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Spatial and Temporal Structure of a Mesocarnivore Guild in Midwestern North America

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Factors Influencing the Spatial and Temporal Structure of a Carnivore Guild in the Central Hardwood Region

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ABSTRACT Ecological communities are most commonly structured by a mixture of bottom-up processes such as habitat or prey, competition within the same trophic level, and top-down forces from higher trophic levels. Carnivore guilds play a vital role in the broader ecological community by stabilizing or destabilizing food webs. Consequently, factors influencing the structure of carnivore guilds can be critical to ecosystem patterns. Coyotes (*Canis latrans*),

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bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and striped skunks (*Mephitis mephitis*) occur sympatrically throughout much of their geographic ranges in North America and overlap in resource use, indicating potential for interspecific interactions. Although much is known about space use, habitat relationships, and activity patterns of the individual species separately, little is known about factors that facilitate coexistence and how interactions within this guild influence distribution, activity, and survival of the smaller carnivores. For example, gray fox populations appear to have declined in Illinois since the early 1990s and it is unknown if the increase in bobcat and coyote populations during the same time period is the cause. We conducted a large-scale non-invasive carnivore survey using an occupancy modeling framework to quantify factors affecting the structure of this widely-occurring carnivore guild. We used baited remote cameras during 3-week surveys to detect carnivores at 1,118 camera-points in 357 2.6-km^2 sections (clusters of 3–4 cameras/section) in the 16 southernmost counties of Illinois (16,058 km^2) during January–April, 2008–2010. We collected microhabitat data at each camera-point and landscape-level habitat data for each camera-cluster. In a multi-stage approach, we used information-theoretic methods to develop and evaluate models for detection, species-specific habitat occupancy, multi-species co-occupancy, and multi-season (colonization and extinction) occupancy dynamics. We developed hypotheses for each species regarding the occupancy of areas based on anthropogenic features, prey availability, landscape complexity, and vegetative landcover. We used photographic data, Poisson regression, and mixed-model logistic regression to quantify temporal activity of carnivores in the study area and how interspecific factors influence temporal patterns of activity.

Of the 102,711 photographs of endothermic animals we recorded photographs of bobcats (*n* = 412 photographs), coyotes (*n* = 1,397), gray foxes (*n* = 546), raccoons (*n* = 40,029), red foxes (*n* = 149) and striped skunks (*n* = 2,467). Bobcats were active primarily during crepuscular periods, and their activity was reduced with precipitation and higher temperatures. The probability of detecting bobcats at a camera point decreased after a bobcat photograph was recorded, suggesting avoidance of remote cameras. Across southern Illinois, bobcat occupancy at the camera-point and camera-cluster scale ($\hat{\psi}_{\text{point}} = 0.24 \pm 0.04$, camera-cluster $\hat{\psi}_{\text{cluster}} = 0.75 \pm 0.06$) was negatively influenced by anthropogenic features and infrastructure. Bobcats had high rates of colonization ($\hat{\gamma} = 0.86$) and low rates of extinction ($\hat{\varepsilon} = 0.07$) during the study, suggesting an expanding population, but agricultural land was less likely to be colonized. Nearly all camera clusters were occupied by coyotes ($\hat{\psi}_{\text{cluster}} = 0.95 \pm 0.03$) during the entire study. At the camera-point scale, coyote occupancy (overall $\hat{\psi}_{\text{point}} = 0.58 \pm 0.03$) was higher in hardwood forest stands with open understories than in other habitats.

Compared to coyotes, gray foxed occupied a lower portion of the study area ($\hat{\psi}_{\text{point}} = 0.13 \pm 0.01$, $\hat{\psi}_{\text{cluster}} = 0.29 \pm 0.03$) at all scales. At the camera-cluster scale, gray fox occupancy was highest in spatially-complex areas with high proportions of forest, and positively related to anthropogenic features within 100% estimated home-range buffers. Red foxes occupied a similar proportion of the study area as gray foxes ($\hat{\psi}_{\text{point}} = 0.12 \pm 0.02$, $\hat{\psi}_{\text{cluster}} = 0.26 \pm 0.04$), but were more closely associated with anthropogenic features. Indeed, at all three scales of red fox occupancy analysis, only anthropogenic feature models occurred in the 90% confidence set. Camera-cluster extinction probabilities were higher for both gray foxes ($\hat{\varepsilon} = 0.57$) and red foxes ($\hat{\varepsilon} = 0.35$) than their colonization rates (gray fox $\hat{\gamma} = 0.16$, red fox $\hat{\gamma} = 0.06$), suggesting both species may be declining in southern Illinois. Striped skunks occupied a large portion of the study area ($\hat{\psi}_{point} = 0.47 \pm 0.01$, $\hat{\psi}_{cluster} = 0.79 \pm 0.03$) and were associated primarily with anthropogenic features, especially if the features were surrounded by agricultural land and not forest. Raccoons were essentially ubiquitous within the study area, being photographed in 99% of camera clusters.

In some instances, the presence of other carnivores appeared to be an important factor in the occupancy of the 4 smaller species, but in general, habitat models were more supported than co-occurrence models. Habitat had a stronger influence on the occupancy of gray foxes and red foxes than did the presence of bobcats. However, the level of red fox activity was negatively correlated with bobcat activity. Gray fox occupancy and level of activity were reduced in camera-clusters occupied by coyotes, but were not related to bobcat occupancy. When not considering the presence of coyotes, gray foxes appeared to use camera points with fewer hardwood and more conifer trees, which was counter to previous findings. However, when adding the effect of coyote presence, gray fox ψ_{point} models indicated a positive relationship with hardwood stands. Therefore, gray foxes were more likely to occupy camera points in hardwood stands than conifer stands if coyotes were also present; suggesting that hardwood stands may enhance gray fox-coyote coexistence.

The 2 fox species appeared to co-occur with each other at the camera-point scale more frequently than expected on the basis of their individual selection of habitat. Similarly, camera-point occupancy of red foxes was higher when coyotes were present. These apparent canid associations may be a response to locally-high prey abundance or an unmeasured habitat variable. Activity levels of raccoons, bobcats, and coyotes were all positively correlated.

Collectively, our results suggest that although gray foxes and red foxes currently coexist with bobcats and coyotes, the foxes have reduced activity in the areas occupied by larger

carnivores, especially when bobcats and coyotes are highly active. Further, hardwood stands may contain trees with structure that enhances tree-climbing by gray foxes, a behavior that probably facilitates coexistence with coyotes. Therefore, efforts to manage gray foxes should focus on maintaining and increasing the amount of mature oak-hickory forest. Additionally, the varying results from different scales of analyses underscore the importance of considering multiple spatial scales in carnivore community studies.

KEY WORDS activity, bobcat (*Lynx rufus*), carnivore guild structure, central hardwoods, co-occupancy, coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), habitat occupancy, multi-scale ecological sorting, raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*).

