

OCCUPANCY MODELING OF FOREST CARNIVORES IN MISSOURI

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Degree of Doctor of Philosophy

By

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.....To my wife, Suzie,
Thanks Champ, I Love You!

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OCCUPANCY MODELING OF FOREST CARNIVORES IN MISSOURI

Harvey Mundy Hackett IV

Dr. Matthew Gompper, Dissertation Advisor

ABSTRACT

My research focused on patterns of distribution and co-occurrence of the carnivore guild in forested ecosystems of southern Missouri. Carnivores have the ability to structure and drive the dynamics of entire ecosystems, and these effects are disproportionate to their abundance on the landscape. I used infrared remote cameras, trackplate boxes, and scat transects to survey sites throughout the southern forested region of Missouri. My goals were to assess the validity of noninvasive techniques and use the ensuing survey data to document the distribution of forest carnivores, to analyze habitat associations and patterns of occurrence for forest carnivores, and to model carnivore species occupancy for the Ozarks region.

The study of carnivore communities across landscapes has become more feasible and economical with the advent of modern noninvasive technologies. To better understand the value and limitations of these methods and approaches I examined presence data collected non-invasively in 2005-06 from 53 forested sites. I estimated latency to detection (LTD) and probability of detection (POD) given presence for seven species, compared these metrics across detection devices, and evaluated the effects of altering the order of implementation of the method on detectability. I also performed scat transects at 40 of 53 sites to validate the use of remote cameras for discerning the

presence of coyotes (*Canis latrans*). Cameras and track-plates both detected Eastern spotted skunk (*Spilogale putorius*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*) and opossum (*Didelphis virginiana*), but with differing effectiveness. Bobcat (*Lynx rufus*) and gray fox (*Urocyon cinereoargenteus*) were only effectively documented with remote cameras. Daily detection rates by cameras ranged from 0.003 (bobcat) to 0.05 (opossum), and rates by track-plates ranged from 0.09 (striped skunk) to 0.29 (opossum). Cameras and track-plates performed poorly at capturing images of coyotes where their presence was known from scat transects, but cameras also obtained photographic evidence of coyote presence at 63% (5/8) sites where no coyote scat was collected. I found that by combining methods a more accurate picture of the community composition is obtained, and that it is necessary to tailor survey methodology to target species over an extended period.

Relatively little is known about eastern spotted skunk ecology, a state endangered species in Missouri. Model results for it and the striped skunk revealed that forested habitat was a predictor of eastern spotted skunk occupancy, while urban features of a landscape were better predictors of striped skunk occupancy. However, neither species had a single model for occupancy that had a high weight of evidence ($w_i > 0.90$), so data were further analyzed using model averaging. Results suggest the most influential variables in predicting high occupancy by eastern spotted skunk were those related to proportion of an area covered by forest. Conversely, the best striped skunk occupancy variables in model averaging were characterized by a positive relationship to distance to nearest road and an inverse relationship with percent area settled. The regional predictive map for eastern spotted skunk indicated generally low occupancy rates across the region,

with several large patches of habitat related to forest cover that had predicted occupancy of $\Psi > 0.20$. The map for striped skunk revealed an association between areas of habitat transitions from forested to urban landcover type and a relatively higher occupancy rate across the region. One of the most significant findings was that incorporation of the other carnivore species into each species occupancy model (e.g. including striped skunk presence as a covariate in the spotted skunk models) resulted in an improved model. This suggests that there is some habitat component that is being accounted for indirectly by the incorporation of the other species, and may also imply the potential for competition between the two species.

The two most commonly detected mammalian mesopredators in my surveys were the opossum and raccoon. Raccoons were detected at 94% of sites and opossum at 89% of sites. Model averaging was also used for these two species due to weak resolution of a single important model set in occupancy model selection analyses. As was observed for the skunk species, model averaging revealed that by incorporating knowledge of the presence of one species (e.g. raccoon) into the modeling process for other species (e.g. opossum) the predictive ability of the resulting model is improved. Odds ratios revealed that the most important predictors of raccoon occupancy at a landscape level were knowledge of opossum presence (OR = 1.60) and distance to water (OR = 1.16). Core area index (OR = 4.37) and knowledge of raccoon presence (OR = 2.08) were the most important predictors of opossum occupancy. The predictive models for both species lack much resolution, however, because both species were so common and because of the binary nature of modeling presence-absence data. Nonetheless, my results do suggest a high degree of habitat overlap in the general distribution of these two forest

mesopredators, and a that a modeling approach that uses abundance data for each may allow for a more effective result.

In the past century the coyote has become an abundant apex predator in much of eastern North American temperate forest habitats. How coyotes may influence the distribution of other forest carnivores such as bobcat and gray fox is unclear. Again, due to a lack of a single important model set I used model averaging to predict occupancy of coyote, bobcat, and gray fox. The probability of actual occupancy (PAO) for coyotes was best predicted by measures of human disturbance and prey distribution. Bobcats were primarily influenced by coyote presence and prey availability. Gray foxes were the most heterogeneous of the species in their regional predicted distribution, and were best predicted by measures of coyote and bobcat presence as well as by landscape elements related to humans and settled areas. These results allude to the potential for coyotes to dynamically alter and structure the distribution of bobcat and gray fox in the Ozarks.

CHAPTER 1

OVERVIEW

Harvey Mundy Hackett IV

A fundamental problem in ecology is the issue of scale, and in particular, the appropriate scale at which research needs to be focused to ascertain the dynamics that function to drive and organize a community (Levin 1992). Ecologists have realized that if their research is designed to ask and answer questions related to patterns of species distribution and occupancy, then they need to focus on patterns and processes that may operate at multiple spatial scales (Hansson and Angelstam 1991; Pickett et al. 1992, 1997; Englund 1997; Keitt et al. 1997; Tilmon and Kareiva 1997; Hochberg and Van Baalen 1998; Ritchie 1998; Buskirk et al. 1999).

My research focused on such issues within the carnivore guild in the forested ecosystems of southern Missouri. Carnivores play important and unique roles in the natural functioning of ecosystems by virtue of their apex trophic position (Estes 1996; Crooks and Soulé 1999; Terborgh et al. 1999, 2001; Soulé et al. 2003). They have the ability to structure and drive the dynamics of entire ecosystems, and these effects are disproportionate to their abundance on the landscape. Indeed, an important ecological question is: How, and to what degree, do individual species of carnivores, as well as the broader carnivore assemblage, influence their respective ecosystems (Mech 1996)?

Because extensive intraguild competition and agonism have emerged as general rules for carnivores (MacDonald and Thom 2001), when examining such questions, it is necessary to examine the broader carnivore guild rather than just a select one or two species.

To address these issues, I examined carnivore species patterns of distribution, habitat associations, and co-occurrence patterns at multiple spatial scales in the Ozarks of southern Missouri. I used affordable and efficient non-invasive sampling techniques (infrared remote cameras, track-plate boxes, and scat surveys) to allow for a region-wide survey effort. I combined my results from noninvasive sampling of carnivore distribution with landscape level information about habitat and other factors thought to drive carnivore distributions, and analyzed this information with a geographic information system (GIS) approach to assess habitat structure and predicted levels of species occupancy at multiple spatial scales. The results are powerful models that can become important management tools, aiding wildlife managers and conservation planners (Carroll et al. 1999; Soulé and Terborgh 1999; Zielinski et al. 2000).

At the community level, the primary goal of my study was to systematically survey the carnivore guild throughout the Ozarks of Missouri, focusing on dynamics and patterns of distribution. My project had three objectives: (1) to describe the presence/absence and distribution of the forest carnivore guild; (2) to quantify the habitat associations and intraguild patterns of co-occurrence of these species at a landscape scale; (3) to develop and test multi-scale predictive occupancy models for these species.

Within the confines of these broader guild level questions, I was especially interested in the ecology of the eastern spotted skunk (*Spilogale putorius*). In 1991, the subspecies *S. p. interrupta* or plains spotted skunk was listed as endangered in Missouri

following a precipitous downward trend in furbearer harvest numbers from a high of 55,000 in 1941 to one in 1990 (Sampson 1980; Gompper and Hackett 2005). This pattern is alarmingly evident throughout the Midwest distribution of the species (DeSanty-Combes 2003; Gompper and Hackett 2005). Little is known about the basic habitat ecology of this species or its present distribution throughout its range. To better understand this species of conservation concern, I assessed the distribution and habitat associations of this rare carnivore throughout the Ozarks. I also examined the distribution of the eastern spotted skunk in light of survey data on the distribution of striped skunks, as the later represents a potential intraguild competitor. My efforts were oriented not only towards identifying baseline information about the species distribution and habitat associations, but also gaining information that can be used to help design future studies that are geared towards asking more specific questions related to topics such as demographics, dispersal, and competitive interactions with other carnivores, as well as broader applied concerns such as habitat protection and reintroduction strategies.

Most other species of carnivores in the Ozarks are not necessarily of conservation concern. Indeed, several are widespread and abundant. However the landscape ecology of these species is not well understood, and the extent to which an understanding of intraguild dynamics might give insight into the landscape distributions of the community members is also unclear. To address this, I examined two mesopredator groups: (1) raccoon (*Procyon lotor*) and opossum (*Didelphis virginiana*), and (2) coyote (*Canis latrans*), bobcat (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*). In both cases, I attempted to create predictive models of landscape occupancy and to determine how the presence of one species might influence the models for the other(s).

The raccoon and opossum were the two most commonly detected species throughout my research, and due to their commonness occupancy modeling efforts failed to effectively characterize their distributions at a landscape level. As was the case with all other species models, model averaging had to be used because there was no single occupancy model that sufficiently predicted their distributions based on weight of evidence. Model averaging revealed that by incorporating knowledge of species A (e.g. raccoon) presence within the study area into the modeling process for species B (e.g. opossum) the predictive ability of the resulting model is improved. Nonetheless, given the generalist nature of both of these species and their commonness throughout a variety of Ozark environments, future modeling efforts would be more effective modeling occupancy based upon abundance instead of simple presence/absence.

Model averaging also had to be used for the coyote, bobcat and gray fox. The probability of actual occupancy for coyotes was best predicted by measures of human disturbance and prey distribution. Bobcats were primarily influenced by coyote presence and prey availability. Gray foxes were the most heterogeneous in their regional predicted distribution, and were best predicted by measures of coyote and bobcat presence and landscape elements related to humans and settled areas. These results suggest that coyotes produce a structuring dynamic on these other two forest mesocarnivores in the Ozarks, and this structuring may trickle down to other mesocarnivores as well as the other levels within the trophic web.

My findings indicated that cameras and track-plates, as well as scat transects for coyotes, all have value for community-wide surveys but that no single technique allows collection of sufficient data on all members of the carnivore guild in Missouri. Cameras

detected the most species but are biased in favor of the large bodied species such as the raccoon and against smaller species such as the long-tailed weasel (*Mustela frenata*) and species that may be especially wary of survey apparatus such as the coyote. Track-plates are only suitable for small and medium-sized species, and may also be biased against warier species. Scat transects are the most reliable method for detecting the presence of coyotes. The differences in technique efficacy suggest that future ecological research that derives from data generated using these techniques can be drastically improved by understanding the limitations of these techniques and quantitatively incorporating these limitations into any subsequent modeling or management protocol. Such an approach should help researchers tailor their survey design to their target species in other parts of the Midwestern United States as well as other regions of the globe.

The use of noninvasive surveys has rapidly increased in recent years, making it easier to obtain larger sample sizes for carnivore research, but along with an increased ease of implementing this type of research comes the necessity to pay close attention to the limitations and nuances of each technique as future research projects incorporating these methods are designed. Whenever possible, I recommend that researchers incorporate more than one technique, that these techniques be run consecutively and not concurrently since biases related to the order of method implementation and pre-baiting or habituation effects can be dealt with by including detection covariates in occupancy modeling. Further, whenever possible, data researchers should incorporate occupancy data for other guild members as site covariates in predictive occupancy modeling to assess indirect effects that may be present but are not captured in the environmental variables modeled for each species. The incorporation of other guild members in the

modeling process can lead to interesting theoretical questions about carnivore community dynamics, and should be a first step when the goal is to understand these dynamics at a landscape scale across the overall community of carnivore species.

The management and ecological implications of my study will not be fully realized until further work is undertaken on the community of carnivores in forest habitats in Missouri. My results suggest that the coyote is an apex predator that can have important negative influences on the distribution of gray fox and bobcat. The indirect effect on the lower levels of the trophic web remains unclear. My results also find evidence of a seemingly disjunct distribution of the endangered eastern spotted skunk in the Ozarks, but whether or not these populations are robust and stable, or even increasing, or still declining is also an area that future research should examine closely. The raccoon and Virginia opossum are the most common mid-sized mesopredators in forested habitat in southern Missouri. My occupancy models for both of these species failed to effectively parse the landscape variables I used in analyses, suggesting that these two species are so common and so generalist in nature that it will be a challenge for future research to identify and effectively model landscape scale variables for them in the Ozark region. It is more likely that these two species can be modeled better at a microhabitat scale and with use of abundance data instead of simple presence data for added species distribution resolution. Perhaps a more robust examination of how their spatial distributions are affected by the other members of the carnivore guild in the region will help elucidate more clearly what drives their occupancy of certain areas.

An interesting facet of this work was the observation that incorporation of the presence data for other members of the carnivore community often improved the fit of the

occupancy models for a particular species over the fit derived from habitat variables alone. The distributions of eastern spotted and striped skunks (*Mephitis mephitis*), opossum and raccoon, and the triumvirate of coyote, bobcat and gray fox were all better understood when examined together rather than in the context of habitat alone. If the incorporation of distribution information on another carnivore guild member species is selected in the process of creating predictive occupancy models, as is the case with my results, then at a minimum there is some indirect relationship via habitat selection that should be explored in the future in more detail. It is also possible that there is direct interaction, such as competition, and there are procedures within the modeling framework that can be used to examine these more specific scenarios utilizing detection history data such as that collected from my study.

My study found that knowledge of patterns of species co-occurrence can improve the fit of carnivore landscape models, a clear indication that sufficient knowledge of the selection pressures that shape the life-history strategies of carnivore species (e. g. Gittleman 1994) and the development of conservation strategies for carnivores go hand in hand (Ferguson and Lariviere 2002). If future research can connect life-history variation for these members of the carnivore guild to landscape-scale patterns of environmental predictability and community processes (e. g. competition), critical insights into species specific conservation strategies could be provided, and a broader understanding of the carnivore community as a whole would be gained.

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CHAPTER 2

COMPARISON OF NON-INVASIVE TECHNIQUES TO DETECT FOREST CARNIVORES IN THE MISSOURI OZARKS

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Abstract

The study of carnivores as a community across entire landscapes is challenging because these species require large areas, are secretive, and occur at low densities. Recent advancements in non-invasive methods and approaches to data analysis have begun to make the study of the carnivore community across entire landscapes feasible and affordable. To better understand the value and limitations of non-invasive techniques, I assessed several metrics commonly associated with these types of noninvasive surveys using data collected in 2005-2006 while surveying 53 forested sites in southern Missouri to assess the distribution and habitat associations of forest carnivores. I used infrared remote cameras and covered track-plates to assess carnivore community composition, and compare technique effectiveness across the species. I estimated the latency to detection (LTD) and the probabilities of detection (POD) given presence for each species, compared these metrics across detection devices, and I evaluated the effects of altering the order of implementation of the method on detectability. I also performed scat transects at 40 of these same sites to validate the value of remote camera information for discerning the presence of coyotes (*Canis latrans*). Cameras and track-plates were both capable of detecting Eastern spotted skunk (*Spilogale putorius*), striped skunk

(*Mephitis mephitis*), raccoon (*Procyon lotor*) and opossum (*Didelphis virginiana*), but at differing levels of effectiveness. Coyote, bobcat (*Lynx rufus*) and gray fox (*Urocyon cinereoargenteus*) were only effectively documented with remote cameras. Black bear (*Ursus americanus*), long-tailed weasel (*Mustela frenata*) and red fox (*Vulpes vulpes*) were rarely detected. Daily detection rates by cameras ranged from 0.003 (bobcat) to 0.05 (opossum), and rates by track-plates ranged from 0.09 (striped skunk) to 0.29 (opossum). Cameras performed poorly at capturing images of coyotes where their presence was known from scat transects, but cameras also obtained photographic evidence of coyote presence at 63% (5/8) sites where no coyote scat was collected. Thus, combining methods yielded a more accurate picture of the community composition, but overall low daily detection rates for most species and for both methods reveals that it is necessary to tailor the survey methodology to target species, and to run these types of surveys over an extended period. In most instances the detection rates for carnivores increased over the survey period, indicating that whichever method was first implemented likely habituated individuals and facilitated later detection. Regardless of which method was used in the first 2 weeks of sampling, across virtually all species there was a reduction in LTD by one day between weeks 1-2 versus 3-4 due to the habituation effect. This can have important implications for survey design and appropriate data analyses.

Introduction

The study of carnivore ecology often focuses on the distribution of species and their habitat associations, but usually lacks a multi-species, multi-scale approach from which generalized conclusions can be drawn. While the need for large-scale and multi-species studies has been noted, numerous logistic problems arise when researchers contemplate how such multi-scale studies can be implemented using traditional survey methods that require capture or direct observation of the animal (Zielinski and Kucera 1995). Such studies are potentially costly and in some cases may simply be infeasible given local regulations and norms. Yet, if carnivore habitat use studies are to achieve their desired objectives, they must be implemented at a scale that allows for inferences to be made at more than one set of ecological conditions. Such scale specific studies must also rely on methods that are effective and efficient, ensuring that sample sizes and survey efforts are sufficient to meet project goals (Gerrodette 1987; Cohen 1988).

The increasing sophistication of non-invasive survey methods such as infrared remote cameras and covered track-plates may provide researchers with tools to implement multi-scale, community level studies of carnivore ecology despite a limited budget and personnel (Zielinski and Kucera 1995; Gompper et al. 2006). However, where the value of these techniques has been assessed, results suggest that the efficacy of detection is intrinsically linked to species behavior and detection method (Gompper et al. 2006). Thus, a key characteristic that must be considered in the design phase of studies that use non-invasive methods is whether the methods ensure repeatable detection of the target species when present. If a goal is the surveying of multiple species across a landscape, and then using this information to draw inferences about species-level patterns of distribution and habitat

associations and community-level interactions of species, then the non-invasive methods used should have a high probability of detecting all species present at a given sampling area. If no single technique works for all target species in the community, the use of multiple methods is warranted, and this seems particularly true when surveying for forest carnivores (Sauer and Droege 1990; Reed and Blaustein 1995; Thomas and Martin 1996; Nichols et al. 1998; Mackenzie et al. 2002; Gompper et al. 2006).

I examined the distribution patterns, habitat associations, and implied patterns of species interactions for the forest carnivore community throughout the Missouri Ozarks by surveying across the landscape with noninvasive techniques. Here I summarize the general characteristics of the detection data provided by track-plates, infrared remote cameras, and scat transects (coyote only). I examined the effects of the relative timing of implementation of a particular method during a multi-technique survey on the probability of detection (POD) and latency to detection (LTD) of multiple species. Finally, I quantify species-specific estimates of survey effort required to detect the presence of a species as a function of method and the *a priori* desired POD.

Probability of detection is the probability of detecting at least one individual of a given species in a particular sampling effort, given that individuals of that species are present in the area of interest during the survey (Boulinier et al. 1998). Latency to detection is defined as the number of days it takes for a species to be detected. Latency to detection is distinct from POD, in that it allows for the assessment of precisely how effective a specific survey method is at detecting the targeted species (Foresman and Pearson 1998; Moruzzi et al. 2002). In theory, by comparing LTD for the same species at different survey sites,

populations at higher densities should be detected sooner due to higher encounter rates with sampling stations (Gompper et al. 2006).

In non-invasive surveys, if a species goes undetected it is due to 2 possibilities: either that species was absent (true absence) in the survey site during the time sampling occurred, or the method failed to detect the species (false absence) even though it was present when sampling occurred. False absences are problematic for predictive modeling efforts, because they skew attempts towards under representing the area where a species is likely to occur (Tyre et al. 2003). Therefore, likelihood of false absences must be taken into consideration when a method's detection efficiency is evaluated (Mackenzie et al. 2002). Because of this, and because sampling for rare or cryptic species such as carnivores can be challenging, it is important to identify methods that efficiently and reliably detect the carnivore species of interest with minimal likelihood of false absence. By combining multiple methods as done with this work, one may be able to minimize the potential pitfalls associated with technique-specific deficiencies, as although one method may work poorly on particular species, another method suitably detects them when present, and thus the potential exists for a substantially higher POD for all species of a community.

Methods

Throughout this chapter, the term “technique” refers to the type of sampling method employed (e.g. enclosed track plate, remote camera, scat transect) and is distinct from “design” which is how the methods are employed (e.g. 9 enclosed track-plates visited every 2-3 days for 14 days). “Sample unit design” is used to refer to the combination of methods used at a survey site.

Study Area and Survey Sites

My study area included a large portion of forested regions of southern Missouri, commonly referred to as the Missouri Ozarks (Figure 1). The dominant forest vegetation in the study areas was primarily oak (*Quercus* spp.) and hickory (*Carya* spp.) species. Coniferous trees, primarily short-leaf pine (*Pinus echinata*), were intermixed over the broader study area.

The selection of potential survey sites began with an initial identification of a pool of forested areas of sufficient size to carry out linear transect surveys equivalent to 5 km in length. This initial group of sites was defined by the presence of large tracts ($> 15 \text{ km}^2$) of forest cover, a proximity to reliable sightings of Eastern spotted skunks (cross-referenced to a database of species sighting information from Missouri Department of Conservation, MDC; Desanty-Combes 2003) and the goal of having sites in most counties in the Ozarks Region. The eastern spotted skunk was a key component of the study site selection process because it is a species of conservation concern. The Eastern spotted skunk has experienced a precipitous decline throughout its geographic range in the last 50-60 years, is currently listed as endangered (S1) in the state of Missouri, and is an important conservation priority for MDC (Gompper and Hackett 2005; Hackett et al. 2007). With this database as a starting point, sites were selected based on the presence of accessible forested tracts and the need to survey across the entire study area while maintaining a minimum inter-site dispersal distance of 5 km. Time and financial constraints eventually yielded the 53 survey sites. These sites were located in a variety of forested habitats, and across broad gradients of human disturbance, forest fragmentation, elevation, and topographic complexity (Figure 1).

Field Data Collection

Carnivore occurrence was recorded using track-plates and infrared remote cameras from February to May 2005 and August 2005 to May 2006. The results of a validation study for eastern spotted skunks using this same methodology in eastern Missouri indicated that it was ineffective to implement these surveys during the months of mid-May to August (Hackett et al. 2007). Nine species of carnivores and one marsupial mesopredator were predicted to occur within the study area (Table 1) based upon the known species occurring in Missouri and their associated ecology. Survey stations (n=9) were established in a 3 x 3 grid with a spacing of ~250 m between stations, and a minimum distance of 5 km between survey sites. This spacing was chosen to maximize the likelihood of detecting the smallest species (eastern spotted skunk) when present, while also maintaining spatial independence for this species between sites based upon its average home range size discerned from the existing literature.

At each survey station a camera (DeerCam Model Nontypical matched with 400 speed film) was placed 0.5-1.0 m above the ground on the bole of a tree, and pointed at an opposing tree upon which a partially opened can of sardines was nailed 0.25-1.0 m above the ground. Distance between the camera and the bait tree was 2-4 meters. In instances where there were not two suitable trees I used a downed tree or log. Once a camera station was set and activated, it was revisited on day 7-8 to replace film and batteries (if necessary), re-bait, and re-align the camera if necessary. Camera stations ran 14-15 days.

Track-plates comprised a 24 x 100 cm aluminum plate, one half of one side of which was coated with carbon toner to act as a tracking medium, while the other half was covered with adhesive contact paper (sticky side exposed). This plate was placed inside an enclosure

of corrugated plastic sign material. Because the track plate enclosure box was open on both ends, it would have the end with the bait and adhesive paper backed against the bole of a tree or other object of suitable size so as to prevent animals from accessing the sardine bait from the box without entering it from the front. Animals attempting to obtain the bait would walk over the tracking medium and onto the adhesive paper, leaving a track set behind. Track plates were checked every 2-3 days.

Coyotes defecate regularly on trails and unpaved roads, and measures of coyote scat abundance can be used to assess the presence and relative abundance of coyote populations (Knowlton 1984; Stoddart et al. 2001; Gompper et al. 2006; Kays et al. 2008). Scat surveys were performed along dirt roads that bisected survey sites to gain an index of presence for coyote. To minimize the confusion of scat identification, since there can be overlap between large fox scat and small coyote scat, only scats measuring >21 mm in diameter were recorded as being from coyote. On day 1 all scats were cleared from each transect to be surveyed. Scats were thereafter collected and their location recorded with GPS along all transects on days 15, 30, and 45, and quantified as scat/km/day. All coyote scat transects were ≥ 5 km in length.

Data Analysis

General characteristics of survey methods were evaluated using seven metrics: species richness, LTD, and POD. Species richness for each method was: 1) the total number of species detected by each method; 2) the mean number of species detected at a sample unit by each method; 3) the proportion of species detections accounted for by each device type; and 4) the number of times a species detection by a device represented the only detection of

that species at a sample unit (i.e. unique detection). Since the detection of species at survey sites drives the description of its distribution, examining the number of unique detections by method provides an indication of the relative contribution of each method to the depiction of that distribution. Differences among the number of species detected by a method at a sample unit were evaluated using Chi-square test with a Yates continuity correction (SAS 2005).

For most purposes, only a single detection of a species is required to document presence. In fact, it may be advantageous to cease sampling at a location once a detection is recorded, allowing investigators to move to new sampling locations. Consequently, a more efficient method will be one that detects a species earlier (lower LTD), especially if some species are wary of the detection apparatus (Gompper et al. 2006). To this end, mean LTD at a sample unit for each species were compared by survey method (Kruskal-Wallis test, SAS 2005). The raw LTD values were converted to per day LTD value by subtracting 1.5 from the result for direct comparisons to camera detection data, because track-plates were checked every 2-3 days and not everyday.

Program Presence (Mackenzie et al. 2002) was used to calculate POD given that a species was present. Program Presence uses repeated visits to a survey site to provide a detection history. This method assumes that the occupancy status of the sample location does not change during the survey period and that species detections are independent. Maximum likelihood estimation is used to estimate the probability that a species is detected at least once when it is present (Mackenzie et al 2002). Probabilities of detection by each method were estimated for each species. The estimated probabilities provided by Presence represent the mean POD for a species by that method at each site (n = 53). Estimates of detection probability were carried out at the site level, based upon assumed independence of

sites. Track-plate POD (initially over 3 days) was converted into daily probability, comparable with camera POD. I converted the survey length POD ($p_{\text{total survey}}$) into a per-check probability (p_{check}) using Gompper et al's (2006) modification of Campbell's (2004) equation such that $p_{\text{check}}=1-(1-p_{\text{total survey}})^n$, where n is the conversion metric (1/number of survey intervals). I used the same formula to extrapolate POD for 14-day survey periods for cameras and track-plates.

Results

Neither track-plates nor cameras detected all 10 target species occurring throughout the study region (Table 1). Track-plates did not detect coyote and black bear, and rarely detected bobcat, long-tailed weasel, and gray fox. Cameras did not detect long-tailed weasel and rarely detected black bear and red fox. Remote cameras and track-plates have been used to effectively survey for black bear, weasel and red fox in other parts of their range. I presumed, given the habitat type and the techniques used, that a lack of detections for red fox, black bear and weasel reflects their relative scarcity in the survey areas. The mean number of species detected at a sample unit by track-plates versus cameras was significantly different ($p < 0.01$); cameras averaged 2.46 species per site versus 1.9 species for track-plates, and combining the two techniques yields an average of 3 species.

Cameras accounted for 75.5% of unique species detections (71/94) and were more effective for detecting presence of the larger species, including coyote (100% of unique detections), bobcat (92.9%), gray fox (92.9%), and raccoon (92.3%) (Table 1). Raccoon and opossum were the most commonly detected species with cameras, together accounting for 80.8% of detection events ($n=906$ total occurrences), while bobcat were the least detected

species accounting for 1.3% (n= 15 total occurrences) of detections (Table 1). Cameras detected 9 of 10 members of the target community (Table 2). The percent of sites at which individual species were detected by camera varied from 92.5% (raccoons) to 1.9% (red fox and black bear). At sites where a species was documented by track-plates, cameras failed to detect raccoons 3.0% of the time, opossum 25.0%, spotted skunk 41.7%, gray fox 50%, and striped skunk 63.6% (Table 2).

Track-plates accounted for 24.5% of unique species detections (23/94) and were most effective for detecting presence of the smaller species, including striped skunk (66.7%), spotted skunk (62.5%), and opossum (61.5%) (Table 1). Opossum were the most commonly detected species with track-plates (n=316 occurrences) followed by raccoon (n=150), striped skunk (n=32), spotted skunk (n=30) and gray fox (n=2). As expected based on the size of the species, track plates did not detect coyote or black bear, but did detect the 8 other target species. Overall, track-plates detected species at 75.5% (opossum; 40/53) to 1.9% (long-tailed weasel; 1/53) of sites (Table 2). At sites where species presence was documented by cameras, track-plates failed to detect opossum 11.8% of the time, spotted skunk 30.0%, raccoon 34.7%, striped skunk 60.0%, and gray fox 92.9% (Table 2).

