily detection recorded in an encounter history could be the result of a single sequence or multiple independent sequences over a 24-hour period. Similarly, a sequence could be the result of a single trigger (e.g., an animal quickly passing in front of the camera) or multiple triggers (e.g., from an animal remaining in front of the camera for an extended period). The presence of an attractant may increase (or decrease) the number of triggers per sequence, number of sequences per detection, or both. For each species, we tested (i) if the number of triggers per sequence was different when a lure was applied or not, (ii) and if the number of sequences per daily detection was different when a lure was applied or not. Data were not normally distributed for all comparisons and, therefore,

comparisons were completed with nonparametric Mann-Whitney U tests (Mann and Whitney 1947).

Results

From May to September 2019, we surveyed 180 stations for a total of 5,514 camera days (mean = 30.6 ± 7.5 SD), consisting of 2,692 with a lure and 2,822 days without a lure. Time characterized as a linear covariate was more supported than a quadratic effect of time for all species except raccoon. However, the raccoon detection model with a quadratic effect of time had estimation issues and was not a significant improvement over the linear time model (ΔAIC = 0.54). Consequently, we used the linear time covariate to model detection for all species.

We detected bobcats at 24 stations and had more independent photo sequences without a lure than with one (Table 1). The most-supported bobcat detection model structure included lure and precipitation. Bobcat detection was negatively associated with lure ($\hat{\beta}$ = −0.96, $\widehat{SE}$ = 0.36, 95% CI = −1.66, −0.25) and precipitation ($\hat{\beta}$ = −0.03, $\widehat{SE}$ = 0.03, 95% CI = −0.09, 0.02), although the effect of precipitation was not as strong with confidence intervals overlapping 0. When considering the full candidate model set, the two covariates in the most-supported model, lure and precipitation, and temperature had the highest relative importance (Table 2). Lure had the highest relative importance followed by precipitation and temperature. Other covariates had lower relative importance values (cumulative model weights < 0.5; Table 2). Daily *p* was lower with a lure (0.025, $\widehat{SE}$ = 0.008, 95% CI = 0.014, 0.046) than without one (0.063, $\widehat{SE}$ = 0.014,

95% CI = 0.040, 0.098; Fig. 1A). Daily *p* estimates indicated that 63 survey days were required to achieve a $p^* \geq 0.8$ with a lure compared to 25 days at a station without a lure (Fig. 1A). The lure did not significantly influence the number of sequences per detection for bobcat, but stations with lure never had >1 sequence for a daily detection (Table 1). The number of triggers per sequence was marginally lower when a lure was applied (Table 1).

We detected coyotes at 111 stations and had more independent photo sequences with a lure than without (Table 1). Lure age and time were important predictors of coyote detection (Table 2) and were the only covariates in the most-supported model of coyote detection. Coyote daily *p* increased with lure age ($\hat{\beta} = 0.017$, $\widehat{SE} = 0.008$, 95% CI = 0.001, 0.032; Fig. 2) and time ($\hat{\beta} = 0.003$, $\widehat{SE} = 0.002$, 95% CI = −0.001, 0.007), although the effect of time was weak with the confidence intervals overlapping 0. Only covariates in the most-supported model had cumulative model weights >0.5 (Table 2). The presence of a lure did not meaningfully impact the survey effort required to achieve a $p^* \geq 0.8$ (Fig. 1B). For coyotes, sequences per detection and triggers per sequence were both significantly higher when a lure was applied (Table 1).

We detected raccoons at 159 stations and had more independent photo sequences with a lure than without one (Table 1). The most-supported raccoon detection model included lure, camera model, trail, temperature, and time covariates. Daily *p* of raccoon was positively associated with lure ($\hat{\beta} = 0.35$, $\widehat{SE} = 0.07$, 95% CI = 0.21, 0.48). Daily *p* of raccoons was higher when stations were set by game trails ($\hat{\beta} = 0.31$, $\widehat{SE} = 0.08$, 95% CI = 0.15, 0.47). Detection increased over time ($\hat{\beta} = 0.007$, $\widehat{SE} = 0.001$, 95% CI = 0.005, 0.009), and decreased with increasing temperature ($\hat{\beta} = -0.02$, $\widehat{SE} = 0.01$, 95% CI =

−0.03, −0.01). Relative to Moultrie cameras (represented by the intercept), raccoon detection was higher for Browning ($\hat{\beta}$ = 0.28, $\widehat{SE}$ = 0.09, 95% CI = 0.10, 0.46) and Bushnell ($\hat{\beta}$ = 0.92, $\widehat{SE}$ = 0.12, 95% CI = 0.68, 1.15) camera models (Fig. 3). Only covariates in the most-supported model had cumulative model weights >0.5 (Table 2). Daily *p* of raccoon was higher with a lure than without one (Fig. 1C). However, *p* was sufficiently high for both treatments that lure did not meaningfully impact the survey effort required to achieve $p^* \geq 0.8$ (Fig. 1C). Lure did not significantly influence sequences per detection or triggers per sequence for raccoons (Table 1).

We detected eastern cottontails at 121 stations and had more independent photo sequences without a lure than with one (Table 1). The most-supported detection model included lure, lure age, camera model, temperature, and illumination. Eastern cottontail detection was negatively associated with lure ($\hat{\beta}$ = −0.20, $\widehat{SE}$ = 0.11, 95% CI = −0.41, 0.01), although 95% confidence intervals slightly overlapped 0. Detection was negatively associated with lure age ($\hat{\beta}$ = −0.02, $\widehat{SE}$ = 0.01, 95% CI = −0.04, −0.01) and temperature ($\hat{\beta}$ = −0.02, $\widehat{SE}$ = 0.01, 95% CI = −0.03, −0.005) and positively related to illumination ($\hat{\beta}$ = 0.002, $\widehat{SE}$ = 0.001, 95% CI = 0.00, 0.005), although confidence intervals for illumination included 0. Relative to Moultrie cameras, eastern cottontail detection was comparable with Browning cameras ($\hat{\beta}$ = 0.04, $\widehat{SE}$ = 0.10, 95% CI = −0.16, 0.23) and higher for Bushnell ($\hat{\beta}$ = 0.52, $\widehat{SE}$ = 0.13, 95% CI = 0.27, 0.77) camera models (Fig. 3). Only covariates in the most-supported model had cumulative model weights >0.5 (Table 2). Daily *p* of eastern cottontail was lower with a lure than without one (Fig. 1D). The presence of the lure increased the effort required to achieve a $p^* \geq 0.8$ from 4 days without the lure to 6 days (Fig. 1D). For eastern cottontails, the number of sequences was

not significantly different for stations with and without a lure, but triggers were significantly lower when a lure was applied (Table 1).

Discussion

The use of an olfactory attractant to increase species-specific detection rates can be problematic for multi-species monitoring when the direction and magnitude of the effect differs among target species (Holinda et al. 2020). Holdinda et al. (2020) focused on guilds (i.e., all predators, large carnivores, small carnivores, all prey, small mammals, and ungulates) and four target species and found that lure increased predator detections but did not influence prey. We found that the influence of an olfactory lure varied across the focal species, even between the two most carnivorous species. The presence of a lure largely positively influenced detection of coyotes and generally had a negative influence on detection of bobcats. Our results suggest that evaluating the influence of attractants on groups or guilds of species can mask differences in detection among species. Studies investigating the influence of an olfactory attractant on species-specific detection rates focused largely on testing differences in the number of sequences (i.e., presumably independent observations; Tobler et al. 2008, Wellington et al. 2014, Holinda et al. 2020) or differences in detection probability over a defined sampling occasion (e.g., 1-week sampling occasion). The temporal scale at which camera trap data is applied may alter the resulting inferences but has received little attention (Fidino et al. 2020). Fidino et al. (2020) investigated the influence of a lure on the number of triggers and daily *p* for multiple species, including three species we investigated, and found that the temporal scale of inquiry influenced conclusions related to the influence of lure on detection. In

addition to triggers and daily *p*, we also considered the influence of a lure on the commonly used scale of sequences. Similar to our results, Fidino et al. (2020) found that lure decreased detection of eastern cottontails at both temporal scales but influenced coyote detection only at the scale of triggers (not daily *p*). For raccoons, our results indicating no effect of lure aligned with those of Fidino et al. (2020) at the scale of triggers, whereas our finding that lure increased daily *p* was in contrast to the patterns reported by Fidino et al. (2020). The different results for raccoons emphasize that species-specific responses are context dependent and, therefore, caution should be used when extrapolating results from one system to another.

The most relevant temporal scale of detection depends on the research objectives. For occupancy-based studies, the *p* at the scale of temporal replication (e.g., daily or weekly) is often most relevant. In our system, lure influenced the daily *p* for bobcats, raccoons, and eastern cottontails, but only bobcats had a daily *p* that was low enough (with or without a lure) for it to significantly impact the sampling design or survey intensity required for occupancy modeling. Studies using cameras to investigate the spatial ecology of predators have used the number of prey observations (triggers or sequences) detected from the same cameras as a predictor of predator occupancy (Díaz-Ruiz et al. 2016, Van der Weyde et al. 2018). Although this may be appropriate when all camera sets are the same, our results demonstrated that the number of prey triggers may be influenced by lures (or camera type) and that careful consideration should be used to either select the appropriate scale for prey detections where differences in treatment do not influence results or explicitly account for differences in the analyses (e.g., co-occurrence modeling; Richmond et al. 2010). For camera-based studies interested in

identification of individuals through unique pelage markings or tags (Jordan et al. 2011, du Preez et al. 2014), the scale of triggers or sequences may be important, as increasing the number of images per daily detection may increase the probability of identifying distinguishing markings. The presence of an attractant, a carcass, aided in individual identification of leopards (*Panthera pardus*) based on spot patterns by increasing the time spent at the camera (du Preez et al. 2014). Similarly, we found lures increased triggers per sequence, a measure of time spent at the camera, of coyotes, the most dominant carnivore, but had no effect or decreased triggers for subordinate carnivores and prey. Results may differ for subordinate carnivores and prey due to increased activity or scent making by dominant carnivores because the presence of dominant carnivores has been shown to suppress the detection of subordinate carnivores (Lazenby and Dickman 2013, Ramesh et al. 2017) and prey (Murphy et al. 2019). Bobcat densities have been estimated using cameras and unique pelage markings (Clare et al. 2015, Jacques et al. 2019) and our results suggest that an olfactory lure may decrease the number of photos per sequence, decreasing the probability of individual identification.

When developing occupancy studies, researchers are challenged with balancing the number of sites surveyed and the duration of the surveys while maximizing detection at a site in order to have a sufficient sample size and have the ability to generate accurate and precise results (MacKenzie and Royle 2005). Consequentially, researchers often employ attractants to increase detection (Burton et al. 2015). We identified two scenarios where an olfactory lure did not sufficiently increase detection at the daily detection scale to meaningfully reduce effort and facilitate surveying of additional sites. First, when the target species did not respond to (i.e., coyote), or negatively responded to (i.e., bobcat),

the lure. Second, when the effort required to achieve the desired probability of detecting the target species is only marginally reduced because *p* was sufficiently high with or without a lure (i.e., raccoon).

Camera trapping results may be influenced by the size of target species, the type of camera and settings employed, or both (Tobler et al. 2008, Rowcliffe et al. 2011, Wellington et al. 2014). Using a single camera type, Tobler et al. (2008) found that smaller-bodied mammals had lower detection rates (i.e., photos/1000 days) than larger-bodied mammals. Similarly, Rowcliffe et al. (2011) suggested smaller mammals (≤4 kg) were less likely to be detected than larger mammals (≥8 kg) due to camera sensitivity. Wellington et al. (2014) compared the performance of two camera types (i.e., Reconyx and Cuddeback) and found that detection rates were significantly different between the camera types for smaller- and medium-bodied mammals, but not for larger-bodied mammals. We observed similar patterns, with camera model influencing daily *p* for smaller-bodied raccoons (average mass ~ 6 kg; Lotze and Anderson 1979) and eastern cottontail (average mass ~ 1 kg; Chapman and Ceballos 1990), but not for larger-bodied bobcats (average mass ~10 kg; Tycz 2016) and coyotes (average mass ~ 16 kg; Way 2007). Failure to account for variation in camera model performance and difference in detectability by body mass can bias estimates and lead to erroneous conclusions (Meek et al. 2015, Anile and Devillard 2016). These patterns highlight the importance of using caution when interpreting indices of relative abundance (e.g., among species, for prey of a target predator, or across studies employing different cameras for the same species). Minimizing variation among cameras (e.g., using a single camera type) could alleviate concerns for single species monitoring (Meek et al. 2015), but practitioners often have an

assortment of camera models due to limited funding (e.g., borrowing equipment) or changing camera availability (e.g., replacing damaged cameras with newer models). Alternatively, explicit consideration of camera model in the analyses, as we have done here, can produce more robust inferences regarding species-specific detection rates.