Contents

INTRODUCTION

Ecological communities are considered structured by bottom-up processes such as habitat or prey, competition within the same trophic level or guild, or by top-down forces from higher trophic levels (Paine 1980, Ware and Thomson 2005, Terborgh et al. 2010, Schmitz 2010). However, the most likely and common scenario is that these processes jointly determine community patterns and organization (Hairston et al. 1960, Menge 2000, Soule et al. 2003, Wilson et al. 2010). Indeed, it is misleading to view top-down and bottom-up processes as a dichotomy because no system is regulated exclusively by either process (Bowyer et al. 2005, Terborgh et al. 2010).

In largely bottom-up controlled ecosystems, food chain length and trophic structure are controlled by level of production and nutrients at the lowest trophic levels (White 1978, Oksanen et al. 1981, Fretwell 1987, Chen and Wise 1999). Highly productive and complex ecosystems have longer food chains and tend to be structured by bottom-up processes (Oksanen et al. 1981, Fretwell 1987, Gruner 2004, McCann 2012). In these ecosystems, the characteristics of predator communities are determined by the availability of prey or habitat, which are themselves limited by resources at lower trophic levels (White 1978, Menge 2000). Not only are the number of trophic levels influenced by primary productivity, but the type of successful predators can be influenced by the type of prey available and the quality of the diet of the prey species (Toft and Wise 1999, Mayntz and Toft 2001). Mesopredator populations appear to be primarily controlled by larger predators, but ecosystem productivity may determine the strength of those top-down forces (Henke and Bryant 1999, Elmhagen and Rushton 2007).

Top-down processes vary in strength, extend beyond predator communities to the broader ecosystem, and may have dramatic influence on the distribution and abundance of other species within those ecosystems (Schmitz 2010, Terborgh et al. 2010). Indeed, some ecosystems are so influenced by top-down effects that if predators are removed, the ecosystem could shift to an alternative stable state that may not be reversible by simply allowing the predator population to recover (Scheffer 2010). Much emphasis has been placed on trophic cascades involving top-down effects of large predators on 2 or more lower trophic levels, but the interactions among predators at the same trophic level can also have dramatic effects on carnivore demography as well as an entire ecosystem (Linnell and Strand 2000, Brashares et al. 2010). Predators may interact through exploitative or interference competition; of these, interference is likely more important because it can have a strong negative effect on population growth, especially at low densities of the losing species (Linnell and Strand 2000).

Intraguild predation, the most extreme form of interference competition, is a key component in structuring carnivore communities (Creel and Creel 1996, Henke and Bryant 1999, Wise and Chen 1999). Powell and Zielinski (1983) suggested that, theoretically, local colonization and extinction is the mechanism by which carnivores are able to coexist, but Rosenzweig (1966) concluded that Carnivora coexistence depends on size-based variation within carnivore guilds. The latter hypothesis states that if 2 carnivores share prey and the smaller carnivore is more efficient at hunting that prey, then the larger carnivore may need to kill their smaller competitors to persist. Empirical evidence of larger carnivores killing smaller carnivores as intraguild prey has been documented by many researchers (e.g., King 1989, Gese et al. 1996, Crooks and Soulé 1999, Henke and Bryant 1999). In this situation, the balance of advantage between carnivore species will shift based on the temporal fluctuation in the size distribution and abundance of prey. However, the effect that close competitors of different sizes have on each other involves a whole suite of spatial, temporal, and other components more difficult to quantify than simple linear hierarchy based on body size, prey size, and dominance (King 1989, Gehrt and Prange 2007).

Spatial and temporal factors influencing interactions among mammalian predators can affect individual carnivore species, as well as the functioning of entire ecosystems (Linnell and Strand 2000, Terborgh et al. 2010). In small closed ecosystems, predators can destabilize food webs with strong top-down suppression of prey populations (Holt and Loreau 2001, McCann et al. 2005). However, in large spatially complex landscapes, predators tend to stabilize food webs and enhance the persistence of individual food-chains by their ability to rapidly respond behaviorally to variance in resources. Mobile predators move between communities and switch prey, responding opportunistically to shifts in prey abundance, which is an important governor of prey populations by dampening oscillations in abundance, and in turn food-web stability is maintained (McCann et al. 2005, McCann 2012). Additionally, predator functional diversity, based on habitat selection and hunting behavior, can affect lower trophic levels in various ways and ultimately have cascading effects to ecosystem function and stability (Schmitz 2007, Otto et al. 2008). Mammalian carnivores represent a predator guild that can efficiently move between communities in response to available resources, and thus can dramatically influence an ecosystem.

Coyotes (*Canis latrans*; 7.0–18.0 kg), bobcats (*Lynx rufus*; 4.1–15.3 kg), gray foxes (*Urocyon cinereoargenteus*; 3.0–7.0 kg), raccoons (*Procyon lotor*; 2.0–12.0 kg), red foxes

(*Vulpes vulpes*; 4.1–5.4 kg), and striped skunks (*Mephitis mephitis*; 0.7–2.5 kg) occur sympatrically and compose the majority of the mammalian carnivore guild throughout much of their geographic ranges in North America, which suggests potential for interspecific interactions (Haroldson and Fritzell 1984, Gosselink et al. 2003, Chamberlain and Leopold 2005, Constible et al. 2006, Riley 2006, McDonald et al. 2008). Red fox ecology has been investigated on 5 continents and all 6 species have been extensively studied throughout North America (see citations in Feldhamer et al. 2003 and Wilson and Mittermeier 2009), thus much is known about space use and habitat relationships of the individual species. Based on differences in body size and diet, these species differ physiologically (e.g., metabolic rate, respiration, temperature), resource needs (e.g., ingestion rate, home-range size), population growth, and population density (Peters 1983, Gompper and Gittleman 1991). Therefore, the 6 species coexist putatively through diet, spatial, and temporal partitioning of resources; however, patterns of spatial and temporal co-occurrence are poorly understood. If members of Carnivora occupy different microhabitats, exhibit different diel activity cycles, or have varied diets, direct interspecific interactions may be low even with a high degree of space-use overlap (Bowers and Brown 1982, Kronfeld-Schor and Dayan 2003, Davies et al. 2007).

All 6 mesocarnivores select a variety of habitats, using both open and wooded habitats (Haroldson and Fritzell 1984, Bixler and Gittleman 2000, Fedriani et al. 2000, Kolowski and Woolf 2002, Gosselink et al. 2003, Chamberlain and Leopold 2005, Constible et al. 2006, Riley 2006, Wilson and Nielsen 2007). However, habitat selection differs among the species. Coyotes mainly select open grasslands, brush, and fragmented forests (Litvaitis and Shaw 1980, Chamberlain et al. 2000, Atwood et al. 2004, Randa and Yunger 2006, Kays et al. 2008). Bobcats are mainly terrestrial, but will readily climb trees, and select forested habitat, rocky mountainous areas, semi-deserts, brush, and those areas with high prey density (Litvaitis et al. 1986, Kolowski and Woolf 2002, Nielsen and Woolf 2002, Woolf et al. 2002, Tucker et al. 2008). Similarly, gray foxes select mature hardwood and brushy habitat in rocky or broken terrain with abundant prey (Chamberlain and Leopold 2000, Temple et al. 2010). To seek refuge from predators, gray foxes will often climb trees, which is an unusual behavior for a canid and may permit coexistence with coyotes (Yeager 1938, Haroldson and Fritzell 1984).