At study sites where a species was detected at least once by either cameras or track-plates, LTD at a sample station for species ranged from mean = 10 days for raccoon to 18 days for coyote when survey methods were combined (Figure 2a). Only raccoon and opossum exhibited significant differences among methods in mean LTD (Figure 2b). Across species, mean LTD declined when a technique was used following a period of habituation with another technique for cameras, and was 6.7 days when cameras were installed during the first 14 day sampling period, 5.9 days during second 14 day period, and 6.3 days overall

(Figure 2c). Cameras were more effective in detecting gray fox ($p=0.05$) in weeks 3-4, raccoons ($p=0.03$) in weeks 1-2, and marginally more effective for detecting striped skunk ($p=0.08$) in weeks 3-4 (Figure 2c). Mean LTD for track-plates (corrected for survey check interval) across species was 7.2 days during weeks 1-2, 6.1 days during weeks 3-4 and 8.0 days overall (Figure 2c). Track-plates were significantly better at detecting striped skunk ($p=0.0001$) in weeks 3-4.

Both cameras and track-plates exhibited lower LTD across all species for both cameras (6.70 v. 5.92) and track-plates (7.17 v. 6.14) when that technique was run in the second half of the survey period. Both raccoon and opossum were detected sooner at stations, regardless of technique, in weeks 1-2. All of these values for LTD are uncorrected for survey period (i.e. if an animal was detected on day 1 of the week 3-4 survey period then it's corrected LTD would be 14 days + 1 day effectively making it 15 days).

Based on the frequency of repeat detections, some species were less likely than others to return to a given station or the overall survey site following an initial detection event. At sites with at least one detection, raccoon were detected a second time at 92% of sites, opossum at 89% of sites, spotted skunks at 79% of sites, gray fox at 53% of sites, striped skunks at 50% of sites, coyote at 45% of sites, and bobcat at 8% of sites. Some species were more likely to visit the same station at the same site on consecutive days, with striped skunks the most likely at 50%, spotted skunks at 47%, raccoon at 40%, opossum at 41%, gray fox 31%, coyote at 11%, and bobcat at 0%.

The combination of techniques resulted in a species richness value for a site greater than either technique represented alone for that site 38% (20/53) of the time. Overall, POD for either method for a species ranged from 0.02 (bobcat) to 0.74 (opossum) (Figure 3). Daily

POD for cameras ranged from 0.003 (bobcat) to 0.05 (opossum), and for track-plates ranged from 0.09 (striped skunk) to 0.29 (opossum) (Figure 3). As the number of survey days increased, POD for most species achieved reasonable levels by day 14 for track-plates but not for cameras (Figure 4). Even a doubling of the camera trapping period would fail to achieve a POD of 0.75; to reach this level would require a significant increase in the number of survey stations or number of survey days.

The effectiveness of cameras at detecting coyote when present were compared to scat transects for 40 survey sites. Coyote scat was detected at 80% (32/40) of transects, and of those a coyote was also photographed 46.9% (15/32) of the time. Number of scat/km/day ranged from 0 to 2.07 (Figure 5). There was no significant difference between sites with and without photographs and sites with and without scat found for coyote (Yates's Corrected Chi-square = 1.50, $p = 0.22$). Of sites where scat was collected and a photograph taken ($n=10$), a significant relationship was observed between scat/km/day value and LTD ($r^2 = 0.70$, $p = 0.001$; Figure 6). Results of analyses examining the relationships of POD versus scat/km/day, LTD versus scat/km/day, and POD versus LTD for all scat transect sites ($n = 40$) resulted in the identification of no significant relationships.

Discussion

Neither track-plates nor infrared remote cameras recorded detections of all 10 species documented in my surveys. Track-plates were more effective for smaller species, while cameras were more effective for larger species. For black bear and long-tailed weasel the low number of detections overall (≤ 2) regardless of survey method indicates their probable scarcity in the study area, as these species are generally identified using non-invasive

techniques when present (Gompper et al. 2006). For most carnivore species however, a survey length of 28 days was sufficient to record presence. While detectable differences for cameras and track-plates for specific carnivore species exist, overall these results were similar to those of other recent surveys for forest carnivores (Campbell 2004; Gompper et al. 2006; Long 2006).

The use of multiple techniques in tandem resulted in an increased species richness estimate at 24.5% (13/53) of the survey sites compared to species richness estimates for each survey technique individually. Mean number of species detected by cameras was higher than for track-plates even excluding detection data for coyote, bobcat, and black bear. This result speaks to the broad applicability of infrared remote cameras, whereas track-plates are more suited for smaller bodied species. Thus, variation in detectability among species and by method (Bull et al. 1992; Foresman and Pearson 1998; Mackenzie et al. 2002; Hackett et al. 2007) must always be taken into consideration when analyzing data derived from these sorts of large-scale non-invasive studies.

Overall, LTD values for the combined data from cameras and track-plates indicate performance similar to the results found in other studies implementing these techniques (Zielinski et al. 2005; Long 2006). Specifically, it appears to take 10-14 days on average for the most common carnivores such as raccoon and opossum to show-up at survey stations, and as long as 3-4 weeks for the more elusive species such as coyote and bobcat. Combined average LTD values ranged from mean = 10 days for raccoon to 18 days for coyote. These results are dependent upon the order of each technique's implementation. Mean LTD was almost a full day shorter across species when examining the LTD values for weeks 3-4

versus 1-2. This is due to the habituation to the survey apparatus that likely occurs in weeks 1-2.

Variation in detectability among species and by method (Bull et al. 1992; Foresman and Pearson 1998; Mackenzie et al. 2002; Hackett et al. 2007) must always be taken into consideration when designing these types of non-invasive studies. Overall POD was similar to those values observed by other studies using these same techniques (Zielinski et al. 2005; Long 2006). My survey efforts resulted in POD estimates ranging from 0.02 for bobcat to 0.74 for opossum. Daily POD was lower on average for cameras than track-plates for species that were detectable by both methods. As the number of survey days increased, the POD for most species achieved reasonable levels (0.75) by the end of the 2 week survey period for track-plates, but not for cameras. This difference between the two sampling techniques is further magnified by the fact that body size and or behavioral characteristics of some carnivores like the coyote preclude them from being sampled by track-plates. This result indicates that if a study used solely cameras as a detection device the survey period would have to be extended or the number of detection devices greatly increased. For the rarer or more secretive carnivores such as bobcat and coyote, the threshold to achieve POD values of 0.75 far exceeded the 28-day sample period implemented here.

Coyote are cautious and wary around camera traps (Séquin et al. 2003; Gompper et al. 2006), and in general are slow to approach these types of survey apparatus even when the species are common throughout the study area. In this study, at only 1 of 13 sites where bobcats were detected was the species detected repeatedly. Thus bobcats may be similarly wary around survey methods. For coyotes, the use of scat collection and identification to document the presence was more reliable than infrared remote cameras. Coyote may be

wary of camera setups because of their association of the new object in their habitat with the presence of humans, and it can be weeks before coyote will approach a camera even though coyote may be abundant in the study area (Harris and Knowlton 2001; Séquin et al. 2003). It is highly likely that the combination of wariness to human elements in the landscape, in this case the camera stations, and the propensity to simply utilize road features to move around a home range (Gompper 2002; Séquin et al. 2003; Arjo and Pletscher 2004) results in a low likelihood of coyotes being detected with camera stations.

Track-plates and cameras had similar LTD for species that were detectable by both methods, and track-plates had higher POD than cameras. One of the key drawbacks to track-plates, however, is that they are capable of sampling from a reduced species pool, as large bodied carnivores are not adequately surveyed with track-plates. This is a negative factor that must be heavily weighed if a study goal is to document the presence and composition of the entire carnivore community. Nonetheless, track-plates are suitable for sampling smaller species, and the cost of a track-plate apparatus is approximately 1/10th that of an infrared remote camera. The relatively high POD values of track-plates for small carnivores also implies that they are particularly valuable for surveys with durations of only 1-2 weeks, allowing a greater number of sites to be surveyed.

Management implications

My findings show that noninvasive techniques such as track-plates and infrared remote cameras are appropriate for surveys of carnivores in forested regions in Missouri. The ability to use these techniques in tandem as part of a comprehensive carnivore community study can offer managers and biologists an important tool for quickly,

inexpensively, and effectively censusing species assemblages. Cameras detected the greatest number of species overall, but their lower efficiency at reliably detecting the smallest species necessitates the simultaneous use of track-plates, which while not suited for the larger species, are ideal for surveying smaller bodied species like foxes. Scat transects provide a necessary and inexpensive means for detecting coyote presence. The use of noninvasive techniques is gaining favor throughout North America, and it is important that future research efforts maintain the use of multiple techniques to provide a series of checks and balances on the efficiency of the survey design.

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Table 1. Summary statistics for track-plates and cameras used in carnivore surveys in Missouri 2005-2006. Each of 53 survey sites was composed of 9 enclosed track-plates and 9 infrared remote cameras run in consecutive 14-day survey periods.

¹ Number of sites in which detections of a species by this method represent the only occurrences of that species at a sample unit.

Common name	Species	camera occurrences	track-plate occurrences	N _{uniques} – cameras ¹	N _{uniques} – trackplates ¹
eastern spotted skunk	<i>Spilogale putorius</i>	32	30	3	5
striped skunk	<i>Mephitis mephitis</i>	49	32	4	8
coyote	<i>Canis latrans</i>	51	na	21	na
bobcat	<i>Lynx rufus</i>	15	na	13	1
gray fox	<i>Urocyon cinereoargenteus</i>	66	2	13	1
raccoon	<i>Procyon lotor</i>	518	150	12	1
opossum	<i>Didelphis virginiana</i>	388	316	5	8
black bear	<i>Ursus americanus</i>	4	na	2	na
red fox	<i>Vulpes vulpes</i>	2	1	2	1
long-tailed weasel	<i>Mustela frenata</i>	na	1	na	1
	Total	1127	532	75	25

Table 2. Percent of survey sites (n = 53) at which each species was detected by any technique (n=8586 checking intervals), by cameras (n=6678 survey nights), and by track-plates (n=1908 checking intervals) during 2005-2006. The columns showing the species missed by a technique are the percentage of sites where a species was detected with one technique but not the other.

species	detected	detected	detected	missed	missed
	overall	cameras	track-plates	cameras	track-plates
coyote	na	41.5	na	na	na
opossum	83.0	64.2	75.5	25.0	11.8
bobcat	24.5	24.5	1.9	0.0	92.3
eastern spotted skunk	28.3	18.9	22.6	41.7	30.0
striped skunk	32.1	18.9	20.8	63.6	60.0
long-tailed weasel	1.9	0	1.9	100	0
raccoon	94.3	92.5	62.3	3.0	34.7
black bear	na	1.9	na	na	na
gray fox	28.3	26.4	3.8	50.0	92.9
red fox	1.9	1.9	0	0	100

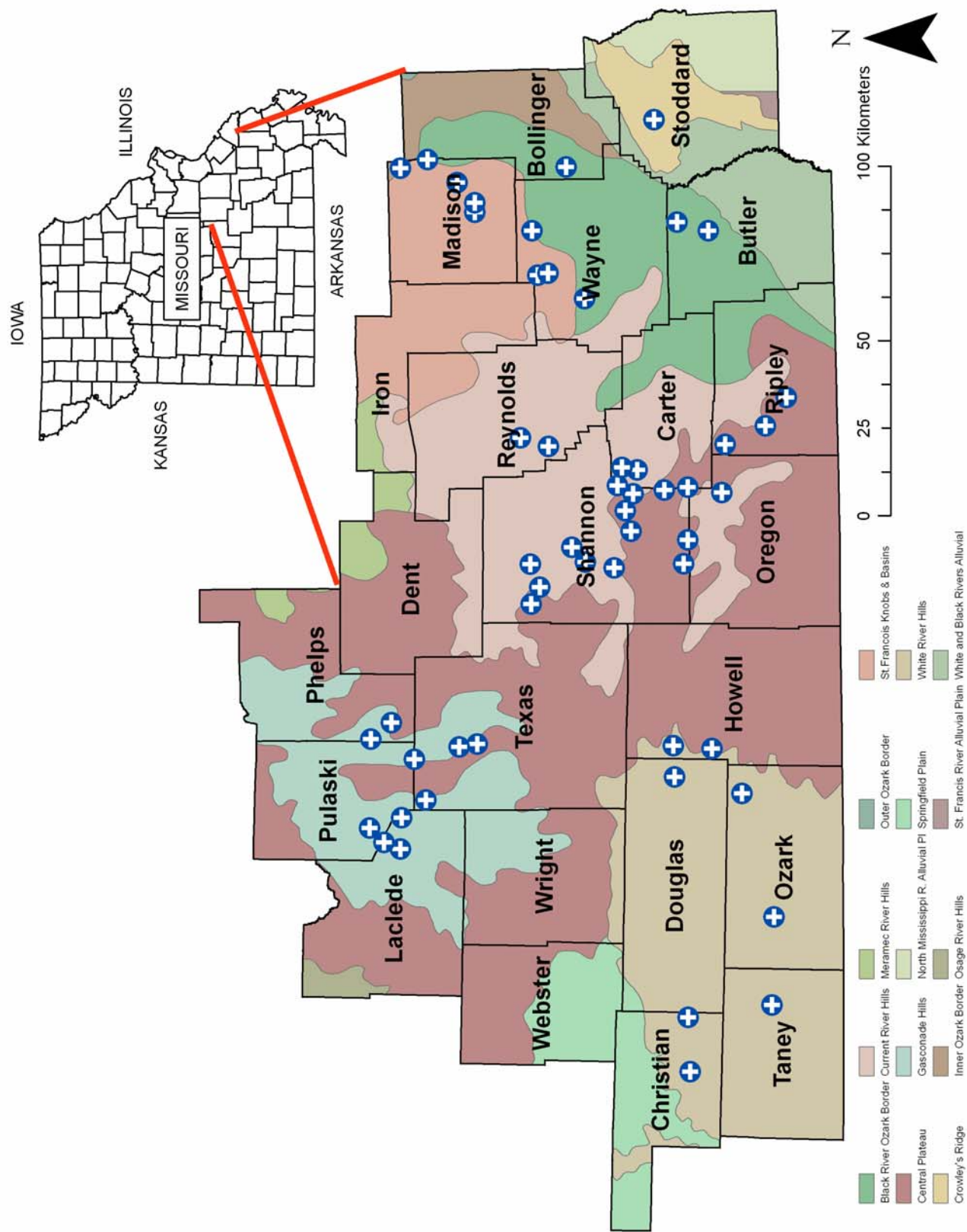


Figure 1. Map of survey sites (n = 53) and corresponding ecological subsections in southern Missouri.

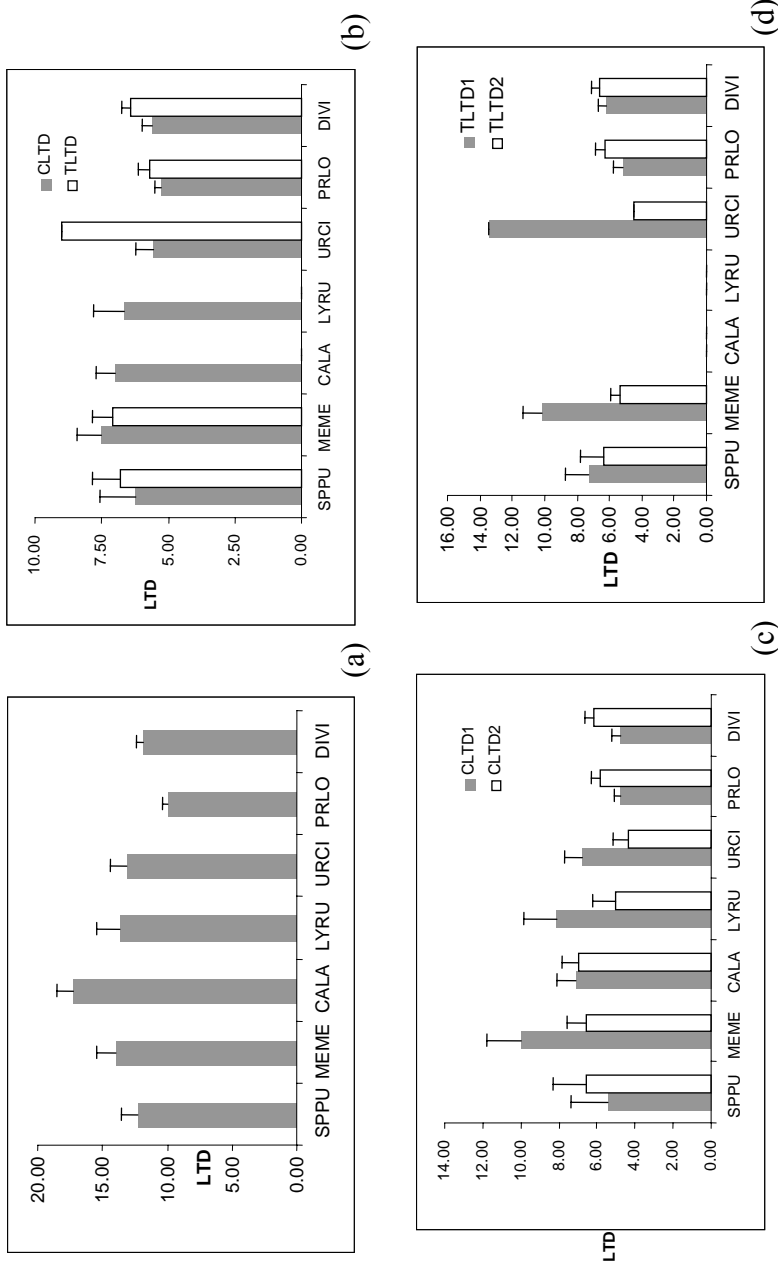


Figure 2. Mean (\pm SE) latency to first detection (LTD) in survey nights for (a) infrared remote cameras and track-plates combined, (b) overall infrared remote cameras and track-plates, not taking into account the order of implementation (c) LTD of cameras implemented in weeks 1-2 (CLTD1) versus weeks 3-4 (CLTD2), and (d) LTD of track-plates implemented in weeks 1-2 (TLTD1) versus weeks 3-4 (TLTD2). Data missing error bars (b and d) result from only one data point used to create value. Species abbreviations: SPPU – eastern spotted skunk, MEME – striped skunk, CALA – coyote, LYRU – bobcat, URCI – gray fox, PRLO – raccoon, DIVI – Virginia opossum.

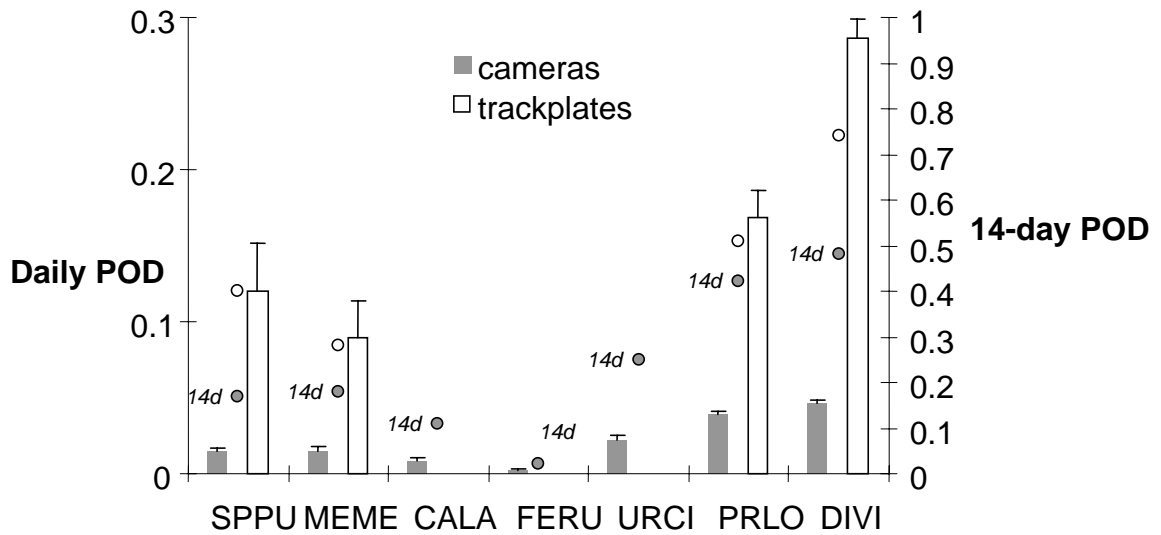
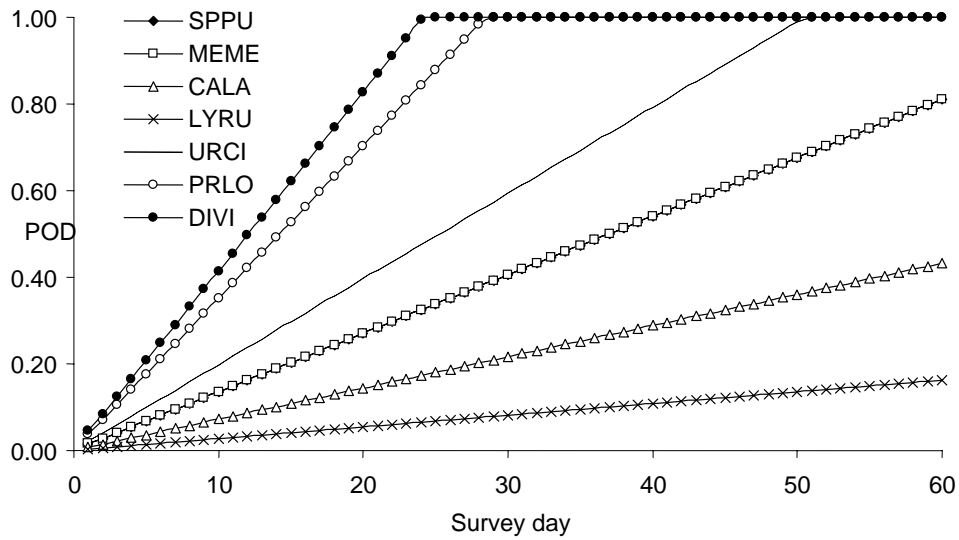
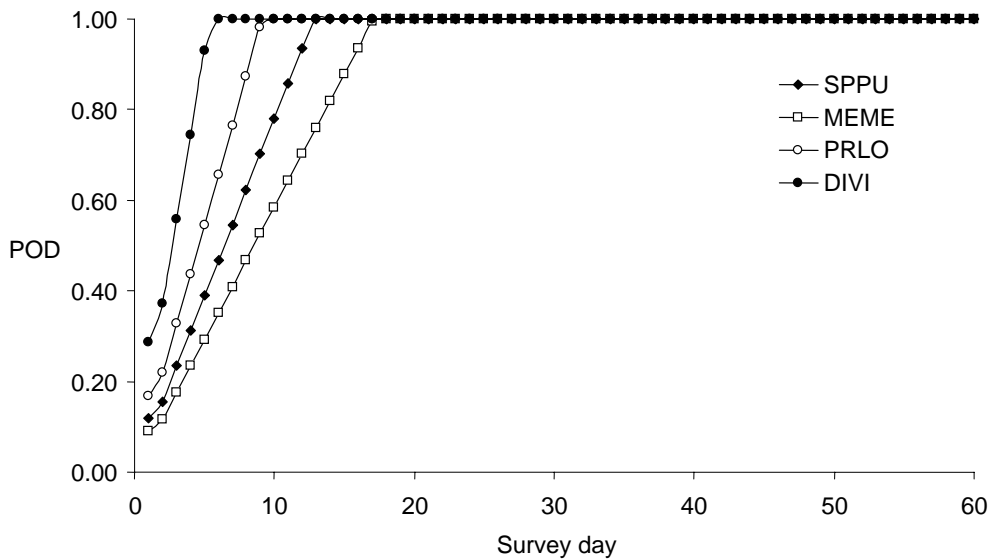


Figure 3. Probability of detection (POD) for eastern spotted skunk (SPPU), striped skunk (MEME), coyote (CALA), bobcat (LYRU), gray fox (URCI), raccoon (PRLO) and Virginia opossum (DIVI). Bars are mean daily POD (\pm SE) and dots are and 14-day estimates.



(a)



(b)

Figure 4. Relationship of probability of detection (POD) and survey effort in Missouri for eastern spotted skunk (SPPU), striped skunk (MEME), coyote (CALA), bobcat (LYRU), gray fox (URCI), raccoon (PRLO) and Virginia opossum (DIVI). (a) infrared remote cameras (note-the eastern spotted and striped skunk data points overlay one another and therefore only one set shows in figure) and (b) track-plates

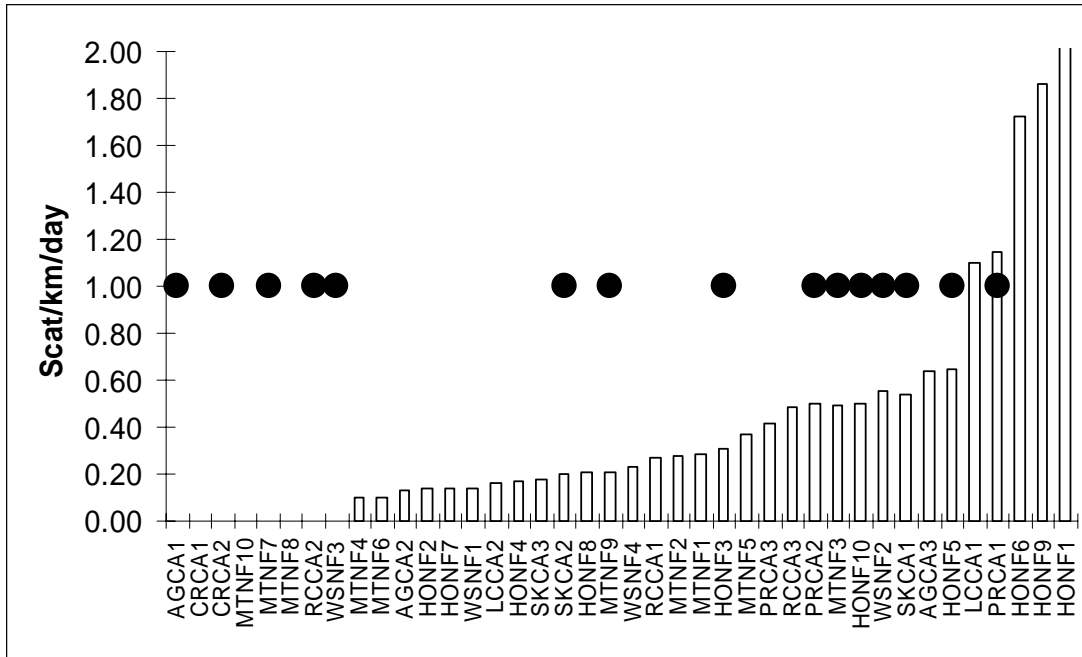


Figure 5. The number of coyote scats per kilometer transect surveyed per survey day for n=40 sites in Missouri. Black dots represent sites where cameras detected coyote.

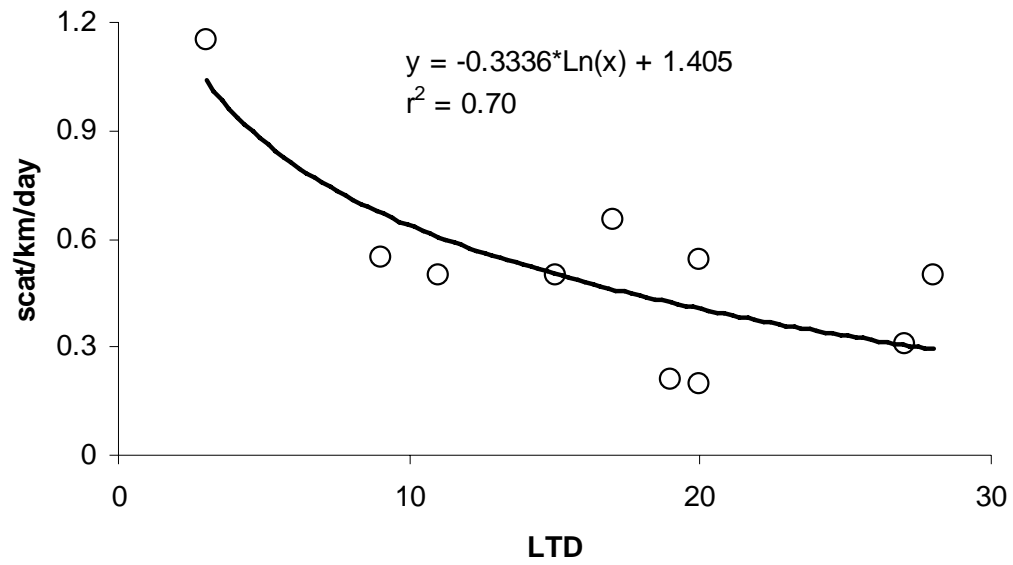


Figure 6. Relationship of coyote scat/km/day and latency to first detection (LTD; m) of sites where coyote scat was observed and where cameras detected coyote presence (n = 10 sites).

CHAPTER 3

THE DISTRIBUTION OF EASTERN SPOTTED AND STRIPED SKUNKS IN THE MISSOURI OZARKS AS A FUNCTION OF HABITAT AND GUILD MEMBER CO-OCCURRENCE

Harvey Mundy Hackett IV and Matthew E. Gompper

Abstract

Accurately predicting the distribution of forest carnivore species in an increasingly fragmented landscape requires understanding both habitat associations and intraguild interactions. I used noninvasive techniques to survey for eastern spotted skunk (*Spilogale putorius*) and striped skunk (*Mephitis mephitis*) in the Ozarks region of southern Missouri from 2005-2006. The eastern spotted skunk is listed as an endangered species in the state of Missouri, and relatively little is known about its habitat preferences and its relationship to the larger striped skunk. I analyzed habitat associations and patterns of occurrence for both skunk species using data collected from 53 sites, and created models of predicted detection rates and occupancy. The global detection model, the most parsimonious using AIC_c, predicted actual occupancy (Ψ) of 41% for eastern spotted skunk and 47% for striped skunk. Neither species had a single model for occupancy that had a high weight of evidence ($w_i > 0.90$), and therefore model averaging was used. Both species model sets were comprised of covariates measured at multiple

spatial scales. The variables indicated as being the best predictors for high occupancy by eastern spotted skunk were those related to proportion of an area covered by forest habitat. Conversely, the best striped skunk occupancy model related to human presence on the landscape, characterized by a positive relationship to distance to nearest road and an inverse relationship with percent area settled. Predictive maps created for each species using model averaging revealed a wide, but heterogeneous distribution across the Ozarks. The map for eastern spotted skunk indicated generally low occupancy rates across the region, but with several large patches of habitat related to forest cover that had predicted occupancy of $\Psi > 0.20$. The map for striped skunk revealed an association between areas of habitat transitions from forested to urban landcover type and a relatively higher occupancy rate across the region. A significant finding from a conservation standpoint was that incorporation of the competitor species into that species occupancy model (e.g. including striped skunk presence as a covariate in the spotted skunk models) resulted in an improved model. This suggests that there is some habitat component that is being accounted for indirectly by the incorporation of the other species, and may also imply the potential for competition between the two species.