In recent years, camera-based community/citizen science projects have been developed for large-scale monitoring of wildlife communities (e.g., Snapshot Wisconsin, Locke et al. 2019; Snapshot USA, Cove et al. 2021). Data collected through community science camera trapping projects have contributed to peer-reviewed research in recent years (Kays et al. 2017, Parsons et al. 2018), highlighting the emerging role of large-scale camera trapping in wildlife management and conservation. Furthermore, data generated from species-specific camera trapping sampling designs are often used to make inferences about prey (e.g., index of prey availability) or wildlife communities. The growing prevalence of large-scale community science projects and multi-species analyses underscore the importance of understanding how variation in sampling strategies influences detection of species at different trophic levels.

This study is limited in that camera trapping was only conducted during summer months when resource availability was presumably the highest. The influence of an olfactory attractant may be stronger during winter when resources are more limited. The factors that influence detection are likely to vary throughout the year including changes in precipitation, weather, and anthropogenic disturbance. Similarly, the factors that drive the intensity of interspecific interactions may change with temporal or spatial variability in resource availability, reproduction, and rearing of young. Furthermore, we only tested an olfactory attractant consisting of sardines in an enclosed container that prevented

consumption. A consumable bait that has a reward may have a stronger effect on detection.

Management Implications

Camera trapping is increasing in popularity as a tool for multi-species, wildlife community, and large-scale community/citizen science research. In our study system, the factors that could be controlled for in the sampling design (e.g., lure, camera model, trail) tended to influence detection more than environmental factors (e.g., precipitation, temperature, illumination). We suggest that multi-species camera trapping research minimize variation in camera sets, account for camera-set variation in analyses, or both. We suggest that multi-species camera trapping research use caution when employing attractants and consider potential variation in response among trophic levels or species of the same guild (i.e., bobcat and coyote). For occupancy studies, the attractant had limited efficacy as a method for increasing detection of carnivores and thus, reducing the survey effort. If attractants are used, we recommend pilot studies to evaluate attractant efficacy. We stress the importance of identifying the resolution that data will be used at and identifying sources of variation at the appropriate temporal scale.

References

Anderson, E. M. and Lovallo, M. J. 2003. Bobcat and lynx. - In: Feldhamer, G. A. et al. (eds), Wild mammals of North America: biology, management, and conservation. 2nd edn. John Hopkins University Press, pp. 758–786.

Anile, S. and Devillard, S. 2016. Study design and body mass influence RAIs from camera trap studies: Evidence from the Felidae. - Anim. Conserv. 19: 35–45.

Arguez, A. et al. 2012. NOAA's 1981-2010 U.S. climate normals. - Bull. Am. Meteorol. Soc. 93: 1687–1697.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. - J. Wildl. Manage. 74: 1175–1178.

Braczkowski, A. R. et al. 2016. Scent lure effect on camera-trap based leopard density estimates (R Arlettaz, Ed.). - PLoS One 11: e0151033.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. - Springer US.

Burton, A. C. et al. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. - J. Appl. Ecol. 52: 675–685.

Cepek, J. D. 2004. Diet composition of coyotes in the Cuyahoga Valley National Park, Ohio. - Ohio J. Sci. 104: 60–64.

Chapman, J. A. and Ceballos, G. 1990. The cottontails. - In: Chapman, J. A. and Flux, J. E. C. (eds), Rabbits, hares, and pikas: Status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources (IUCN), pp. 95–110.

Chapman, J. A. and Litvaitis, J. A. 2003. Eastern cottontail. - In: Feldhamer, G. A. et al. (eds), Wild mammals of North America: biology, management, and conservation. 2nd edn. John Hopkins University Press, pp. 101–125.

Clare, J. D. J. et al. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. - J. Wildl. Manage. 79: 469–480.

Cove, M. V. et al. 2013. Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. - Trop. Conserv. Sci. 6: 781–795.

Cove, M. V. et al. 2021. SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. - Ecology 102: e03353.

Díaz-Ruiz, F. et al. 2016. Drivers of red fox (Vulpes vulpes) daily activity: Prey availability, human disturbance or habitat structure? - J. Zool. 298: 128–138.

Doherty, P. F. et al. 2012. Comparison of model building and selection strategies. - J. Ornithol. 152: 317–323.

Dormann, C. F. et al. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. - Ecography (Cop.). 36: 27–46.

du Preez, B. D. et al. 2014. To bait or not to bait: A comparison of camera-trapping methods for estimating leopard Panthera pardus density. - Biol. Conserv. 176: 153–161.

Erb, P. L. et al. 2012. Seasonal and daily shifts in behavior and resource selection: How a carnivore navigates costly landscapes (B Fenton, Ed.). - PLoS One 7: e42574.

Fidino, M. et al. 2020. Effect of Lure on Detecting Mammals with Camera Traps. - Wildl. Soc. Bull. 44: 543–552.

Fisher, J. T. et al. 2014. Spatial patterns of breeding success of grizzly bears derived from hierarchical multistate models. - Conserv. Biol. 28: 1249–1259.

Greenwood, R. J. 1982. Nocturnal activity and foraging of prairie raccoons (Procyon lotor) in North Dakota. - Am. Midl. Nat. 107: 238–243.

Heilbrun, R. D. et al. 2006. Estimating bobcat abundance using automatically triggered cameras. - Wildl. Soc. Bull. 34: 69–73.

Henke, S. E. and Bryant, F. C. 1999. Effects of coyote removal on the faunal community in western Texas. - J. Wildl. Manage. 63: 1066–1081.

Holinda, D. et al. 2020. Effects of scent lure on camera trap detections vary across mammalian predator and prey species. - PLoS One 15: e0229055.

Iannarilli, F. et al. 2021. Evaluating species-specific responses to camera-trap survey designs. - Wildlife Biol. 10.2981/wlb.00726

Jacques, C. N. et al. 2019. Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture-recapture data from camera traps. - Wildl. Soc. Bull. 43: 256–264.

Jordan, M. J. et al. 2011. Camera trapping estimates of density and survival of fishers Martes pennanti. - Wildlife Biol. 17: 266–276.

Kamler, J. F. et al. 2002. Seasonal food habits of coyotes in northeastern Kansas. - Prairie Nat. 34: 75–84.

Karanth, K. U. 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. - Biol. Conserv. 71: 333–338.

Kays, R. et al. 2017. Does hunting or hiking affect wildlife communities in protected areas? - J. Appl. Ecol. 54: 242–252.

Knowlton, F. F. et al. 1999. Coyote depredation control: An interface between biology and management. - J. Range Manag. 52: 398–412.

Kolowski, J. M. and Forrester, T. D. 2017. Camera trap placement and the potential for bias due to trails and other features. - PLoS One 12: e0186679.

Kolowski, J. M. et al. 2021. High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. - Ecosphere 12: e03350.

Kucera, T. E. and Barrett, R. H. 1993. In my experience: The Trailmaster camera system for detecting wildlife. - Wildl. Soc. Bull. 21: 505–508.

Lazenby, B. T. and Dickman, C. R. 2013. Patterns of detection and capture are associated with cohabiting predators and prey. - PLoS One 8: e59846.

Lesmeister, D. B. et al. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. - Wildl. Monogr. 191: 1–61.

Locke, C. M. et al. 2019. Managing a large citizen science project to monitor wildlife. - Wildl. Soc. Bull. 43: 4–10.

Lonsinger, R. C. et al. 2017. The roles of habitat and intraguild predation by coyotes on the spatial dynamics of kit foxes. - Ecosphere 8: e01749.

Lotze, J.-H. and Anderson, S. 1979. Procyon lotor. - Mamm. Species 119: 1.

Mackenzie, D. I. et al. 2018. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. - Academic Press.

MacKenzie, D. I. and Royle, J. A. 2005. Designing occupancy studies: General advice and allocating survey effort. - J. Appl. Ecol. 42: 1105–1114.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. - Ecology 83: 2248–2255.

Mann, H. B. and Whitney, D. R. 1947. On a test of whether one of two random variables is stochastically larger than the other. - Ann. Math. Stat. 18: 50–60.

Meek, P. D. et al. 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. - Aust. Mammal. 37: 13–22.

Melville, H. I. A. S. et al. 2020. Abiotic variables influencing the nocturnal movements of bobcats and coyotes. - Wildlife Biol. 10.2981/wlb.00601

Mills, D. et al. 2019. Maximizing camera trap data: Using attractants to improve detection of elusive species in multi-species surveys. - PLoS One 14: e0216447.

Moeller, A. K. et al. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. - Ecosphere 9: e02331.

Moll, R. J. et al. 2020. The effect of camera-trap viewshed obstruction on wildlife detection: Implications for inference. - Wildl. Res. 47: 158–165.

Mosby, C. E. 2011. Habitat selection and population ecology of bobcats (Lynx rufus) in South Dakota, USA.

Murphy, A. et al. 2019. Using camera traps to investigate spatial co-occurrence between exotic predators and native prey species: a case study from northeastern Madagascar. - J. Zool. 307: 264–273.

National Oceanic and Atmospheric Administration (NOAA) 2020. National Centers for Environmental Information - 1991-2020 climate normals.

National Oceanic and Atmospheric Administration (NOAA) 2021a. Climate data online.

National Oceanic and Atmospheric Administration (NOAA) 2021b. Astronomical data.

Nomsen, D. E. 1982. Food habits and placental scar counts of bobcats in South Dakota.

O'Connor, K. M. et al. 2017. Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. - PLoS One 12: e0175684.

Parsons, A. W. et al. 2018. The value of citizen science for ecological monitoring of mammals. - PeerJ 6: e4536.

Prugh, L. R. and Golden, C. D. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles (S Boutin, Ed.). - J. Anim. Ecol. 83: 504–514.

Ramesh, T. et al. 2017. Staying safe from top predators: Patterns of co-occurrence and inter-predator interactions. - Behav. Ecol. Sociobiol. 10.1007/s00265-017-2271-y

Rich, L. N. et al. 2019. Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. - Biol. Conserv. 233: 12–20.

Richmond, O. M. W. et al. 2010. Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. - Ecol. Appl. 20: 2036–2046.

Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. - J. Agric. Biol. Environ. Stat. 14: 322–337.

Robinson, Q. H. et al. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. - Ecology 95: 3112–3123.

Robinson, L. et al. 2017. Winter bait stations as a multispecies survey tool. - Ecol. Evol. 7: 6826–6838.

Rocha, D. G. et al. 2016. Baiting for carnivores might negatively affect capture rates of prey species in camera-trap studies. - J. Zool. 300: 205–212.

Rockhill, A. P. et al. 2013. The effect of illumination and time of day on movements of bobcats (Lynx rufus). - PLoS One 8: e69213.

Rolley, R. E. and Warde, W. D. 1985. Bobcat habitat use in southeastern Oklahoma. - J. Wildl. Manage. 49: 913–920.

Rota, C. T. et al. 2016. A multispecies occupancy model for two or more interacting species (D Warton, Ed.). - Methods Ecol. Evol. 7: 1164–1173.

Rowcliffe, J. M. et al. 2011. Quantifying the sensitivity of camera traps: An adapted distance sampling approach. - Methods Ecol. Evol. 2: 464–476.

Santos, F. et al. 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. - PLoS One 14: e0213671.

Si, X. et al. 2014. How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. - PeerJ 2: e374.

Thorn, M. et al. 2009. Estimating brown hyaena occupancy using baited camera traps. - South African J. Wildl. Res. 39: 1–10.

Tobler, M. W. et al. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. - Anim. Conserv. 11: 169–178.

Tobler, M. W. et al. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data (P Lukacs, Ed.). - J. Appl. Ecol. 52: 413–421.