Raccoons, red foxes, and striped skunks readily use and are adapted to urban habitats. Raccoons use a variety of habitats and readily associate with human-derived resources (Prange et al. 2003). Human-derived foods can be more concentrated than food in more natural habitats, thus raccoons have smaller, more stable home ranges and occur at higher densities in urban settings (Prange et al. 2004). In more natural settings, raccoons select forest edges near agricultural land and streams, especially those areas with higher concentrations of den and resting sites (Dijak and Thompson 2000, Wilson and Nielsen 2007). Following humans and gray wolves (*Canis lupus*), red foxes have the third greatest natural distribution of any terrestrial mammal, and inhabit a wide range of habitats including tundra, prairie, farmland, forest, urbanized areas, and areas of highly diverse vegetation (Jones and Theberge 1982, Dekker 1983, Adkins and Stott 1998, Kurki et al. 1998, Gosselink et al. 2003, Van Etten et al. 2007). Striped skunks use a wide range of habitats, but appear to be most associated with edge habitat and grasslands, and readily use human structures for denning and resting (Shirer and Fitch 1970, Larivière and Messier 1998, Bixler and Gittleman 2000).

At large spatial scales, resource partitioning among carnivores occurs based on morphological characters such as body size and dentition. Carnassial teeth shape predicts the geographical range overlap among carnivores, suggesting that interspecific competition for food is a critical factor determining carnivore coexistence (Davies et al. 2007). Additionally, differences in prey and strategy of hunting, which may be associated with habitat, may enable coexistence among carnivores (Rosenzweig 1966). For example, most canids use coursing hunting strategies and are more adapted to open habitat, whereas most felids are ambush and stalking predators and more commonly use forested habitats. This divergence in morphology and behavior may be driven by competition, or the species may have diverged in isolation and competition was only important when the species became sympatric (Schluter 2000). Whatever the evolutionary importance of competition for character divergence, it affects contemporary ecological species sorting, in which range overlap is inhibited among similar species competing for the same resource base (Davies et al. 2007). In North America the maximum number of sympatric canids and felids is 4 and 3, respectively (Feldhamer et al. 2003). The carnivore community in southern Illinois is devoid of large carnivores, but represents the most common carnivore guild in eastern North America. Therefore, the spatial and temporal patterns observed in this study are likely similar to patterns in other regions of the continent where these species co-occur in the absence of large predators such as gray wolves and cougars (*Puma concolor*).

The overlap in diet among species within this mesocarnivore guild creates additional potential for interspecific interactions, but diet partitioning does occur in many regions of North America, especially in the summer (Schoonover and Marshall 1951, Toweill and Anthony 1988a, 1988b, Litvaitis and Harrison 1989, Cypher 1993, Greenwood et al. 1999, Azevedo et al. 2006). Competition for food has likely led to carnivore guilds having species with teeth adapted for various dietary functions (e.g., cutting, crushing, and grinding; Van Valkenburgh 1989, Davies et al. 2007). The guild also exhibits overlap in activity patterns, as each species is mostly active during nocturnal and crepuscular diel periods (Haroldson and Fritzell 1984, Doncaster and

Macdonald 1997, Larivière and Messier 1997, Patterson et al. 1999, Tigas et al. 2002, Atwood et al. 2004). Mammalian carnivores may adjust their daily activity pattern based on several factors, including environmental conditions, interference from competitors, behavioral thermoregulation, and prey availability (Larivière and Messier 1997, Pereira 2010).

Observations of interactions within Carnivora can provide insight into coexistence and distribution (Andren 1994, Fedriani et al. 2000, Crooks 2002, Andren et al. 2006). In the absence of larger predators, coyote populations appear to be experiencing a “mesopredator release” and are transitioning into an ecologically pivotal role as the apex predator throughout much of North America (Crooks and Soulé 1999, Brashares et al. 2010). Buskirk’s (1999) definition of a mesocarnivore included the size (1–15 kg) and the functional role of the group in landscapes with large carnivores. The description of a mesocarnivore may include coyotes; however, it does not account for the extirpation of gray wolves and thus the shifting functional role of coyotes as an apex predator (Ritchie and Johnson 2009). Coyotes may limit the abundance and distribution of smaller predators (especially foxes) and primary prey species (Henke and Bryant 1999). Researchers have directly observed coyotes killing and displacing foxes or inferred antagonistic interactions based on spatial segregation between the species (Major and Sherburne 1987, Sargeant and Allen 1989, Gese et al. 1996, Kitchen et al. 1999, Fedriani et al. 2000, Gosselink et al. 2003, Chamberlain and Leopold 2005). However, Neale and Sacks (2001a) found no evidence that gray foxes avoided areas inhabited by coyotes and bobcats, so spatial segregation within this guild is not universal. Coyotes negatively influence populations of several fox species (Sargeant et al. 1987, Cypher and Spencer 1998, Farias et al. 2005), and during experimental removals of coyotes, fox populations have increased (Henke and Bryant 1999, Kamler et al. 2003). With the increase in coyote populations in North America

(Gompper 2002, Thornton et al. 2004), gray and red fox populations may decrease as a result of increased intraguild predation and resource competition by coyotes. Additionally, changes in the predator community may indirectly facilitate the emergence of zoonotic diseases. The reduction of fox populations caused by the range expansion of coyotes can have cascading impacts to increase small-mammal populations that are hosts for Lyme disease; therefore, may negatively affect human health (Levi et al. 2012).

The Illinois Archery Deer Hunter Survey (ADHS) administered by the Illinois Department of Natural Resources (IDNR) between 1992 and 2010 suggested that gray fox and red fox populations were declining in Illinois while bobcats and coyotes were increasing. Hunters reported 81% and 58% decreases in gray and red fox sightings, respectively (Bluett 2011). This apparent decline has resulted in the gray fox being identified as a critical species in greatest need of conservation by the Illinois Comprehensive Wildlife Conservation Plan and Strategy (IDNR 2005). Recent research indicates that although the distribution of gray foxes is relatively wide in southern Illinois, gray foxes are scarce compared to bobcats and coyotes (Cooper 2008, Nielsen and Cooper 2012). Furthermore, ADHS data collected during 1992–2010 indicate increases in sightings of 31% and 480% for coyotes and bobcats, respectively (Bluett 2011). Although gray foxes and red foxes may adjust their space use to avoid interactions with sympatric coyotes and bobcats, the larger carnivores may dominate, kill, and displace individuals of both fox species. Overall, these observations suggest that intraguild interactions may be a contributing factor to the decline of foxes in Illinois.