Introduction

How a species perceives the availability of resources in its environment, and what other species are also present that may compete for these resources, both determine the distribution of that species on the landscape. Species distributions are influenced by these multiple factors at different spatial and temporal scales (Thomson et al. 1996), and a common approach to discern these relationships is to analyze habitat selection (Mackey and Lindenmayer 2001). Such analytical approaches generally do not explicitly account for the presence of competitors or predators. Yet for some taxa such as the Carnivora, the landscape ecology of a species may be especially dependent on intraguild interactions (Linnell and Strand 2000; St. Pierre et al. 2006; Berger and Gese 2007). Consequently, examination of carnivore habitat associations and the effects of other carnivore species present on those selection choices may be most insightful when looked at in tandem.

Furthermore, such analyses should be examined across multiple spatial scales. Single scale studies risk spurious conclusions if habitat selection is assessed at a spatial scale irrelevant to the species actual distribution (Mackey and Lindenmayer 2001; Wiens 1989). For example, the distribution of a species that selects habitat based upon fine scale characteristics would be misrepresented by models derived from attributes measured at the landscape scale. Thus an understanding of the relationship between the species and its environment at multiple spatial scales is required, and integration of information across multiple spatial scales will more accurately reflect species distributions and habitat associations (Mazerolle and Villard 1999).

Recent research suggests large-scale habitat characteristics drive forest carnivore habitat selection instead of, or in addition to, the microhabitat and stand-level

characteristics traditionally assumed to drive behavior and distribution (Zielinski and Kucera 1995; Zielinski and Stauffer 1996; Carroll et al. 1999; Zielinski et al. 2000, Campbell 2004). Although larger species have larger home ranges and are likely best modeled by the largest spatial scales available, while smaller species with small home ranges are probably best modeled at smaller spatial scales, this generalization may not always hold (Wiens 1989; Holling 1992; Kelt and Van Vuren 1999; Bowman et al. 2002). A multi-scale approach which combines measures from different spatial scales therefore has the potential to be insightful for assessing habitat occupancy by a carnivore species.

Here I investigate these related issues of habitat use, intraguild interactions, and spatial scale for two species of small carnivores, the eastern spotted skunk (*Spilogale putorius*) and the striped skunk (*Mephitis mephitis*). The former is a rare species of conservation concern (Gompper and Hackett 2005) while the latter is fairly ubiquitous across much of temperate North America (Rosatte and Larivière 2003). For each species I created multi-scale models that combine variables related to forest cover, human use, and the presence of the other skunk species. Each of these models represents a distinct hypothesis about the underlying drivers of the distribution of these species.

I focus on these two species because of conservation concerns related to the eastern spotted skunk (Gompper and Hackett 2005). This species is perhaps the least understood carnivore in eastern North America, and more precisely understanding the distribution of this species is a conservation priority. Prior to this study and concurrent research in western Arkansas (Lesmeister 2007), the only substantive research on the species and its habitat associations came from a study performed in the 1940s (Crabb

1948). This paucity of data makes selection of appropriate spatial scales relevant to species occupancy of a site for predictive modeling tenuous. Historical accounts suggest that the eastern spotted skunk was a species closely tied to prairie ecosystems and open mixed environments, but contemporary data indicate an association with forested ecosystems (McCullough and Fritzell 1984; Lesmeister 2007).

In contrast to the eastern spotted skunk, the landscape ecology of striped skunks is better studied. The species generally selects habitat that is characterized by abundant edge features and landscapes that provide a matrix of heterogeneous habitat types (Bixler and Gittleman 2000). Striped skunks are also associated with human-dominated habitats. Rosatte et al. (1991) observed high densities of striped skunks in settled areas comprised of forested parklands and older suburban neighborhoods with large old trees compared to surrounding habitats. However, Crooks (2002) found that striped skunk occurrences at tracking stations increased as the distance from settled edge increased, and Larivière and Messier (2000) observed striped skunk selected for large habitat patches only when near edge features. Thus it appears that striped skunks are associated with human dominated habitats in so much as these habitats are affiliated with edges.

No evidence exists of antagonistic behavior or conspecific competition between the two skunk species. Rosenzweig (1966) noted that although the western spotted skunk (*S. gracilis*) is smaller in size than the striped skunk, it tends to consume prey that is larger relative to its body size, which may facilitate co-occurrence. The striped skunk has been characterized as a more generalist mesopredator found in many different types and sizes of habitat patches, whereas the western spotted skunk is a more specialized carnivore that only seems to occur in the largest habitat patches (Crooks 2002). Crooks

(2002) also suggested that specialized carnivores like the spotted skunk are likely found in patchy distributions because of their high sensitivity to habitat fragmentation.

Methods

Study Area and Survey Site Selection

Study sites were distributed over the extensive forested regions of southern Missouri (63,252 km²) commonly referred to as the Missouri Ozarks (Figure 1). Selection of survey sites was initially based on three factors: presence of large, contiguous patches of forest cover; close proximity to reliable sightings of eastern spotted skunks (cross-referenced to a database of species sighting information from the Missouri Department of Conservation; Desanty-Combes 2003); and an attempt to distribute surveys over most counties in the Ozarks region. Ultimately, 53 sites were selected based on site accessibility and a minimum inter-site dispersal distance of 5 km (Figure 1; Appendix 1). These sites represent a variety of forested habitats and levels of human settlement and disturbance, fragmentation, elevation, and topographic complexity.

Carnivore surveys

Species occurrences were documented using track-plates and remote camera traps from January to May 2005 and September 2005 to April 2006. At each site I surveyed an area bound by a 0.25 km² grid consisting of 9 station nodes arranged in a 3 x 3 pattern oriented north-south. At each node a track-plate was placed or a camera (DeerCam Model Nontypical with 400 speed film) was placed 0.5-1.0 m above the ground on the bole of a tree, and pointed at an opposing tree upon which a partially opened can of

sardines was nailed 0.25-1.0 m above the ground. Distance between the camera and the bait tree was 2-4 meters. Once a camera station was set and activated, it was revisited on day 7-8 to replace film and batteries, re-bait, and re-align the camera if necessary.

Camera stations ran 14-15 days. Track-plates comprised a 24 x 100 cm aluminum plate, one half of one side of which was coated with carbon toner to act as a tracking medium, and the other half was covered with adhesive contact paper (sticky side exposed). All of this was then placed within a Coroplast enclosure (Gompper et al. 2006). The end of the track plate apparatus with the bait and adhesive paper backed the bole of a tree or other object of suitable size so as to prevent animals from taking the sardine bait without walking over the contact paper. Track plates were checked every 2-3 days for 14-15 days. Track plates and cameras were run consecutively at each site, with the initial technique randomly chosen (Chapter 2).

GIS layers

Spatial data used to quantify the model variables were obtained from the Missouri Spatial Data Information Systems (MSDIS) online database (<http://msdisweb.missouri.edu>). All manipulations of spatial data and analyses were conducted using ArcGIS (ESRI, Redlands, California, USA) software. Forest data were extracted from 30-m resolution Landsat-based raster land cover data for Missouri. This layer was based on circa 2000-2004 satellite imagery. Data for stream networks, the National Wetlands Inventory, and the Wetlands Restoration Program lands were used to improve the mapping of open water, woody-dominated wetland, and herbaceous-dominated wetland. Overall accuracy of this layer was not assessed, but for the specific

land cover type forest and its components, 94% (50 of 53) of survey sites were properly classified into the forest category. I extracted, merged, and reclassified deciduous forest, evergreen forest, mixed forest, deciduous-woody herbaceous, evergreen-woody herbaceous, and woody-dominated layers into a single forest layer for analyses. Areas in the 2005 Land-use Land-cover (LULC) that were identified residential, commercial, industrial, or “other settled” were extracted and merged together into a single “settled” layer. A poly-line map layer that combined primary rivers, all permanent water sources, and all year-round stream reaches was extracted from the Missouri surface water dataset. These data were originally in separate raster layers available from MSDIS. Roads were extracted from the 2005 MODOT Roads of State of Missouri (1:100,000) layer. No discrimination between different categories of roads was made other than the requirement that they be “improved”, because the goal was to document and assess the relationship of patterns of species distributions to the general concept of a “road” as a manmade linear feature bisecting the environment. However, due to the rural nature of the majority of these survey site locations, most roads came from the category county roads. I used the Vector-based Landscape Analysis Tools Extension for ArcGIS 9 (V-Late version 1.1) for analysis of polygon layers. This extension is similar to the commonly used, raster-based Fragstats (Riley et al. 1999), and was used to characterize patch metrics and spatial characteristics related to fragmentation.

A priori species models

I considered preliminary results and published studies on the natural history of each species to develop a set of preliminary predictor variables and *a priori* model sets

(Table 1). Specifically, I tested five model sets that included variables assessed at three spatial scales. The Disturbance model incorporated distance to roads (m), distance to settled landcover type (m), and proportion of settled area (km²/ha). The Species model was simply the presence-absence history of the other skunk species at each site. Three Habitat models contained measures of area and shape related to forest landcover (Table 1).

In addition to the fine scale (grid-level) assessment of the presence of the two target species, I selected two spatial scales for analyses based on the approximate maximum home range size of the eleven species that comprise the carnivore community of the Ozarks. A medium scale (9 km²), and coarse scale (650.25 km²) corresponded with the average size of the survey grid (0.5 km on a side) plus a 2.5 km radius buffer, and the survey grid plus a 25 km radius buffer, respectively. Values for each predictor variable at each survey site were calculated for both medium and coarse scales (where applicable) from the center survey node in the 3x3 grid.

Modeling framework

I used likelihood-based occupancy modeling (MacKenzie et al. 2002; MacKenzie and Bailey 2004; MacKenzie et al. 2005) in a two-stage process to estimate site occupancy (Ψ ; the probability that a species occurs at a site) and detectability (p ; the probability that the species will be detected, given that it is present) from the presence/absence data collected at my sites. Because cameras and track plates differ in their detection rates for skunks and because the order and timing of a survey influences detection likelihood (Hackett et al. 2007; chapter 2), covariates incorporated into models

included one site covariate (month) and four sample covariates (survey apparatus, survey order, survey day, and interaction of survey apparatus x survey order). These covariates were modeled together and individually, and then the two highest weighted single covariate models were combined. The most parsimonious set as indicated by the lowest Aikake's Information Criterion adjusted for small sample size (AIC_c) was used as the null model during the model selection process for occupancy rates.

Model development and selection

I modeled probability of occupancy (PAO) as the dependent variable. Candidate models were compared using AIC_c (Burnham and Anderson 2002). Goodness-of-fit statistics and an index of over-dispersion ($\hat{c} = \chi^2 / df$) were calculated from the global model (Burnham and Anderson 2002). The global model consisted of all model subsets and all detection covariates carried forward from the most parsimonious detection model. Models were ranked using ΔAIC_c . Models with ΔAIC_c values ≤ 2 from the most parsimonious model were considered strongly supported, and their variables were considered to be the most determinant of species occurrence patterns in the best averaged model.

To further interpret the relative importance of each model's independent variable, given the *a priori* model set, Aikake's weights (w) were used. ΔAIC_c values were used to compute w_i , which is the weight of evidence in favor of a model being the best approximating model given the model set (Burnham and Anderson 2001). Unless a model has a $w_i > 0.9$, then other models should be considered when drawing inferences about the data (Burnham and Anderson 2001). A 90% confidence model set was created

by summing all w_i until 0.90 was achieved. I assessed the relative importance of each variable by summing normalized w_i values for every model in which that variable appears (Anderson et al. 2001). I anticipated differences in the numbers of models in which different variables were likely to occur, and therefore calculated an adjusted weight for all parameters using the formula:

$$\text{Adjusted } w_i = (\# \text{ models} * w_i) / ((\# \text{ models with variable}) * (\text{total } \# \text{ variables})).$$

A null model that only included the intercept term was included to ensure that variables used were relevant to the data set. To evaluate the effectiveness of top models from each spatial scale, I assessed the classification success for those models. This provided a diagnostic tool to determine how well each model differentiated between sites of presence versus absence for each species.

Detection and occurrence models were fit to species detection histories with Program Presence 2.0 with the single-season option (MacKenzie et al. 2006). I modeled all model subsets for detection covariates to determine the most parsimonious detection model, which would then be incorporated into all occurrence models. I modeled Ψ by creating a set of *a priori* candidate occurrence models (Table 1) for each species (see Appendix II for range of values for each landscape covariate). The single season occupancy model of MacKenzie et al. (2006) uses multiple surveys on a collection of survey sites to construct a likelihood estimate using a series of probabilistic arguments. False negative surveys can be somewhat corrected for via estimation of probability of detection (POD), providing a more accurate assessment of site occupancy values (MacKenzie et al. 2002). Both occupancy and POD were modeled with site- and visit-specific covariates by introducing a logit link function, thereby performing logistic

regression analyses on occupancy and detectability simultaneously (MacKenzie and Royle 2005). All continuous covariates were standardized to z-scores prior to analysis, allowing model coefficients to be interpreted as the change in the log-odds ratio of occupancy relative to a 1-standard deviation change in the covariate from its mean. Models that did not result in convergence, or for which convergence was questionable due to inestimable parameters (Cooch and White 2005), were eliminated from the candidate set.

Model Validation

I validated accuracy of final models created from model averaging by calculating the area under the curve (AUC) for receiver operating characteristic (ROC) curve and by creating confusion matrices for each dataset. I used web-based ROC analysis software (Eng 2005) to generate ROC curves and to calculate AUC values. This process works by taking the existing dataset of presence/absence values (1/0), and matching it with POD values for each site using the model averaged equation (i.e. averaged coefficients carried forward in 90% confidence model set). The program then computes the ROC curve, provides the AUC value and the parameters needed to plot the ROC curve in a spreadsheet program of ones choosing. ROC curves were obtained by plotting all sensitivity values (true positive proportion; 1-false-negative rate) against the false positive proportion (1-specificity [true negative proportion]) values (Fielding and Bell 1997). The area under the curve (AUC) is a threshold-free (i.e., does not require designation of an arbitrary cutoff for specifying presence or absence from probability values) index model of classification performance and indicates overall ability of the

model (Fielding and Bell 1997) to accurately predict the data used to create it. AUC values range from 0.5 to 1.0, with 1.0 indicating perfect accuracy and 0.5 indicating a model performing no better than a null model (Fielding and Bell 1997). Values of AUC > 0.7 were interpreted as indicating excellent similarity between predicted and observed values for that species, whereas values between 0.5 and 0.7 were good.

Confusion matrices were created, and the accuracy and precision calculated. A confusion matrix (Provost and Kohavi 1998) contains information about actual and predicted classifications done by a classification system. Performance of such systems is commonly evaluated using the data in the matrix. Because the estimated accuracy may be an inadequate performance measure when the number of negative cases is much greater than the number of positive cases (Kubat et al. 1998), I also calculated the geometric mean (g-mean) (Kubat et al. 1998) which accounts for this by including the true positive (*TP*) proportion in a product.

Model prediction

For each model in the 90% confidence set I calculated PAO for each 30 x 30-km grid cell in the study region using the averaged model-specific coefficient estimates and covariate information for that grid cell and the raster calculator function in ArcGIS.

Results

Skunk surveys

Combining cameras and track-plates, raw detection rates were 28.3% (15 sites) for eastern spotted skunks and 32.1% (17 sites) for striped skunk. These values are

minimal estimates of occupancy, as they do not account for variability in the POD for each species. The global model was the most parsimonious model for detectability for both species (Table 2, 3). The global detection model predicted actual occupancy of $\Psi = 41\%$ for eastern spotted skunk with detection rates between $p = 0.03$ and 0.45 . The global detection model predicted $\Psi = 47\%$ for striped skunk with $p = 0.07$ to 0.45 .

Eastern spotted skunk modeling

Fourteen occurrence models were fitted for the eastern spotted skunk (Table 4). The 5 detection covariates selected in the best detection model were incorporated into every spotted skunk occurrence model. No evidence of over dispersion was detected for the global spotted skunk occurrence model ($p = 0.9$, $c\text{-hat} = 0.59$) (i.e., the model “fit” the data), as indicated by the boot-strapped chi-square value from the global model which was greater than the chi-square value calculated with the actual detection data. All other models, which are more specific subsets of this model, were therefore also assumed to fit the data. The global occurrence model for which the goodness-of-fit test was conducted often ranked near the bottom of all models and far outside the 90% confidence interval set, also suggesting higher-ranking models fit the data well.

The occurrence model with the greatest support for eastern spotted skunk was the HABITAT3 model containing only percent cover forest (OR = 555.57, CI = 65.37-4722) (Table 5). Two models were within 2 AIC_c units for eastern spotted skunk, the NULL ($\Delta AIC_c = 1.71$) and HABITAT3 + SPECIES models ($\Delta AIC_c = 1.83$) (Table 4). No other models for eastern spotted skunks were within 2 AIC_c units. However, there was model selection uncertainty for the eastern spotted skunk, (i.e., no single model received $w_i > 0.9$;

Table 4). Therefore model averaging was performed on the 90% confidence model set. The number of models that comprised the 90% model set for eastern spotted skunk was comprised of 4 models: (1) HABITAT3, (2) HABITAT3 + SPECIES, (3) NULL, (4) DISTURBANCE, (5) HABITAT3 + DISTURBANCE. The number of variables present in the 90% confidence model set for eastern spotted skunk, excluding the 5 detection covariates, was four (distance to nearest road, area settled cover, competitor presence, and area forest cover). I recalculated model AIC_c weights using only the 90% confidence model set, and calculated model-averaged estimates for each coefficient. The final model used for predictive mapping was therefore comprised of the model averaged coefficients created through model averaging, and indicated that all four occurrence covariates were significant predictors because none encompassed 0 in their 95% confidence intervals (Table 5). Based upon model averaging, eastern spotted skunks were more likely to be found in or near habitats containing larger proportions of forest cover than the surrounding areas, which are also more likely to contain striped skunks, and are farther away from developed roads and settled related landcover. Estimated proportion of sites occupied from model averaging was 0.32 (SE = 0.08), an increase of 0.04 over observed occupancy. Examination of weights of evidence for individual model variables across all models revealed that forest cover was the most important variable across all models (importance = 0.73) followed by presence of striped skunk ($w = 0.21$). The AUC calculated for eastern spotted skunk was 0.63 (Figure 2). The accuracy based upon the confusion matrix was 0.77, the precision was 0.21, and the geometric mean accuracy was 0.43 (Table 6).

The predictive map for the eastern spotted skunk revealed a fairly uniform pattern of very low occupancy (< 0.1 predicted occupancy), with areas of highest predicted spotted skunk occupancy corresponding to the centers of the largest forested portions of the region (Figure 3a). The areas of the eastern spotted skunk map that contained areas of zero predicted occupancy corresponded to defined urban centers. The eastern spotted skunk map predicted occupancy ranged from 0.001 to 0.45 (Figure 3a), and greater than 85% of the predicted occupancy map for eastern spotted skunk was less than 0.1. Less than 0.1% of the map for eastern spotted skunk was in the highest category of predicted occupancy (0.40-0.45).

Striped skunk modeling

The GLOBAL model, comprised of five detection covariates, was the most parsimonious detection model ($w_i = 0.85$; Table 4) and was carried forward in the modeling process to become the NULL model in occupancy modeling for striped skunk. The global occurrence model indicated no evidence of over dispersion for striped skunk ($p = 0.89$, $\hat{c} = 0.39$). Like with the eastern spotted skunk modeling this is a good indication that all other models which are subsets of the global model also fit the dataset well.

The single most parsimonious occupancy model for striped skunk was the NULL model ($w_i = 0.27$) (Table 4), but overall there was greater evenness across all occupancy models for this species in contrast to the results for eastern spotted skunk. There were four other models within 2 AIC_c units; in order of weight of evidence they were DISTURBANCE ($w_i = 0.21$), DISTURBANCE + SPECIES ($w_i = 0.16$), HABITAT3 (w_i

= 0.15), and SPECIES ($w_i = 0.10$) (Table 4). There was a positive association between the distance to paved roads (OR = 1.26, CI = 1.14-1.39), area settled cover (OR = 4.10, CI = 2.91-5.75) and spotted skunk presence (OR = 1.12, CI = 1.07-1.26) and higher values of predicted occupancy for striped skunk. There was strong negative relationship indicated between high striped skunk occupancy and the area of forest cover (OR = 0.67, CI = 0.27-1.69).

However, no single model garnered enough support to be selected solely as the most parsimonious model for striped skunk (i.e., no single model received $w_i > 0.9$), and therefore as with the eastern spotted skunk model averaging was performed using the 90% confidence set of models. This resulted in five models being used in model averaging for striped skunk: (1) NULL, (2) DISTURBANCE, (3) DISTURBANCE + SPECIES, (4) HABITAT3, (5) SPECIES. The number of variables present in the 90% confidence model set, excluding the three detection covariates, was four (distance to nearest road, area settled cover, competitor presence, and area forest cover). Model variables for striped skunk models also revealed uncertainty on a single most parsimonious model across all variables when weights of evidence were examined for each variable used in model averaging. The environmental variables related to human related features of disturbance to the landscape, area settled cover (+) and distance to nearest paved road (+), were equally important overall ($w = 0.34$). The presence of eastern spotted skunk (+) ($w = 0.28$) was also an important predictor coupled with area forest (-) ($w = 0.21$). Estimated proportion of sites occupied increased by 6% over observed occupancy to 0.38 (SE = 0.12) as a result of model averaging. The AUC calculated for striped skunk was 0.65, and the associated values for accuracy, precision,

and geometric mean accuracy as determined from the confusion matrix were 0.68, 0.38, and 0.57 respectively (Table 6; Figure 2).

The predictive striped skunk occupancy map showed a far greater heterogeneous distribution and a much higher average and overall predicted probability of occupancy compared to the eastern spotted skunk map (Figure 3b). This map did not contain areas of zero predicted occupancy. The values for striped skunk PAO ranged from 0.03 to 0.89 (Figure 3b). Predicted occupancy for the striped skunk was predominantly in the 0.3-0.5 category (65% by area). Only 2% of the study area was predicted to be occupied by striped skunk occupancy of > 0.50 .

Discussion

Habitat versus Guild Member Co-occurrence

Modeling efforts for eastern spotted skunk revealed that habitat components were the best predictors of occupancy but knowledge about the presence of striped skunk was also important. The most parsimonious model for eastern spotted skunk before model averaging was HABITAT3 ($w_i = 0.44$). This model was more than twice as important as the next closest model, and indicated a strong positive association with areas of higher forested cover and higher values of predicted eastern spotted skunk occupancy. This result agrees with the findings of McCullough and Fritzell (1984) and Lesmeister (2007) who found that forested areas in southern Missouri and western Arkansas were selected over open areas. Similarly, western spotted skunks (*S. gracilis*) in the Pacific Northwest have been more frequently captured in old-growth forests (Carey and Kershner 1996),

and in Texas western spotted skunks den in areas with denser cover (Doty and Dowler 2006).

The NULL model was the second most selected for single model, but the third best model again reflected the importance of forested cover in conjunction with knowledge of an area being suitable for the striped skunk. This suggests that the incorporation of other guild member's distribution in relation to the species of focus in predictive modeling can improve the predictive distribution models. Model averaging was used because the top eastern spotted skunk model had relatively low weight ($w = 0.44$, Table 4), and the resulting averaged model used for prediction indicated that knowledge of both habitat and striped skunk gave the most insight; the species was positively associated with forested habitat, more likely to be found where striped skunks were also observed, and negatively associated with more disturbed habitats represented by paved roads and settled habitat features. Thus, understanding the distribution of one member of the carnivore guild can enhance the prediction strengths of models that focus on other guild members. The likelihood that some knowledge of habitat selection by striped skunks could also serve to help identify areas of higher occupancy for eastern spotted skunks is an important finding since relatively little is known about how these two species interact with each other, a scenario typical for most carnivores. Given their differences in body size and mobility, it is unclear whether the two species segregate their habitat spatially or temporally where they overlap, or whether there is some means by which they partition their resources to reduce competition, as seen between western spotted skunks and striped skunks (Doty and Dowler 2006).

While considering these results in a framework of intraguild interference competition may be useful, such an assumption is not necessary. No evidence exists for interference competition between these two species. An alternative is simply that some degree of habitat associated with striped skunk presence that went unmeasured for eastern spotted skunk is important and is indirectly being incorporated in the eastern spotted skunk models via the inclusion of the striped skunk. An example of such a component might be the interaction of human presence on the landscape and the amount of edge in the habitat matrix resulting from fragmentation. The summation of weighted evidence for all model variables used indicated that forest cover was the most important variable across all models ($w_i = 0.73$) followed by presence of striped skunk ($w_i = 0.21$).

Predicted striped skunk occupancy in the Ozarks was negatively related to area forest cover and positively associated with shorter distances to paved roads. Areas that were very close to roads and had lower proportions of forest cover were more likely to be occupied by striped skunks. The striped skunk is capable of surviving in settled as well as forested environments, but prefers the areas of transition between ecological habitat types where there is abundant resources for denning, food, and water (Larivière and Messier 2000; Baldwin et al. 2004). The summation of weighted evidence for all model variables used indicated that environmental features related to a human presence and disturbance of the landscape were the most important variables across all models ($w = 0.33$) followed by presence of eastern spotted skunk (+) ($w = 0.29$) and area forest cover (-) ($w = 0.28$). The incorporation of eastern spotted skunk presence into the striped skunk modeling process, as was also observed in the eastern spotted skunk model results, indicated that the knowledge of the distribution of an intraguild species was not only an

important predictor of striped skunk presence but also suggests the incorporation may indirectly account for unmeasured habitat components associated with the species. Thus the identification of disturbance variables as the best predictors of striped skunk occupancy, in conjunction with presence of eastern spotted skunks, can likely be explained in part by the general ability of the striped skunk to take advantage of heterogeneous habitats in a human-dominated landscape where open cover is available with sufficient amounts of area of transition (Rosatte 1987). These findings agree with those of other researchers. For instance, Crooks (2002) observed that striped skunks exhibited increased visitation to scent stations the further they were located from urban centers. Frey and Conover (2006) observed that striped skunks incorporated existing roads into their home ranges more often than would be expected. Similarly, Prange and Gehrt (2004) observed that increasing urbanization appeared to favor decreased use by striped skunks.

My results give little insight about the extent of competition between these two species. However, understanding species coexistence is a central concern for community ecologists, and community interactions can potentially influence single species viability and conservation, especially for carnivores (Linnell and Strand 2000). Sympatric species of carnivores have coexisted long enough to allow that niche differentiation to occur, and so competition is potentially difficult to observe (Glen and Dickman 2005). To my knowledge, no evidence exists of antagonistic or intraguild competition between these two species of skunk, but future research into the specifics of exactly how these two taxa interact in the landscape seems warranted given my findings that the presence of one species is an important predictor of presence of the other.

Studies of this nature can provide valuable and affordable distribution and habitat association data vital to effective management and conservation planning efforts of rare species, forest carnivores, and fragmented landscapes. This study showed that the inclusion of conspecific species occurrence information can improve the predictive modeling of species occupancy across the landscape, even if their relationship is based upon some indirect relationship not revealed explicitly by the available data. Thus, usage of presence-absence data gathered from noninvasive surveys of forest carnivores where multiple techniques are utilized can yield good results when used in a predictive modeling framework, and holds promise for the interpretation of how rare species such as the eastern spotted skunk view the landscape and at what level they seem to select resources related to their general distribution. Lastly, studies such as this can be useful in elucidating the relationships of conspecifics and the identification of landscape species that can be used in an umbrella capacity to effectively manage for a broader suite or guild of related organisms.

Modeling with covariates

A methodological insight from this work was the importance of incorporating covariates to account for the techniques and timing of survey efforts. I found that the season as characterized by the use of Julian date, the type and order of a survey technique, the day over the course of the sampling period and the interaction of trap day and trap type all were important predictors of detectability for both species. While detection probability has an indirect association with the actual occupancy of an animal on the landscape at a given location, its proper treatment and estimation in a predictive

modeling framework is essential for creating accurate and parsimonious models. When studies use presence-absence data and multiple survey techniques, differences in the detection rates of the techniques must be accounted for in the modeling process. Generally, it is assumed that all species have probability of detection < 1 (MacKenzie et al. 2002; Gehring and Swihart 2004). Gehring and Swihart (2004) suggested that variables which are interpreted as affecting occupancy rates may in fact be affecting detectability, leading to spurious conclusions in the modeling process. Despite this, most survey efforts do not explicitly incorporate assessment of biases in detection rates. This can be especially detrimental when examining species that are both rare on the landscape and difficult to detect.

Skunk ecology

A primary goal of this work was to create a predictive model for occupancy of the eastern spotted skunk, a species that is considered endangered (S1) in Missouri. My results suggest a distribution for the eastern spotted skunk that is driven by forested habitat and the existence of landscape features that also allow for the presence of the striped skunk. The regional surveys and predictive occupancy map for eastern spotted skunk suggest that the species is distributed across the Ozarks at an overall low probability, with very low predicted occupancy rates at any given site. Less than 1% of the region had predicted occupancy rates of > 0.40 . However, these isolated locations of high predicted occupancy based upon my model should be examined in the future for eastern spotted skunk populations. If future survey efforts locate spotted skunks in these regions of high predicted occupancy it would serve to validate the map and allow for

greater consideration of the environment in which this increasingly rare carnivore can still be found.