Tycz, B. M. 2016. Evaluation of bobcat (Lynx rufus) survival, harvest, and population size in the west-central region of South Dakota.

Van der Weyde, L. K. et al. 2018. Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. - Biol. Conserv. 220: 21–28.

Wang, Y. et al. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. - Biol. Conserv. 190: 23–33.

Way, J. G. 2007. A Comparison of body mass of Canis latrans (coyotes) between eastern and western North America. - Northeast. Nat. 14: 111–124.

Wellington, K. et al. 2014. Identifying performance differences among trail cameras used to monitor forest mammals. - Wildl. Soc. Bull. 38: 634–638.

White, G. C. and Burnham, K. P. 1999. Program MARK: Survival estimation from populations of marked animals. - Bird Study 46: S120–S139.

White, G. C. et al. 1982. Capture-recapture and removal methods for sampling closed population. - Los Alamos National Laboratory LA-8787-NERP.

Wilson, R. R. et al. 2010. Prey-mediated avoidance of an intraguild predator by its intraguild prey. - Oecologia 164: 921–929.

Zielinski, W. J. and Kucera, T. E. 1995. American marten, fisher, lynx, and wolverine: Survey methods for their detection. - Gen. Tech. Rep. PSW-GTR-15.

Figure 1. Estimated daily probability of detection (*p*) with 95% confidence intervals (left column) and daily *p** curves (right column; the cumulative probability of detecting a species at least once during *K* surveys of a used station) with (solid line) and without (dotted line) an olfactory lure from 180 camera stations surveyed for (A) bobcat (*Lynx rufus*), (B) coyote (*Canis latrans*), (C) raccoon (*Procyon lotor*), and (D) eastern cottontail rabbit (*Sylvilagus floridanus*) in southcentral South Dakota during summer, 2019.

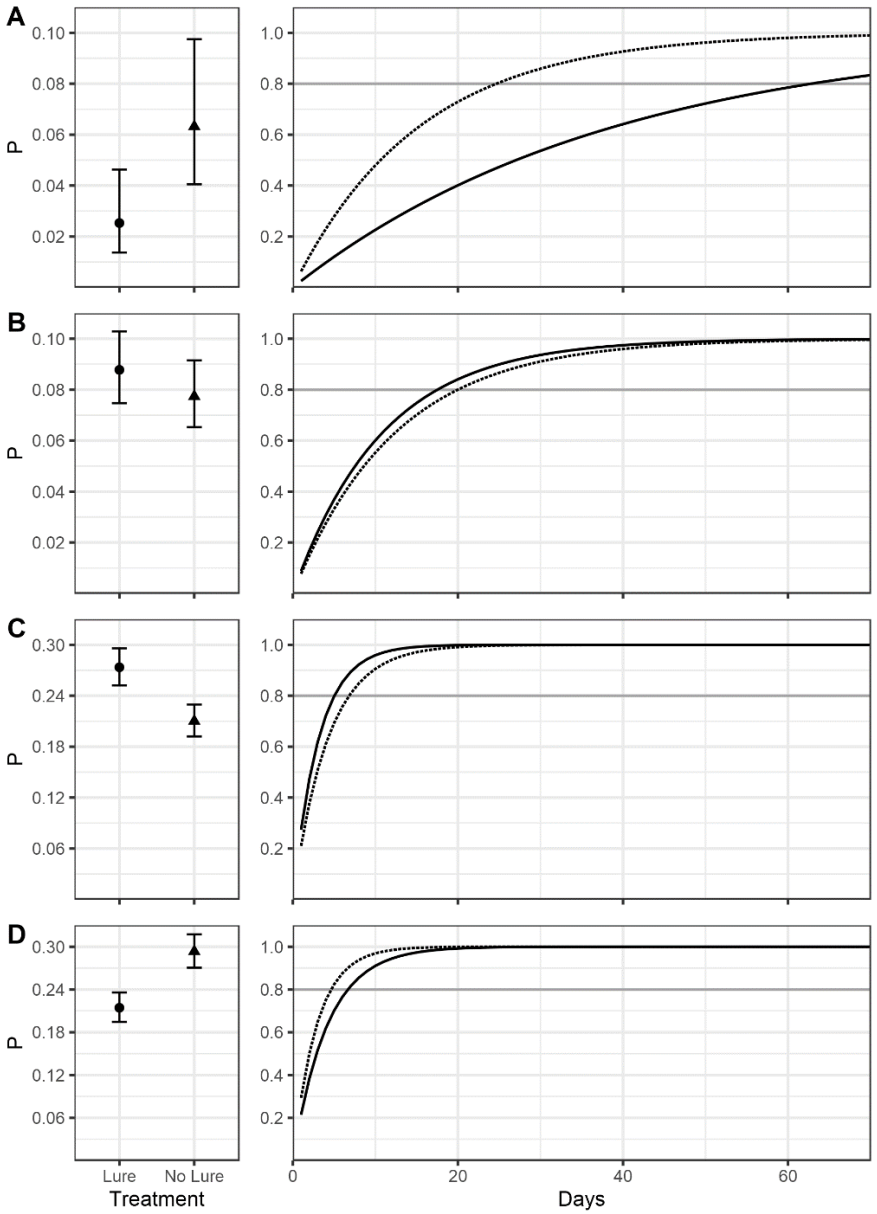


Figure 2: Estimated daily probability of detection of coyote (*Canis latrans*) as a function of lure age with 95% confidence interval band from 180 camera stations surveyed in southcentral South Dakota during summer, 2019.

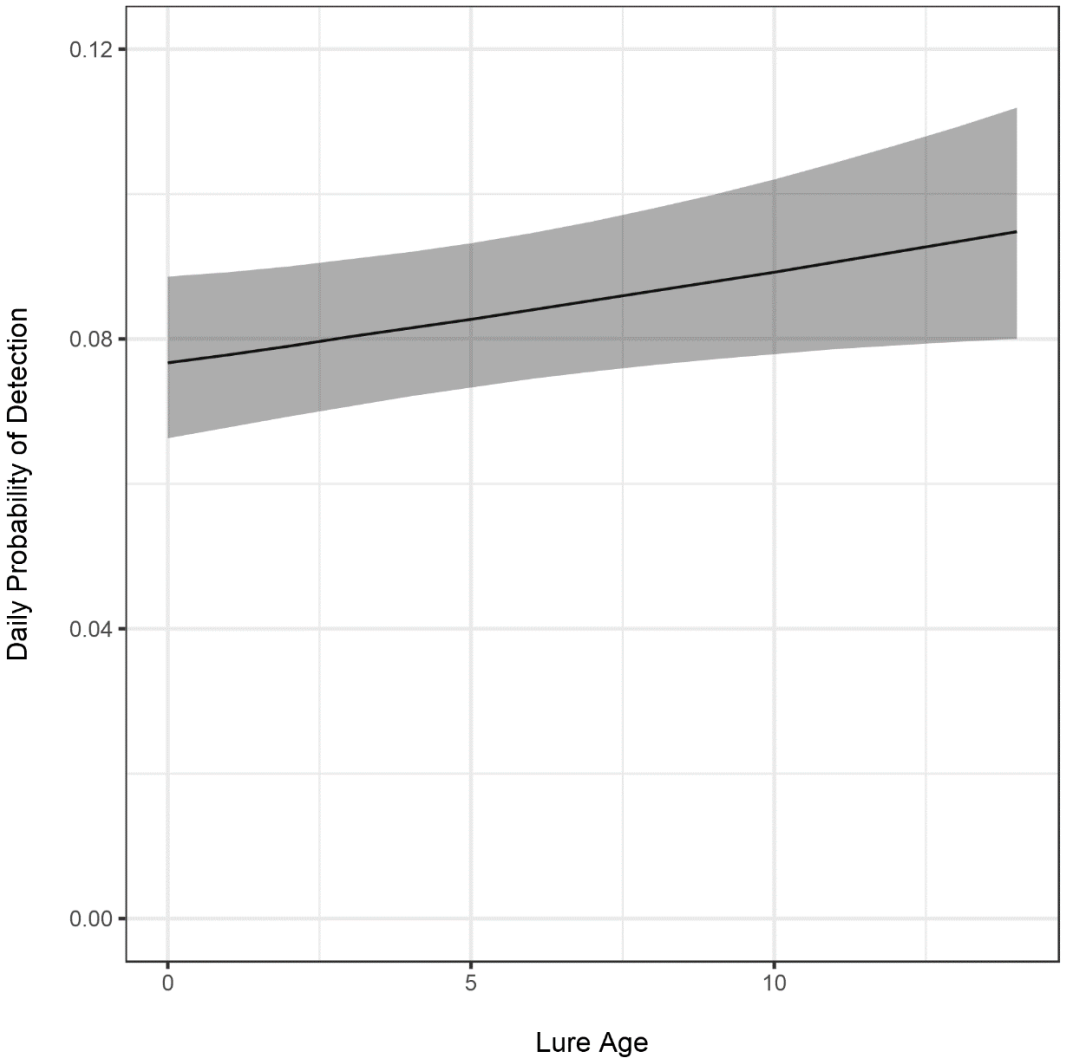


Figure 3: Daily probability of detection of raccoon (*Procyon lotor*) and eastern cottontail rabbit (*Sylvilagus floridanus*) by camera model with (●) and without (▲) lure applied from 180 camera stations surveyed in southcentral South Dakota during summer, 2019.

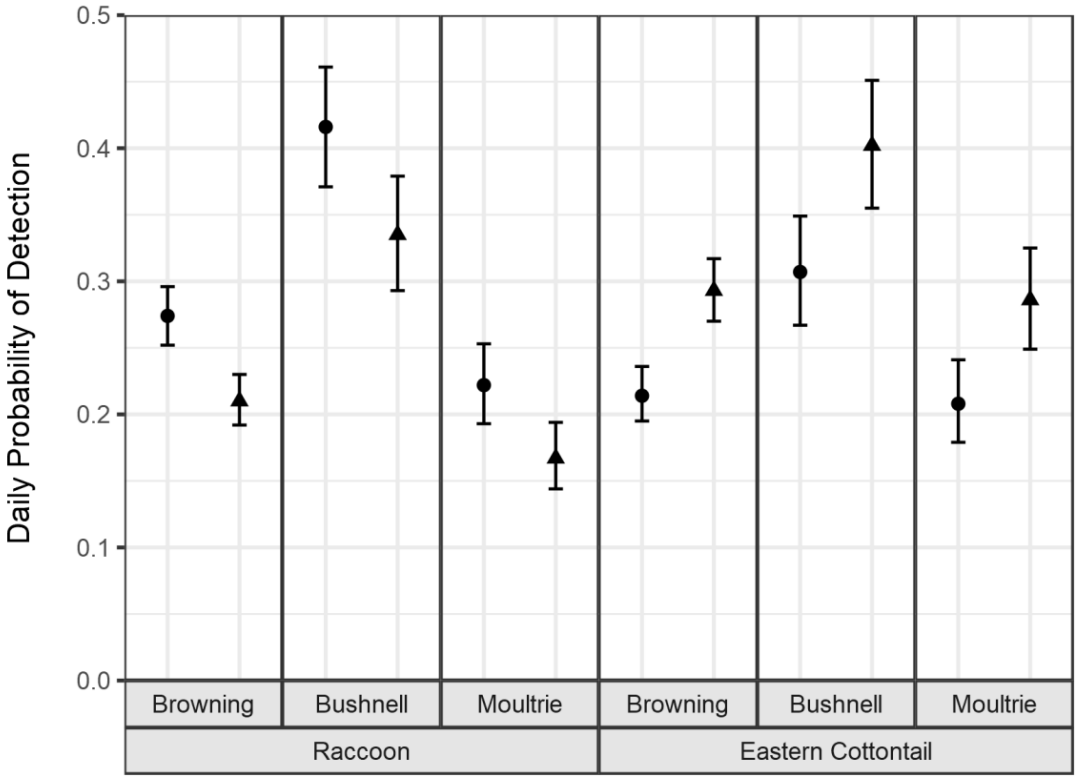


Table 1: Number of independent photo sequences, mean number of sequences (± SE) per detection, mean number of triggers (± SE) per sequence, and *p*-values for Mann-Whitney U tests at camera stations with and without a sardine lure applied for bobcat (*Lynx rufus*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), and eastern cottontail (*Sylvilagus floridanus*) surveyed in southcentral South Dakota during summer, 2019.