Considerable research has been conducted on these 6 carnivores in Illinois (Storm 1972, Nielsen and Woolf 2001a, 2002, Kolowski and Woolf 2002, Gosselink et al. 2003, Prange et al. 2004, Wilson and Nielsen 2007, McDonald et al. 2008, Cooper et al. 2012) and throughout North

America; however, few large-scale occupancy-type surveys and analyses have been conducted, especially for all the species simultaneously (e.g., O’Connell et al. 2006). The importance of scale in ecological research has been demonstrated repeatedly (Johnson 1980, Wiens 1989, Carroll et al. 2001, Bowyer and Kie 2006, Mayor et al. 2009). For example, animals may make decisions on spatial distribution beyond the scale of the home range, whereas feeding and resting sites are selected within a home range and food items are selected at an even smaller scale (Johnson 1980, Bowyer and Kie 2006). Because carnivores play such a vital role in the broader ecological community it is critical to understand factors influencing the structure and interactions at multiple scales within this predator guild. Therefore, our objectives were to quantify temporal and spatial factors at multiple scales that influence the structure of the carnivore guild in a large region of southern Illinois, an area with a carnivore community similar to that found throughout the majority of the conterminous United States. We hypothesized that the factors (habitat features, species interactions, or both) that influence occupancy would differ with scale of analysis. We expected landscape-level occupancy by each species would be influenced by the amount of anthropogenic features, complexity of the landscape, or vegetative landcover of that area. At small scales, we expected occupancy of all species to be influenced by anthropogenic features, predator avoidance, or prey availability.

I hypothesized that bobcat occupancy would be strongly and positively associated with forest landcover at large scales and negatively related to anthropogenic features at fine scales. Given cursorial hunting techniques and human-related persecution, we predicted that coyotes would have lower occupancy near anthropogenic features and associate with highly complex landscapes at large scales, but be linked to habitat factors associated with prey availability at small scales. At large scales, we hypothesized that the spatial distribution of gray foxes would be closely associated with forest cover, but reduced at the site-level when bobcats and coyotes were present. It is well established that red foxes use urban landscapes and are often killed by coyotes; therefore, we expected red foxes to have higher rates of occupancy with anthropogenic features at coarse scales and lower occupancy in coyote-occupied areas at fine scales. Furthermore, we predicted that when coexisting with bobcats and coyotes, both gray foxes and red foxes would adjust activity patterns to reduce temporal overlap the larger carnivores. We expected to find striped skunk occupancy lower in the highly forested region of the study area and relatively unaffected by the presence of larger carnivores. Likewise, we hypothesized that raccoon activity would not differ based on the activity of other carnivores, and based on ADHS information, we predicted that raccoons would be fairly ubiquitous in the study area.

To accomplish our objectives, we conducted a regional remote camera survey and a 4-stage occupancy modeling (MacKenzie et al. 2002, 2003, 2004, 2006) approach to examine each of our distribution hypotheses and thereby elucidate factors influencing the spatial and temporal structure of the southern Illinois carnivore guild. We also used multiple years of occupancy data to estimate site colonization and extinction rates. In our analysis, we incorporated local and landscape-level scales of use by carnivores individually and evaluated both habitat and co-occurrence patterns influencing the spatial distribution of the 4 smallest species in the guild. We also used the spatial and temporal detection data to quantify species-specific periods of high activity and the effect of bobcats and coyotes on the activity patterns of the 4 smaller species (gray foxes, raccoons, red foxes, striped skunks).

STUDY AREA

This study was conducted in Alexander, Franklin, Gallatin, Hamilton, Hardin, Jackson, Johnson, Massac, Perry, Pope, Pulaski, Randolph, Saline, Union, White, and Williamson counties of southern Illinois (16,058 km^2; Figure 1). The study area was human-dominated (ca. 21.5 persons/km^2) and comprised portions of the Southern Till Plain, Wabash Border, Shawnee Hills, Ozarks, Lower Mississippi River bottomlands, and Coastal Plain natural divisions of Illinois (Schwegman 1973, Neely and Heister 1987). The Shawnee National Forest (1,074.91 km^2), Crab Orchard National Wildlife Refuge (177.62 km^2), Cypress Creek National Wildlife Refuge (61 km^2), 6 Illinois State Parks, and 15 other state-managed public natural areas were located within the study area. Streams and roads were abundant on the landscape with densities of ca. 1.1 km/km^2 and 1.5 km/km^2, respectively. Elevation ranged from 92 to 316 m, with a mean slope of 6.6°. During the study period, the mean temperature was 5.4 ± 0.4 °C (± SE throughout) with average precipitation of 2.6 ± 0.2 cm per week (NOAA 2010). The study area was dominated by light-colored Alfisols that developed beneath deciduous forest vegetation (Fehrenbacher et al. 1984). Highly productive dark-colored Mollisols were found in the bottomlands near the Mississippi and Ohio rivers and were associated with cropland. Throughout the study area, Entisols were found in sandy floodplains along riparian areas and on slopes prone to erosion (Barnhardt 2010). Soil parent materials were mainly loess followed by alluvium and outwash (Fehrenbacher et al. 1967). Landcover of the central portion of the study area consisted primarily of closed-canopy mixed hardwood forests (21% of study area; primarily *Acer*, *Carya*, and *Quercus* spp.) with primary ownership by the Shawnee National Forest (Figure 1; Luman et al. 1996). The northern region and areas along large rivers were dominated by agriculture cropland (44%; Figure 1), which was non-irrigated land under annual crops and may have temporarily been left fallow. The crops were primarily rotations of corn (*Zea mays*), soybeans (*Glycine max*), and winter wheat (*Triticum aestivum*). The remaining landcover of the study area comprised grassland (20%; primarily cattle pasture and hay fields), wetlands (8%), open water (3%), and urban (4%; Figure 1; IDNR 1996).

METHODS

Site Selection

Using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) and township and range political boundaries, we divided the study area into 2.6-km^2 political sections to be surveyed by stratified random sampling, including both public and private lands (ISGS 2004a). Sections were delineated as part of the public land survey system, which was ordered by the Land Ordinance of 1785 and Northwest Ordinance of 1787 (USDOI 2008). We used the 2005 United States Geological Survey's National Land Cover Database (USGS 2007) and ArcGIS 9.3 to determine the percentage of forest cover within each section of the study area. Because bobcats and gray foxes are unlikely to occupy areas with little forest cover (Chamberlain and Leopold 2000, Nielsen and Woolf 2002), we eliminated sections with <11% forest cover and stratified the remaining sections by the percentage of forest cover in 10% increments. We then randomly selected 360 potential sample sections among increments proportional to the total number of sections within each increment.

I determined ownership of forested areas within each section using county plat books and landcover data (Figure 1). We requested permission to conduct carnivore surveys from private landowners or management authorities controlling potential survey locations. If access was not granted or possible, we identified a nearby section with a similar percentage of forest cover to request access. We gained access and conducted carnivore surveys in 357 sections during January–April 2008–2010 (Figure 2). We chose to survey during these months because of constraints with access to land during fall hunting seasons and reduction in carnivore detectability during summer (O’Connell et al. 2006, Hackett et al. 2007, Crimmins et al. 2009). Within forested areas of each selected section, we placed cameras at 3–4 points composing a camera cluster (1,188 total camera points, 357 camera clusters).