Lesmeister (2007) examined habitat use of eastern spotted skunks in the Ouachita region of western Arkansas, and found that they selected areas of dense cover associated with young shortleaf pine mixed with hardwoods that provided sufficient overstory cover. The results of my research also suggest a correlation between some degree of forest cover and occupancy by the eastern spotted skunk. This is contrary to historical data collected in Iowa in the 1940s suggesting that the species was most closely associated with open prairie and agricultural landscapes (Crabb 1948). The reasons for this difference in habitat, shifting from open prairies where they were commonly found prior to their documented decline in the 1940s (Gompper and Hackett 2005) back to areas comprised more of a matrix of young and older forests, could have been precipitated by a change in the agricultural practices and lifestyles of the human inhabitants of the prairie region. At the peak of their population numbers in open areas of Missouri based upon furbearer harvest records they were clearly most abundant in these regions compared to the Ozarks (Gompper and Hackett 2005), and the numbers of pelts obtained from the Ozarks over this same period of time were a fraction of those taken in the northwestern parts of Missouri. However, given that no data exists for what the true population densities were for the eastern spotted skunk prior to human settlement of the region, the possibility exists that they are indeed a species associated with forested habitats as found in my study and by Lesmeister (2007) and that the expansion of their populations into these regions of open prairie was a result of the abundance of resources available to them as a

side effect of the farming style that was so prevalent prior to the species range wide declines (Choate et al. 1974).

The predictive map for striped skunk indicates that this species is common across the Ozark region, with predicted occupancy ranging as high as $p = 0.89$ in some areas. The close association of striped skunk to edge habitat, often found in the transition zone where the settled and natural interface, makes the increasingly heterogeneous landscape suitable for this habitat generalist. The primary habitat for striped skunk has been shown to be forest-field edge environments (Stout and Sonenshine 1974; Bixler and Gittleman 2000). Based on my findings and the degree to which the predicted occupancy of striped skunk across the region is associated with these edge-type features, it suggests that areas where striped skunks are found may be at the outskirts of the most suitable areas for eastern spotted skunks.

My study is the first to examine the contemporary distribution of the eastern spotted skunk using noninvasive techniques. The insights gained from this study can be used as a base upon which future research examining the species ecology can be founded upon. The protection status of the eastern spotted skunk in Missouri is S1 (state endangered), but this study suggests there may well be areas of the state beyond the Ozarks that are suitable for the species. The question of reintroduction inevitably arises where rare carnivores are concerned. The feasibility of reintroducing the eastern spotted skunk into formerly occupied areas of Missouri should only be considered after further research more fully discerns the life history characteristics of the species in the region as well as the specific forest structure preferences in Missouri. The species is dispersed in

forested pockets across the Ozarks, but the reasons why it is absent from particular forested habitat is unclear.

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Table 1. Model variables used to model occupancy of eastern spotted skunk and striped skunk based upon 53 survey sites in the Ozarks, Missouri USA.

Model name	Model variables	Variable value range	Scale	k ^a
Disturbance model	Distance to nearest road	200 – 4626 m	medium	8
	Area Settled	0.1 – 9%	coarse	
Species model	Striped skunk presence	0 – 1	fine	6
	Spotted skunk presence	0 – 1	fine	
Habitat 1 model	Core area index	0 – 54	medium	8
	Mean perimeter edge	14 – 610547 m	medium	
	Area Forest	1 – 36%	coarse	
Habitat 2 model	Core area index	0 – 54	medium	7
	Mean perimeter edge	14 – 610547 m	medium	
Habitat 3 model	Area Forest	1 – 36%	coarse	6

^a – Number of model parameters including five detection covariates: season, trap type, trap order, interaction term (trap type x trap day), trap day.

Table 2. Detection models for eastern spotted skunk in the Ozarks, Missouri USA.

Covariate components of each model listed with the number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c) and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i represent models with more substantial support. The sample size for all models was $n = 53$ sites, and the number of model parameters of each model is denoted by k .

Model	k	AIC_c	ΔAIC_c	w_i
global	7	322.54	0.00	0.99
julian2 + julian3	3	331.21	8.67	0.01
julian2 + interaction	3	338.04	15.50	0.00
julian2 + type	3	339.23	16.69	0.00
julian2 + day	3	339.43	16.89	0.00
julian2 + order	3	340.56	18.02	0.00
julian2	2	342.10	19.56	0.00
interaction + day	3	347.79	25.25	0.00
order + day	3	356.60	34.06	0.00
day	2	359.81	37.27	0.00
julian3 + day	3	360.04	37.50	0.00
type + day	3	360.60	38.06	0.00
order + type	3	374.95	52.41	0.00
julian3 + order	3	378.13	55.59	0.00
interaction + order	3	381.48	58.94	0.00

order	2	387.68	65.14	0.00
julian3 + type	3	423.92	101.38	0.00
julian3	2	424.03	101.49	0.00
julian3 + interaction	3	426.18	103.64	0.00
type	2	436.21	113.67	0.00
interaction + type	3	438.24	115.70	0.00
interaction	2	439.25	116.71	0.00

Table 3. Detection models for striped skunk presence in the Ozarks, Missouri USA. Covariate components of each model listed with the number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c) and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i represent models with more substantial support. The sample size for each model is $n = 53$ survey sites and the number of model parameters is denoted by k .

Model	k	AIC_c	ΔAIC_c	w_i
global	6	357.66	0.00	0.85
julian2 + order	3	361.23	3.57	0.14
julian2 + day	3	370.66	13.00	0.00
julian2	2	373.63	15.97	0.00
julian2 + interaction	3	375.12	17.46	0.00
julian2 + type	3	375.39	17.73	0.00
order + day	3	391.27	33.61	0.00
type + day	3	408.39	50.73	0.00
interaction + day	3	410.92	53.26	0.00
day	2	411.80	54.14	0.00
interaction + order	3	431.32	73.66	0.00
order + type	3	432.78	75.12	0.00
order	2	432.54	74.88	0.00
type	2	511.71	154.05	0.00
interaction + type	3	512.51	154.85	0.00
interaction	2	531.66	174.00	0.00

Table 4. *A priori* predictive occupancy models for eastern spotted skunk and striped skunk presence in the Ozarks, Missouri USA. Covariate components of each model listed with the number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c) and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i represent models with more substantial support. The sample size for each model is $n = 53$ survey sites, and the number of model parameters is denoted by k.

Model	<u>Eastern spotted skunk</u>				<u>Striped skunk</u>			
	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i
HABITAT3	4	326.70	0.00	0.44	6	348.50	1.20	0.15
NULL	4	328.41	1.71	0.19	6	347.30	0.00	0.27
HABITAT3 + SPECIES	5	328.52	1.83	0.18	7	351.50	4.20	0.03
DISTURBANCE	5	331.10	4.40	0.05	7	347.80	0.50	0.21
HABITAT3 + DISTURBANCE	6	331.26	4.56	0.04	8	352.05	4.75	0.03
HABITAT1	6	331.55	4.85	0.04	8	354.69	7.39	0.01
SPECIES	4	333.21	6.52	0.02	6	349.20	1.90	0.10
DISTURBANCE + SPECIES	6	333.59	6.90	0.01	8	348.40	1.10	0.16

SPECIES + HABITAT1	7	333.71	7.01	0.01	9	357.34	10.04	0.00
HABITAT1 + DISTURBANCE	7	334.28	7.59	0.01	10	355.11	7.81	0.01
HABITAT2	5	334.32	7.62	0.01	7	351.96	4.66	0.03
HABITAT2 + DISTURBANCE	8	336.19	9.50	0.00	8	354.56	7.26	0.01
HABITAT2 + SPECIES	6	336.22	9.52	0.00	10	355.11	7.81	0.01
GLOBAL	9	338.72	12.02	0.00	11	357.52	10.22	0.00

Table 5. Model averaged parameter estimates, SE, odds-ratio, lower and upper odds-ratio interval, and summed weights of evidence (relative importance) for eastern spotted and striped skunk.

Parameter	Eastern spotted skunk					Striped skunk						
	Coeff.	SE	OR	Lower	Upper	relative importance	Coeff.	SE	OR	Lower	Upper	relative importance
Area forest	6.32	2.14	555.57	65.37	4722	0.73	-0.40	0.92	0.67	0.27	1.69	0.28
Distance to road	0.02	0.00	1.02	1.01	1.02	0.06	0.23	0.10	1.26	1.14	1.39	0.34
Area settled	-32.30	3.70	0.00	0.00	0.00	0.06	1.41	0.34	4.10	2.91	5.75	0.34
Competitor presence	0.10	0.05	1.11	1.05	1.17	0.21	0.11	0.04	1.12	1.07	1.16	0.21

Table 6. Confusion matrices, accuracy, precision, and geometric mean accuracy values for predictive models of eastern spotted skunk and striped skunk using model averaging.

	<u>eastern spotted skunk</u>		<u>striped skunk</u>	
	<u>Predicted</u>			
<u>Actual</u>	positive	negative	positive	negative
positive	11	8	15	13
negative	4	30	4	21
accuracy	0.77		0.68	
precision	0.21		0.38	
g-mean	0.43		0.57	

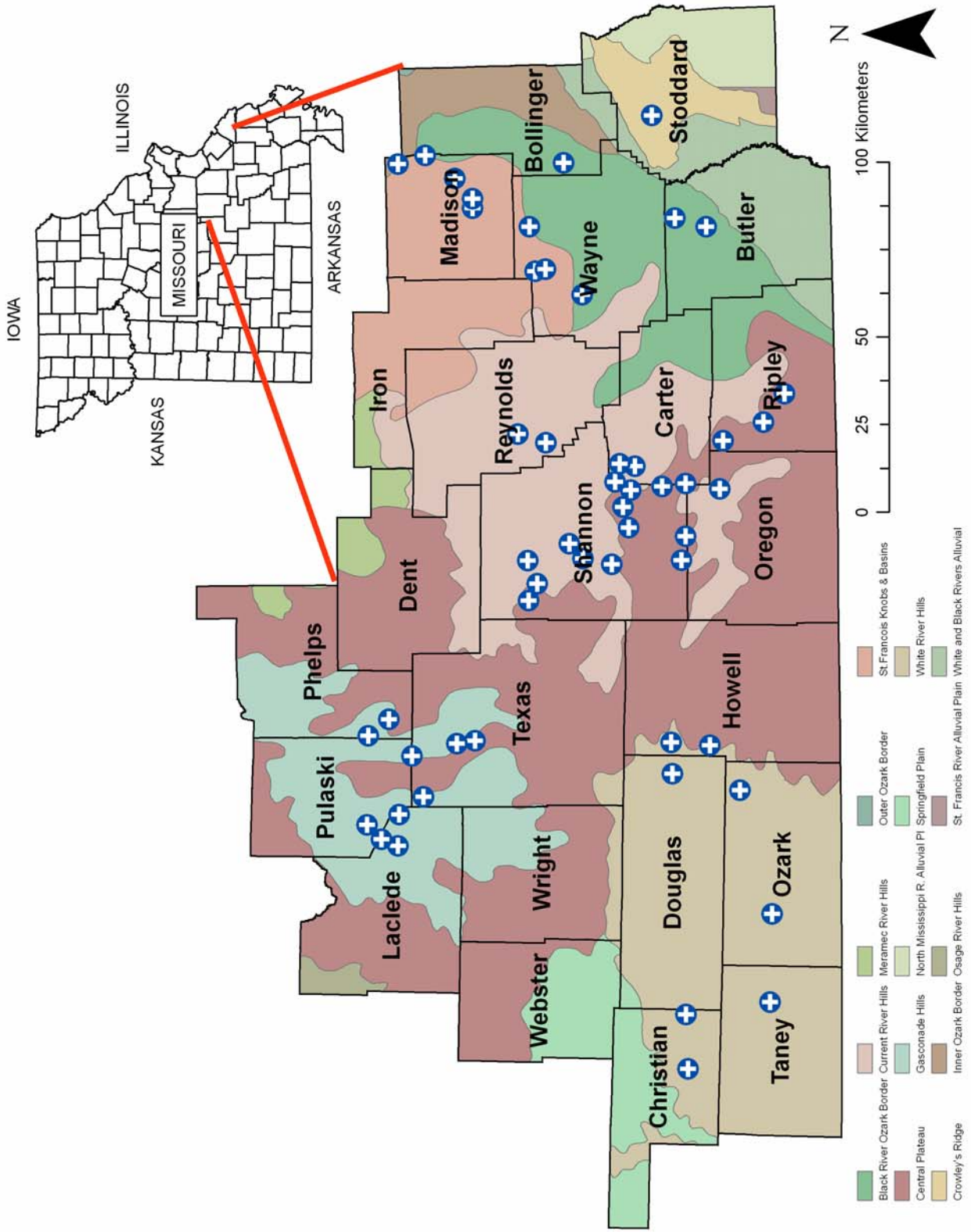


Figure 1. Map of survey sites (n = 53) and corresponding ecological subsections in southern Missouri.

Figure 2. ROC curves for (a) spotted and (b) striped skunk predictive model in the Missouri Ozarks. Dashed lines represent 95% confidence intervals.

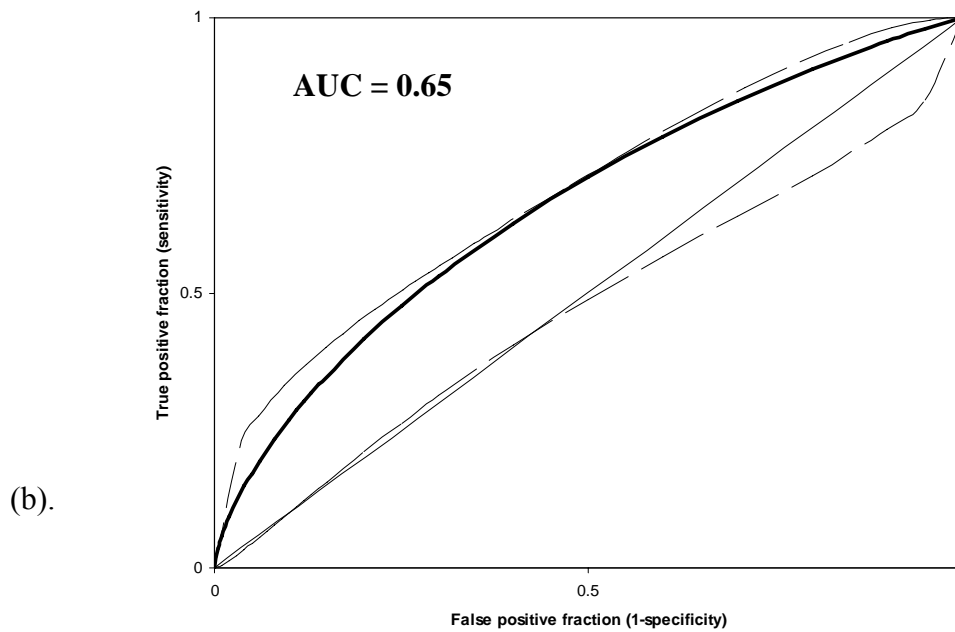
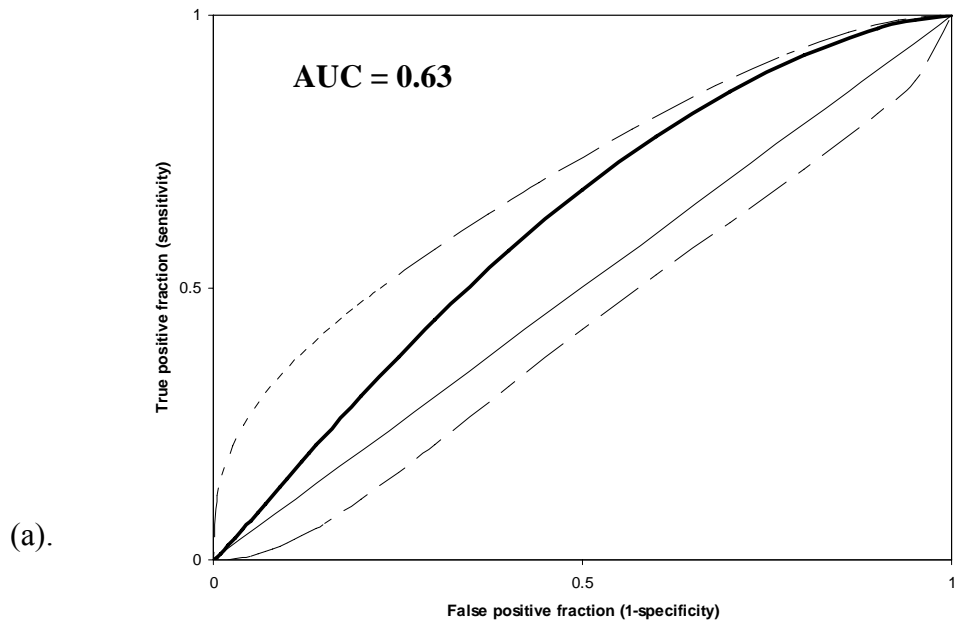
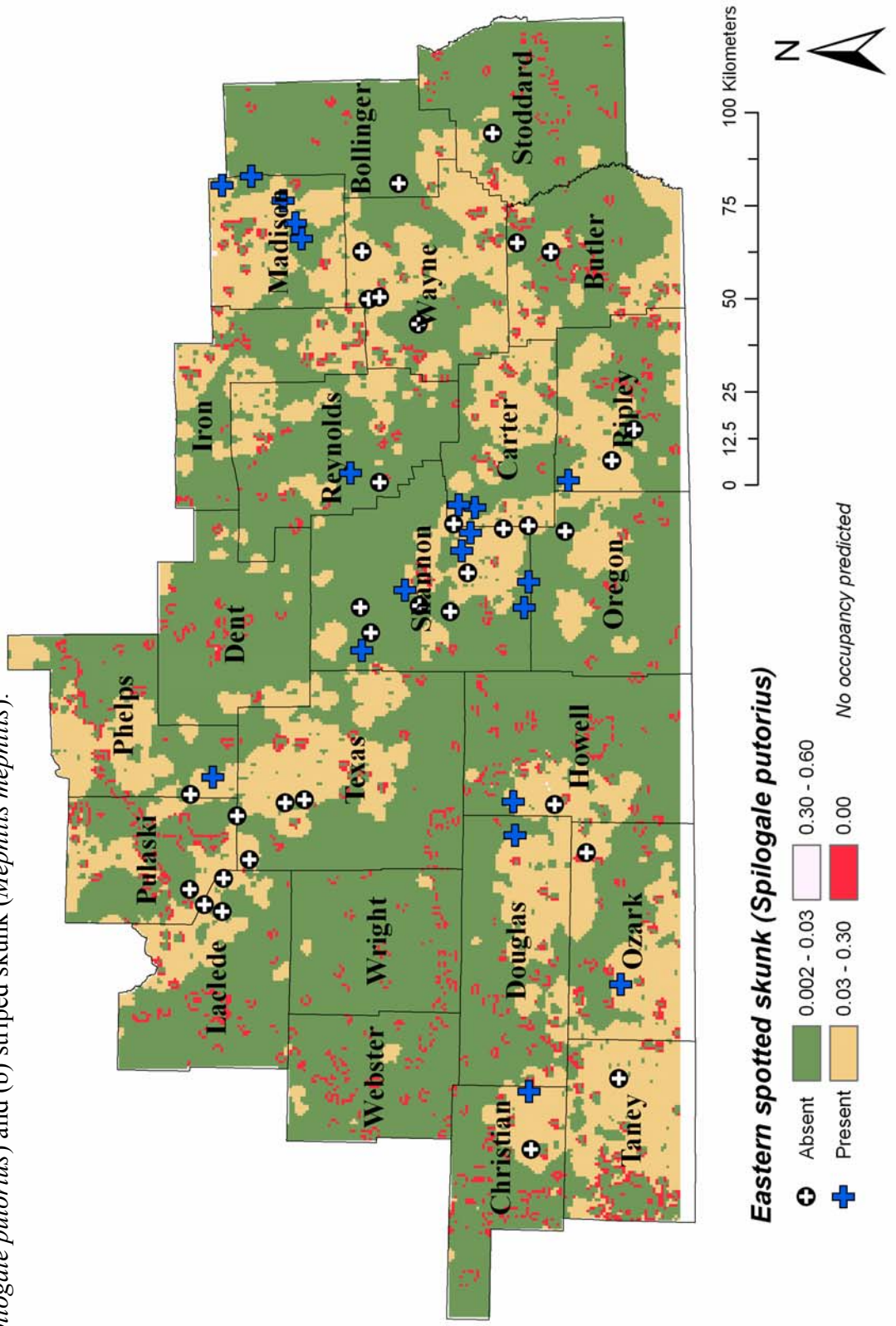
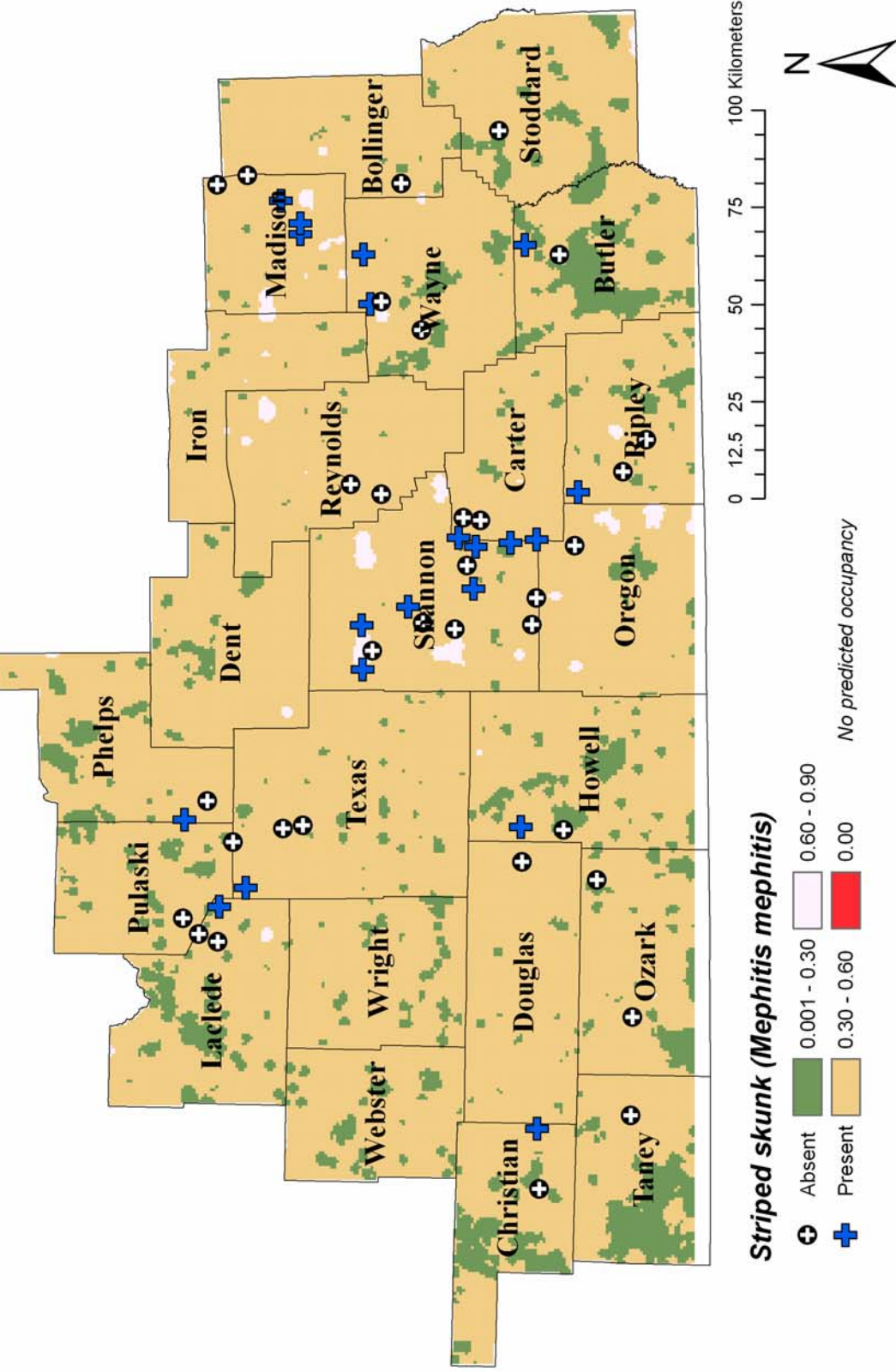


Figure 3. Map of study region depicting predicted actual occupancy (PAO) based upon model averaging results for (a) eastern spotted skunk (*Spilogale putorius*) and (b) striped skunk (*Mephitis mephitis*).

(a)





(b)

Appendix I. Site name, county, UTM location, and species presence/absence history of survey sites (n = 53) for eastern spotted (SPPU) and striped skunk (MEME) in the Missouri Ozarks

Site	County	Northing	Easting	SPPU	MEME
Angeline 1	Shannon	4113348	637193	no	no
Angeline 2	Shannon	4116949	641284	yes	yes
Ava 1	Ozark	4059212	535704	yes	no
Ava 2	Taney	4059841	510428	no	yes
Ava 3	Christian	4083960	507022	no	no
Ava 4	Christian	4083296	491444	no	no
Castor	Bollinger	4118635	750608	no	no
Coldwater	Bollinger	4128368	731898	no	yes
Clearwater 1	Bollinger	4111708	674540	no	no
Clearwater 2	Bollinger	4117795	674306	no	no
CWCA	Stoddard	4093367	233905	no	no
Donaldson	New Madrid	4047308	281159	no	no
Flatwoods	Wayne	4113482	712319	no	no
Houston 1	Texas	4143947	585358	no	no
Houston 10	Laclede	4166408	555153	no	no
Houston 2	Texas	4149054	584570	no	no
Houston 3	Texas	4162213	580846	no	no
Houston 4	Phelps	4168770	591318	yes	no
Houston 5	Phelps	4174801	586600	no	yes
Houston 6	Laclede	4158898	569092	no	yes

Houston 7	Laclede	4170984	556982	no	no
Houston 8	Texas	4175034	561138	no	no
Houston 9	Laclede	4165843	564127	no	no
Krooked Arrow	Bollinger	4162529	752363	yes	yes
Logan 1	Ripley	4123840	670658	no	no
Logan 2	Ripley	4131663	673107	yes	no
Lanford	Madison	4144940	737386	yes	no
Mark Twain 1	Shannon	4099350	657164	yes	yes
Mark Twain 10	Ripley	4055454	684647	no	no
Mark Twain 2	Shannon	4100052	646264	no	no
Mark Twain 3	Carter	4085339	636392	no	no
Mark Twain 4	Carter	4083703	643471	yes	no
Mark Twain 5	Oregon	4090448	657670	no	yes
Mark Twain 6	Oregon	4083814	658353	no	yes
Mark Twain 7	Oregon	4074069	656856	no	no
Mark Twain 8	Oregon	4073026	670652	yes	yes
Mark Twain 9	Ripley	4061446	675830	no	no
Poplar Bluff	Butler	4077728	731746	no	no
Peck Ranch 1	Carter	4098267	663865	yes	yes
Peck Ranch 2	Carter	4103865	658902	no	yes
Peck Ranch 3	Carter	4102447	664616	yes	no
Rocky Creek 1	Shannon	4108054	638136	no	no
Rocky Creek 2	Shannon	4104843	635858	yes	yes

Sam Baker 1	Wayne	4124280	719666	no	yes
Sam Baker 2	Wayne	4127206	718974	no	no
Sunklands 1	Shannon	4128841	636963	no	no
Sunklands 2	Shannon	4125988	630265	no	no
Sunklands 3	Shannon	4128577	625414	yes	yes
University Forest	Butler	4086734	734522	no	yes
Willow Springs 1	Ozark	4068181	570977	no	no
Willow Springs 2	Howell	4076767	583647	no	no
Willow Springs 3	Howell	4087835	584997	yes	yes
Willow Springs 4	Douglas	4087463	575989	yes	no

Appendix II. Mean, standard deviation (SD), and range of values for landscape variables used in occupancy modeling for eastern spotted (SPPU) and striped skunk (MEME).

	n	distance to road (km)			area settled			core area index			mean perimeter edge			area forest		
		mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
SPPU																
presence	19	0.70	1.29	0.05 to 5.8	0.01	0.01	0 to 0.03	0.06	0.50	-0.2 to 1.0	-0.20	0.85	-1.4 to 1.9	0.10	0.08	0.02 to 0.26
absence	34	0.46	0.35	0.11 to 1.2	0.01	0.02	0 to 0.06	-0.14	0.16	-0.2 to 0.6	0.11	1.07	-1.6 to 3.4	0.07	0.05	0.01 to 0.17
MEME																
presence	17	0.40	0.31	0.14 to 1.2	0.01	0.01	0 to 0.02	-0.10	0.21	-0.2 to 0.6	-0.14	1.01	-1.6 to 2.1	0.09	0.08	0.01 to 0.25
absence	36	0.63	0.97	0.05 to 5.8	0.01	0.02	0 to 0.09	-0.12	0.248	-0.2 to 1.0	0.07	1.00	-1.3 to 3.4	0.08	0.06	0.01 to 0.26

CHAPTER 4

USE OF OCCURRENCE DATA TO CREATE LANDSCAPE_SCALE PREDICTIVE MAPS OF TWO COMMON MESOPREDATORS IN THE MISSOURI OZARKS

Harvey Mundy Hackett IV and Matthew E. Gompper

Abstract

Common mesopredators can produce large effects on plant and animal communities. In North American temperate forest environments, two of the most common mammalian mesopredators are the Virginia opossum (*Didelphis virginiana*) and raccoons (*Procyon lotor*). To better understand the landscape ecology of these species in the Missouri Ozarks and to discern whether the incorporation of potential competitive dynamics between the two species might increase model precision, I conducted field surveys and created multi-scale predictive models for the two species. Noninvasive surveys of 53 sites detected raccoon at 94.3% (n = 50) and Virginia opossum at 88.7% (n = 47) of sites. Predictive modeling efforts indicated neither species was suitably characterized by a single model at the landscape scale, therefore model averaging was used to assess the level of importance of landscape variables in the prediction of occupancy of these two forest mesopredators. A positive relationship existed between the presence of raccoon and opossum. Model averaging revealed that by incorporating knowledge of species A (e.g. raccoon) presence within the study area into the modeling process for species B (e.g. opossum) the predictive ability of the resulting model was

improved. Odds ratios revealed that the most important predictors of raccoon occupancy at a landscape level were knowledge of opossum presence (OR = 1.60) and distance to water (OR = 1.16). Core area index (OR = 4.37) and knowledge of raccoon presence (OR = 2.08) were the most important predictors of opossum occupancy. WATER models were also selected for inclusion in the 90% Confidence Interval model sets for each species upon which model averaging of model coefficients was performed. While the ubiquitous nature of both species limited insights on the landscape ecology of the species, my results nonetheless suggest that there exists a high degree of habitat overlap in the distribution of these two forest mesopredators. The ability to incorporate knowledge of one species into the predictive process for another species has implications not only for single species modeling efforts but also for community dynamics research, and is an approach that should be explored further.