	Independent Sequences			**Sequences**			**Triggers**		
Species	**Lure**	**No lure**	**Total**	**Lure**	**No lure**	***P*-value**	**Lure**	**No lure**	***P*-value**
Bobcat	14	38	52	1.00 ± 0.00	1.23 ± 0.12	0.172	1.07 ± 0.07	1.58 ± 0.27	0.098
Coyote	229	174	403	1.34 ± 0.06	1.12 ± 0.04	0.003	1.39 ± 0.06	1.09 ± 0.03	<0.001
Raccoon	878	708	1,586	1.32 ± 0.02	1.35 ± 0.03	0.771	1.41 ± 0.04	1.44 ± 0.06	0.121
Eastern Cottontail	743	999	1,742	1.71 ± 0.06	1.79 ± 0.06	0.196	1.35 ± 0.04	1.50 ± 0.04	<0.001

Table 2: Detection covariate predictor importance based on cumulative model weights from single-species, single-season occupancy modeling for bobcat (*Lynx rufus*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), and eastern cottontail (*Sylvilagus floridanus*) surveyed in southcentral South Dakota during summer, 2019. Bold indicates predictors in the most-supported detection model.

	Species			
Covariate	**Bobcat**	**Coyote**	**Raccoon**	**Eastern cottontail**
Lure	**0.87**	0.31	**0.98**	**0.71**
Lure age	0.32	**0.77**	0.36	**0.93**
Trail	0.26	0.27	**1.00**	0.43
Camera model	0.27	0.32	**1.00**	**1.00**
Precipitation	**0.51**	0.36	0.25	0.44
Temperature	0.51	0.27	**0.96**	**0.92**
Illumination	0.27	0.27	0.40	**0.66**
Time	0.39	**0.65**	**1.00**	0.27

Notes: Predictors: Lure = lure applied at time of survey; lure age = days since lure applied; Trail = camera set adjacent to game trail; Camera Model = categorical identification of camera model; Precipitation = daily precipitation total (mm) from nearest weather station; Temperature = daily max temperature (ºC) from nearest weather station; Illumination = scaled range of moon phase; 0 (new moon) to 100 (full moon); Time = Julian day during survey.

CHAPTER 2: SPATIAL AND TEMPORAL PATTERNS OF SYMPATRIC BOBCATS (*LYNX RUFUS*) AND COYOTES (*CANIS LATRANS*) IN AN AGRICULTURAL LANDSCAPE

Abstract

In the Northern Great Plains, habitat loss and fragmentation are driven by the conversion of grasslands to agricultural land. Bobcats (*Lynx rufus*) are a species of management interest in South Dakota that are potentially vulnerable to habitat loss and fragmentation due to their large home ranges, low densities, and low reproductive rates. Additionally, bobcats may be influenced by interspecific interactions with coyotes (*Canis latrans*). Coexistence of sympatric carnivores can be facilitated through spatial, temporal, or dietary niche partitioning. We evaluated the influences of landscape features on space use of bobcats and coyotes using occupancy modeling and generated activity curves to quantify species temporal overlap using detection data collected from motion-activated cameras during the summers of 2019 and 2020. Coyote space use was high and positively related to slope and small-scale percent agriculture in 2019 and positively related to edge density in 2020. Bobcat space use was limited and positively associated with coyote activity in both years, and distance to roads and large-scale percent woodland/shrubland in 2020. We did not find evidence of temporal partitioning. Our results indicate that bobcats are using smaller, less-disturbed patches of woodland/shrubland, which are also associated with higher levels of coyote activity.

Introduction

Habitat loss and degradation are among the leading causes of mammalian biodiversity loss (Schipper et al. 2008, Newbold et al. 2015) and are projected to be the primary drivers of biodiversity loss in the future (Sala et al. 2000). Temperate grassland ecosystems, including grasslands of the Northern Great Plains, are threatened by high levels of conversion coupled with the lowest levels of protection (Hoekstra et al. 2005). In the Northern Great Plains, habitat loss is driven by conversion of grasslands to agricultural lands (Stephens et al. 2008). The life history characteristics of mammalian carnivores including low densities, large home ranges, and low reproductive rates relative to other terrestrial mammalian orders and persecution by humans can make them susceptible to habitat loss and fragmentation (Woodroffe and Ginsberg 1998, Crooks 2002). Consequently, carnivore population declines have resulted in the largest range contractions among mammalian biodiversity (Di Minin et al. 2016).

Carnivores are an essential component of the environment that influences ecosystem structure and function through regulating prey and their impact on vegetative communities (Ripple et al. 2014). Declines in populations of large carnivores can result in mesocarnivore population growth (i.e., “mesopredator release”), which can impact prey and vegetative communities through trophic cascades (Crooks and Soulé 1999, Berger et al. 2008, Prugh et al. 2009). Sympatric carnivore coexistence can be facilitated through spatial, temporal, or dietary niche partitioning (Schoener 1974). Habitat loss and fragmentation can reduce the potential for spatial partitioning by restricting movement and use to smaller, more-isolated patches of habitat (Hanski 2008, Šálek et al. 2014). With reduced opportunity for spatial partitioning, coexistence of carnivores may be

facilitated through temporal partitioning (Schoener 1974). Temporal partitioning may be more restricted in landscapes with greater anthropogenic disturbances as carnivores decrease diurnal activity in response to anthropogenic disturbance (Riley et al. 2003, George and Crooks 2006, Wang et al. 2015).

Bobcats (*Lynx rufus*) are a species of management interest in South Dakota due to their value as a furbearer and vulnerability to overharvest (Knick 1990). Bobcats are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), which requires that management agencies demonstrate that harvest and exportation is not detrimental to the survival of the species (Anderson and Lovallo 2003). Bobcats may be influenced by sympatric coyotes (*Canis latrans*) through interference competition including interspecific killing (Knick 1990, Fedriani et al. 2000, Gipson and Kamler 2002) or exploitative competition (Litvaitis and Harrison 1989, Henke and Bryant 1999). Bobcats have relatively large home ranges, tend to be solitary as adults, and are elusive, making monitoring their populations difficult (Sargeant et al. 1998, Ruell and Crooks 2007). Motion-activated camera traps have improved monitoring of elusive carnivores by enabling monitoring over large spatial and temporal scales and can be used to evaluate patterns of occurrence (Burton et al. 2015, Lesmeister et al. 2015).

Habitat conservation is improved through a better understanding of how habitat characteristics influence the spatial dynamics of species (Mackenzie et al. 2018). Evaluating patterns of use and occurrence without accounting for imperfect detection (Mackenzie et al. 2018), the influence of interspecific interactions (McLoughlin et al. 2010), or both can lead to biased inferences of factors associated with use. Occupancy

modeling uses detection-nondetection data to estimate and examine the factors that influence probability of detection (*p*) and occupancy while accounting for imperfect detection (MacKenzie et al. 2002).

We combined detection data from camera traps with occupancy modeling (MacKenzie et al. 2002) and activity curves (Wang et al. 2015, Lashley et al. 2018) to investigate patterns of space use and temporal activity, respectively, for bobcats and coyotes (a potential intraguild predator) in an agriculturally-dominated landscape in southcentral South Dakota. Consistent with previous research (Tucker et al. 2008, Clare et al. 2015, Wait et al. 2018), we predicted that bobcat use would be positively associated with woodland/shrubland (WS) cover due to their reliance on cover as ambush predators (Rollings 1945, Anderson and Lovallo 2003). We also predicted that bobcat space use would be positively associated with terrain ruggedness (Mosby 2011, Reed et al. 2017) and positively associated with distance from paved roads due to sensitivity to anthropogenic disturbance (Poessel et al. 2014, Lesmeister et al. 2015). We also predicted that bobcat space use would be negatively associated with coyote activity because bobcat space use has been shown to be influenced by the intensity of coyote activity (Wilson et al. 2010). Consistent with previous research (Theberge and Wedeles 1989, Lesmeister et al. 2015, Ellington et al. 2020) and cursorial hunting techniques, we predicted that coyote space use would be positively associated with edge density and distance from paved roads due to increased persecution in an agriculturally-dominated landscape (Lesmeister et al. 2015). Lastly, we predicted that bobcats and coyotes would temporally partition resources if space use of both species was limited to the same areas.

Methods

Study Area

The study area was located along the Missouri River in Charles Mix and Brule counties in southcentral South Dakota. The study area was ~4,275 km^2 and was bound by the borders of Charles Mix and Brule counties and by Interstate 90 to the north. The majority of the area was dominated by flat, privately-owned rangelands used for domestic cattle (*Bos taurus*) grazing and croplands (primarily corn [*Zea mays*] and soybean [*Glycine max*]) interspersed with woodland shelterbelts. Conversely, the western extent of the study area along the river was characterized by rugged drainages that had been impacted by eastern red cedar (*Juniperus virginiana*) encroachment. Dominant plant species included smooth bromegrass (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), big bluestem (*Andropogon gerardii*), porcupine grass (*Hesperostipa spartea*), eastern red cedar, and green ash (*Fraxinus pennsylvanica*). The study area experienced cold winters and moderate summers with the coldest month being January (average = -6.5°C) and the warmest month being July (average = 23.8°C). Average monthly precipitation, defined as the liquid equivalent of precipitation not including snowfall (Arguez et al. 2012), ranged from 12.7 mm (December) to 98.8 mm (June). Average annual precipitation and snowfall of 609 mm and 1054 mm, respectively (National Oceanic and Atmospheric Administration [NOAA] 2020).

Camera Trapping Design

Our sampling design was primarily intended to evaluate occupancy of bobcats. We divided the study area into 25 km^2 sites (5 km x 5 km), which approximated the home range size of female bobcats in South Dakota (Mosby 2011). We randomly selected 60 sites for surveying, excluding sites where land-access permissions could not be obtained. Single cameras within a site can fail to produce reliable assessments of occupancy and spatial replication within sites has been recommended (O'Connor et al. 2017, Kolowski et al. 2021). We used three cameras (hereafter, stations) to survey each site, which ensured that we surveyed a range of conditions within each site. We set stations ≥1.2 km from one another (both within and among sites), which represented the approximate home range diameter of eastern spotted skunks (*Spilogale putorius*) in the Midwest (Lesmeister et al. 2015). Eastern spotted skunks were of management interest in South Dakota and were a secondary target of our broader survey efforts. We surveyed selected sites over two summer field seasons from May to September in 2019 and May to August in 2020. Each station within a site was surveyed concurrently.

We set stations near habitat features frequented by carnivores (e.g., edge habitat, fence lines). We set all stations within a site with one of three passive infrared game camera models (Browning model BTC-6HDP, Bushnell Trophy Cam No Glow, or Moultrie model M-880), keeping models consistent within a site. We set cameras ~1 m high with a slight downward angle and trimmed vegetation within 4 m in front of each camera to increase visibility of smaller species and minimize false triggers (Si et al. 2014). We hung a quarter of an aluminum pie tin ~1 m high and ~4 m in front of each camera as a visual lure. In 2019, we ran a pilot study to test the influence of an olfactory

lure on *p* of bobcats by randomly assigning one of three olfactory lure treatments to each station within a site without replacement; details of this pilot study are described in Chapter 1. Briefly, treatments included (i) an olfactory lure, (ii) no olfactory lure, or (iii) an olfactory lure only during only the latter half of the survey. For treatments with an olfactory lure, we used 3.75 ounces of sardines in soybean oil enclosed in a perforated polyvinyl chloride pipe (5" length x 2" diameter) to prevent consumption and secured to the ground with a rebar stake ~4 m in front of the camera. Based on our pilot study (*see* Chapter 1), olfactory lures were not applied in 2020. We set cameras to operate 24 hours a day and capture three photos per trigger with a one-minute delay between triggers. Stations were set for ~28 nights. In 2019, we checked cameras after ~14 nights to replace memory cards and batteries (if necessary) and replace or add attractants for sites receiving an attractant during the entire survey or latter half of the survey, respectively. Cameras were not checked in 2020.