Field Methods

Remote cameras.—To detect carnivores at each camera point, we used 1 digital remote camera (Cuddeback Excite [2.0 megapixel] or Capture [3.0 megapixel], Non Typical, Inc., Park Falls, WI) with passive infrared sensors (requiring both heat and motion to trigger photographic event) and incandescent flash illumination. We used remote cameras because the method has been successful to detect many carnivores in various habitats and climates (Silveira et al. 2003, Maffei et al. 2004, O'Connell et al. 2006, Linkie et al. 2008, Vine et al. 2009, Nielsen and McCullough 2009, Reed 2011). Conducting simultaneous surveys for multiple species can provide insight into spatial and temporal co-occurrence patterns and inform inferences about interspecific interactions and potential causes of changes in mesopredator populations (MacKenzie et al. 2004, Olson et al. 2005, O'Connell et al. 2006). Data from carnivore surveys often do not reflect actual abundance, but provide indices to describe trends and occurrence patterns (Ralls and Eberhardt 1997, MacKenzie et al. 2002). Most mammalian carnivores are cryptic, elusive, nocturnal, solitary, uncommon, and use rugged terrain with limited human access; characteristics that make them difficult to inventory or monitor (Gese 2001). Further, multispecies monitoring efforts are hindered because carnivores have broad differences in body size and morphology that often require species-specific sampling methods, which create financial and temporal constraints (Field et al. 2005). For example, covered track-plates are effective for eastern spotted skunk surveys (Hackett et al. 2007, Lesmeister et al. 2013), but are ineffective for detecting coyotes (Hackett 2008, Kays et al. 2008). Although no single survey technique is optimal for all carnivores in all habitats, remote cameras can be effective for non-invasive surveys of multiple species of forest mesocarnivores (Foresman and Pearson 1998, Tigas et al. 2003, Zielinski et al. 2005, O'Connell et al. 2006, Kelly and Holub 2008). Indeed, remote cameras have been identified as the most appropriate detection method for medium-size and large mammal inventories in most environments (Silveira et al. 2003) and used as the method to evaluate the effectiveness of other survey methods (Comer et al. 2011). Additionally, remote cameras are relatively easy to operate and deploy, do not require daily monitoring, and are not as negatively influenced by inclement weather as other survey methods such as track surveys and sightings. Remote cameras can be used to quantify occupancy within various habitat types for multiple species and patterns of spatial co-occurrence within a mesocarnivore guild (Davis et al. 2010b, O'Connell and Bailey 2010, Reed 2011, Sollmann et al. 2012). Furthermore, remote cameras record the date and time of photographs, and thus can be used to elucidate activity patterns of detected species.

I deployed 3–4 cameras in a section, so that we was able to conduct spatial hierarchical analyses of habitat with camera points being the smallest scale and camera clusters the larger scale. Animals typically have a hierarchical nature of habitat selection with 4 orders of selection (Johnson 1980). For example, a forest-adapted carnivore may select areas of high prey abundance (third-order selection) within a forested landscape (second-order selection). Because results can be quite different depending on the order of selection being studied, Johnson (1980) suggested recognizing which of 4 orders of selection a study is assessing. For this study, we used second-order selection (features of an animal’s entire home range) and third-order selection (usage of habitat components within the home range) as guides for determining scales used in our analyses. We used camera points to represent third-order selection and camera clusters to represent second-order selection.

I randomly selected camera-points ≥ 250-m apart within a section in woody or brushy cover to promote maximum coverage and independence of camera points (Kays and Slauson 2008). Once a general random location was selected for a camera-point, we secured cameras to trees (with braided steel cable and padlocks) approximately 0.5 m off ground. When game trails were present, we pointed the camera toward the trail to maximize detection probability. We baited cameras with sardines and fatty acid scent disks (United States Department of Agriculture Pocatello Supply Depot, Pocatello, ID) placed ~2-m in front of camera. At each camera point, we recorded Universal Transverse Mercator (UTM) coordinates and set cameras to be active 24-hours each day with a 1-minute delay between photographs. The remote cameras recorded date and time of each photograph. We visited camera points weekly for 3 weeks to rebait and collect digitally recorded photographs; after those 3 weeks, we redeployed cameras to points in other sections. After photographs were collected, we identified carnivore species based on coloration and body shape, and extracted date and time data for each photograph. We also used photographs to determine the presence of other endothermic animals.

I deployed 4 cameras in each of 117 sections (*n* = 468 total camera points) in 2008 and randomly selected 60 of those sections to survey again in 2010. In a preliminary analysis of detection probability (at the camera-cluster scale) for each focal species with random removals of 1, 2, and 3 camera-points from each camera-cluster, we observed no difference in detection probability between 3 and 4 camera-points per camera-cluster (D. Lesmeister, unpublished data). Therefore, in 2009, we deployed 3 cameras in each of 157 sections (*n* = 471 camera points), which increased camera-cluster sample size over 2008 with similar total cameras deployed. In

2010 we deployed 3 cameras in each of 83 new sections (249 camera-points) and 4 cameras in the same 60 sections (240 camera-points) from 2008. The camera-clusters surveyed in both 2008 and 2010 were used to inform multi-season occupancy models (MacKenzie et al. 2003, 2006).

Habitat characteristics.—I used point-level metrics to build third-order habitat occupancy models for each species (Table 1). At each camera point, we recorded ownership (public or private) and measured 8 microhabitat variables using methods similar to those used by Lesmeister et al. (2008) for eastern spotted skunk den/resting site selection. Originating at the camera, we established 4 10-m transects in cardinal directions and measured coarse woody debris and stem density along transects (Table 1). We measured total basal area, hardwood basal area, and slope at each camera. Using ArcGIS 9.3, we measured distance to nearest paved road (ISGS 2004b) and permanent stream or shoreline (IDNR 1994; Table 1). We digitized human structures using 2005 Illinois Digital Orthophotography Quadrangle (DOQ) files and measured distance from each camera-point to the nearest human structure (ISGS 2005).

I used a combination of broad-scale habitat metrics from remotely-sensed landscape layers for each camera cluster to model second-order habitat selection for each species (Table 1). We measured habitat metrics at or within buffers around each camera point, and then we averaged data from the camera points within each camera cluster. We created 2 buffers (100% and 20% of estimated home-range size for each species) surrounding each camera point and averaged habitat variables measured within each buffer size across the points within each camera cluster. Throughout we refer to 20% of home-range size, recognizing it does not represent the expected core-area use by a species, but rather 20% of the 100% estimated home-range size. Carnivore home-range sizes differ based on species body size and diet, where larger and more carnivorous species typically have larger home ranges (Peters 1983, Gompper and Gittleman 1991). We used home-range size estimates reported by Nielsen and Woolf (2001a) for bobcats (18.15 km^2), Cooper (2008) for gray foxes (2.75 km^2), Gosselink et al. (2003) for coyotes (21.90 km^2) and red foxes (7.09 km^2), and Prange et al. (2004) for striped skunks (2.75 km^2). Buffer radii representing 100% and 20% of home ranges were 2.4 and 1.1 km (bobcat), 2.6 and 1.2 km (coyote), 0.9 and 0.4 km (gray fox and striped skunk), and 1.5 and 0.7 km (red fox), respectively.