Introduction

Increases in mesopredator populations, whether from mesopredator release (Palomares et al. 1995; Soulé et al. 1988) or increased landscape heterogeneity (Litvaitis and Villafuerte 1996; Oehler and Litvaitis 1996), can impact many aspects of an ecosystem (Estes 1996). Mesopredators can act as surrogate top predators and produce effects that ripple through plant and animal communities (Terborgh et al. 1999), such as by decreasing population densities of smaller vertebrate prey (Crooks and Soulé 1999) or indirectly causing important top-down changes in vegetation structure and species diversity (Asquith et al. 1997). Mesopredator release has been implicated in driving some species towards extinction (Courchamp et al. 1999), and there is mounting evidence of the phenomenon in several systems (Crooks and Soulé 1999; Goodrich and Buskirk 1995; Palomares et al. 1995; Rogers and Caro 1998; Sieving 1992; Soulé et al. 1988).

Predator selection of key resources is influenced by interspecific competition, spatial distribution of resources, landscape heterogeneity, and the spatial scale at which the required resources are available. Landscape ecologists commonly deal with problems related to these relationships (Mackey and Lindenmayer 2001), and in an effort to assess and identify important habitat components among mammalian predators it is especially important to identify the appropriate scale of analysis. How these patterns of landscape use depend on intraguild interactions should also be taken into account (Linnell and Strand 2000; St. Pierre et al. 2006; Berger and Gese 2007), although this is rarely done. The most common outcome of multi-resolution investigations is the inference that species respond to local- and landscape-level conditions (Pearson 1993). Consequently, examination of carnivore habitat associations and the effects of other carnivore species

present on those selection choices are most insightful when looked at in tandem and across multiple scales. Furthermore, recent research suggests large-scale habitat characteristics drive forest carnivore habitat selection instead of, or in addition to, the microhabitat and stand-level characteristics traditionally assumed to drive behavior and distribution (Carroll et al. 1999; Ray 2000). However for more omnivorous and ubiquitous mesopredators such as raccoon (*Procyon lotor*) and Virginia opossum (*Didelphis virginiana*), several studies have shown strong associations to finer-scale habitat characteristics (Pedlar et al. 1997; Dijak and Thompson 2000; Disney 2005; Wilson and Nielsen 2007). Therefore, mixed-scale approaches, which combine habitat associations observed at multiple spatial scales, may have the potential for defining landscape-scale patterns in habitat occupancy, especially if intraguild interactions are accounted for.

The Virginia opossum and raccoon are two of the most common mammalian mesopredators throughout much of temperate North America. Dijak and Thompson (2000) observed these species were efficient and dynamic predators of forest songbird populations and other studies have implicated these species as leading causes of decline in many migratory songbirds (Robinson et al. 1995; Donovan et al. 1997). One study in Tennessee found a positive association existed between the two species (Kissell and Kennedy 1992) with habitat overlap between both species as high as 95%. Ladine (1995) observed spatial overlap between the two species for habitat attributes and use, but the species apparently partitioned the same habitat by temporally segregating their use of like components and areas (Ladine 1997). Apparently little or no interference competition occurs between these species (Kissell and Kennedy 1992; Ladine 1995).

To better understand the landscape scale occurrence of raccoons and Virginia opossums as a function of both habitat preferences and the distribution of one another, I created mixed-scale models to test a variety of hypotheses put forth to explain the predicted presence of the species across the landscape. I predict models created for both species should have similar values for covariates and should result in a large similarity between predicted occurrence maps for both species. Thus the approach used here is an opportunity to assess whether competitive interactions between these two species may exist and whether knowledge of these interactions may aid the precision of our predictive models.

Methods

Study Area and Survey Site Selection

My study sites were distributed over the extensive forested regions of southern Missouri (63,252 km²) commonly referred to as the Missouri Ozarks (Figure 1). Selection of survey sites was initially based on three factors: presence of large, contiguous patches of forest cover; proximity to sightings of eastern spotted skunks (Desanty-Combes 2003; Chapter 3); and an attempt to distribute surveys over most counties in the Ozarks region. Ultimately, 53 sites were selected (Figure 1; Appendix 1), with these sites representing a variety of forested habitats and levels of human disturbance, fragmentation, elevation, and topographic complexity.

Mesopredator surveys

From January to May 2005 and September 2005 to April 2006, I used a 3 x 3 grid with sampling stations 250 m apart (0.25 km²) to document occurrences of raccoon and Virginia opossum. At each site, survey grids were oriented north-south, and at each station a track-plate or camera station was established. Whichever technique, track-plates or cameras, was established initially would run for a period of 14-15 days and then was switched to the other technique for a second 14-15 day survey. Track-plates were comprised of a 24 x 100 cm aluminum plate, one half of one side of which was coated with carbon toner to act as a tracking medium, and the other half was covered with adhesive contact paper (sticky side exposed). The plate was then placed within a Coroplast enclosure (Gompper et al. 2006). The end of the track plate apparatus with the bait and adhesive paper backed the bole of a tree or other object of suitable size so as to prevent animals from taking the sardine bait without walking over the contact paper. Track plates were checked every 2-3 days. Infrared remote cameras, DeerCam Model Nontypical, were equipped with 400 speed print film, placed 0.5-1.0 m above the ground on the bole of a tree and pointed at an opposing tree 2-4 m away and upon which a partially opened can of sardines was nailed 0.25-1.0 m above the ground. Camera stations were revisited on day 7-8 to replace film and batteries, re-bait, and realign the camera if necessary.

GIS layers

Spatial data used to quantify the model variables were obtained from the Missouri Spatial Data Information Systems (MSDIS) online database (<http://msdisweb.missouri.edu>). All manipulations of spatial data and analyses were conducted using ArcGIS (ESRI, Redlands, California, USA) software. Forest data were extracted from 30-m resolution Landsat-based raster land cover data for Missouri. This layer was based on circa 2000-2004 satellite imagery. The data used to create an area water layer and to estimate distance to nearest water was collected from the land cover data as well as from stream networks, the National Wetlands Inventory, and the Wetlands Restoration Program lands. These data sources were all used to improve the mapping of open water, woody-dominated wetland, and herbaceous-dominated wetland. Overall accuracy of this layer was not assessed, but for the specific land cover type forest and its components, 94% (50 of 53) of survey sites were properly classified into the forest category. I extracted, merged, and reclassified deciduous forest, evergreen forest, mixed forest, deciduous-woody herbaceous, evergreen-woody herbaceous, and woody-dominated layers into a single forest layer for analyses. Areas in the 2005 Land-use Land-cover (LULC) that were identified residential, commercial, industrial, or “other urban” were extracted and merged together into a single “urban” layer. A poly-line map layer that combined primary rivers, all permanent water sources, and all year-round stream reaches was extracted from the Missouri surface water dataset. These data were originally in separate raster layers available from MSDIS. Roads were extracted from the 2005 MODOT Roads of State of Missouri (1:100,000) layer. No discrimination between different categories of roads was made other than the requirement that they be

“improved”, because the goal was to document and assess the relationship of patterns of species distributions to the general concept of a “road” as a manmade linear feature bisecting the environment. However, due to the rural nature of the majority of these survey site locations, most roads came from the category county roads. I used the Vector-based Landscape Analysis Tools Extension for ArcGIS 9 (V-Late version 1.1) for analysis of polygon layers. This extension is similar to the commonly used, raster-based Fragstats (Riley et al. 1999), and was used to characterize patch metrics and spatial characteristics related to fragmentation.

A priori species models

Based on results of preliminary analyses and published studies on the natural history of each species, I developed a set of preliminary predictor variables and *a priori* model sets (Table 1). I tested four model sets that included variables assessed at three spatial scales. A Disturbance model incorporated distance to roads (m), distance to urban landcover type (m), and proportion of urban area (km²/ha). A Species model was simply the presence-absence history of the other species at each site. Four Topographical variables were incorporated into models containing measures of area and shape related to forest landcover (Table 1). Finally, a Water model incorporated riparian features that have been shown (Kaufman 1992) to have a positive effect on the presence of raccoon, including distance to nearest permanent water feature (m) (Table 1).

In addition to the fine scale (grid-level) assessment of the presence of the two target species, I selected two spatial scales for analyses based on the approximate maximum home range size of the eleven species that comprise the mesopredator

community of the Ozarks. A medium scale (9 km²), and coarse scale (650.25 km²) corresponded with the average size of the survey site (0.5 km on a side) plus a 2.5 km radius buffer, and the survey site plus a 25 km radius buffer, respectively. Values for each predictor variable at each survey site were calculated from the center survey station in the 3x3 grid.

Modeling framework

I used likelihood-based occupancy modeling (MacKenzie et al. 2002; MacKenzie and Bailey 2004; MacKenzie et al. 2005) in a two step process to estimate site occupancy (Ψ ; the probability that a species occurs at a site) and detectability (p ; the probability that the species will be detected, given that it is present) from the presence/absence data collected at my sites. I incorporated detection covariates into models because cameras and track plates differ in their detection rates and because the order and timing of a survey influences detection likelihood (see Chapter 2). They included three forms of Julian date (Julian, Julian², Julian³), survey method (camera or trackplate), survey order (weeks 1-2 or 3-4), survey day (1-18), and interaction of survey method x survey order. The global model included all covariates, and all single and two variable models were also assessed. The most parsimonious individual model (Table 2) as indicated by the lowest Aikaike's Information Criterion adjusted for small sample size (AIC_c) was used as the null model during occupancy model selection (Burnham and Anderson 2002). Where the global model indicated lack-of-fit, Quasi Aikaike's Information Criterion (QAIC_c) was implemented.

Model development and selection

I modeled probability of actual occupancy (PAO) as the dependent variable. Candidate models were compared using AIC_c . Goodness-of-fit statistics and an index of over-dispersion ($\hat{c} = \chi^2 / df$) were calculated from the global model (Burnham and Anderson 2002). The global model consisted of all model subsets and all detection covariates carried forward from the most parsimonious detection model. Models were ranked using ΔAIC_c . Models with ΔAIC_c values ≤ 2 from the most parsimonious model were considered strongly supported, and their variables were considered to be the most determinant of species occurrence patterns in the best averaged model.

To further interpret the relative importance of each model's independent variable, given the *a priori* model set, Aikake's weights (w) were used. ΔAIC_c values were used to compute w_i , which is the weight of evidence in favor of a model being the best approximating model given the model set (Burnham and Anderson 2001). Where there was no single model with $w_i > 0.9$, other models were considered to draw inferences (Burnham and Anderson 2001). A 90% confidence model set was created by summing all w_i until 0.90 was achieved. I assessed the relative importance of each variable by summing normalized w_i values for every model in which that variable appears (Anderson et al. 2001). I anticipated differences in the numbers of models in which different variables were likely to occur, and therefore calculated an adjusted weight for all parameters using the formula:

$$\text{Adjusted } w_i = (\# \text{ models} * w_i) / ((\# \text{ models with variable}) * (\text{total } \# \text{ variables})).$$

A null model that only included the intercept term and the aforementioned detection covariates was included to ensure that variables used were relevant to the data set.

Detection and occurrence models were fit to species detection histories with Program Presence 2.0 with the single-season option (MacKenzie et al. 2006). I modeled Ψ by creating a set of *a priori* candidate occurrence models (Table 1) for each species. The single season occupancy model of MacKenzie et al. (2006) uses multiple surveys on a collection of survey sites to construct a likelihood estimate using a series of probabilistic arguments. False negative surveys can be somewhat corrected for via estimation of probability of detection (POD), providing a more accurate assessment of site occupancy values (MacKenzie et al. 2002). Both PAO and POD were modeled with site- and sample-specific covariates by introducing a logit link function, thereby performing logistic regression analyses on occupancy and detectability simultaneously (MacKenzie and Royle 2005). All continuous covariates were standardized to z-scores prior to analysis, allowing model coefficients to be interpreted as the change in the log-odds ratio of occupancy relative to a 1-standard deviation change in the covariate from its mean. Models that did not result in convergence, or for which convergence was questionable due to inestimable parameters (Cooch and White 2005), were eliminated from the candidate set.

Model Validation

I analyzed the accuracy of final models using confusion matrices (Provost and Kohavi 1998) which contain information about actual and predicted classifications done by a classification system. Performance of such systems is commonly evaluated using the data in the matrix. Confusion matrices were created, and the accuracy and precision calculated. The estimated accuracy may not be an adequate performance measure when

the number of negative cases is much greater than the number of positive cases (Kubat et al. 1998). Therefore, the geometric mean (g-mean) was calculated to account for this by including the true positive proportion in a product (Kubat et al. 1998).

Model prediction

For each model in the 90% confidence set I calculated PAO for each 30 x 30-km grid cell in the study region using the averaged model-specific coefficient estimates and covariate information for that grid cell and the raster calculator function in ArcGIS.

Results

Species surveys

Combining cameras and track-plates, raw detection rates were 94.3% (50 sites) for raccoon and 88.7% (47 sites) for Virginia opossum. These are minimal estimates of occupancy, as they do not account for variability in POD for each species. The most parsimonious model for detectability for raccoon was the JULIAN² + ORDER + DAY model with PAO of 94% with per check detection rates ranging from 0.33 to 0.47 (Table 2). The JULIAN² + INTERACTION model was the most parsimonious detection model for Virginia opossum, predicting 84% PAO and detection ranged from 0.4 to 0.7 per check (Table 2).

Raccoon modeling

I developed and attempted to fit 16 occupancy models for raccoon (Table 3). All raccoon occupancy models contained three detection covariates, JULIAN², ORDER, and DAY. Evidence of over dispersion was detected for the GLOBAL raccoon model ($p =$

0.02, $c\text{-hat} = 1.58$) as indicated by the boot-strapped chi-square value from the global model. Therefore, all model sets for species occupancy were further analyzed using QAIC_c. All other model subsets can not be assumed to fit, because the GLOBAL model did not fit, and this also means that they can only serve as a guide under an exploratory analysis design and have no predictive power.

The NULL model was the single most parsimonious model for predicting raccoon occupancy (Table 3). Model results indicated model selection uncertainty (i.e., no single model received $w_i > 0.9$), and therefore model averaging was used. Model averaging based on the 90% confidence model set for raccoon selected 3 models (NULL, SPECIES, WATER). The number of variables present in the 90% confidence model subset, not including detection covariates, was 3 (opossum presence, distance to nearest water, area water). I recalculated model QAIC weights using just the models selected in the 90% CI set, and calculated model-averaged estimates for each coefficient. The final best fit model used to create a predictive map for raccoon was based upon the averaged model coefficients. There were several significant predictors as indicated by the model-averaging coefficient 90% CI not overlapping zero (Table 4). The raccoon predictive model accuracy based upon the confusion matrix was 0.81, the precision was 0.67, and the geometric mean accuracy was 0.27 (Table 5).

The occupancy model with the greatest support for raccoon was the NULL model ($w_i = 0.83$). No other models were within 2 QAIC_c units for raccoon, and the next closest model was the SPECIES model (Virginia opossum presence; odds ratio 1.60, SE = 0.65; Table 5), separated by QAIC_c = 5.62 (Table 3). The third model incorporated into model averaging was the WATER model (distance to water; odds ratio 1.16, SE = 0.39; area

water; odds ratio 1.03, SE = 0.03; Table 5). The estimated proportion of sites occupied by raccoon from model averaging was 0.97 (SE = 0.04), an increase of 0.03 over observed occupancy. The summation of weighted evidence for individual model variables used in model averaging indicated that none of the variables were overwhelmingly important. The presence of Virginia opossum was the most important variable across all models (importance = 0.05) followed by variables associated with the presence of water (importance = 0.04).

The predictive occupancy map for raccoon revealed a high occupancy rate throughout the study region (i.e. PAO \geq 0.90; Figure 2a). This map did not contain areas of zero predicted occupancy, and the overall predicted occupancy ranged from 0.70 to 1.00 (Figure 2a). This map was characterized by a heterogeneous distribution, within which the southwestern third of the study region had the highest proportion of high occupancy area.

Virginia opossum modeling

Sixteen occupancy models were developed and fitted for Virginia opossum (Table 3). The two detection covariates used in all occupancy models for the Virginia opossum were JULIAN² and INTERACTION. Evidence of over dispersion was detected for Virginia opossum ($p = 0.20$, $c\text{-hat} = 1.09$) as indicated by the boot-strapped chi-square value from the global model. Therefore, occupancy models were further analyzed using QAIC_c. Because the GLOBAL model did not fit the data, all other models that are subsets of the GLOBAL model can not be assumed to fit and may only serve as a guide under an exploratory analysis design.

The NULL model was the single most parsimonious for Virginia opossum at predicting occupancy (Table 3). There was a fair amount of model selection uncertainty (i.e., no single model received $w_i > 0.9$), and so model averaging was used. The 90% CI model set for Virginia opossum was comprised of 4 models (NULL, SPECIES, SPECIES + WATER, HABITAT). The 90% CI model subset, not including detection covariates, contained 7 variables for Virginia opossum (raccoon presence, mean perimeter edge, core area index, fractal dimension, area forest, distance to water, and area water). The final model averaged variables for Virginia opossum indicated some of these predictor variables were significant influences on predicting opossum occupancy as indicated by the model-averaging coefficients not overlapping zero (Table 4). The Virginia opossum predictive model accuracy based upon the confusion matrix was 0.75, the precision was 0.14, and the geometric mean accuracy was 0.22 (Table 5).

The best single occupancy model for Virginia opossum was the NULL model, but with a smaller overall weight of evidence than the results from raccoon modeling ($w_i = 0.50$) (Table 3). There was less certainty across all occupancy models for Virginia opossum, as indicated by the incorporation of 4 models into the 90% CI set and the fact that all 4 models were within < 2 QAIC units of each other. Overall, the SPECIES model had a weight of evidence value of 0.20, the highest of all models after the NULL model. As with the raccoon model set, there was a direct relationship between the presence of raccoon and Virginia opossum (odds ratio = 2.08, SE = 1.03). Estimated proportion of sites occupied from model averaging was 0.93 (SE = 0.11), an increase of 0.06 over observed occupancy. Following presence of raccoon as the most important variable in

the average model based upon relative weighted evidence (importance = 0.39) were features related to water ($w_i = 0.15$) and forest ($w_i = 0.05$) (Table 5).

The Virginia opossum predictive maps, like the raccoon map, exhibited a heterogeneous distribution for occupancy region wide, but it also was characterized by a wider range of predicted occupancies (PAO = 0.55 – 0.99; Figure 2b). This map did not contain areas of zero predicted occupancy. The areas of highest predicted Virginia opossum occupancy were dispersed in smaller regions throughout the area's central mountainous core.

Discussion

None of the landscape characteristics associated with raccoon and Virginia opossum presence in the Ozarks of southern Missouri were good predictors of occupancy by themselves for either species. Therefore model averaging was used to obtain a predictive equation for assessing predicted occupancy for each species throughout the region. Given the ubiquitous nature of both species, their generalist behaviors, and the fact that the predominant habitat was forest and therefore many distinct landscape types were not surveyed, it is quite possible that regardless of the variables selected *a priori* for modeling of these two species, results could remain relatively un-insightful because using presence-absence data rather than relative density data does not yield as much variability for these species between survey sites. If I had surveyed over a broader range of habitat types, then perhaps there would be more differentiation and incorporation of sites that were less than ideal for either species. However, given that the observed occupancy rate

for both species was over 85% there is little resolution between presence and absence sites.

The most parsimonious single raccoon occupancy model was the NULL model, indicating that either the landscape variables I modeled did not capture enough variation on a scale relative to how raccoons select habitat within the landscape or because raccoons are so generalist in nature that relatively few if any landscape level habitat variables are good predictors of raccoon occupancy in Ozark-type forests. Thus my results contrast with those of Dijak and Thompson (2000) who found macrohabitat variables could be good predictors of putative raccoon abundance. The lack of significant results therefore lends support to research suggesting that attempts to understand raccoon landscape ecology should focus more on the local scale microhabitat (Wilson and Nielsen 2007).

There were no single raccoon occupancy models within 2 AIC_c values of the NULL model, but there was some support for the WATER model in the model averaging process. The incorporation of WATER in the model averaging process improved the overall ability of predicting high occupancy by raccoons in a given area. This finding agrees with previous studies that revealed the critical importance of water to raccoon distribution, and showed it to be a primary limiting factor to raccoon abundance (Endres and Smith 1993; Henner et al. 2004; Wilson and Nielsen 2007).

Knowledge about the presence of Virginia opossum was also important in the model averaging process, and improved the predictive model for raccoon occupancy. Previous work that examined the ecological relationships of raccoon and opossum revealed only minor evidence of competition in terms of habitat use (Kissell and

Kennedy 1992; Ladine 1995), although direct interference in the form of the killing of opossums by raccoons in enclosure experiments has been observed (Stuewer 1943). Their association to one another may range from simple coexistence to exploitation, and future research examining this type of direct interaction could be illuminating. There are studies suggesting that the removal of raccoons in an area may release opossum to broaden their dietary niche (Ginger et al. 2003). The amount of overlap in habitat effectively used by both species is quite high (Ginger et al. 2003), as high as 95% in some habitats (Kissell and Kennedy 1992), yet Kasparian et al. (2002) found minimal if any competition between the two for essential resources. However, I conclude that either there is indeed exploitation competition, or that some characteristic of the habitat associated with Virginia opossum that went unmeasured for raccoon is nonetheless important and is indirectly being incorporated in the raccoon models via the inclusion of the Virginia opossum. An example of such a component might be the dynamics of edge habitat created from the interaction of anthropogenic influences and the size of forested patches.

There was greater uncertainty in single models predicting Virginia opossum occupancy, but unlike the case for raccoon there was less support for NULL and greater support for some of the landscape variables modeled. The NULL model was still the most supported single model for opossum, but unlike for raccoon models for which no other models were within 2 AIC units of the NULL model, there were three other models for opossum that were within this range. Results of model averaging for Virginia opossum, unlike those of raccoon, revealed greater uncertainty and support for a single model. The presence of the raccoon (SPECIES model) was the most important variable based upon relative weighted evidence (relative importance = 0.39), occurring in two of

the four models used in model averaging of coefficients. This was followed by features related to water ($w_i = 0.16$) and habitat structure and size ($w_i = 0.06$). The SETTLED occupancy models based on urban related landscape features represent environmental components that fragment the landscape in the form of roads and urban areas. They may still be indirectly important to the distribution of opossum, but not measured at a scale relevant to the scale at which opossum perceive that element. There was some form of landscape level fragmentation selected for, but these components of the landscape may be more important to the opossum at a local scale and not at a landscape scale.

These results for the Virginia opossum speak to their preference for a more heterogeneous landscape (Dijak and Thompson 2000), and past studies have revealed a close association of the species with a habitat matrix comprised of forest and anthropogenic (i.e. agriculture) elements (Pedlar et al. 1997). Dijak and Thompson (2000) found no association between Virginia opossum occurrence and edge dynamics at the landscape level, but they did observe a relationship between Virginia opossum abundance and stream density, contagion, and mean nearest-neighbor distance between forest patches, concluding that Virginia opossum in Missouri were associated with heterogeneous landscapes with dispersed forested patches and abundant riparian habitat. Prange and Gehrt (2004) found a higher proportion of Virginia opossum in areas of raccoon co-occurrence in rural areas versus urban areas. Increased perimeter edge would allow Virginia opossum to more readily access sites with higher quantities of preferred foods.

My results give further support to the observation of a high degree of overlap in the general distribution and habitat associations of these two common forest

mesopredators. As a whole, the improved predictive power of the models when the presence of the other mesopredator was included as an additional independent variable suggests the potential for indirect or exploitation competition. From a predictive modeling perspective, how these two species spatially or functionally share their habitat is of little consequence as these results indicate the presence of one can be a good predictor of the presence of the other. The ability to incorporate something about the habitat of one species by including the distribution of another guild member is something that to date has not been done for mesopredators. This is perhaps the most illuminating finding of this research, and holds promise for future efforts to model single species and community dynamics.

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Table 1. Model name, covariates, range of data values of each covariate, and the scale the covariate was derived from to be included in *a priori* models used to explain raccoon and Virginia opossum occupancy in the Ozarks, Missouri, USA.

Model name	Covariates	Covariate value range	Scale	k ^a
DISTURBANCE	Distance to nearest road	200 – 4626 m	medium	4 / 5
	Distance to nearest urban	53 – 17908 m	medium	
	Area Urban	0.1 – 9 %	coarse	
SPECIES	Raccoon presence	0 – 1	fine	2 / 3
	Opossum presence	0 – 1	fine	
HABITAT	Core area index	0 – 54	medium	5 / 6
	Mean perimeter edge	14 – 610547 m	medium	
	Fractal dimension	1.2 – 2.5	medium	
WATER	Area Forest	1 – 36 %	coarse	
	Area Water	1 – 36 %	coarse	3 / 4
	Distance to nearest water	7 – 19173 m	medium	

^a – Number of model parameters including detection covariates (raccoon/opossum).

Table 2. Detection models for raccoon and Virginia opossum presence in the Ozarks, Missouri, USA. Columns represent covariate components of each model, number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c), and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i indicate models with more substantial support. The sample size for each model is 53 sites.

Model	<u>Raccoon</u>				<u>Virginia opossum</u>			
	k	AIC_c	ΔAIC_c	w_i	k	AIC_c	ΔAIC_c	w_i
JULIAN ² + ORDER + DAY	4	998.25	0.00	0.28	4	1152.55	21.12	0.00
JULIAN ² + INTERACTION + ORDER + DAY	5	998.26	0.01	0.28	5	1135.69	4.26	0.07
GLOBAL	8	999.92	1.67	0.12	8	1132.15	0.72	0.38
JULIAN ² + DAY	3	1000.08	1.82	0.11	3	1151.21	19.78	0.00
JULIAN ³ + DAY	3	1000.23	1.98	0.11	3	1173.21	41.78	0.00
DAY	2	1002.86	4.61	0.03	2	1171.46	40.03	0.00
ORDER + DAY	3	1003.17	4.92	0.02	3	1173.70	42.27	0.00
JULIAN + DAY	3	1003.94	5.69	0.02	3	1173.33	41.90	0.00
INTERACTION + DAY	3	1004.66	6.41	0.01	3	1152.02	20.59	0.00
TYPE + DAY	3	1005.19	6.94	0.01	3	1168.32	36.89	0.00

INTERACTION + ORDER + TYPE + DAY	5	1006.68	8.43	0.00	5	1152.97	21.54	0.00
JULIAN ³ + ORDER	3	1011.03	12.77	0.00	3	1173.65	42.22	0.00
ORDER	2	1011.81	13.56	0.00	2	1171.77	40.34	0.00
ORDER + TYPE	3	1013.24	14.99	0.00	3	1165.50	34.07	0.00
JULIAN + ORDER	3	1013.53	15.27	0.00	3	1173.71	42.28	0.00
INTERACTION + ORDER	3	1014.07	15.81	0.00	3	1152.80	21.37	0.00
JULIAN ² + ORDER	3	1014.16	15.90	0.00	3	1156.70	25.27	0.00
JULIAN + JULIAN ² + JULIAN ³	4	1018.72	20.47	0.00	4	1152.61	21.18	0.00
JULIAN ² + JULIAN ³	3	1019.60	21.35	0.00	3	1152.29	20.86	0.00
JULIAN + JULIAN ²	3	1023.86	25.61	0.00	3	1156.72	25.29	0.00
JULIAN ²	2	1024.48	26.23	0.00	2	1158.28	26.85	0.00
JULIAN ² + TYPE	3	1025.39	27.14	0.00	3	1147.06	15.63	0.00
JULIAN ² + INTERACTION	3	1025.45	27.20	0.00	3	1131.43	0.00	0.55
JULIAN ³ + TYPE	3	1026.21	27.96	0.00	3	1171.12	39.69	0.00
JULIAN ³ + INTERACTION	3	1026.52	28.27	0.00	3	1161.32	29.89	0.00
TYPE	2	1026.58	28.33	0.00	2	1168.91	37.48	0.00

JULIAN + TYPE	3	1027.60	29.35	0.00	3	1171.00	39.57	0.00
JULIAN + INTERACTION	3	1027.89	29.64	0.00	3	1161.39	29.96	0.00
INTERACTION	2	1027.25	29.00	0.00	2	1159.14	27.71	0.00
INTERACTION + TYPE	3	1028.68	30.43	0.00	3	1158.27	26.84	0.00
JULIAN ³	2	1029.47	31.21	0.00	2	1171.87	40.44	0.00
JULIAN	2	1030.07	31.82	0.00	2	1171.83	40.40	0.00
JULIAN + JULIAN ³	3	1031.73	33.48	0.00	3	1174.08	42.65	0.00

Table 3. *A priori* predictive occupancy models for raccoon and Virginia opossum in the Ozarks, Missouri, USA. Detection covariate components of each model are included with the number of parameters (k), Quasi Akaike's Information Criterion adjusted for small sample size (QAIC_c), distance from the most parsimonious model (Δ QAIC_c) and QAIC_c weight (w_i). Lower QAIC_c and Δ QAIC_c and greater w_i represent models with more substantial support. The sample size for each model was 53 sites.