Habitat Sampling

We used line-point intercept sampling to characterize vegetation cover at each station (Herrick et al. 2005). We cleared vegetation and selected camera locations to maximize visibility; therefore, habitat sampling was conducted at randomly generated sampling cores using random bearings (0−359°) and distances (<100 m) from which three 100 m transects were conducted at randomly generated angles spaced equally apart by 120°. We used sampling core distances <100 m to ensure that the circular area sampled by the transects included the camera. We dropped a pin at 5 m increments along the transect and recorded the functional group (i.e., grass, forbs, sub-shrub [height <1 m],

shrub [1 m – 2 m], and tree [>2 m]) of every species that intercepted a line extending vertically from the pin (Herrick et al. 2005). We recorded four measurements of both visual obstruction (VO) using a Robel Pole (Harris et al. 2020) and concealment using a concealment board (Camp et al. 2012, McMahon et al. 2017) from a viewing height of 1 m and distance of 4 m in the four cardinal directions from the sampling core. Concealment was measured using a 39 x 30 cm concealment board with 3 x 3 cm checkerboarded squares and was recorded as the percentage of squares concealed by vegetation (Camp et al. 2012). We averaged the four directional measures to get a single measurement for both visual obstruction and concealment for each station.

Occupancy Modeling Covariates

We identified covariates expected to influence detection of carnivores. Cameras set near game trails may influence detection (Tobler et al. 2015, Kolowski and Forrester 2017), so we included a covariate (trail) to indicate if the camera was set adjacent to a game trail or not. Detection can be influenced by precipitation and temperature (Lesmeister et al. 2015). We obtained daily precipitation totals (mm) and maximum temperatures (ºC) for 5 NOAA weather stations near the study area (NOAA 2021a) and characterized each camera station with weather data from the nearest reporting weather station. Predators may alter movement patterns with changes in lunar illumination (Rockhill et al. 2013, Prugh and Golden 2014, Melville et al. 2020). We generated a daily illumination covariate from recorded moon phase data (NOAA 2021b) by scaling illumination from a range of 0 (new moon) to 100 (full moon). We included a covariate for time based on Julian day to account for temporal variation in detection. The effect that

time has on detection may change within a season (i.e., detection increases, then decreases), so we also considered time with a quadratic effect (i.e., time + time^2). For analysis of 2019 detection data, we included two covariates, lure and lure age, to characterize the influence of the olfactory lure on detection. Lure indicated if a lure was present at the time of the survey and lure age characterized the number of days since the lure was applied or refreshed because the influence of an attractant can change over time (Mills et al. 2019).

We identified covariates expected to influence space use of bobcats and coyotes. Bobcats are ambush predators that rely on the dense cover and increased prey availability associated with WS cover (Rollings 1945). Previous research has found that bobcat space use and occupancy was positively associated with WS cover (Tucker et al. 2008, Clare et al. 2015, Wait et al. 2018), edge (Clare et al. 2015, Wait et al. 2018), and terrain ruggedness (Mosby 2011, Reed et al. 2017), and negatively associated with human disturbance (Lesmeister et al. 2015, Wang et al. 2015) and agriculture landcover (Reed et al. 2017). Similarly, coyotes have been found to be associated with WS habitats in some systems (Gese et al. 1988, Lonsinger et al. 2017), terrain ruggedness (Bender et al. 2017), edge density (Theberge and Wedeles 1989, Lesmeister et al. 2015) and may avoid areas with higher human disturbance in some systems (Lesmeister et al. 2015, Wait et al. 2018).

We used ArcMap 10.8 (Environmental System Research Institute [ESRI], Redlands, CA, USA) to calculate a distance to the nearest paved road, which tends to reflect areas with greater human activity. We also used ArcMap and a digital elevation model (https://www.landfire.gov, accessed 18 Nov 2020) to calculate two covariates that

characterize terrain ruggedness at each station, slope and terrain ruggedness index (TRI), defined as the standard deviation of the slope (Riley et al. 1999). We used FRAGSTATS 4.2 (University of Massachusetts, Amherst, MA, USA) and a National Vegetation Classification (NVC) land cover layer (https://www.landfire.gov, accessed 17 Nov 2020) to calculate two covariates to characterize fragmentation for each station, mean patch size and edge density, and to calculate large-scale percent WS cover and percent agriculture (row crop). All FRAGSTATS landscape metrics were calculated within a 600-m buffer. We used line-point intercept habitat sampling data to calculate small-scale percent WS cover and percent agriculture by dividing the number of transect points with WS (tree, shrub, and sub-shrub) or agriculture functional groups by the total number of points (Lonsinger et al. 2015). We also used habitat sampling data to generate VO (Harris et al. 2020) and concealment (McMahon et al. 2017) covariates for each station. Because we were unable to use co-occurrence models, we characterized relative coyote activity at each camera station as the proportion of survey days with a coyote detection and included relative coyote activity as a covariate on bobcat space use (Lonsinger et al. 2017, Wait et al. 2018).

Occupancy Modeling

We intended to evaluate species-specific patterns of detection, occupancy, and spatial dynamics using multi-season single-species occupancy models for bobcats and coyotes, and then combine results of species-specific analyses into a multi-season conditional two-species analysis to investigate the influence of coyotes on bobcat patterns of occurrence (MacKenzie et al. 2002, 2003, Richmond et al. 2010). Preliminary site-

level analyses revealed that coyote occupancy was high and prevented us from formally assessing patterns of co-occurrence. Insufficient variation in the occurrence of coyotes, the dominant species, limited our ability to evaluate their influence on patterns of occurrence of bobcat, the subordinate species. High occurrence of coyote at the site level also limited our ability to evaluate how environmental predictors influenced coyote occurrence. Station-level patterns of detection suggested coyote occurrence was lower at the station-level scale. Although we were unlikely to satisfy the closure assumption of occupancy modeling at the station level, occupancy results can be interpreted as the probability of use when the closure assumption is not met and movement between sites is random (Mackenzie 2006, Gould et al. 2019). Consequently, we performed the analyses at the station-level scale to facilitate identification of factors driving coyote space use and interpreted results as the probability of use. Very few stations that were used by bobcats in 2019 were not used in 2020. This limited our ability to generate reliable estimates of extinction which can lead to erroneous use estimates in year 2 and prevented multi-season occupancy modeling. Consequently, we evaluated the factors influencing space use of bobcats and coyotes separately for 2019 and 2020 using daily encounter histories and single-species, single-season occupancy models (MacKenzie et al. 2002).

We used a sequential-by-sub-model modeling approach (Lonsinger et al. 2017, Morin et al. 2020). We tested for correlations between all pairwise covariate combinations using a Kendall's rank correlation test (Robinson et al. 2014, Lonsinger et al. 2017). Covariates with a Kendall's $|\tau| \geq 0.7$ were not included in the same model (Dormann et al. 2013). For each species, we first identified the most-supported global models for detection and occupancy. We fit two global detection models (i.e., including

all detection covariates), which varied only by how time was characterized (i.e., time versus quadratic effect of time), while holding the occupancy model for occupancy at the null model. We retained the most parsimonious characterization of time for each species for subsequent analyses. We fit eight competing global occupancy models that compared support for covariates that were correlated (i.e., slope vs. TRI, mean patch size vs. edge density, and VO vs. concealment), including all possible combinations of characterizations for these covariates along with all other occupancy covariates. We retained the characterization of each covariate in the most parsimonious global model for subsequent analyses. Finally, we developed a candidate model set for occupancy that included all possible additive combinations of occupancy covariates (Doherty et al. 2012), while holding the model for detection at the most-supported model (Lonsinger et al. 2017). Relative support for competing models was ranked using an information-theoretic approach with Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We estimated daily *p* and use, and inferred the influence of covariates, based on the structure of the most-supported models. Detection and use were estimated at the mean value for continuous covariates and the mode for categorical covariates (i.e., trail = adjacent to trail; camera type = Browning). To account for model-selection uncertainty, we also reported covariate predictor importance based on cumulative model weights. Analyses were completed separately for each species and each year.

The influence of mean patch size on bobcat space use (*see* Results) contradicted patterns observed in other studies (Nielsen and Woolf 2002, Crooks 2002). Consequently, we conducted a post-hoc analysis to assess the relationship between patch size and WS cover using a Spearman's rank correlation test. Additionally, we replaced mean patch

size with edge density in the top model to ensure that we had identified the most-parsimonious model.

Temporal Activity Curves

We evaluated temporal activity patterns separately for 2019 and 2020 using a non-parametric kernel density approach (Ridout and Linkie 2009). Photo sequences of the same species separated by ≥30 minutes were considered independent (Wang et al. 2015, Iannarilli et al. 2021). We converted detection times to radians, generated a probability density distribution using a kernel density estimation, and calculated a coefficient of overlap between bobcats and coyotes ($\hat{\Delta}$; Ridout and Linkie 2009, Wang et al. 2015, Lashley et al. 2018). Ridout and Linkie (2009) suggested using $\hat{\Delta}_1$ if the number of independent photo sequences of the smaller sample was <50 and $\hat{\Delta}_4$ if >75. We used $\hat{\Delta}_1$ because bobcat had <75 photo sequences for both years (2019: 52 and 2020: 45). Using program R (R Core Team 2020), we estimated $\hat{\Delta}$ 95% confidence intervals from 10,000 bootstrap samples with *overlap* package (Ridout and Linkie 2009; Wang et al. 2015, Lashley et al. 2018) and conducted a Watson's two-sample test of homogeneity in the *CircStats* package (Lund and Agostinelli 2018) to test for homogeneity between samples, (i.e., if the two samples come from the same population). We interpreted results to evaluate for evidence of temporal partitioning (Lashley et al. 2018).

Results

We surveyed 180 stations for a total of 5,514 camera days (mean = 30.6 ± 7.5 SD) from May to September 2019, and 174 stations for a total of 5000 camera days (mean = 27.8 ± 6.2 SD) from May to August 2020. Six stations from 2019 were not resurveyed in 2020 due to camera failure or changes in land-access permission. Coyotes had more independent photo sequences, days with ≥1 sequence, and were detected at more stations than bobcats (Table 1). Coyote independent photo sequences and days with ≥1 sequence decreased from 2019 and 2020, while those of bobcat were comparable between years (Table 1).

Time characterized as a linear covariate was more supported than a quadratic effect of time for bobcats and coyotes for both years. Only covariates that characterized the same habitat characteristics were correlated either year, including TRI and slope (Kendall's $|\tau| = 0.81$), VO and concealment ($|\tau| = 0.70$), and mean patch size and edge density ($|\tau| \geq 0.72$), which were not included in the same model.

Bobcat

The most-supported models of bobcat detection suggested that detection was negatively associated with lure in 2019 (Table 2). The most-supported models also suggested that bobcat detection may have been influenced by precipitation in 2019 and trail, illumination, and time in 2020, however, the influence of these predictors was not different from 0 (Table 2). When considering the full candidate model set, only lure, precipitation, and temperature in 2019 and only trail and time in 2020 had cumulative

model weights >0.5, with lure having the highest relative importance (Table 3). Daily *p* was higher in 2019 (daily $\hat{p}$ without lure, 0.063, $\widehat{\text{SE}}$ = 0.014, 95% CI = 0.040, 0.097) than in 2020 (0.027, $\widehat{\text{SE}}$ = 0.007, 95% CI = 0.017, 0.044).

Eight of the 512 bobcat space use models for 2020 were removed from the model set due to convergence issues. The most-supported models of bobcat space use suggested space use was positively associated with coyote activity (Table 2; Fig. 1) and negatively associated with patch size in both years, but the influence of patch size was not different from 0 in 2020 (Table 2). Cumulative model weights supported the importance of coyote activity and patch size in both years (Table 3). Bobcat space use in 2020 was also positively associated with distance to the nearest paved road and the large-scale percent WS cover (Table 2), both of which had high cumulative model weights (Table 3). Although the most-supported models also suggested that bobcat space use may have been influenced by concealment in 2019 and the large-scale proportion of agriculture in 2020, the influence of these predictors was not different from 0 (Table 2) and both had relatively low cumulative model weights (Table 3). Estimates of bobcat space use were similar across years (Fig. 2).

A post-hoc analysis found that mean patch size was negatively correlated with large-scale percent WS (Spearman's rho = –0.69, $p < 0.001$). The model with mean patch size was more supported than the model with edge density, and the 95% confidence intervals for the estimated beta coefficient of edge density overlapped 0 in 2020.