I used ArcGIS 9.3 to measure distances from each camera point to 4 nearest anthropogenic features (i.e., municipality boundary, major road, minor paved road, human structure) and used the average distance for camera-cluster scale analyses. Within 100% and 20% of home-range buffers, we calculated the density of major roads, minor paved roads, and human structures for each camera point and averaged values for each camera cluster. We used U.S. census data from 2000 for incorporated municipality boundaries (ISGS 2006), Illinois DOQ files from 2005 (ISGS 2005) for digitized human structures, and Federal Highway Administration data (FHWA 2000) for road classification. Additionally, we measured the density of streams within buffer areas. Using FRAGSTATS 3.3 (McGarigal et al. 2002) and landcover data (USGS 2007), we quantified an additional 33 remotely-sensed habitat variables within buffers surrounding each camera point. To address multicollinearity among variables, we used cluster analysis to identify and eliminate correlated variables, which resulted in 19 remotely-sensed habitat variables used in subsequent analyses (Table 1). Based on literature for the ecology of focal species, we predicted the direction of effects of habitat and survey variables on species detection and occupancy (Table 1).

Data Analysis

I incorporated detection probabilities (p) in estimates of habitat occupancy (ψ), co-occurrence (φ), camera-cluster colonization (γ), and camera-cluster extinction (ε) patterns among bobcats, coyotes, gray foxes, raccoons, red foxes, and striped skunks. In a 4-stage modeling approach, we used information-theoretic methods to: (1: detection) estimate species-specific detectability (p) and model factors influencing it; (2: single-species occupancy) compare support for *a priori* models that represent 2 primary sets of hypotheses (anthropogenic features/larger predator avoidance, prey availability) for occupancy at the camera-point scale (ψ_{point}) and 3 primary sets of hypotheses (anthropogenic features, landscape complexity, vegetative land cover) to explain patterns of occupancy at the camera-cluster scale (ψ_{cluster}) of each species individually (bobcats, coyotes, gray foxes, red foxes, and striped skunks; Table 2); (3: co-occupancy) examine factors that may influence co-occurrence among these species; and (4: multi-season dynamics) estimate rates of and factors affecting colonization and extinction between 2008 and 2010 for each species at the camera-cluster scale. Raccoons were not included in occupancy analyses because they were detected at nearly all camera clusters (see Results).

Detectability.—Incorporating detection probabilities in site occupancy surveys provides the most appropriate methodology for conducting effective wildlife inventories and subsequent monitoring at large spatial scales (O'Connell et al. 2006, Karanth et al. 2011, Lesmeister and Nielsen 2011). Although some studies have shown similar results between logistic regression models (without accounting for detection probabilities) and occupancy models (e.g., *Oryzomys palustris*, Eubanks et al. 2011), those results are likely driven by the high detection probability of the species. However, for species with low to moderate detection probabilities, this finding likely will not hold true. Indeed, it has been repeatedly demonstrated that incorporating imperfect detection can alter forecasted population trends and estimated species distributions (Gu and Swihart 2004, Field et al. 2005, Martin et al. 2005, Rota et al. 2011). Further, little is known about the factors (e.g., season, weather, attraction to bait, avoidance of detection device) that may influence a researcher’s ability to detect the focal carnivores.

Detection of carnivores is imperfect and likely varies among species and sites. Therefore, we used single-species models in Program PRESENCE 3.1 (Hines 2006, MacKenzie et al. 2002, 2006) to estimate the probability of detection (p) and occupancy (ψ) for each species. The method involves estimating p by visiting sites multiple times during a period when site occupancy does not change, and during each visit the target species is either detected, which requires occupancy and occurs with probability ψ x p, or not detected. Non-detection during a visit arises when either the species is present but not detected [$\psi \times (1 - p)$] or when it is absent ($1 - \psi$). The photographic history for a site during our 3-week sampling periods permitted the estimation of p, which was incorporated into probabilistic models of occupancy for each species (MacKenzie et al. 2006).

I used a logit link function to model ψ and p with covariates that varied among camera-points and camera-clusters for each rate parameter (ψ and p) in each stage of analysis. For each model set, we ranked models based on their Akaike’s Information Criterion (AIC) values and model weights (w) (Burnham and Anderson 2002, MacKenzie et al. 2006). We considered only the top-ranked models composing 0.90 cumulative w (i.e., the 90% confidence set) for interpretation. We calculated the model-averaged p and ψ estimates for each species at camera-point and camera-cluster scales. Given that data collected at a camera cluster integrated data collected at each within-cluster camera point, estimates of p and ψ estimates at the camera-cluster scale were necessarily greater than estimates at the camera-point scale. We standardized all continuous covariates to z-scores prior to analysis, so we interpreted model β coefficients as the change in the log-odds ratio of occupancy relative to 1 standard deviation change in the covariate from its mean (Cooch and White 2005). We used model-averaging for all β coefficients, and estimates of *p* and ψ.

I held occupancy constant [i.e., unaffected by site features; this null model is designated as ψ (.)] for stage 1 (detectability modeling), and modeled species-specific *p* as a function of several variables that may influence an animal's activity or a researcher's ability to detect the species (Table 1). The assumption that animals move independently of cameras might be violated if animals develop shyness, caused by avoidance of either the flash of remote cameras or the cameras themselves (Séquin et al. 2003, Wegge et al. 2004, Jackson et al. 2006). Alternatively, animals may increase visits to camera points over time due to bait attractiveness. Trends in photographic rate over time (either increases or decreases) could also result from factors unrelated to behavioral response to the camera or bait. Consequently, we modeled *p* for each species on the basis of detection of that species at the camera point on a previous visit (yes/no), total precipitation, mean temperature, interaction of precipitation and temperature, month of survey, year of survey, and a separate intercept for each week of the 3-week survey (Table 1). Including a week-specific intercept allowed *p* to vary among the 3 1-week sample periods, which estimated differences between the detection probabilities of survey weeks. We used precipitation and temperature data recorded during each week at the nearest National Weather Service climatological station (NOAA 2010). We considered the null model [*p*(.)], where detection probability was held constant and equal for all survey weeks, in the model set to provide a reference for the relative strength of survey covariates to explain heterogeneity in detection probabilities. We used the best-supported (lowest AIC) species-specific p model for all subsequent stages of analysis.

Single-species occupancy.—I fit *a priori* occupancy models to species-specific photographic histories and habitat covariates after identifying the most-supported p model for each species. Occupancy models included various combinations of landscape and vegetation characteristics that may affect ψ (Table 2). We repeated this procedure for each species to model occupancy at the camera-point scale (ψ_{point}), measuring habitat characteristics near each camera point, and twice at the camera-cluster scale (ψ_{cluster}), measuring habitat characteristics within buffers representing 100% and 20% of home ranges. We included the null occupancy model [$\psi(.)$] in each model set to compare parameter estimates and provide a reference to determine the relative strength of habitat covariates used in other models (Boulinier et al. 1998).