Model	<u>Raccoon</u>			<u>Virginia opossum</u>				
	k	QAIC _c	Δ QAIC _c	w_i	k	QAIC _c	Δ QAIC _c	w_i
NULL	4	790.80	0.00	0.83	3	1041.07	0.00	0.50
SPECIES	4	796.42	5.62	0.05	3	1042.85	1.78	0.20
WATER	5	797.34	6.54	0.03	4	1047.76	6.69	0.02
HABITAT	7	797.37	6.57	0.03	6	1045.48	4.41	0.05
SPECIES + HABITAT	8	797.57	6.77	0.03	7	1048.36	7.28	0.01
SPECIES + WATER	6	798.50	7.70	0.02	5	1043.50	2.43	0.15
SPECIES + DISTURBANCE	7	801.72	10.93	0.00	5	1075.63	34.56	0.00
DISTURBANCE	6	801.74	10.94	0.00	5	1063.64	22.57	0.00
HABITAT + WATER	9	802.76	11.96	0.00	8	1047.64	6.56	0.02
SPECIES + HABITAT + WATER	10	803.08	12.28	0.00	9	1050.65	9.58	0.00

SPECIES + HABITAT + DISTURBANCE	11	803.88	13.08	0.00	10	1050.27	9.20	0.00
DISTURBANCE + WATER	8	804.61	13.81	0.00	7	1055.05	13.98	0.00
HABITAT + DISTURBANCE	10	804.84	14.04	0.00	9	1047.08	6.01	0.02
SPECIES + DISTURBANCE + WATER	9	806.60	15.80	0.00	8	1049.85	8.77	0.01
GLOBAL	13	809.99	19.19	0.00	12	1053.87	12.80	0.00
HABITAT + DISTURBANCE + WATER	12	811.11	20.31	0.00	11	1050.41	9.34	0.00

Table 4. Model averaged parameter estimates, SE, odds-ratio, lower and upper odds-ratio interval, and summed weights of evidence for raccoon and Virginia opossum.

Raccoon parameter	Coefficient	SE	OR	Lower	Upper	importance
distance to water	0.15	0.39	1.16	0.78	1.71	0.03
area water	0.03	0.03	1.03	0.99	1.06	0.03
mean perimeter edge	na	na	na	na	na	na
fractal dimension	na	na	na	na	na	na
core area index	na	na	na	na	na	na
area forest	na	na	na	na	na	na
other species presence	0.47	0.65	1.60	0.83	3.06	0.05
Opossum parameter	Coefficient	SE	OR	Lower	Upper	importance
distance to water	-0.14	0.13	0.87	0.77	0.99	0.16
area water	-0.19	2.37	0.83	0.08	8.84	0.16
mean perimeter edge	0.01	0.02	1.01	0.99	1.03	0.06
fractal dimension	0.24	2.32	1.27	0.13	12.95	0.06
core area index	1.47	0.34	4.37	3.11	6.13	0.06
area forest	-0.03	0.83	0.97	0.42	2.23	0.06
other species presence	0.73	1.03	2.08	0.74	5.80	0.39

Table 5. Confusion matrices, accuracy, precision, and geometric mean (g-mean) accuracy values for predictive models of raccoon and Virginia opossum using model averaging.

		<u>raccoon</u>		<u>Virginia opossum</u>		
		<u>Predicted</u>				
		positive	negative	positive	negative	
<u>Actual</u>	positive	42	2	positive	34	1
	negative	8	1	negative	12	6
accuracy	0.81			0.75		
precision	0.67			0.14		
g-mean	0.27			0.22		

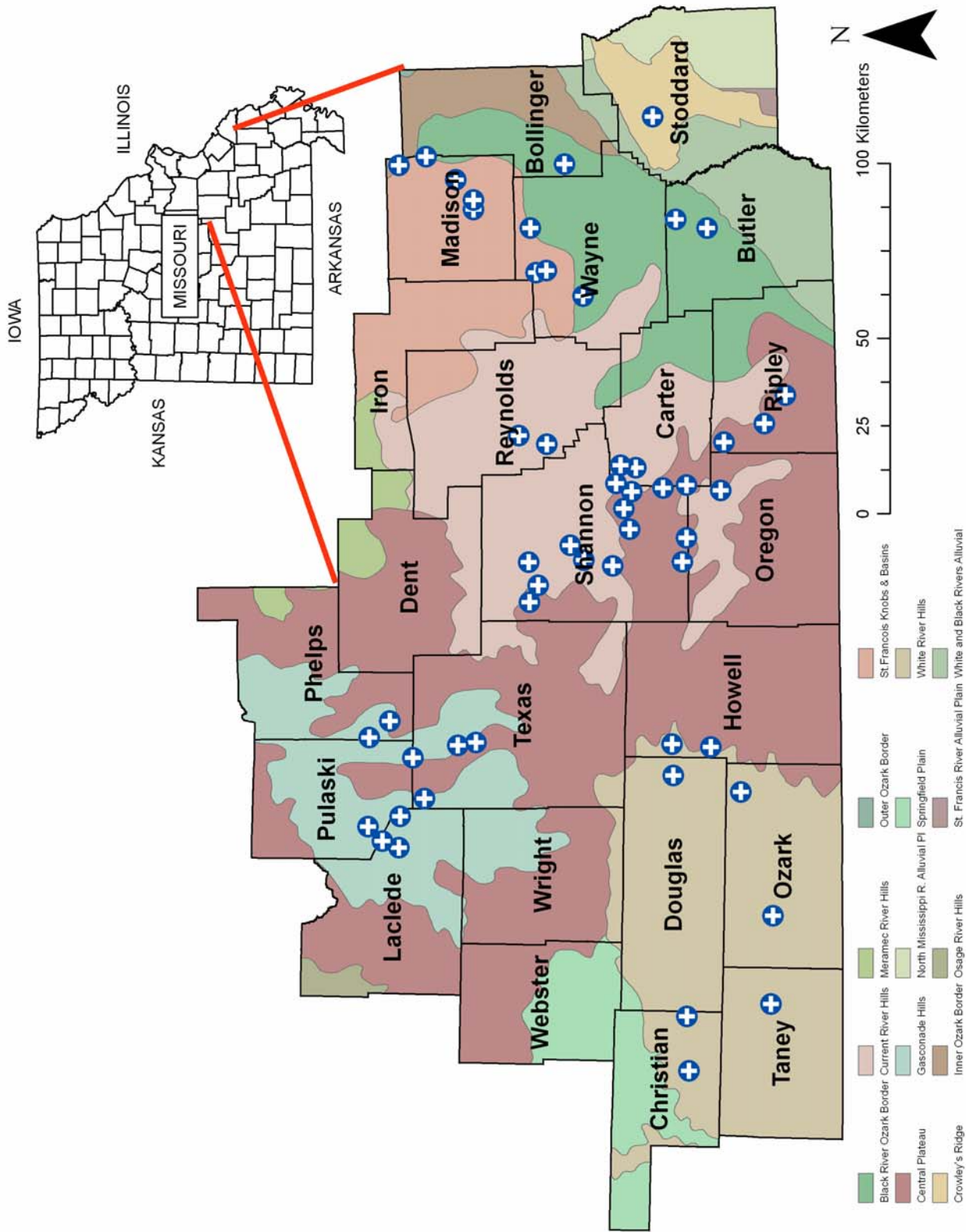


Figure 1. Map of survey sites (n = 53) and corresponding ecological subsections in southern Missouri.

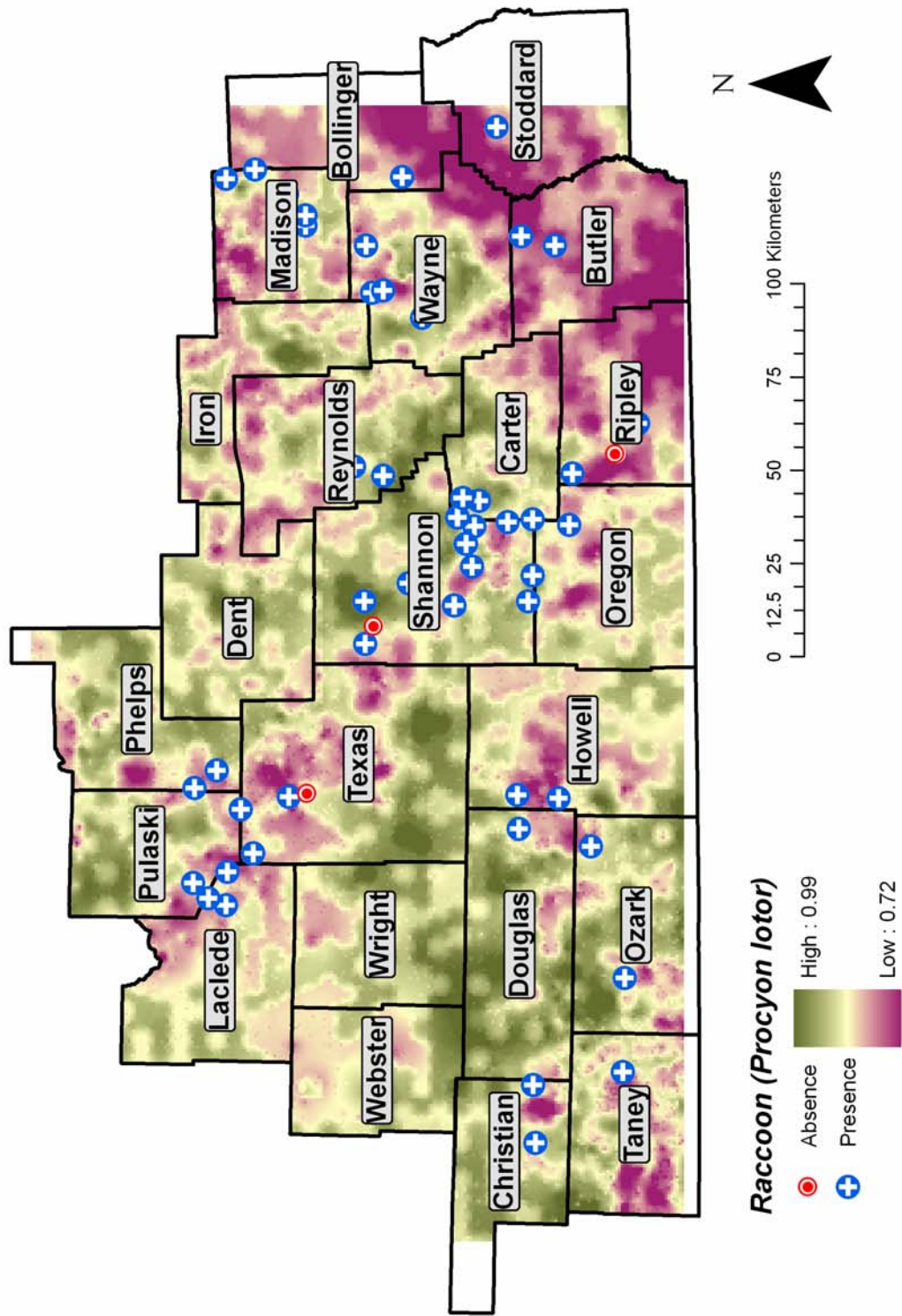


Figure 2a. Map of study region depicting predicted actual occupancy (PAO) for raccoon (*Procyon lotor*) based upon results of model averaging.

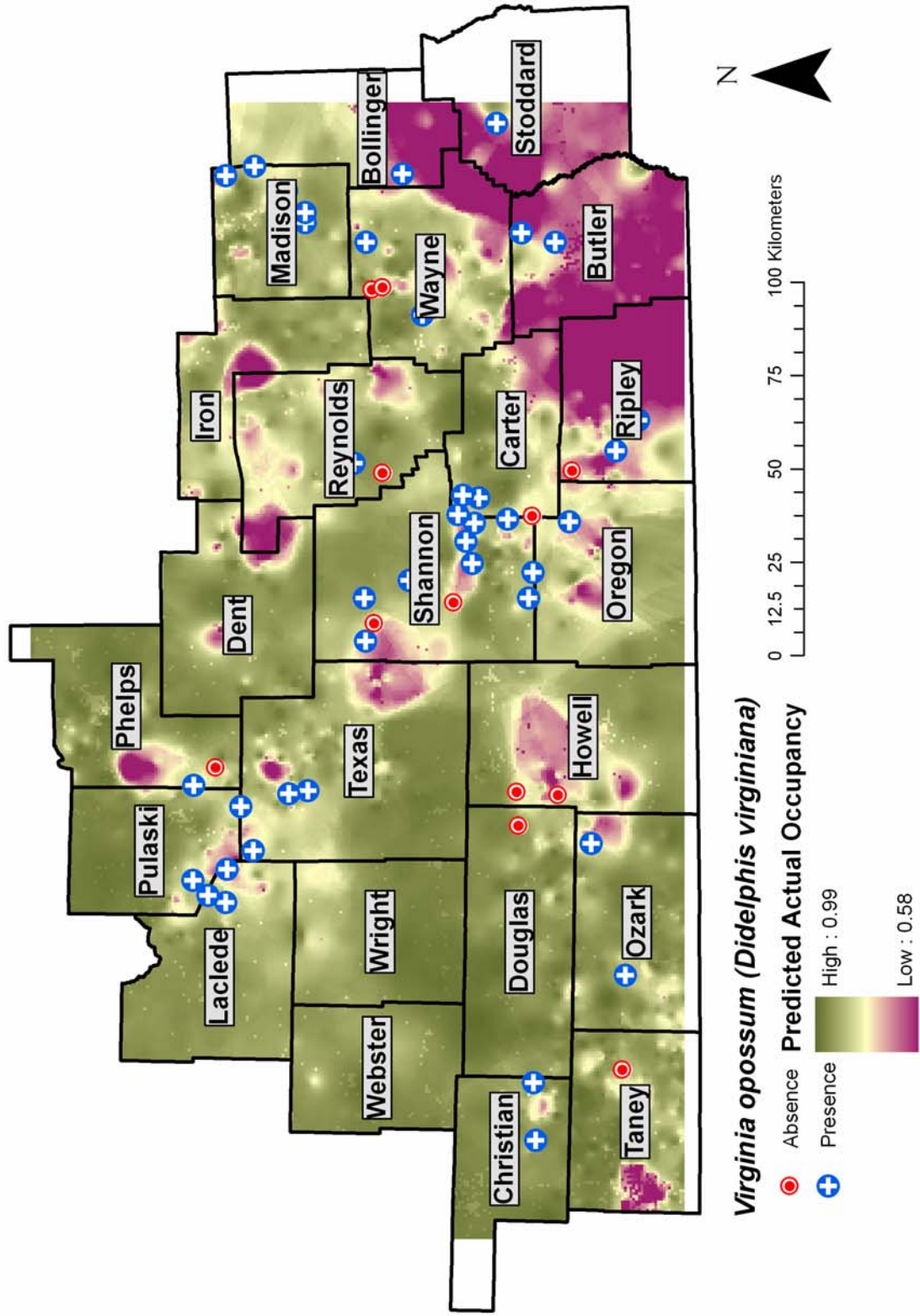


Figure 2b. Map of study region depicting predicted actual occupancy (PAO) for Virginia opossom (*Didelphis virginiana*) based upon results of model averaging.

Appendix I. Locations of surveys for raccoon (PRLO) and opossum (DIVI) in the Missouri Ozarks

Site	County	Northing	Easting	PRLO	DIVI
Angeline 1	Shannon	4113348	637193	yes	yes
Angeline 2	Shannon	4116949	641284	yes	yes
Ava 1	Ozark	4059212	535704	yes	yes
Ava 2	Taney	4059841	510428	yes	no
Ava 3	Christian	4083960	507022	yes	yes
Ava 4	Christian	4083296	491444	yes	yes
Castor	Bollinger	4118635	750608	yes	yes
Coldwater	Bollinger	4128368	731898	yes	yes
Clearwater 1	Bollinger	4111708	674540	yes	yes
Clearwater 2	Bollinger	4117795	674306	yes	yes
CWCA	Stoddard	4093367	233905	yes	yes
Donaldson	New Madrid	4047308	281159	yes	yes
Flatwoods	Wayne	4113482	712319	yes	yes
Houston 1	Texas	4143947	585358	no	yes
Houston 10	Laclede	4166408	555153	yes	yes
Houston 2	Texas	4149054	584570	yes	yes
Houston 3	Texas	4162213	580846	yes	yes
Houston 4	Phelps	4168770	591318	yes	no
Houston 5	Phelps	4174801	586600	yes	yes
Houston 6	Laclede	4158898	569092	yes	yes
Houston 7	Laclede	4170984	556982	yes	yes

Houston 8	Texas	4175034	561138	yes	yes
Houston 9	Laclede	4165843	564127	yes	yes
Krooked Arrow	Bollinger	4162529	752363	yes	yes
Logan 1	Ripley	4123840	670658	yes	no
Logan 2	Ripley	4131663	673107	yes	yes
Lanford	Madison	4144940	737386	yes	yes
Mark Twain 1	Shannon	4099350	657164	no	yes
Mark Twain 10	Ripley	4055454	684647	yes	yes
Mark Twain 2	Shannon	4100052	646264	yes	yes
Mark Twain 3	Carter	4085339	636392	yes	yes
Mark Twain 4	Carter	4083703	643471	yes	yes
Mark Twain 5	Oregon	4090448	657670	yes	yes
Mark Twain 6	Oregon	4083814	658353	yes	yes
Mark Twain 7	Oregon	4074069	656856	yes	yes
Mark Twain 8	Oregon	4073026	670652	yes	yes
Mark Twain 9	Ripley	4061446	675830	yes	yes
Poplar Bluff	Butler	4077728	731746	yes	yes
Peck Ranch 1	Carter	4098267	663865	yes	yes
Peck Ranch 2	Carter	4103865	658902	yes	yes
Peck Ranch 3	Carter	4102447	664616	yes	yes
Rocky Creek 1	Shannon	4108054	638136	yes	yes
Rocky Creek 2	Shannon	4104843	635858	yes	no
Sam Baker 1	Wayne	4124280	719666	yes	no

Sam Baker 2	Wayne	4127206	718974	yes	yes
Sunklands 1	Shannon	4128841	636963	yes	yes
Sunklands 2	Shannon	4125988	630265	no	yes
Sunklands 3	Shannon	4128577	625414	yes	yes
University Forest	Butler	4086734	734522	yes	yes
Willow Springs 1	Ozark	4068181	570977	yes	yes
Willow Springs 2	Howell	4076767	583647	yes	no
Willow Springs 3	Howell	4087835	584997	yes	no
Willow Springs 4	Douglas	4087463	575989	yes	no

Appendix II. Mean, standard deviation (SD), and range of values for landscape variables used in occupancy modeling for raccoon (PRLO) and opossum (DIVI).

	n	distance to water			area water			other species presence			mean perimeter edge		
		mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
PRLO presence	50	0.02	1.01	-1.6 to 2.6	0.21	0.11	0.04 to 0.41	0.86	0.35	0 to 1	na	na	na
absence	3	-0.62	0.74	-1.2 to -0.1	0.25	0.15	0.14 to 0.35	1	0	na	na	na	na
DIVI presence	47	-0.02	1.01	-0.2 to 2.6	0.21	0.11	0.04 to 0.44	0.96	0.21	0 to 1	0.004	0.99	-1.6 to 3.4
absence	8	0.13	1.01	-1.4 to 1.5	0.19	0.11	0.08 to 0.33	1	0	na	-0.03	1.15	-1.4 to 2.1

	n	core area index			fractal dimension			area forest		
		mean	SD	range	mean	SD	range	mean	SD	range
PRLO presence	50	na	na	na	na	na	na	na	na	na
absence	3	na	na	na	na	na	na	na	na	na
DIVI presence	47	-0.05	0.35	-0.2 to 1	1.57	0.05	1.4 to 1.7	0.08	0.06	0.01 to 0.26
absence	8	-0.20	0.00	na	1.60	0.01	1.59 to 1.61	0.07	0.04	0.02 to 0.13

CHAPTER 5

USING HABITAT ASSOCIATION AND INTERSPECIFIC OCCURRENCE DATA TO CREATE PREDICTIVE LANDSCAPE MODELS FOR COYOTE, BOBCAT, AND GRAY FOX IN THE MISSOURI OZARKS

Harvey Mundy Hackett IV and Matthew E. Gompper

Abstract

The composition of the typical North American temperate forest carnivore community has changed greatly in the last century, with the coyote becoming an abundant apex predator. How coyotes may influence the distribution of other forest carnivores is unclear. I used infrared remote cameras and scat transects to detect coyote, bobcat and gray fox at 53 sites across the Ozark region of southern Missouri. These distribution data were combined with habitat and environmental variables at multiple spatial scales to model the habitat associations of each species as well as to assess the effects on models of predicted occupancy by including the presence data for the other guild member during the model building process. None of these species had single occupancy models that alone were good predictors of observed occupancy, so model averaging was used for all three species to obtain model averaged values for coefficients used to create predictive distribution maps. The probability of actual occupancy (PAO) for coyotes was best predicted by measures of human disturbance and prey distribution.

Bobcats were primarily influenced by coyote presence and prey availability. Gray foxes were the most heterogeneous in their regional predicted distribution, and were best predicted by measures of coyote and bobcat presence as well as by landscape elements related to humans and settled areas. As a whole, these results suggest that coyotes produce a structuring dynamic on these other two forest mesocarnivores in the Ozarks.

Introduction

Members of the mammalian order Carnivora are important components of a functioning ecosystem. This group of species receives a disproportionate amount of attention from conservation managers, much of which is tied directly to their charismatic public image, direct competition with humans for prey, and an historical importance as an important natural resource (Gittleman et al. 2001; Ray et al. 2005). More recently, there has been renewed interest in these species as a critical component of various landscape ecology approaches to resource management, in part due to their potential to fundamentally influence communities and ecosystems in ways that are disproportional to their biomass in the system (Estes et al. 1998; Crooks and Soulé 1999; Post et al. 1999; Terborgh et al. 1999; Fortin et al. 2005; Ray et al. 2005).

The landscape of the Midwestern United States has changed a great deal over the last two hundred years. Prairies have given way to streamlined agricultural operations, forests have been converted to family farms and then back to forest, and an expanded human footprint has occurred in the form of cities and roads. The historical apex carnivore species, gray wolf (*Canis lupus*) and cougar (*Felis concolor*), have been replaced by the coyote (*Canis latrans*). Most knowledge of coyote ecology and behavior

comes from studies conducted in the open western North America (Camenzind 1978; Andelt 1982, 1985; Gese 1988a, 1988b, 1989, 1996; Mills and Knowlton 1991; McClennen et al. 2001), but in recent years more has become known about their ecology in forested Midwestern and eastern regions (Ray 2000; Gompper 2002; Chamberlain and Leopold 2001, 2005; Chamberlain et al. 2000, 2003; Kays et al. 2008). Part of the coyote's successful range expansion can be linked to the species ability to use forested regions where white-tailed deer (*Odocoileus virginianus*) are abundant (Gehring and Swihart 2003; Kays et al. 2008). Thus the coyote has assumed the apex role within forested temperate ecosystems. It remains unclear, however, how this may influence other forest carnivore species.

Two co-occurring forest predators that may be influenced by coyotes are bobcat (*Lynx rufus*) and gray fox (*Urocyon cinereoargenteus*). The bobcat is intermediate in its sensitivity to urbanization and fragmentation (Kamradt 1995; Crooks 2002) relative to the coyote, and is strictly carnivorous (Anderson and Lovallo 2003) whereas the coyote is more omnivorous and capable of taking advantage of anthropogenic food resources (McClure et al. 1995; Quinn 1997; Fedriani et al. 2001). Gray foxes are thought to be common throughout their range (Fritzell and Haroldson 1982), and relative to the coyote and bobcat are presumably the most heavily dependent on forest environments (Alderton 1994; Harrison 1997). Despite their apparent abundance, however, knowledge gaps exist as to how gray foxes as well as bobcats respond to increases in coyote distribution and habitat fragmentation (but see Constible et al. 2006).

Research has revealed little information about the level and effects of interaction between the coyote, bobcat, and gray fox in forested ecosystems where they co-occur

(Gehrt and Prange 2006), and even less is understood with respect to their response to alterations of large landscape patterns (Sargeant et al. 1998; Crooks 2002). Bobcats may react to the effects of fragmentation at a landscape level, but coyote and gray fox seem less affected (Constible et al. 2006). Gehrt and Prange (2006) found that the theory of carnivore community dynamics and structuring related to body size did not hold for this triumvirate in Illinois, raising the questions of how mesocarnivores segregate their environment, at what spatial scale can these relative differences be observed, and whether their effects on the broader community can be examined through the use of multi-scale predictive occupancy modeling

Recent years have seen a surge in research techniques and studies that allow large-scale assessment of spatial patterns and relative abundance of carnivores. Yet for the effective management and conservation of top carnivores, two major knowledge gaps must be addressed. First, most studies focus on just one or two species and their habitat use at the home range level, hindering understanding of forest carnivore habitat relationships at the landscape scale (Ruggiero et al. 1994). Second, the relative importance of habitat characteristics at various scales (e.g., stand vs. landscape) is unknown (Bissonette and Broekhuizen 1995), but these species likely select their resources at different spatial magnitudes depending upon resource distribution and rarity. If conservation priorities for forest carnivores are to be effective, these knowledge gaps must be filled.

I used data on the forest carnivores in southern Missouri to determine patterns of distribution for coyote, bobcat, and gray fox, and integrated this information with habitat data gathered from multiple spatial scales to create predictive models of species

occupancy patterns in the region. My primary objective was to identify factors related to presence of coyote, bobcat and gray fox in the Ozarks and use that information to predict the occurrence of each species in the Ozarks. If the assumed hierarchy of this community based upon past research and carnivore community theory (see Dayan and Simberloff 1996; Palomares and Caro 1999; Linnell and Strand 2000; Carbone and Gittleman 2002) holds, I predict the coyote and bobcat maps will be driven by habitat and prey selection, but the bobcat will also be influenced by the distribution of coyote. The gray fox will be driven by habitat as well as the distribution of both the coyote and perhaps to a lesser degree the bobcat (Fritzell and Haroldson 1982).

Study area

Study sites were distributed over the extensive forested regions of southern Missouri (63,252 km²) commonly referred to as the Missouri Ozarks (Figure 1). The initial survey site pool was based on the presence of large, contiguous patches of forest cover, a close proximity to reliable sightings of eastern spotted skunks (Desanty-Combes 2003), and an attempt to distribute survey efforts across as large an area of the region as feasible. I ended up with 53 sites where camera surveys were implemented based on site accessibility and a minimum inter-site buffer distance of 5 km (Figure 1; Appendix 1). These sites represented a variety of forested habitats and levels of human disturbance, fragmentation, elevation, and topographic complexity. Of these 53 sites, 40 were also sampled using scat transects for coyote. There were fewer sites where scat transects were conducted due to limitations of available roads suitable for scat surveys.

Methods

Occupancy surveys

Occurrence of bobcat and gray fox was documented with infrared remote cameras and occurrence of coyote was documented via scat transects, implemented from February to May 2005 and August 2005 to May 2006. Coyotes have been characterized as being wary of elements introduced into their home ranges by humans (e.g. traps or cameras), but they readily use roads and trails to traverse their home range and to mark their territory. Therefore, I used scat transects to document their presence. Survey stations (n=9) were established in a 3 x 3 grid with a spacing of ~250 m between stations, and a minimum distance of 5 km between survey sites. At each survey grid node a camera (DeerCam Model Nontypical with 400 speed film) was placed 0.5-1.0 m above the ground on the bole of a tree, and pointed at an opposing tree upon which a partially opened can of sardines was nailed 0.25-1.0 m above the ground. Distance between the camera and the bait tree was 2-4 meters. In instances where there no suitable trees were available, a downed tree or log was substituted. Once a camera station was set and activated, it was revisited on day 7-8 to replace film and batteries, re-bait, and re-align the camera if necessary. Camera stations ran 14-15 days. This data allowed me to create a detection history and estimate probability of detection (POD) for bobcats and gray foxes. Probability of detection is the probability of detecting an animal during a specified survey period in an area given that the animal is present during the survey attempt.