Coyote

The most-supported models of coyote detection suggested that detection was positively associated with lure age in 2019 and precipitation and varied across camera models in 2020 (Table 2). Relative to Moultrie cameras (represented by the intercept), detection was higher for Browning and Bushnell camera models (Table 2). Cumulative model weights supported the importance of lure age in 2019 and camera model and precipitation in 2020 (Table 3). Although the most-supported models also suggested that coyote detection may have been influenced by time in 2019, the influence of this predictor was not different from 0 (Table 2) and had a lower cumulative model weight than lure age in 2019 (Table 3). Daily *p* was similar between 2019 (0.070, $\widehat{\text{SE}}$ = 0.005, 95% CI = 0.061, 0.080) and 2020 (0.074, $\widehat{\text{SE}}$ = 0.007, 95% CI = 0.062, 0.088).

The most-supported models of coyote occupancy suggested space use was positively associated with slope and small-scale percent agriculture in 2019 and edge density in 2020 (Table 2). The most-supported models also suggested that coyote space use may have been influenced by large-scale percent WS cover in 2019, however, the influence of this predictor was not different from 0 (Table 2). When considering the full candidate model set, only slope, small-scale percent agriculture, and large-scale percent WS cover in 2019 and edge density and concealment in 2020 had cumulative model weights >0.5, with slope and edge density having the highest relative importance in 2019 and 2020, respectively (Table 3). Estimates of coyote space use were similar across years and significantly higher than bobcat space use (Fig. 2).

Temporal overlap

Bobcats and coyotes had marginally higher levels of activity during nocturnal and crepuscular periods with more detections (bobcat: 2019 = 56%, 2020 = 58%; coyote: 2019 = 61%, 2020 = 62%) occurring between sunrise and sunset than during diurnal periods. Bobcat activity was similar between years ($\hat{\Delta}_1$ = 0.89, 95% CI = 0.77, 0.99) and was not significantly different (p-value > 0.10). Coyote activity was similar between years ($\hat{\Delta}_4$ = 0.92, 95% CI = 0.86, 0.96) and was not significantly different (p-value > 0.10). Seasonal bobcat activity had high temporal overlap with coyote activity in both years, $\hat{\Delta}_1$ = 0.91 (95% CI = 0.81, 0.98) in 2019 and $\hat{\Delta}_1$ = 0.86 (95% CI = 0.76, 0.94; Fig 3) in 2020. We did not find evidence of temporal partitioning between bobcats and coyotes in either year (2019: p-value > 0.10; 2020: p-value > 0.10).

Discussion

Previous research investigating bobcat space use in habitats similar to southcentral South Dakota (Iowa, Tucker et al. 2008; Wisconsin, Clare et al. 2015; Kansas, Wait et al. 2018) found that landcover type influenced bobcat space use. Bobcat space use is often positively associated with natural landcover types such as woodlands and shrublands (Tucker et al. 2008, Clare et al. 2015, Wait et al. 2018) and can be negatively associated with agricultural land (Tucker et al. 2008). Based on telemetry data and habitat selection ratios, Tucker et al. (2008) found that bobcats were almost twice as likely to select for woodland than other habitat types and avoided agricultural land. Clare et al. (2015) found that bobcat space use was positively associated with the proportion of

wooded cover (forest, shrubland, and wooded wetland combined) and that neither the proportion of cropland or urban were significant predictors of space use. As we predicted, we found that large-scale percent WS was a significant predictor of bobcat space use in 2020. Percent agriculture was not a significant predictor either year. These results highlight the importance of WS cover to bobcats in an agricultural landscape.

Roads and anthropogenic disturbances can negatively influence the spatial dynamics of bobcats. Roads can be a direct source of mortality (Litvaitis et al. 1987, Knick 1990, Chamberlain et al. 1999, Riley et al. 2003) and can contribute to increased harvest mortality of carnivores (Basille et al. 2013). Bobcat home ranges in California had lower road densities than the overall road density in the study extent (Poessel et al. 2014). Likewise, Reed et al. (2017) found that collared bobcats avoided areas with high road densities. Riley et al. (2003) found that bobcat home ranges consisted primarily of natural areas, but most particularly adult females had the lowest percentage of urban landcover and hypothesized that females perceived disturbed areas as unsafe for rearing young. Occupancy of bobcat in southern Illinois was most influenced by anthropogenic disturbances, including negative associations with distance to paved roads and anthropogenetic structures (Lesmeister et al. 2015). We observed similar patterns. As we predicted, space use was greater in areas that were farther from roads, but only in 2020. These results highlight the importance of conserving undisturbed remote habitat. Undisturbed habitat may be important for females rearing young and may provide refugia from human-related disturbance and mortality.

Both edge density and patch size have been used to investigate bobcat space use or occupancy. Clare et al. (2015) found that bobcat use was positively associated with

wetland edge density (but not forest edge density) and suggested that wetland edge density had increased foraging value. Similarly, Wait et al. (2018) found that bobcat occupancy was positively associated with edge density. Nielsen and Woolf (2002) found that bobcat core areas had similarly high levels of mean patch size in comparison to the rest of the study area. Crooks (2002) found that the probability of occurrence of bobcats was positively related to fragment area. Our results that bobcat space use was negatively associated with mean patch size contradicts previous results (Nielsen and Woolf 2002, Crooks 2002). However, this is likely a consequence of landcover patterns in our study area and the scale of our mean patch size covariate. In our study area, relatively small, and presumably higher-quality, WS patches were interspersed among larger agricultural patches. This highlights the importance of understanding how covariate selection can influence the interpretation of results and how covariates and their influence can be scale and context dependent.

Ubiquitous use of study areas by coyotes has been found in other regions (Lesmeister et al. 2015, Lonsinger et al. 2017). Despite being able to exploit anthropogenically-dominated landscapes (Grinder and Krausman 2001, Gehrt et al. 2009), coyote space use and occupancy can still be negatively influenced by anthropogenic disturbance (Lesmeister et al. 2015, Wait et al. 2018). Our results did not indicate that coyote space use was influenced by anthropogenic disturbance. Rather, coyote space use was positively associated with slope and large-scale percent agriculture in 2019 and edge density in 2020. Coyotes in North Carolina selected for agricultural fields over woodland but territories normally consisted of core areas dominated by agricultural land with woodland more prevalent on the periphery (Hinton et al. 2015). In

2019, we found that coyote space use was positively associated with small-scale percent agriculture with large-scale percent WS potentially having a weak effect on coyote space use. Similar to other studies examining coyote space use (Theberge and Wedeles 1989, Lesmeister et al. 2015, Ellington et al. 2020), we found that space use was positively associated with edge density, which has been attributed to their cursorial hunting technique and increased prey availability in edge habitats (Theberge and Wedeles 1989).

The competitive exclusion principle suggests that two sympatric species competing for the same resources cannot coexist (Hardin 1960). Coyotes have been shown to influence bobcat space use (Wilson et al. 2010), influence bobcats through interference competition (Knick 1990, Fedriani et al. 2000, Gipson and Kamler 2002), and suppress bobcat populations through exploitative competition (Litvaitis and Harrison 1989, Henke and Bryant 1999). Coexistence of sympatric carnivores can be facilitated through dietary, spatial, or temporal niche partitioning (Schoener 1974, Di Bitetti et al. 2010). Despite evidence of competition between bobcat and coyote, previous research examining the spatial dynamic of bobcats and coyotes has generated mixed results on spatial partitioning. Wilson et al. (2010) found that bobcat space use was most influenced by the intensity of coyote activity. Bobcats avoided areas with high coyote activity when prey was abundant, but were more likely to use areas with high coyote activity when prey availability was low (Wilson et al. 2010). Bobcat space use or occurrence has been shown to not be influenced by (Lesmeister et al. 2015, Wait et al. 2018) or even be positively associated with coyote occupancy (Wang et al. 2015, Bender et al. 2017, Lombardi et al. 2020). Wang et al. (2015) and Wait et al. (2018) did not account for prey availability. The spatial patterns that they observed may have been influenced by underlying resource

availability that was not accounted for. Lombardi et al. (2020) did not include prey availability in analyses but suggested that prey availability in the study area was high due to no harvest and limited habitat manipulation. Bender et al. (2017) found that bobcat and coyote were more likely to co-occur than would be expected under a hypothesis of independence (Richmond et al. 2010) but that space use of each species was influenced by different-sized prey. Lesmeister et al. (2015) accounted for prey availability and found no effect for bobcat but found that coyote occupancy was higher in hardwood forest stands and suggested that hardwood forests had higher prey abundance than conifer stands. Contradicting our prediction, we found that bobcat space use was positively associated with coyote activity. These results suggest that bobcats are more likely to use areas that have more coyote activity. This may suggest that prey resources are sufficiently low in our study area (Wilson et al. 2010) or that landscape patterns in our agriculturally-dominated landscape concentrate prey in areas and results in increased interactions at the spatial scale between bobcats and coyotes. We were unable to include prey availability in our modeling of space use because detection of eastern cottontail, presumably one of the primary prey of bobcats in South Dakota (Nomsen 1982), was influenced by differences across camera sets (e.g., camera model and lure) that would have invalidated any relative measure of prey availability.

Consistent with our results that bobcats and coyotes do not spatially partition resources, our results aligned with previous research findings that activity of bobcats and coyotes have high levels of temporal overlap (Witmer and DeCalesta 1986, Neale and Sacks 2001, Lesmeister et al. 2015). This may be a consequence of decreased diurnal activity of carnivores in response to anthropogenic disturbance (Riley et al. 2003, George

and Crooks 2006, Wang et al. 2015) in our agriculturally-dominated landscape. In the absence of spatial and temporal partitioning, co-occurrence can still be facilitated through dietary niche partitioning (Schoener 1974), but we were unable to evaluate dietary patterns between bobcats and coyotes in our study system. Neale and Sacks (2001) found slight differences in diets between bobcat and coyote and no evidence of spatial or temporal partitioning. Bobcat diets consisted primarily of small mammals, while coyotes diets consisted primarily of ungulates (Neale and Sacks 2001). Bender et al. (2017) found that bobcat and coyote space use was influenced by different-sized prey. Lesmeister et al. (2015) and Bender et al. (2017) suggested that despite high spatial overlap, that co-occurrence can be facilitated through differences in hunting techniques between cursorial predators and ambush predators. Beyond dietary niche partitioning, Lombardi et al. (2020) hypothesized that co-occurrence was facilitated by an abundance of suitable cover with high prey availability and fine-scale avoidance was facilitated through olfactory cues.

We found that the factors that influenced patterns of use varied between years. Our study area experienced major flooding before and during our 2019 field season. Flooding altered human activity by limiting farming and altering human movement and access. In our study area, most WS cover is adjacent to rivers, creeks, and drainages. Flooding may have altered prey availability or displaced bobcats in these areas. Our 2020 field season took place during the SARS-CoV-2 (coronavirus disease 2019) outbreak, which likely had impacts on human activity and road traffic around recreation areas and campgrounds in the study area.

Our study was restricted to spatial and temporal patterns of bobcats and coyotes during summer months. The factors that potentially influence space use and interspecific interactions (e.g., resource availability, weather, harvest, reproduction, and anthropogenic disturbance) are likely to vary throughout the year. Summer is important for understanding bobcat and coyote space use because abundance should be highest due to reproductive pulses. Harvest in winter months complicates using occupancy modeling to investigate space use because harvest mortality likely violates the closer assumption required for occupancy modeling. Furthermore, trapping activity is difficult to quantify and is likely to influence space use of bobcats and coyotes.

Management Implications

This research adds to the growing body of evidence of the importance of remnant, undisturbed WS cover for bobcat space use in an agricultural landscape. Eastern red cedar encroachment could benefit bobcat populations and management of encroachment is likely to influence bobcat populations in the Northern Great Plains. Managers should consider conserving and limiting the development of undisturbed WS habitats because it may provide refugia from human-related disturbance and mortality. Our results also provide insight into patterns of spatial and temporal resource partitioning between competing sympatric carnivores in agricultural landscapes. Agricultural landscapes may limit the availability of high-quality habitat, which may concentrate or suppress prey availability, and increase spatial overlap of sympatric carnivores. Wildlife managers should consider limiting further conversion of natural habitats to agriculture to limit

further concentration or reduction of prey availability which could further decrease opportunities for resource partitioning between bobcats and coyotes.