I developed 2 general hypotheses concerning local habitat features driving occupancy of focal species at the camera-point scale. The first hypothesis was a combined effect of anthropogenic features and predator avoidance (AF-PRED) because habitat features likely serve multiple purposes for carnivores. We expected bobcat and coyote occupancy to be negatively related to AF-PRED habitat features, and the 4 smaller carnivores to be either unaffected or positively associated with those habitat features. For example, red foxes may use urban landscapes to reduce predation by coyotes. To capture that potential effect, we included distance to roads and human structures, as well as private vs. public ownership as variables (Table 2). We hypothesized that sites with higher woody stem density would enhance protection for gray foxes and red foxes from larger predators; therefore, we included it as a variable for the AF-PRED hypothesis. We predicted gray foxes would use sites with greater slope to provide additional avenues to escape coyote predation. We expected occupancy for all carnivores to be positively related to habitat features associated with the second hypothesis at the camera-point scale, which was prey availability (PREY). We did not directly measure prey density at sites; rather, habitat variables likely associated with winter prey species. The abundance of small mammals — the primary prey of Midwestern carnivores in winter — can be predicted from structural and landscape variables (Pearson and Ruggiero 2001). Therefore, we used 4 habitat variables that were likely associated with prey availability (Table 2). Compared to conifer stands, we predicted that hardwood stands would have higher abundance of small mammals because of hard mast availability; therefore, all carnivores would have higher occupancy in hardwood stands (Table 1). Because coarse woody debris is an important habitat component for many taxa used as prey by carnivores (Loeb 1999, Bunnell and Houde 2010), we hypothesized that more dead organic matter availability would be associated with higher biodiversity (Freedman et al. 1996) and small mammal prey available, thus higher carnivore occupancy (Table 1). We predicted bobcats and gray foxes to be more associated with mature forest (greater basal area) than the other species. We expected stream corridors to have more prey available; therefore, we expected carnivore occupancy to decrease with distance from streams (Table 1).

I generated 3 general hypotheses concerning habitat features within buffers surrounding cameras that may influence occupancy of focal species at the camera-cluster scale. The first hypothesis, represented by 10 variables (Table 2), was that red fox and striped skunk occupancy would be associated with anthropogenic features (AF), whereas gray foxes would be relatively unaffected, and bobcats and coyotes would be negatively related to AF (Table 1). Because of their ability to adapt to urban landscapes, we expected red foxes and striped skunks to have higher occupancy on private land and in camera clusters with more human structures, roads, and urban patch density within buffered areas (Table 1). As distance to roads, structures, and municipalities increased, we expected red fox and striped skunk occupancy to decrease (Table 1). For each AF variable, we predicted the opposite direction of effect for bobcats and coyotes. The second hypothesis was represented by the effect of up to 8 landscape complexity (LC) variables in a model (Table 2). We expected that association with those variables would differ among species, but rather than related to body size, we hypothesized differences would be driven by variation in hunting techniques and use of highly fragmented landscapes. Many canids use cursorial hunting techniques; therefore, we hypothesized that coyotes and red foxes would be positively related to most LC variables, whereas the other carnivores would mostly be negatively associated. The third camera-cluster hypothesis was represented by 5 vegetative landcover (VEG) variables (Table 2). We expected bobcats and gray foxes to have higher occupancy in camera clusters surrounded by less agricultural land and grassland, and more forest (Table 1). Coyotes, red foxes, and striped skunks appear to use open land more than bobcats or gray foxes, so we predicted the reverse pattern for these 3 species.

I used the model-averaged coefficient estimates from the 100% home-range scale occupancy model results and ArcGIS to map predicted occupancy based on habitat for bobcats, coyotes, gray foxes, red foxes, and striped skunks in southern Illinois. To output a raster file for the 5 predicted occupancy maps, we used created rasters and model-averaged variable estimates in ArcGIS Raster Calculator, which uses Python syntax to create and execute an algebraic expression. We classified landcover in 1-ha cells based on majority landcover type (agriculture, forest, grassland, urban) within each cell. Additionally, we created raster files for density of human structures using the point density tool and the line density tool for major road, minor road, and stream raster files. We used the Euclidean distance tool to create raster files representing distance to structures, major roads, minor roads, municipality, and streams.

Species co-occurrence.—I used the co-occupancy modeling approach described by MacKenzie et al. (2004, 2006) to test the hypothesis that occupancy of gray foxes, red foxes, and striped skunks may be negatively influenced by bobcats, coyotes and each other. We used predicted occupancy of heterospecific carnivores as parameters in co-occurrence models to estimate the influence that presence of 1 species (interacting species) had on the occupancy of another species (focal species), thereby investigating co-occurrence patterns within the guild. Gray foxes, red foxes, and striped skunks were the focal species and other species were interacting species in co-occurrence modeling.

Imperfect detection could lead to misleading inferences about species co-occurrence patterns; therefore, we accounted for species-specific detection probabilities while modeling multispecies camera-point and camera-cluster occupancy (MacKenzie et al. 2004, 2006). In all models in each co-occurrence model set (for both camera-point and camera-cluster scales), we included covariates from the most-supported p model for each species [both p_{focal}(best) and $p_{\text{interacting}}$(best)] at the given scale. We also included the covariates from the best-supported habitat ψ model for interacting species to produce the null co-occurrence model for the focal species [$\psi_{\text{interacting}}$(best ψ model) ψ_{focal}(.) $p_{\text{interacting}}$(best p) p_{focal}(best p)] at a given scale. We used the null model as a reference for all co-occurrence models that varied based on focal species occupancy. We then investigated the relative strength of habitat features vs. interacting species presence to predict focal species ψ at each scale. For each co-occurrence model set, we defined 4 categories for models: (1) habitat-only models (top 3-4 habitat models of the focal species without the influence of the interacting species [$\psi_{\text{interacting}}$(best ψ model) ψ_{focal}(best ψ models) $p_{\text{interacting}}$(best) p_{focal}(best)], [HABITAT-ONLY]), representing the hypothesis that species co-occurrence patterns are driven by species-specific habitat selection with no response to the presence of other species; (2) main effects of habitat plus interacting species (i.e., separate occupancy intercept with vs. without the presence of interacting species [$\psi_{\text{interacting}}$(best ψ model) ψ_{focal}(best ψ models + interacting species) $p_{\text{interacting}}$(best) p_{focal}(best)], [HABITAT + INTERACTING SPECIES]); (3) interaction between habitat and interacting species (i.e. separate intercepts and habitat variable slopes with vs. without presence of interacting species [$\psi_{\text{interacting}}$(best ψ model) ψ_{focal}(best ψ models × interacting species) $p_{\text{interacting}}$(best) p_{focal}(best)], [HABITAT × INTERACTING SPECIES]); and (4) interacting species-only (i.e., without the influence of habitat [$\psi_{\text{interacting}}$(best ψ model) ψ_{focal}(interacting species) $p_{\text{interacting}}$(best) p_{focal}(best)], [INTERACTING SPECIES-ONLY]), representing the hypothesis that species co-occurrence patterns are driven by the presence of other species with no response to the habitat selection of the focal species.