Scat surveys were performed along dirt roads that bisected survey sites to gain an index of presence for coyote. Coyotes defecate regularly on trails and unpaved roads providing data that can be used to measure presence and the relative abundance of coyote

populations (Knowlton 1984; Stoddart et al. 2001; Gompper et al. 2006; Kays et al. 2008). To minimize the confusion of large gray fox scat and small coyote scat, only scats >21mm in diameter were recorded as derived from coyote (Danner and Dodd 1982). On day 1 all scat was cleared from the survey transect, and then on days 15, 30, and 45 all scat were counted and cleared, and their location recorded with GPS. All coyote scat transects were ≥ 5 km in length. The metric used for scats was a scat/km/day

GIS layers

Spatial data used to quantify the model variables were obtained from the Missouri Spatial Data Information Systems (MSDIS) online database (<http://msdisweb.missouri.edu>). All manipulations of spatial data and analyses were conducted using ArcGIS (ESRI, Redlands, California, USA) software. Forest data were extracted from 30-m resolution Landsat-based raster land cover data for Missouri. This layer was based on circa 2000-2004 satellite imagery. Data for stream networks, the National Wetlands Inventory, and the Wetlands Restoration Program lands were used to improve the mapping of open water, woody-dominated wetland, and herbaceous-dominated wetland. Overall accuracy of this layer was not assessed, but for the specific land cover type forest and its components, 94% (50 of 53) of survey sites were properly classified into the forest category. I extracted, merged, and reclassified deciduous forest, evergreen forest, mixed forest, deciduous-woody herbaceous, evergreen-woody herbaceous, and woody-dominated layers into a single forest layer for analyses. Areas in the 2005 Land-use Land-cover (LULC) that were identified residential, commercial, industrial, or “other urban” were extracted and merged together into a single “disturbed”

layer. A poly-line map layer that combined primary rivers, all permanent water sources, and all year-round stream reaches was extracted from the Missouri surface water dataset. These data were originally in separate raster layers available from MSDIS. Roads were extracted from the 2005 MODOT Roads of State of Missouri (1:100,000) layer. No discrimination between different categories of roads was made other than the requirement that they be “improved”, because the goal was to document and assess the relationship of patterns of species distributions to the general concept of a “road” as a manmade linear feature bisecting the environment. However, due to the rural nature of the majority of these survey site locations, most roads came from the category county roads. I used the Vector-based Landscape Analysis Tools Extension for ArcGIS 9 (V-Late version 1.1) for analysis of polygon layers. This extension is similar to the commonly used, raster-based Fragstats (Riley et al. 1999), and was used to characterize patch metrics and spatial characteristics related to fragmentation.

A priori species models

Published studies on the ecology of each species were used to develop a set of preliminary predictor variables and *a priori* occupancy model sets (Table 1). The same variables within each occupancy model set were selected for all three species to facilitate differentiation and comparisons of similarities in habitat association and to provide some elucidation for how each species seems to respond to variables measured at different spatial scales. All three species had LANDSCAPE and SETTLED model sets created. SETTLED was identified as any map feature relating to a manmade feature or alteration of the landscape that resulted in a non-natural environment. Thus the SETTLED layer

was comprised of features relating to roads and urban classified portions of the Missouri LULC GIS layer. Coyote and bobcat each had a PREY model set created, and bobcat and gray fox each had a PREDATOR model set created. Justification for these model sets is detailed below.

To varying degrees, all three species have been associated closely with metrics related to forest cover and landscape form. Chamberlain et al. (2000) and Atwood et al. (2004) noted the importance of forest cover for coyote, and studies have also shown landscape scale relationships between forested habitat and bobcat (Woolf et al. 2002) and gray fox (Haroldson and Fritzell 1984; Chamberlain and Leopold 2005). Chamberlain et al. (2003) observed young and mature pine stands were important to bobcat habitat selection, and Constible et al. (2006) observed that intermixing habitat, the complexity of habitat patches, and the contrast of habitat edges were all key predictors of bobcat space usage. In forested landscapes, Chamberlain and Leopold (2005) observed a high degree of overlap in spatial distribution and home ranges of all three species at the landscape scale. It is suggested that habitat partitioning between these three species happens at the core home range level (Chamberlain et al. 2000, 2003; Chamberlain and Leopold 2000). Therefore, I created a LANDSCAPE model set that characterized these qualities in the landscape. I incorporated core-area-index (cai), fractal dimension (fd), mean-patch-edge (mpe), percent area forest (%/km²), and distance to nearest water (m) into the LANDSCAPE model set to represent these features (Table 1).

Coyotes have shown an aversion for urban related features (Kitchen et al. 2000; Atwood et al. 2004), the presence of gray foxes have been negatively associated with paved roads (Dickson et al. 2005; Markovchick-Nicholls et al. 2008). Bobcats have been

classified by several studies as highly sensitive to habitat fragmentation and disturbance (Crooks 2002; Tigas et al. 2002). Thus, the SETTLED model set was meant to characterize the extent to which a landscape was disturbed by human alteration of the natural environment. I incorporated distance to nearest road (m), distance to urban landcover type (m), road density (m/km²), and proportion of urban area (km²/ha) into the SETTLED model set (Table 1).

The PREY model set incorporated a layer representing potential suitable white-tailed deer (*Odocoileus virginianus*) forage/cover habitat that was first used in Michigan (Strong 2001). It involves reclassifying the Missouri LULC layer in such a fashion that habitat types which could provide forage and browse cover for white-tailed deer are identified. This habitat is comprised of agricultural, woodlot, and transition areas within the landscape. White-tailed deer range from being a year-round (Knowlton 1964) to a seasonal food resource for coyote and bobcat (Leopold and Krausman 1986; Koehler and Hornocker 1991; Neale and Sacks 2001; Gompper 2002; Thornton et al. 2004). The extent to which white-tailed deer comprise the diet of coyote or bobcat in Missouri is unclear since no recent studies have occurred and the relative abundance of coyotes, bobcat and deer have changed dramatically over the past several decades. However, the type of habitat selected for by white-tailed deer will also provide ample areas for numerous other small mammal species (Calvete et al. 2004). One study showed that 53.7% of coyote diet in Missouri was comprised of rabbits (*Sylvilagus* spp.) (Korschgen 1957). The bobcat diet in Missouri has been documented as consisting of 67% rabbits as well as other small mammals and white-tailed deer (Hamilton 1982).

The PREDATOR model was the incorporation of the product of competitor/predator presence created from the detection history for that species. Thus, the bobcat PREDATOR model set incorporated coyote only, but gray fox incorporated coyote and bobcat. The scat transect detection history for coyote was augmented by infrared remote camera at the 13 sites where no scat transect was performed to obtain a sample size of 53 sites for coyote presence to be used in the PREDATOR model. Although documented coyote predation directly on bobcat is rare (but see Toweill 1986; Knick 1990; Fedriani et al. 2000; Gipson and Kamler 2002), coyote may suppress or limit bobcat numbers in an area via exploitation competition (Major and Sherburne 1987; Litvaitis and Harrison 1989; Fedriani et al. 2000). Predation of gray fox by coyote adheres to classic Canidae suppression theory (Fedriani et al. 2000; Farias et al. 2005). Bobcat predation on gray fox has also been documented (Farias et al. 2005), although the extent and importance of interaction is unclear.

In addition to the fine scale (grid-level) assessment of the presence of the two target species, I selected two spatial scales for analyses based on the approximate maximum home range size of the eleven species that comprise the carnivore community of the Ozarks. A medium scale (9 km²), and coarse scale (650.25 km²) corresponded with the average size of the survey grid (0.5 km on a side) plus a 2.5 km radius buffer, and the survey grid plus a 25 km radius buffer, respectively. Values for each predictor variable at each survey site were calculated for its corresponding scale from the center survey node in the 3x3 grid (Table 1).

Modeling framework

I used likelihood-based occupancy modeling (MacKenzie et al. 2002, 2005; MacKenzie and Bailey 2004) in a two part process to estimate species detectability (p ; the probability that the species will be detected, given that it is present) and site occupancy (Ψ ; the probability that a species occurs at a site) from the presence/absence data. First, I modeled the various detection covariates that were surmised to potentially affect survey results. One of the covariates that could play a pivotal role in the actual occupancy of a given study site by a species was the relationship of the time of year or season which sampling occurred within. I modeled Julian date, Julian date squared (Julian^2) and Julian cubed (Julian^3). Once the proper seasonal detection covariate(s) was determined for each species it was then modeled with two more sample covariates for bobcat and gray fox: (survey order (cameras only), survey day (cameras only)). The nature of the scat data collected for coyote did not lend itself to modeling any detection covariates except for the three Julian date parameters. As part of the broader study, track-plates were also incorporated as a survey method (see Chapters 2-4), and because the order of implantation was varied randomly across sites it was necessary to account for the potential pre-baiting effect this could have on target species even though none of these species were sampled with track-plates in survey efforts. These covariates were modeled together and individually, and then the two highest weighted single covariate models were combined. The most parsimonious set as indicated by the lowest Akaike's Information Criterion adjusted for small sample size (AICc) was used as the NULL model during occupancy model selection.

Model development and selection

I modeled probability of occupancy (PAO) as the dependent variable. Candidate models were compared using AIC_c (Burnham and Anderson 2002). Goodness-of-fit statistics and an index of over-dispersion ($\hat{c} = \chi^2 / df$) were calculated from the global model (Burnham and Anderson 2002). The global model consisted of all model subsets and all detection covariates carried forward from the most parsimonious detection model. Models were ranked using ΔAIC_c . Models with ΔAIC_c values ≤ 2 from the most parsimonious model were considered strongly supported, and their variables were considered to be the most determinant of species occurrence patterns in the best averaged model.

To further interpret the relative importance of each model's independent variable, given the *a priori* model set, Aikake's weights (w) were used. ΔAIC_c values were used to compute w_i , which is the weight of evidence in favor of a model being the best approximating model given the model set (Burnham and Anderson 2001). Unless a single model had a $w_i > 0.9$, other models were considered when drawing inferences about the data (Burnham and Anderson 2001). A 90% confidence model set was created by summing all w_i until 0.90 was achieved. I assessed the relative importance of each variable by summing normalized w_i values for every model in which that variable appears (Anderson et al. 2001). I anticipated differences in the numbers of models in which different variables were likely to occur, and therefore calculated an adjusted weight for all parameters using the formula

$$\text{Adjusted } w_i = (\# \text{ models} * w_i) / ((\# \text{ models with variable}) * (\text{total } \# \text{ variables})).$$

A null model with only the intercept term and detection covariates was included to ensure that variables used were relevant to the data set. To evaluate the effectiveness of top models from each spatial scale, I assessed the classification success for those models. This provided a diagnostic tool to determine how well each model differentiated between sites of presence versus absence for each species.

Detection and occurrence models were fit to species detection histories with Program Presence 2.0 with the single-season option (MacKenzie et al. 2006). I modeled all model subsets for detection covariates to determine the most parsimonious detection model, which would then be incorporated into all occurrence models. I modeled Ψ by creating a set of *a priori* candidate occurrence models (Table 1) for each species. The single season occupancy model of MacKenzie et al. (2006) uses multiple surveys on a collection of survey sites to construct a likelihood estimate using a series of probabilistic arguments. False negative surveys can be somewhat corrected for via estimation of POD, providing a more accurate assessment of site occupancy values (MacKenzie et al. 2002). Both occupancy and POD were modeled with sample-specific covariates by introducing a logit link function, thereby performing logistic regression analyses on occupancy and detectability simultaneously (MacKenzie and Royle 2005). All continuous covariates were standardized to z-scores prior to analysis, allowing model coefficients to be interpreted as the change in the log-odds ratio of occupancy relative to a 1-standard deviation change in the covariate from its mean. Models that did not result in convergence, or for which convergence was questionable due to inestimable parameters (Cooch and White 2005), were eliminated from the candidate set.

Model Validation

I validated accuracy of final models created from model averaging by calculating the area under the curve (AUC) for receiver operating characteristic (ROC) curve and by creating confusion matrices for each dataset. I used web-based ROC analysis software (Eng 2005) to generate ROC curves and to calculate AUC values. This process works by taking the existing dataset of presence/absence values (1/0) and matching it with POD values for each site using the model averaging equation (i.e. averaged coefficients carried forward in 90% confidence model set). The program then computes the ROC curve, provides the AUC value and the parameters needed to plot the ROC curve in a spreadsheet program of ones choosing. ROC curves were obtained by plotting all sensitivity values (true positive proportion; 1-false-negative rate) against the false positive proportion (1-specificity [true negative proportion]) (Fielding and Bell 1997) values. The area under the curve (AUC) is a threshold-free (i.e., does not require designation of an arbitrary cutoff for specifying presence or absence from probability values) index model of classification performance and indicates overall ability of the model (Fielding and Bell 1997) to accurately predict the data used to create it. AUC values range from 0.5 to 1.0, with 1.0 indicating perfect accuracy and 0.5 indicating a model performing no better than a null model (Fielding and Bell 1997). Values of AUC > 0.7 were interpreted as indicating excellent similarity between predicted and observed values for that species, whereas values between 0.5 and 0.7 were good.

Confusion matrices were created, and the accuracy and precision calculated. A confusion matrix (Provost and Kohavi 1998) contains information about actual and predicted classifications done by a classification system. Performance of such systems is

commonly evaluated using the data in the matrix. Because the estimated accuracy may be an inadequate performance measure when the number of negative cases is much greater than the number of positive cases (Kubat et al. 1998), I also calculated the geometric mean (g-mean) (Kubat et al. 1998) which accounts for this by including the true positive proportion in a product.

Model prediction

For each model in the 90% confidence set I calculated PAO for each 30 x 30-km grid cell in the study region using the averaged model-specific coefficient estimates and covariate information for that grid cell and the raster calculator function in ArcGIS.

Results

Carnivore surveys

Raw detection rates were 90.0% (36/40 sites) for coyote, 20.8% (11/53 sites) for bobcat and 28.3% (15/53 sites) for gray fox. These are minimal estimates of occupancy, as they do not account for variability in POD for each species. The most parsimonious model for detectability for coyote was a combination of all three covariates related to Julian date with PAO of 91% with per check detection rates ranging from 0.28 to 0.40 (Table 2a). The $\text{Julian}^2 + \text{Julian}^3 + \text{Day of survey period}$ model was the most parsimonious detection model for bobcat, predicting 27% PAO and detection ranged from 0.00 to 0.45 per check (Table 2b). The combination of $\text{Julian}^2 + \text{Day of survey period}$ was the most parsimonious detection model for gray fox, predicting 35.6% PAO and detection ranged from 0.03 to 0.45 per check (Table 2b).

Occupancy model selection

I attempted to fit a total of 8 models related to occurrence for both coyote and gray fox and 16 models for bobcat (Table 3). The numbers of detection covariates for coyote, bobcat, and gray fox were three, three, and two, respectively. The occurrence model with the greatest support for coyote was SETTLED + PREY ($w_i = 0.50$). Based upon this model, coyote were more likely to be found in or near areas where distance to urban areas and developed road features were greatest and where the proportion of potential prey habitat was greatest. The second most parsimonious model was PREY ($w_i = 0.26$), suggesting again a close relationship between coyote occupancy and quality prey habitat.

The best single supported model for bobcat was the PREY model ($w_i = 0.42$). PREDATOR ($w_i = 0.13$) was the third most supported model. The incorporation of these two models into the 90% model subset suggests absence of coyote and higher proportions of prey habitat in an area result in increased predicted occupancy for bobcat.

The PREDATOR model ($w_i = 0.33$) was the best supported single model for gray fox predicted actual occupancy. The next best model for gray fox was SETTLED ($w_i = 0.29$). These results suggest that the presence of coyote negatively affects gray fox predicted occupancy rates, but the presence of bobcat actually has a slightly positive effect. The SETTLED model suggests that areas with higher proportions of urban related features in the landscape that are closer to primary and secondary roads have lower predicted occupancy for gray fox.

Model results indicated some level of model selection uncertainty (i.e., no single model received $w_i > 0.9$) for any of the three species. The global model for all three species was unranked in the 90% confidence interval set of models, and combined with goodness of fit tests was shown to fit the data for all three species (coyote; $p = 0.67$, $c\text{-hat} = 0.70$, bobcat; $p = 0.89$, $c\text{-hat} = 0.40$, gray fox; $p = 0.67$, $c\text{-hat} = 1.01$). Given the model selection uncertainty, I extracted the 90% model confidence set for each species, recalculated model AIC_c weights, and calculated model-averaged estimates for each coefficient. The model averaged coefficients were then combined for each species to create the final occupancy models. The 90% confidence occupancy model set for coyote, bobcat and gray fox were each comprised of three models. These three models were used to create the 90% CI model set for gray fox. The number of variables present in the 90% confidence model subset, excluding detection covariates, was 5 for coyote, 2 for bobcat, and 6 for gray fox.

Model averaged parameters

Analyses of model averaged parameters for coyote revealed a negative association between predicted coyote occupancy and distance to settled areas and the proportion of area comprised of urban related landscape features (Table 4). There was a positive relationship for distance to road, area road and prey habitat (Table 4). The greatest effect was prey habitat ($OR = 42.10$, $\Sigma w_i = 0.76$) followed by distance to nearest road ($OR = 2.18$, $\Sigma w_i = 0.50$) (Table 4).

Model averaged parameters for bobcat indicated a negative association between predicted bobcat occupancy and coyote presence (Table 5). There was a positive

relationship for higher proportions of potentially good prey habitat (Table 5). The greatest effect was prey habitat (OR = 1.64, relative importance = 0.42) followed by the presence of coyote (OR = 0.83, relative importance = 0.13).

For gray fox, model averaged parameters revealed a negative association between predicted occupancy and distance to settled, area settled, and coyote presence (Table 6). A positive relationship was indicated for bobcat presence (Table 6). The greatest effect was coyote presence (OR = 0.71, $\Sigma w_i = 0.33$) followed by bobcat presence (OR = 1.24, $\Sigma w_i = 0.33$) and area settled (OR = 0.78, $\Sigma w_i = 0.269$) (Table 6).

Predictive maps for coyote revealed a distribution of predicted occupancy that was high throughout the majority of the Ozarks (i.e. ~65% of region PAO ≥ 0.75 ; Figure 3a). There was less than 20% of the area predicted to be < PAO 0.20 for coyote. The predictive maps for bobcat and gray fox were more heterogeneous in nature, with patches of high and low PAO throughout the region (Figure 3b-c). The single largest region of high gray fox PAO was located within the central area of United States Forest Service habitat in eastern Shannon, southern Dent, and western Reynolds counties. Overall, the PAO for bobcat was lower region wide compared to the gray fox, but there was an area of the highest PAO located in eastern Shannon and western Reynolds counties that corresponded to the areas of highest gray fox PAO. Approximately 15% of the region had a predicted PAO > 0.30 for bobcat. Gray fox had a predicted PAO > 0.50 in about 30% of the survey region. The gray fox map indicated 6 cores areas of high PAO overall, compared to only 4 for the bobcat. The area of the region that seemed to contain the largest single area of high PAO related to bobcat was located at the northwestern edge of

the Missouri Bootheel region where the Ozarks give way to the lowland floodplains of the Mississippi river.

Model validation

I applied the equation for each species derived from the model averaging coefficients to all 53 sites surveyed to obtain a value for predicted occupancy. Then this value was compared to the actual detection history for each species to construct the ROC curve and obtain the AUC value. The AUC calculated for bobcat was 0.80 and 0.74 for gray fox (Figure 2). There was no ROC/AUC analysis performed on the data for coyote because the values for POD were only 0 or 1, which would result in a ROC curve that was uninformative and an AUC value of 1.0 which is not insightful. Distance to road, area road, area settled, and prey habitat were all considered significant predictors of coyote occupancy because their 90% confidence intervals did not overlap zero (Table 4; Appendix 2). The coyote occupancy model averaging model accuracy based upon the confusion matrix was 0.90, the precision was 0.25, and the geometric mean accuracy was 0.35 (Table 7). Neither prey habitat or coyote presence had their 90% CI overlap zero for bobcat model averaging, and thus were determined to both be significant predictors of bobcat occupancy (Table 5; Appendix 2). The bobcat occupancy model averaging model accuracy based upon the confusion matrix was 0.68, the precision was 0.33, and the geometric mean accuracy was 0.53 (Table 7). There were several significant predictors for gray fox as indicated by the model-averaging coefficient 90% CI not overlapping zero (Table 6; Appendix 2) including the presence of both coyote and bobcat. The gray fox

predictive model accuracy based upon the confusion matrix was 0.42, the precision was 0.79, and the geometric mean accuracy was 0.84 (Table 6).

Discussion

Exploitation competition for food as well as interference competition may exist between coyote and bobcat (Dibello et al. 1990; Litvaitis and Harrison 1989), an interaction that if true in Missouri may help explain the reason why the addition of knowledge about coyote presence in the occupancy modeling process influences and improves the resulting prediction ability of the bobcat model. Combined with the incorporation of coyote presence into the 90% confidence model set for gray fox, this work lends credence to the depiction of the coyote as the apex carnivore in Missouri forested environments.

This work indicates that a proper understanding of forest carnivore ecology should examine relationships between species distribution patterns and habitat characteristics at multiple spatial scales, especially in fragmented environments. In addition to an allometric scaling of carnivore body size with the scale at which a landscape is perceived (Lidicker and Koenig 1996), the breadth of a species niche has also been suggested as influencing the spatial characteristics that best characterize a species distribution pattern (Gehring and Swihart 2003). Smaller carnivores like the gray fox may have a more difficult time perceiving the existing continuity between habitat patches within a larger landscape matrix, but this is less of a problem for a larger bodied species like the coyote. My results suggest that distribution of the coyote in the southern Ozarks is influenced primarily by variables measured at the landscape level, while bobcat

and gray fox patterns of distribution can be more effectively predicted by local and medium scale habitat components and the inclusion of the presence information of other members of the carnivore guild.

Coyote

Coyotes utilize manmade linear features like roads to traverse and delineate territories. Chamberlain and Leopold (2001) observed primitive roads were not a key cause of coyote mortality, and other effects to the spatial distribution of coyotes caused by anthropogenic changes to forest ecosystems are also well studied. Kays et al. (2008) observed a negative correlation between coyote abundance and the amount of rural non-forest landscape and other research has shown that coyote use corridors between habitat patches extensively while avoiding urban elements (Atwood et al. 2004). Distance to roads, distance to settled, fractal dimension of roads, percent area settled, and percent potential prey habitat were all important predictors of coyote occupancy. My results found that greater proportions of suitable prey habitat were positively correlated with increased predicted coyote occupancy. Natural edges and disturbed forests are favored by coyotes in northeastern North American forests, possibly providing refuge from human persecution and hunting (Kays et al. 2008). This selection of habitat based upon the presence of human elements has also been observed in ungulates (Millsbaugh et al. 2000), one of the coyotes primary foods in throughout North America. Distance to nearest developed road and area roads exhibited a positive influence on coyote PAO, while distance to nearest settled and area settled were negatively correlated with predicted coyote occupancy. George and Crooks (2006) observed reduced coyote

activity in areas with greater urban development compared to areas of less urban development. The general consensus is that coyote habitat use in fall to spring is largely determined by their prey (Brundige 1993), and by areas that provide suitable den locations. Thus it is likely that selection of the PREY model is accounting for more than potential prey resource alone.

Bobcat

The model averaging results for bobcat indicated that PAO was driven by areas of higher potential prey habitat and lower presence by coyote. Studies in other regions of North America suggest prey availability is a major determinant of where bobcats locate their home ranges (Litvaitis et al. 1986; Lovallo and Anderson 1996; Kamler and Gipson 2000; Woolf et al. 2002). Thus, land cover type may not be as important to bobcat as the structural nature of that habitat.

Exploitation competition for food may exist between coyote and bobcat (Dibello et al. 1990; Litvaitis and Harrison 1989). Thornton et al. (2004) observed that in areas of sympatry between bobcat and coyote, they segregated their habitat through prey selection at a landscape scale, with coyote feeding mostly on white-tailed deer and bobcat on small mammals such as rabbits, but when examined at a more local spatial scale, spatial segregation was also a determining factor in bobcat patterns of distribution. This suggests that the scale at which an analysis is performed on mesocarnivores can result in different insights. Therefore, it is important to try and examine habitat effects at multiple spatial scales when studying carnivore habitat associations. Chamberlain and Leopold (2005) found that although there was extensive overlap in the general spatial distribution

of bobcat, coyote and even gray fox, at the core area level within each animal's home range there was spatial segregation between bobcat and coyote. Additionally, in areas where both species co-occur, there may be temporal or spatial segregation of resources that takes place on the part of bobcat to minimize potential encounters with coyote. Constible et al. (2006) modeled bobcat habitat using linear mixed modeling, and their results indicated that the habitat matrix or interspersions of various habitat components with one another at varying spatial scales were all potentially important predictors of space use by bobcats. They did not observe this pattern in coyote or gray fox.

Gray fox

The occupancy modeling efforts for gray fox indicated that at the landscape scale the presence of potential competition from other members of the Carnivore guild along with environmental characteristics related to human elements in the form of roads and settled areas were the most important driving forces. These results would seem to indicate that a complex set of variables play a role in the distribution of gray fox, and that both predator-competitor and human related environmental cues drive their patterns of distribution. Harrison (1997) found that gray foxes could coexist with roads, especially if culverts were present. Riley (2006) observed the highest gray fox densities were actually closer to urban edge than natural core areas, again likely allowing them to capitalize on the abundance of resources for food and shelter provided by humans. Gray fox can coexist with coyote (Johnson et al. 1996), but they seem to avoid coyote activity areas temporally and/or spatially as a strategy to avoid fatal encounters (Ingle 1990; Lovell 1996; but see Neale and Sacks 2001).

The lack of overwhelming support for a single model set related to specific land type factors contributing significantly to the final averaged model could also be a function of the more omnivorous diet and generalist habitat requirements of the species within forested landscapes. The selection of PREDATOR importance in the model selection process supports past studies that observed coyote and bobcat intraguild predation as a common cause of mortality for other fox species (O'Farrell 1984; Sargeant and Allen 1989; Ralls and White 1995; Cypher and Spencer 1998; Farias et al. 2005). The relationship between bobcat and gray fox was positive, whereas the relationship between coyote and gray fox was negative. The bobcat and coyote have a negative relationship as was indicated by incorporating coyote presence into bobcat models. Thus, although bobcats may predate on gray foxes, the bobcat presence may act as a surrogate for some aspect of the habitat that was unmeasured but is influential and selected for by gray foxes. Thus, it is possible that gray fox select the same habitat as bobcat at a landscape level, but on a more local scale foxes may spatially segregate from bobcats to minimize risk of predation. The removal of larger predators has resulted in increases in the numbers of gray foxes, suggesting that predation limits some fox populations (Crooks and Soulé 1999; Henke and Bryant 1999). Farias et al. (2005) recorded that coyote accounted for 67% (8/12) of observed gray fox mortalities but only 17% (2/12) could be attributed to bobcat related predation on gray fox.

Conclusions

Three of the most important results from my study of coyote, bobcat, and gray fox spatial ecology in the Ozarks of southern Missouri are noted here. First, the data suggest

hierarchical structuring in the carnivore community with coyote assuming the apex position. Second, that coyote and bobcat are negatively impacted by disturbance at the landscape scale represented by environmental variables that represent human alteration and fragmentation of the habitat. Third, the incorporation of conspecific data in the predictive modeling process of mesocarnivore occupancy can improve models of PAO for forest carnivores.

Coyote seem to be driven mostly by prey related dynamics, by specific human related landscape features to a lesser degree, and relatively little by the variables I measured relating to forest habitat and spatial dynamics. Similarly, bobcat distribution at a landscape scale is driven by the location of both its prey and potential competitor the coyote. Thus the coyote may exert an influential structuring dynamic on bobcat habitat selection. Coyote also is suggested as exerting a negative influence on gray fox presence in an area, but the presence of bobcat may actually indicate an area that is also more likely to contain gray fox. Gray fox, like the coyote, are also negatively affected by the human related landscape elements.

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Table 1. Model name and covariates included in *a priori*, multi-scale models for coyote, bobcat and gray fox.

Model name	Covariates	Covariate		k ^a (coyote/bobcat/gray fox)
		value range	Scale	
Disturbance model	Distance to nearest road	200 – 4. km	fine	
	Distance to nearest urban	53 – 17.9 km	medium	5/6/7
	Area Urban	0.1 – 9 %	coarse	
	Fractal dimension roads	-15 - 48	coarse	
Predator model	Coyote Presence	0 – 1	fine	na/3/5
	Bobcat Presence	0 – 1	fine	
Habitat model	Core area index	0 – 54	medium	
	Mean perimeter edge	14 – 610 km	medium	
	Fractal dimension forests	1.2 – 2.5	medium	6/7/8
	Area Forest	1 – 36 %	coarse	
	Distance to nearest water	7 – 19.1 km	fine	
	Area deer/small game browse/forage habitat	0 – 25 %	coarse	2/3/na

^a – Number of model parameters including detection covariates.

Table 2a-b. Detection models for (a) coyote, (b) bobcat and gray fox presence in the Ozarks, Missouri USA. Covariate components of each model listed with the number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (ΔAIC_c) and AIC_c weight (w_i). Lower AIC_c and ΔAIC_c and greater w_i represent models with more substantial support. The sample size for each model is denoted by k.

(a)

Coyote				
Model	k	AIC_c	ΔAIC_c	w_i
Julian	2	163.17	0.00	0.31
Julian ²	2	164.10	0.93	0.19
Julian ³	2	164.67	1.50	0.15
Julian + Julian ²	3	165.08	1.91	0.12
Julian + Julian ³	3	165.18	2.02	0.11
Julian ² + Julian ³	3	165.76	2.60	0.08
Global	4	167.44	4.27	0.04

(b)

Model	Bobcat				Gray fox			
	k	AIC _c	Δ AIC _c	w _i	k	AIC _c	Δ AIC _c	w _i
Global	4	151.98	0	0.82	3	294.43	0.00	0.56
Julian ²	2	169.36	17.38	0.00	2	308.72	14.29	0.00
Julian ³	2	233.36	81.38	0.00	na	na	na	na
Day	2	166.39	14.41	0.00	2	294.92	0.49	0.44
Julian ² + Julian ³	3	160.67	8.69	0.01	na	na	na	na
Julian ² + Day	3	155.19	3.21	0.17	na	na	na	na
Julian ³ + Day	3	165.19	13.21	0.00	na	na	na	na

Table 3. *A priori* predictive occupancy models for coyote, bobcat, and gray fox in the Ozarks, Missouri, USA. Covariate components of each model listed with the number of parameters (k), Akaike's Information Criterion adjusted for small sample size (AIC_c), distance from the most parsimonious model (Δ AIC_c) and AIC_c weight (w_i). Lower AIC_c and Δ AIC_c and greater w_i represent models with more substantial support. The sample size for each model is denoted by k.