References

Anderson, E. M. and Lovallo, M. J. 2003. Bobcat and lynx. - In: Feldhamer, G. A. et al. (eds), Wild mammals of North America: biology, management, and conservation. 2nd edn. John Hopkins University Press, pp. 758–786.

Arguez, A. et al. 2012. NOAA's 1981-2010 U.S. climate normals. - Bull. Am. Meteorol. Soc. 93: 1687–1697.

Basille, M. et al. 2013. Selecting habitat to survive: The impact of road density on survival in a large carnivore. - PLoS One 8: e65493.

Bender, L. C. et al. 2017. Seasonal occupancy of sympatric larger carnivores in the southern San Andres Mountains, south-central New Mexico, USA. - Mammal Res. 62: 323–329.

Berger, K. M. et al. 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. - Ecology 89: 818–828.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. - Springer US.

Burton, A. C. et al. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. - J. Appl. Ecol. 52: 675–685.

Camp, M. J. et al. 2012. When to run and when to hide: The influence of concealment, visibility, and proximity to refugia on perceptions of risk. - Ethology 118: 1010–1017.

Chamberlain, M. J. et al. 1999. Survival and cause-specific mortality of adult bobcats in central Mississippi. - J. Wildl. Manage. 63: 613.

Clare, J. D. J. et al. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. - J. Wildl. Manage. 79: 469–480.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. - Conserv. Biol. 16: 488–502.

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. - Nature 400: 563–566.

Di Bitetti, M. S. et al. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. - Acta Oecologica 36: 403–412.

Di Minin, E. et al. 2016. Global priorities for national carnivore conservation under land use change. - Sci. Rep. 6: 23814.

Doherty, P. F. et al. 2012. Comparison of model building and selection strategies. - J. Ornithol. 152: 317–323.

Dormann, C. F. et al. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. - Ecography (Cop.). 36: 27–46.

Ellington, E. H. et al. 2020. Seasonal and daily shifts in behavior and resource selection: how a carnivore navigates costly landscapes. - Oecologia 194: 87–100.

Fedriani, J. M. et al. 2000. Competition and intraguild predation among three sympatric carnivores. - Oecologia 125: 258–270.

Gehrt, S. D. et al. 2009. Home range and landscape use of coyotes in a metropolitan landscape: Conflict or coexistence? - J. Mammal. 90: 1045–1057.

George, S. L. and Crooks, K. R. 2006. Recreation and large mammal activity in an urban nature reserve. - Biol. Conserv. 133: 107–117.

Gese, E. M. et al. 1988. Home range and habitat use of coyotes in southeastern Colorado. - J. Wildl. Manage. 52: 640–646.

Gipson, P. S. and Kamler, J. F. 2002. Bobcat killed by a coyote. - Southwest. Nat. 47: 511–513.

Gould, M. J. et al. 2019. Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly-mobile species: A case study using the American black bear. - Biol. Conserv. 234: 28–36.

Grinder, M. I. and Krausman, P. R. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. - J. Wildl. Manage. 65: 887–898.

Hanski, I. 2008. Spatial patterns of coexistence of competing species in patchy habitat. - Theor. Ecol. 1: 29–43.

Hardin, G. 1960. The competitive exclusion principle. - Science. 131: 1292–1297.

Harris, S. N. et al. 2020. Den site selection by the Florida spotted skunk. - J. Wildl. Manage. 84: 127–137.

Henke, S. E. and Bryant, F. C. 1999. Effects of coyote removal on the faunal community in western Texas. - J. Wildl. Manage. 63: 1066–1081.

Herrick, J. E. et al. 2005. Monitoring manual for grassland, shrubland, and savanna ecosystems. Volume II: Design, supplementary methods and interpretation. - USDA - ARS Jornada Experimental Range.

Hinton, J. W. et al. 2015. Space use and habitat selection by resident and transient coyotes (Canis latrans). - PLoS One 10: e0132203.

Hoekstra, J. M. et al. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. - Ecol. Lett. 8: 23–29.

Iannarilli, F. et al. 2021. Evaluating species-specific responses to camera-trap survey designs. - Wildlife Biol. 10.2981/wlb.00726

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. - Wildl. Monogr. 108: 3–42.

Kolowski, J. M. and Forrester, T. D. 2017. Camera trap placement and the potential for bias due to trails and other features. - PLoS One 12: e0186679.

Kolowski, J. M. et al. 2021. High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. - Ecosphere 12: e03350.

Lashley, M. A. et al. 2018. Estimating wildlife activity curves: Comparison of methods and sample size. - Sci. Rep. 8: 4173.

Lesmeister, D. B. et al. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. - Wildl. Monogr. 191: 1–61.

Litvaitis, J. A. and Harrison, D. J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. - Can. J. Zool. 67: 1180–1188.

Litvaitis, J. A. et al. 1987. Influence of season and human-induced mortality on spatial organization of bobcats (Felis rufus) in Maine. - J. Mammal. 68: 100–106.

Lombardi, J. V. et al. 2020. Co-occurrence of bobcats, coyotes, and ocelots in Texas. - Ecol. Evol. 10: 4903–4917.

Lonsinger, R. C. et al. 2015. Fine-scale genetic structure of the ringtail (Bassariscus astutus) in a Sky Island mountain range. - J. Mammal. 96: 257–268.

Lonsinger, R. C. et al. 2017. The roles of habitat and intraguild predation by coyotes on the spatial dynamics of kit foxes. - Ecosphere 8: e01749.

Lund, U. and Agostinelli, C. 2018. CircStats: Circular statistics.

Mackenzie, D. I. 2006. Modeling the probability of resource use: The effect of, and dealing with, detecting a species imperfectly. - J. Wildl. Manage. 70: 367–374.

Mackenzie, D. I. et al. 2018. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. - Academic Press.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. - Ecology 83: 2248–2255.

MacKenzie, D. I. et al. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. - Ecology 84: 2200–2207.

McLoughlin, P. D. et al. 2010. Considering ecological dynamics in resource selection functions. - J. Anim. Ecol. 79: 4–12.

McMahon, L. A. et al. 2017. Habitat selection differs across hierarchical behaviors: Selection of patches and intensity of patch use. - Ecosphere 8: e01993.

Melville, H. I. A. S. et al. 2020. Abiotic variables influencing the nocturnal movements of bobcats and coyotes. - Wildlife Biol. 10.2981/wlb.00601

Mills, D. et al. 2019. Maximizing camera trap data: Using attractants to improve detection of elusive species in multi-species surveys. - PLoS One 14: e0216447.

Morin, D. J. et al. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? - Ecosphere 11: e02997.

Mosby, C. E. 2011. Habitat selection and population ecology of bobcats (Lynx rufus) in South Dakota, USA.

National Oceanic and Atmospheric Administration (NOAA) 2020. National Centers for Environmental Information - 1991-2020 climate normals.

National Oceanic and Atmospheric Administration (NOAA) 2021a. Climate data online.

National Oceanic and Atmospheric Administration (NOAA) 2021b. Astronomical data.

Neale, J. C. C. and Sacks, B. N. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. - Oikos 94: 236–249.

Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - Nature 520: 45–50.

Nielsen, C. K. and Woolf, A. 2002. Habitat-relative abundance relationship for bobcats in southern Illinois. - Wildl. Soc. Bull. 30: 222–230.

Nomsen, D. E. 1982. Food habits and placental scar counts of bobcats in South Dakota.

O'Connor, K. M. et al. 2017. Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. - PLoS One 12: e0175684.

Poessel, S. A. et al. 2014. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. - Biol. Conserv. 180: 224–232.

Prugh, L. R. and Golden, C. D. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles (S Boutin, Ed.). - J. Anim. Ecol. 83: 504–514.

Prugh, L. R. et al. 2009. The rise of the mesopredator. - Bioscience 59: 779–791.

R Core Team 2020. R: A language and environment for statistical computing.

Reed, G. C. et al. 2017. Describing habitat suitability of bobcats (Lynx rufus) using several sources of information obtained at multiple spatial scales. - Mamm. Biol. 82: 17–26.

Richmond, O. M. W. et al. 2010. Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. - Ecol. Appl. 20: 2036–2046.

Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. - J. Agric. Biol. Environ. Stat. 14: 322–337.

Riley, S. J. et al. 1999. Index that quantifies topographic heterogeneity. - Intermt. J. Sci. 5: 23–27.

Riley, S. P. D. et al. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. - Conserv. Biol. 17: 566–576.

Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. - Science. 343: 1241484.

Robinson, Q. H. et al. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. - Ecology 95: 3112–3123.

Rockhill, A. P. et al. 2013. The effect of illumination and time of day on movements of bobcats (Lynx rufus). - PLoS One 8: e69213.

Rollings, C. T. 1945. Habits, foods and parasites of the bobcat in Minnesota. - J. wild 9: 131–145.

Ruell, E. W. and Crooks, K. R. 2007. Evaluation of noninvasive genetic sampling methods for felid and canid populations. - J. Wildl. Manage. 71: 1690–1694.

Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. - Science. 287: 1770–1774.

Šálek, M. et al. 2014. Does spatial co-occurrence of carnivores in a central European agricultural landscape follow the null model? - Eur. J. Wildl. Res. 60: 99–107.

Sargeant, G. A. et al. 1998. Interpreting carnivore scent-station surveys. 62: 1235–1245.

Schipper, J. et al. 2008. The status of the world's land and marine mammals: Diversity, threat, and knowledge. - Science. 322: 225–230.

Schoener, T. W. 1974. Resource partitioning in ecological communities. - Science. 185: 27–39.

Si, X. et al. 2014. How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. - PeerJ 2: e374.

Stephens, S. E. et al. 2008. Predicting risk of habitat conversion in native temperate grasslands. - Conserv. Biol. 22: 1320–1330.

Theberge, J. B. and Wedeles, C. H. R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. - Can. J. Zool. 67: 1285–1290.

Tobler, M. W. et al. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data (P Lukacs, Ed.). - J. Appl. Ecol. 52: 413–421.

Tucker, S. A. et al. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. - J. Wildl. Manage. 72: 1114–1124.

Wait, K. R. et al. 2018. Land-use change structures carnivore communities in remaining tallgrass prairie. - J. Wildl. Manage. 82: 1491–1502.

Wang, Y. et al. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. - Biol. Conserv. 190: 23–33.

Wilson, R. R. et al. 2010. Prey-mediated avoidance of an intraguild predator by its intraguild prey. - Oecologia 164: 921–929.

Witmer, G. W. and DeCalesta, D. S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. - Can. J. Zool. 64: 2333–2338.

Woodroffe, R. and Ginsberg, J. R. 1998. Edge effects and the extinction of populations inside protected areas. - Science. 280: 2126–2128.

Figure 1. Estimated space use ($\widehat{\Psi}$) of bobcats (*Lynx rufus*) as a function of relative coyote (*Canis latrans*) activity (i.e., the proportion of survey days with a coyote detection) with 95% confidence intervals in southcentral South Dakota during summer, 2019 and 2020.

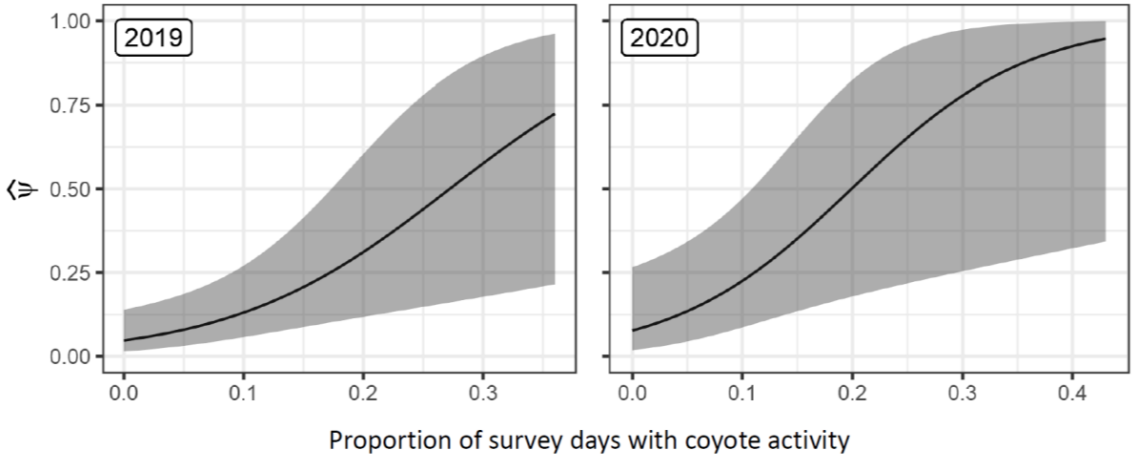


Figure 2. Estimated space use ($\hat{\Psi}$) of bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) with 95% confidence intervals for summer 2019 (●) and 2020 (▲) in southcentral South Dakota.

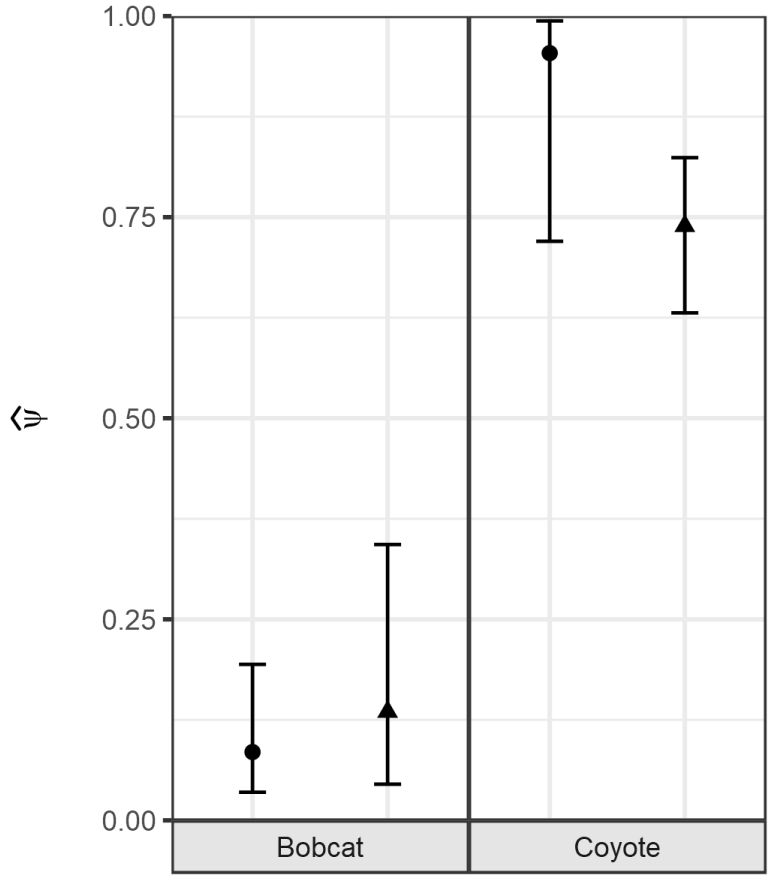
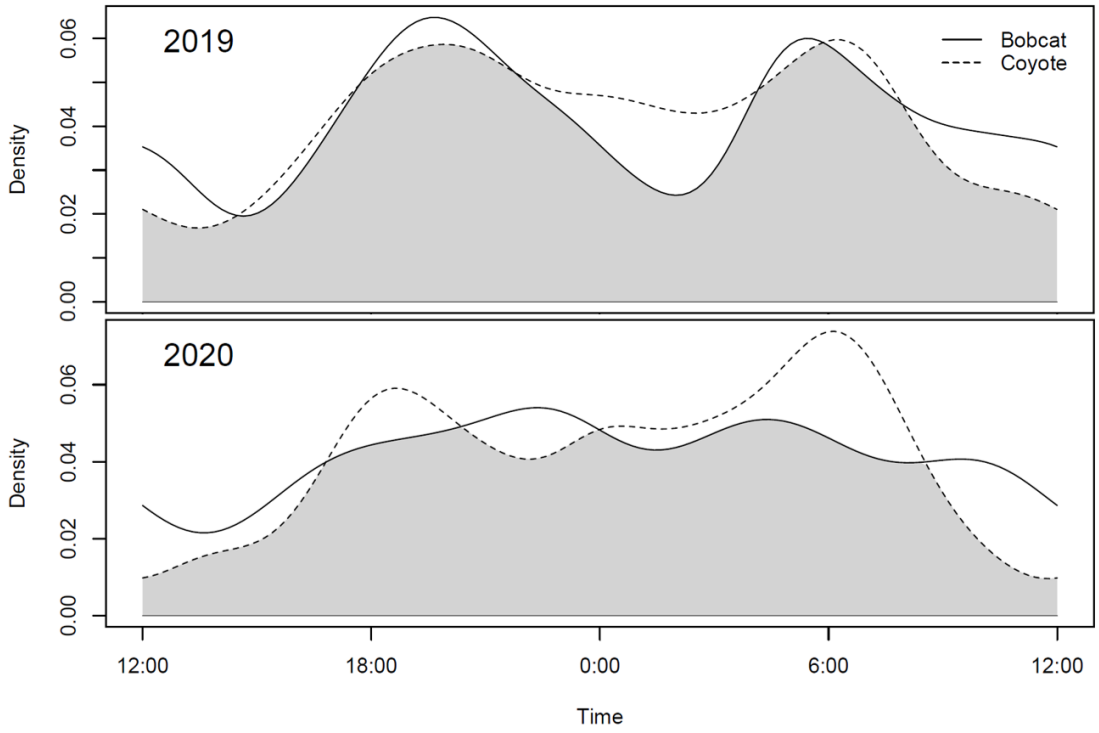


Figure 3. Kernel density estimates of summer daily activity patterns of bobcat (*Lynx rufus*) and coyote (*Canis latrans*) in southcentral South Dakota, 2019 and 2020.



Notes: independent photo sequence totals: 2019: bobcat = 52, coyote = 403; 2020: bobcat = 45; coyote = 302.

Table 1. The number of independent photo sequences, number of days with ≥1 photo sequence, and number of unique stations with detections of bobcat (*Lynx rufus*) and coyote (*Canis latrans*) surveyed in southcentral South Dakota during summer, 2019 and 2020.

	Independent sequences		**Days with ≥1 sequence**		**Unique stations**		
	2019	**2020**	**2019**	**2020**	**2019**	**2020**	**Both years**
Bobcat	52	45	45	44	24	30	43
Coyote	403	302	326	262	111	108	153

Table 2. Estimated beta coefficients ($\hat{\beta}$), standard error (SE), and 95% confidence interval lower (LCL) and upper (UCL) confidence limits for the most-supported models of detection (*p*) and space use (Ψ) for bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) surveyed in southcentral South Dakota during summer, 2019 and 2020.

	Parameter	$\hat{\beta}$	SE	LCL	UCL		Parameter	$\hat{\beta}$	SE	LCL	UCL
Bobcat 2019						*Coyote 2019*					
p	Intercept	−2.548	0.243	−3.025	−2.071	*p*	Intercept	−3.080	0.376	−3.817	−2.343
	Lure	−1.011	0.357	−1.710	−0.311		Lure Age	0.022	0.008	0.006	0.037
	Precipitation	−0.033	0.027	−0.086	0.019		Time	0.003	0.002	−0.001	0.006
Ψ	Intercept	0.403	0.808	−1.180	1.987	Ψ	Intercept	−1.276	0.481	−2.218	−0.334
	Coyote Act.	10.989	3.995	3.158	18.820		Slope	0.594	0.237	0.129	1.058
	Concealment	−0.018	0.010	−0.037	0.001		LS_%WS	0.116	0.071	−0.023	0.255
	Patch	−0.374	0.162	−0.692	−0.056		SS_%Ag	0.019	0.008	0.003	0.035
Bobcat 2020						*Coyote 2020*					
p	Intercept	−1.306	1.769	−4.773	2.160	*p*	Intercept	−3.223	0.212	−3.639	−2.806
	Trail	0.896	0.686	−0.450	2.241		Cam Model				
	Illumination	−0.008	0.005	−0.019	0.002		Browning	0.629	0.229	0.179	1.079
	Time	−0.015	0.009	−0.033	0.002		Bushnell	0.818	0.243	0.342	1.293
Ψ	Intercept	−3.307	1.283	−5.821	−0.793		Precipitation	0.015	0.004	0.007	0.023
	Coyote Act.	12.442	5.083	2.480	22.404	Ψ	Intercept	−0.621	0.572	−1.742	0.500
	Patch	−0.415	0.218	−0.843	0.012		Edge Density	0.018	0.007	0.004	0.031
	Road Dist.	0.599	0.248	0.114	1.085						
	LS_%WS	0.108	0.033	0.044	0.173						
	LS_%Ag	0.031	0.018	−0.004	0.067						

Notes: Predictors: Lure = lure applied at time of survey; lure age = days since lure applied; Trail = camera set adjacent to game trail; Camera Model = categorical identification of camera model; Precipitation = daily precipitation total (mm) from nearest weather station; Temperature = daily max temperature (ºC) from nearest weather station; Illumination = scaled range of moon phase; 0 (new

moon) to 100 (full moon); Time = Julian day during survey; Slope = slope at station; TRI = Terrain ruggedness index at station; concealment = visual cover measured as percent of 39 x 30 cm concealed by vegetation at ground level; VO = vertical density of vegetation measured from ground level (cm); Edge Density = total edge (m) per hectare within 600-m buffer; Patch = mean patch size within 600-m buffer; coyote act = proportion of survey days with a coyote detection; Road Dist = distance to nearest paved road (km); LS_%WS = percent woodland/shrubland cover within 600-m buffer; LS_%Ag = percent agriculture cover within 600-m buffer, SS_%WS = percent woodland/shrubland cover within 100-m buffer, SS_%Ag = percent agriculture cover within 600-m buffer.

Table 3. Detection (*p*) and space use (Ψ) covariate predictor importance based on cumulative model weights from single-species, single-season occupancy modeling for bobcat (*Lynx rufus*) and coyote (*Canis latrans*) surveyed in southcentral South Dakota during summer, 2019 and 2020. Bold indicates predictors in the most-supported detection model. Dash indicates that the covariate was not considered in the model set.

		Bobcat		Coyote	
	Covariate	2019	2020	2019	2020
p	Lure	**0.87**	-	0.31	-
	Lure Age	0.32	-	**0.77**	-
	Trail	0.26	**0.78**	0.27	0.42
	CamModel	0.27	0.15	0.32	**0.97**
	Illumination	0.27	**0.47**	0.27	0.29
	Precipitation	**0.51**	0.26	0.36	**0.99**
	Temperature	0.51	0.41	0.27	0.30
	Time	0.39	**0.85**	**0.65**	0.41
Ψ	Slope	0.26	-	**1.00**	-
	TRI	-	0.47	-	0.27
	Concealment	**0.61**	-	-	0.51
	VO	-	0.54	0.26	-
	Edge Density	-	-	0.36	**0.67**
	Patch	**0.88**	**0.87**	-	-
	Coyote Act.	**0.96**	**0.97**	-	-
	Road Dist	0.26	**0.97**	0.25	0.26
	LS_%WS	0.45	**1.00**	**0.74**	0.31
	LS_%Ag	0.26	**0.48**	0.27	0.27
	SS_%WS	0.31	0.53	0.34	0.38
	SS_%Ag	0.29	0.34	**0.76**	0.31

Notes: Predictors: Lure = lure applied at time of survey; lure age = days since lure applied; Trail = camera set adjacent to game trail; Camera Model = categorical identification of camera model; Precipitation = daily precipitation total (mm) from nearest weather station; Temperature = daily max temperature (ºC) from nearest weather station; Illumination = scaled range of moon phase; 0 (new moon) to 100 (full moon); Time = Julian day during survey; Slope = slope at station; TRI = Terrain ruggedness index at station; concealment = visual cover measured as percent of 39 x 30 cm concealed by vegetation at ground level; VO = vertical density of vegetation measured from ground level (cm); Edge Density = total edge (m) per hectare within 600-m buffer; Patch = mean patch size within 600-m buffer; coyote act = proportion of survey days with a coyote detection; Road Dist = distance to nearest paved road (km); LS_%WS = percent woodland/shrubland cover within 600-m buffer; LS_%Ag = percent agriculture cover within 600-m buffer, SS_%WS = percent woodland/shrubland cover within 100-m buffer, SS_%Ag = percent agriculture cover within 600-m .