Model	Coyote			Bobcat			Gray fox					
	k	AIC _c	Δ AIC _c	w_i	k	AIC _c	Δ AIC _c	w_i	k	AIC _c	Δ AIC _c	w_i
SETTLED + PREY	8	166.10	0	0.50	8	157.11	5.03	0.03	na	na	na	na
PREY	4	167.43	1.34	0.26	4	152.08	0.00	0.42	na	na	na	na
NULL	4	168.43	2.34	0.16	4	152.88	0.80	0.28	3	299.43	0.30	0.28
LANDSCAPE	8	171.51	5.41	0.03	8	160.80	8.72	0.01	7	303.59	4.46	0.04
SETTLED	7	171.79	5.70	0.03	7	158.37	6.29	0.02	6	299.37	0.23	0.29
LANDSCAPE + PREY	9	172.86	6.77	0.02	9	163.72	11.63	0.00	na	na	na	na
LANDSCAPE + SETTLED	12	178.36	12.26	0.00	12	171.05	18.97	0.00	11	310.92	11.79	0.00
GLOBAL	13	182.80	16.71	0.00	14	178.73	26.65	0.00	13	315.03	15.90	0.00
SETTLED + PREY + PREDATOR	na	na	na	na	9	158.56	6.47	0.02	na	na	na	na
PREDATOR	na	na	na	na	4	154.45	2.37	0.13	4	299.13	0.00	0.33
LANDSCAPE + PREDATOR	na	na	na	na	9	163.67	11.58	0.00	9	306.49	7.35	0.01
PREY + PREDATOR	na	na	na	na	5	154.99	2.90	0.10	na	na	na	na

LANDSCAPE + PREY + PREDATOR	na	na	na	na	na	10	166.71	14.62	0.00	na	na	na	na
LANDSCAPE + SETTLED + PREY	na	na	na	na	na	13	173.22	21.14	0.00	na	na	na	na
LANDSCAPE + SETTLED + PREDATOR	na	na	na	na	na	13	175.01	22.93	0.00	na	na	na	na
SETTLED + PREDATOR	na	na	na	na	na	8	161.11	9.03	0.00	8	302.97	3.84	0.15

Table 4. Model averaged parameter estimates, SE, odds-ratio, lower and upper odds-ratio interval, and summed weights of evidence for coyote.

parameter	estimate	SE	OR	lower	upper	weight of evidence
distance to road ¹	0.78	0.15	2.18	1.88	2.53	0.50
area road ¹	0.75	0.15	2.12	1.82	2.46	0.50
distance to settled ¹	-1.43	1.67	0.24	0.05	1.28	0.50
area settled ¹	-0.16	0.02	0.85	0.83	0.87	0.50
area forage/browse ²	3.74	1.02	42.10	15.18	116.75	0.76

¹ – Individual covariate in the SETTLED occupancy model.

² – Individual covariate in the PREY occupancy model.

Table 5. Model averaged parameter estimates, SE, odds-ratio, lower and upper odds-ratio interval, and summed weights of evidence for bobcat.

parameter	estimate	SE	OR	lower	upper	weight of evidence
area forage/browse ¹	0.49	0.38	1.64	1.12	2.40	0.57
coyote presence ²	-0.18	0.11	0.83	0.74	0.93	0.18

¹ – Individual covariate in the PREY occupancy model.

² – Individual covariate in the PREDATOR occupancy model.

Table 6. Model averaged parameter estimates, SE, odds-ratio, lower and upper odds-ratio interval, and summed weights of evidence for gray fox.

parameter	estimate	SE	OR	lower	upper	weight of evidence
distance to road ¹	-0.06	0.01	0.94	0.93	0.95	0.31
area road ¹	0.0004	0.0001	1.00	1.00	1.00	0.31
distance to settled ¹	0.003	0.033	1.00	0.97	1.04	0.31
area settled ¹	-0.25	0.13	0.78	0.68	0.89	0.31
coyote presence ²	-0.34	0.20	0.71	0.58	0.87	0.06
bobcat presence ²	0.21	0.09	1.24	1.13	1.36	0.06

¹ – Individual covariate in the SETTLED occupancy model.

² – Individual covariate in the PREDATOR occupancy model.

Table 7. Confusion matrices, accuracy, precision, and geometric mean accuracy values for predictive models of coyote, bobcat, and gray fox using model averaging.

	<u>coyote</u>	<u>bobcat</u>	<u>gray fox</u>
	<u>Predicted</u>		
<u>Actual</u>			
positive	33	9	14
negative	1	13	30
	3	4	1
	0.90	0.68	0.42
accuracy			
	0.25	0.33	0.79
precision			
	0.35	0.53	0.84
g-mean			

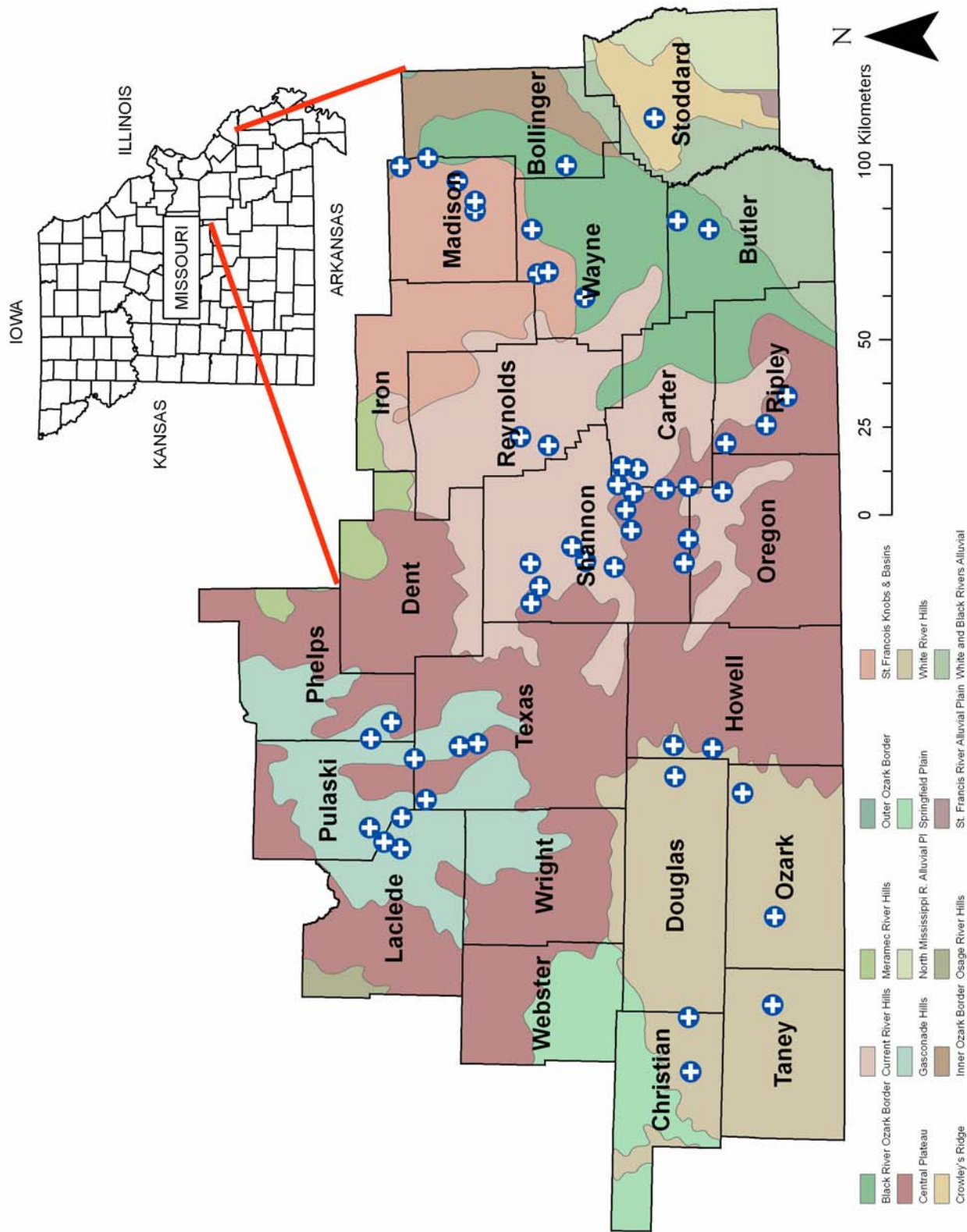
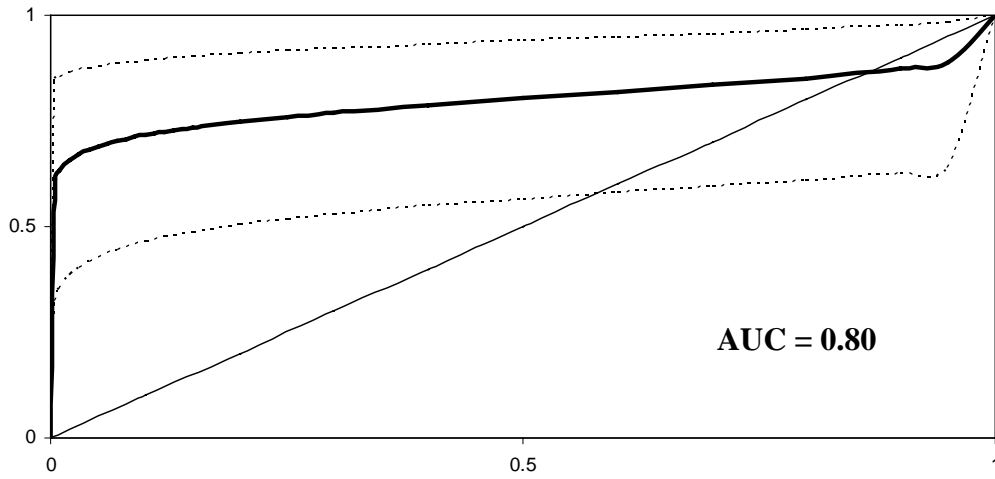


Figure 1. Map of survey sites (n = 53) and corresponding ecological subsections in southern Missouri.

(a)



(b)

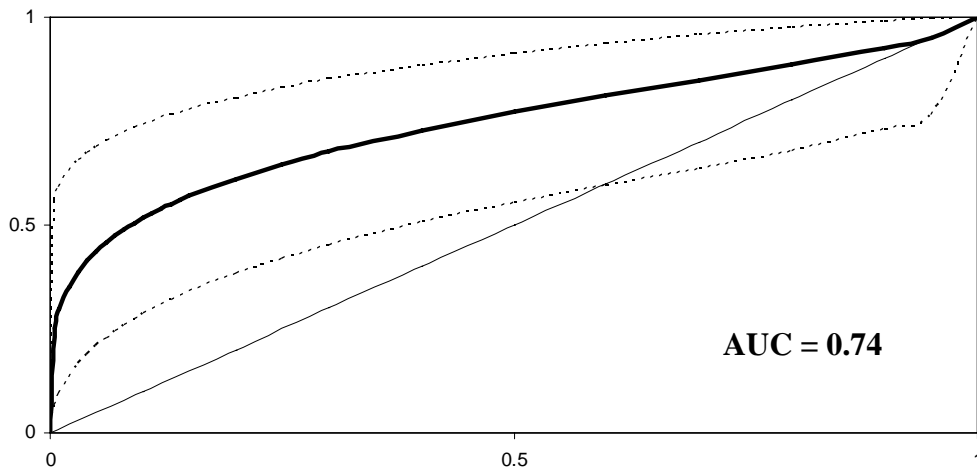
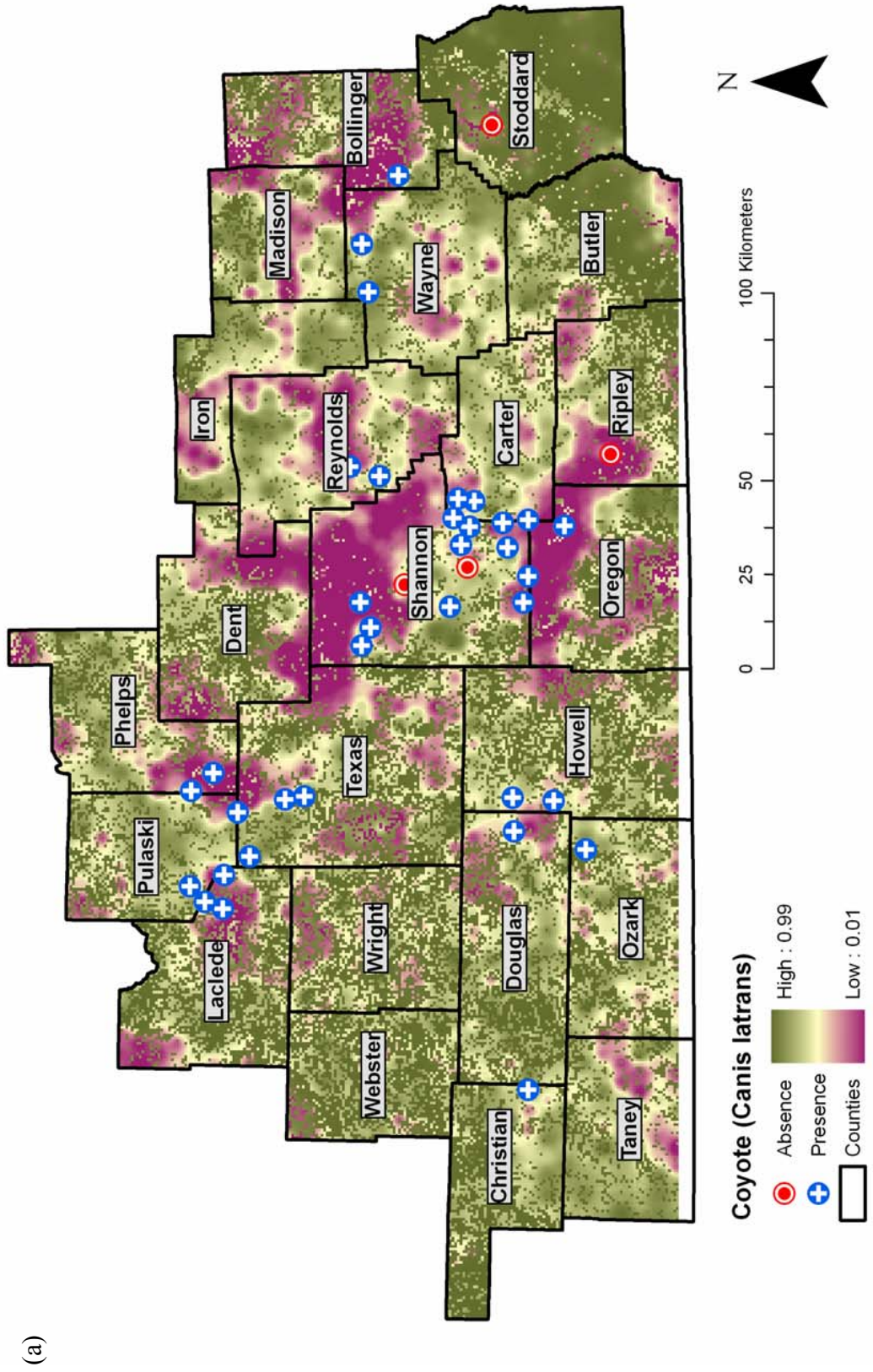
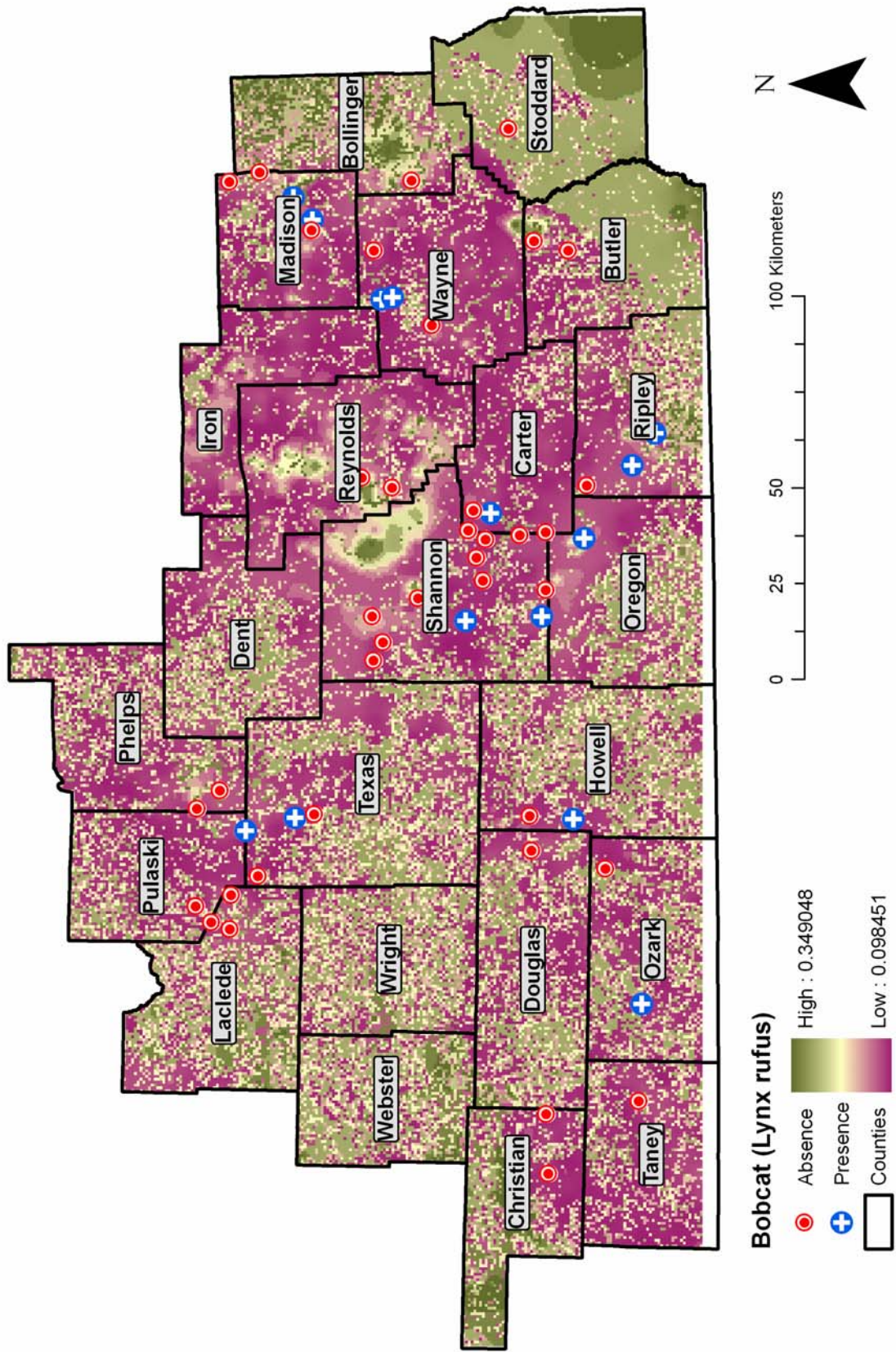


Figure 2. ROC curves (a) bobcat and (b) gray fox predictive model in the Ozarks region of Missouri. Dashed lines represent the 95% confidence intervals.

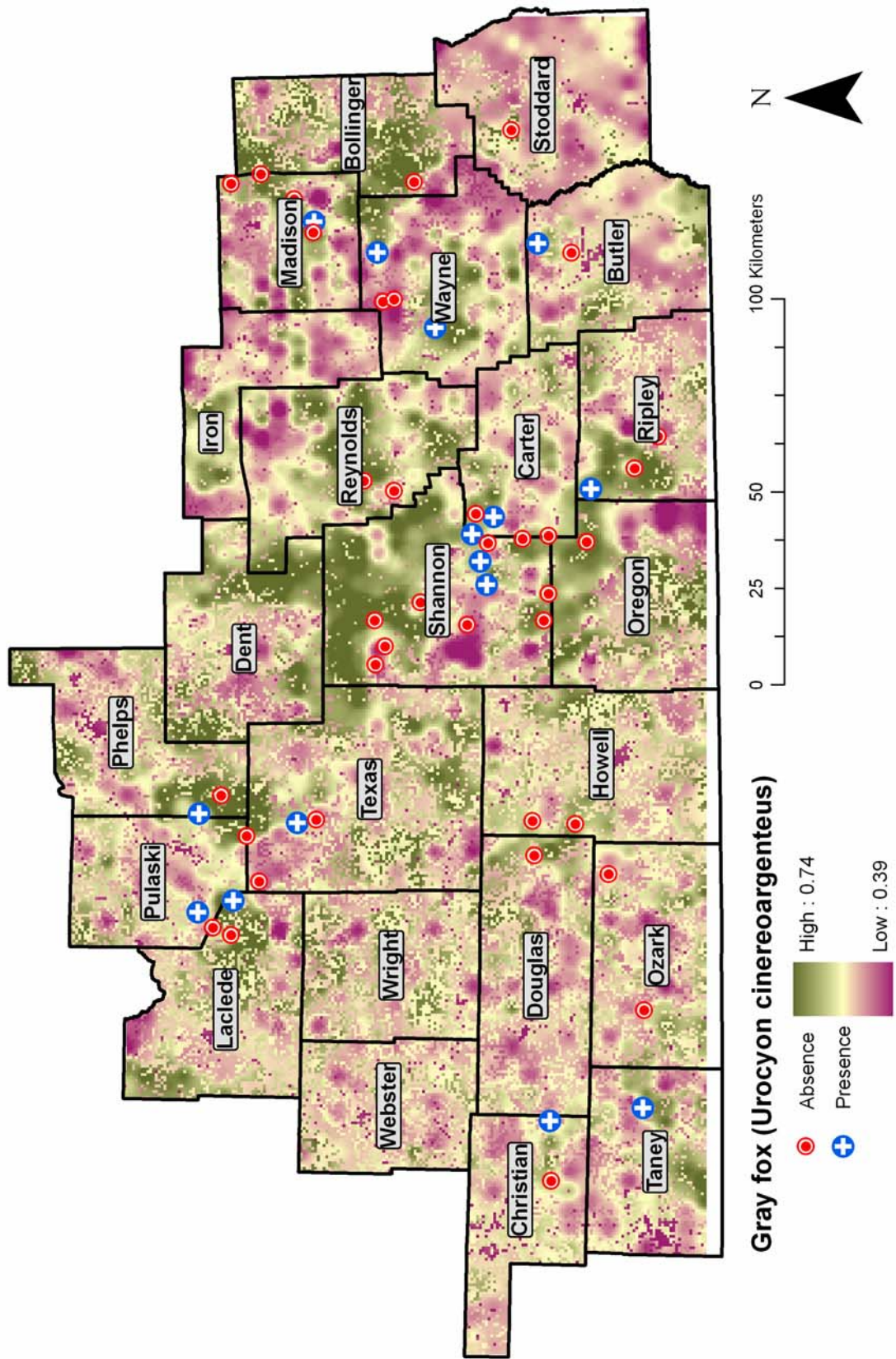
Figure 3. Map of study region depicting the proportion of predicted occupancy for (a) coyote (*Canis latrans*), (b) bobcat (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*) based upon the averaged multi-scale model for coyote bobcat and gray fox.



(b)



(c)



Appendix I. Locations of surveys and detection results for coyote (scat transect/cameras), bobcat, and gray fox in the Missouri Ozarks

Site	County	Northing	Easting	Coyote	Bobcat	Gray fox
Angeline 1	Shannon	4113348	637193	yes/yes	no	no
Angeline 2	Shannon	4116949	641284	yes/no	no	no
Ava 1	Ozark	4059212	535704	na/yes	yes	no
Ava 2	Taney	4059841	510428	na/no	no	yes
Ava 3	Christian	4083960	507022	no/no	no	no
Ava 4	Christian	4083296	491444	na/no	no	no
Castor	Bollinger	4118635	750608	na/no	no	no
Coldwater	Bollinger	4128368	731898	na/no	no	yes
Clearwater 1	Bollinger	4111708	674540	yes/no	no	no
Clearwater 2	Bollinger	4117795	674306	yes/yes	no	yes
CWCA	Stoddard	4093367	233905	no/no	no	no
Donaldson	New Madrid	4047308	281159	na/no	yes	no
Flatwoods	Wayne	4113482	712319	na/no	no	yes

Houston 1	Texas	4143947	585358	yes/no	no	no
Houston 10	Laclede	4166408	555153	no/yes	no	no
Houston 2	Texas	4149054	584570	yes/yes	yes	yes
Houston 3	Texas	4162213	580846	no/no	no	no
Houston 4	Phelps	4168770	591318	yes/no	no	no
Houston 5	Phelps	4174801	586600	no/no	no	yes
Houston 6	Laclede	4158898	569092	yes/no	no	no
Houston 7	Laclede	4170984	556982	yes/no	no	no
Houston 8	Texas	4175034	561138	yes/no	no	yes
Houston 9	Laclede	4165843	564127	yes/no	no	yes
Krooked Arrow	Bollinger	4162529	752363	na/yes	no	yes
Logan 1	Ripley	4123840	670658	yes/no	no	no
Logan 2	Ripley	4131663	673107	yes/no	no	no
Lanford	Madison	4144940	737386	na/yes	no	no
Mark Twain 1	Shannon	4099350	657164	yes/yes	no	no

Mark Twain 10	Ripley	4055454	684647	no/no	yes	no
Mark Twain 2	Shannon	4100052	646264	yes/yes	no	no
Mark Twain 3	Carter	4085339	636392	yes/no	yes	no
Mark Twain 4	Carter	4083703	643471	yes/no	no	no
Mark Twain 5	Oregon	4090448	657670	yes/no	no	no
Mark Twain 6	Oregon	4083814	658353	yes/no	no	no
Mark Twain 7	Oregon	4074069	656856	no/yes	yes	no
Mark Twain 8	Oregon	4073026	670652	no/no	no	yes
Mark Twain 9	Ripley	4061446	675830	yes/no	yes	no
Poplar Bluff	Butler	4077728	731746	na/no	no	no
Peck Ranch 1	Carter	4098267	663865	yes/no	yes	yes
Peck Ranch 2	Carter	4103865	658902	yes/yes	no	yes
Peck Ranch 3	Carter	4102447	664616	yes/yes	no	no
Rocky Creek 1	Shannon	4108054	638136	yes/yes	yes	yes
Rocky Creek 2	Shannon	4104843	635858	yes/yes	yes	no

Sam Baker 1	Wayne	4124280	719666	na/no	yes	no
Sam Baker 2	Wayne	4127206	718974	na/no	yes	no
Sunklands 1	Shannon	4128841	636963	yes/no	no	no
Sunklands 2	Shannon	4125988	630265	yes/yes	no	no
Sunklands 3	Shannon	4128577	625414	yes/no	no	no
University Forest	Butler	4086734	734522	na/no	no	yes
Willow Springs 1	Ozark	4068181	570977	yes/yes	no	no
Willow Springs 2	Howell	4076767	583647	yes/no	yes	no
Willow Springs 3	Howell	4087835	584997	no/no	no	no
Willow Springs 4	Douglas	4087463	575989	yes/no	no	no

Appendix II. The mean, standard deviation (SD), and range of values for landscape variables used in occupancy modeling for coyote (CALA), bobcat (LYRU), and gray fox (URCI).

	distance to road (m)			area road			distance to settled			area settled			
	n	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
CALA presence	4	332	258	200 to 700	0.01	0.01	0 to 0.02	12.1	7.9	4.3 to 23.3	0.01	0.01	0 to 0.01
absence	36	612	981	100 to 5800	0.003	0.003	0 to 0.01	11.2	5.5	4.0 to 24.0	0.02	0.01	0 to 0.03
LYRU presence	11	na	na	na	na	na	na	na	na	na	na	na	na
absence	42	na	na	na	na	na	na	na	na	na	na	na	na
URCI presence	15	292	141	80 to 500	0.01	0.01	0 to 0.01	11.6	6.7	2.8 to 23.3	0.01	0.00	0 to 0.06
absence	38	661	949	500 to 5800	0.004	0.003	0 to 0.02	12.3	6.0	3.9 to 35.9	0.01	0.02	0 to 0.09

	area prey forage/browse			coyote presence			bobcat presence			
	n	mean	SD	range	mean	SD	range	mean	SD	range
CALA presence	36	0.89	0.03	0.81 to 0.90	na	na	na	na	na	na
absence	4	0.92	0.02	0.89 to 0.93	na	na	na	na	na	na
LYRU presence	11	0.92	0.07	0.70 to 0.97	0.69	0.48	0 to 1	na	na	na
absence	42	0.86	0.05	0.88 to 0.93	0.83	0.39	0 to 1	na	na	na
URCI presence	15	na	na	na	0.60	1.0	0 to 1	0.27	0.0	0 to 1
absence	38	na	na	na	0.84	0.4	0 to 1	0.24	0.4	0 to 1

VITA

Harvey Mundy Hackett IV was born on February 19, 1970 in Woodbridge, Virginia, grew up in Mississippi and Virginia, and graduated from Virginia Episcopal School in 1988. He enrolled at the University of Virginia and graduated with a B.A. in Philosophy in 1992. In 1994, he enrolled at Colorado State University, and graduated in 1997 with a B.S. in Wildlife Biology. In 1998, he moved to Washington, D.C., and met Susan Anne King whom he married on May 14, 2000. He also began work towards an M.S. in Biology from Virginia Commonwealth University (VCU) in January 2000. Working under Dr. John F. Pagels, Mundy studied the habitat relationships of the endangered northern flying squirrel in southwestern Virginia. He graduated in 2002 from VCU and immediately moved his family to Missouri to begin research on forest carnivores at the University of Missouri-Columbia working with Dr. Matthew E. Gompper in the Department of Fisheries and Wildlife Sciences. Mundy was vice president for the Missouri Chapter of the Society for Conservation Biology (2004-05), the first intern for the ground breaking Tigers for Tigers (T4T) conservation group (2006), and had a book of his bird photography published by the University of Missouri Press (2007). He earned his Ph.D. in Wildlife Science in 2008, and moved to Richmond, Virginia with his wife where he is hoping to secure a professional position with an international NGO or a research and teaching position in Academia.