For co-occurrence models with habitat included, we included habitat variables identified in the 3–4 most-supported single-species ψ models (scale-specific) for the focal species. Using AIC values and model weights, we ranked co-occurrence models with and without the influence of the presence of interacting species. We selected the most-supported model from each of the 4 categories for comparison to assess the relative importance of habitat versus species interactions for gray fox, red fox, and striped skunk occupancy.

I estimated the magnitude of probable species interaction at a given scale (camera site or cluster) by: $\varphi = \psi^{AB}/(\psi^{A} * \psi^{B})$, where ψ^{A} and ψ^{B} are unconditional (i.e., ignoring other species) probabilities of occupancy by species A and B, respectively, and ψ^{AB} is the predicted probability of joint occupancy by both species (MacKenzie et al. 2004). If species occur independently, $\varphi = 1$. If $\varphi < 1$, then the 2 species co-occur less frequently than if they were distributed independently (possible avoidance), while $\varphi > 1$ indicates a level of co-occurrence higher than expected under independence (possible attraction), or selection of similar features not included in our models.

Using the results from co-occurrence modeling, we mapped predicted occupancy for gray foxes, red foxes, and striped skunks that included camera-cluster scale habitat factors and the effects of co-occurrence with bobcats and coyotes. We used the gray fox raster layer created in stage 2 and the raster layer of interactive species in raster calculator using the logit function for each model to create 3 maps of gray fox predicted occupancy with added effect of co-occupancy with a potential competitor (bobcat, coyote, red fox). We used the same procedure for 3 predictive maps of red fox with potential competitor (bobcat, coyote, gray fox), and 4 predictive maps of striped skunk with interacting species (bobcat, coyote, gray fox, red fox).

Colonization and extinction.—To estimate colonization and extinction, and factors influencing those rates, we fit multi-season occupancy models for bobcats, gray foxes, red foxes, and striped skunks using data from camera clusters that we surveyed in both 2008 and 2010 for stage 4 of the modeling approach. Multi-season occupancy models are appropriate for both short- and long-term monitoring of multiple species, especially those with detection probabilities <1 (Lesmeister and Nielsen 2011). Each week during a 3-week survey period represented an independent sample and each year represented a season. We could not model multi-season dynamics of coyotes and raccoons because models did not converge, due to near 100% occupancy in 2008 and 2010 (see Results). We only used camera-cluster scale data for multi-season models because colonization (γ) and extinction (ε) would more likely be random at the camera-point scale. Multi-season occupancy modeling relies on detection/non-detection data for detection probability (p) and examines factors (in this case, habitat and interacting carnivore presence) that influence initial occupancy in 2008, colonization probability, and extinction probability of a camera-cluster (MacKenzie et al. 2006). We combined survey covariates from the most-supported model from *p* modeling (stage 1) and the 4 top-ranked models from single-species ψ modeling (stage 2) for the initial occupancy estimates of each species. In the multi-season model sets for gray fox, red fox, and striped skunk, we also included the estimated occupancy of bobcat and both fox species as explanatory variables to estimate the effect of interacting species on extinction probability of each focal species.

Activity.—To quantify the daily activity patterns of each species, we calculated average number of photographs per species per camera-cluster and per diel time period. We used the date and time stamp to determine in which period a photograph was recorded: 1) crepuscular (2 hours before sunrise to 2 hours after sunrise, and 2 hours before sunset to 2 hours after sunset); 2) diurnal (2 hours after sunrise to 2 hours before sunset); and 3) nocturnal (2 hours after sunset to 2 hours before sunrise). We adjusted the defined sunrise and sunset times weekly during the study to account for changing day length and daylight savings time. Because some animals remain at a baited site for an extended period, many photographs of the same individual were recorded during a single visit to the camera point. Therefore, we removed from analyses any photographs of a given species at a camera-point taken <2 hours after another photograph of that same species at the same camera-point.

I used Poisson regression (PROC GENMOD) in SAS (SAS Institute Inc., Cary, NC) to test for differences ($\alpha = 0.05$ throughout) in species-specific activity among diel time periods. We also used Poisson regression to test for differences in the number of photographs of the 4 smallest species (gray fox, raccoon, red fox, and striped skunk) in camera-clusters where the 2 largest species (bobcats and coyotes) were and were not detected. We also examined differences in the number of photographs of smaller species based on estimated bobcat occupancy at a camera-cluster and the total number of photographs of each larger carnivore. We used coyote presence (detection/non-detection) and number of coyote photographs as explanatory variables for the total number of bobcat photographs recorded in a camera-cluster. Poisson regression assumes that the number of events at a particular camera-cluster (i.e., number of photographs of a species) follows the Poisson distribution determined by an observation rate (O), related to a vector of independent explanatory variables ($\mathbf{X}$) as: $\log(O) = \log(\mathbf{R}) + \mathbf{X}\boldsymbol{\beta}$ (Loomis et al. 2005), where $\boldsymbol{\beta}$ is a vector of unknown estimated parameters, $\mathbf{R}$ is the time at risk (period correction, or "offset"; Ma and Goulias 2009). We allowed O to vary among 3 diel time periods and included period length as an offset variable ($\mathbf{R}$) in all models to account for the fact that diel periods were of different length and changed in length throughout the study. We used the Tukey-Kramer least-squares-means-adjustment procedure for multiple comparisons to adjust coefficient estimates.

I used mixed-model logistic regression (SAS PROC GLIMMIX) to test for differences in the proportion of photographs during a specific time period of bobcats, gray foxes, raccoons, red foxes, and striped skunks based on the proportion of bobcat and coyote photographs recorded during the same diel period at a camera-cluster. The binary response variable at a camera cluster was the number of photographs recorded of a species during a diel period divided by the total number of photographs recorded of that species, and this analysis was repeated for each diel period separately. We also tested whether crepuscular and diurnal activity of the 4 smaller carnivores was related to the number of bobcat and coyote photographs in the nocturnal period. We treated the camera-cluster as a random effect, and period, bobcat, and coyote variables as fixed effects. We used Tukey's multiple range test to separate means.

RESULTS

I recorded 29,988 camera days and 102,711 photographs (detections) of endothermic animals at the 1,188 camera-points (357 camera-clusters) surveyed. Among those photographs were exactly 45,000 photographs of bobcats, coyotes, gray foxes, raccoons, red foxes, and striped skunks, with >40,000 of those being raccoons (Table 3). Most raccoon photographs were successive records in short time intervals of individuals reacting to the bait. Following raccoons in the number of photographs recorded were striped skunks, coyotes, gray foxes, bobcats, and red foxes. With the exception of red foxes and raccoons, we recorded more photographs in January–February than March–April (Table 3). Most striped skunk photographs were successive records of individuals and primarily occurred during February (Table 3).

The percentage of camera points and camera clusters at which we recorded photographs varied among bobcats (15% of camera points, 47% of camera clusters), coyotes (39%, 79%), gray foxes (8%, 22%), raccoons (85%, 99%), red foxes (5%, 16%), and striped skunks (22%, 48%). Because we detected raccoons at nearly all camera clusters, we did not model their occupancy. We also recorded photographs of >18 other endothermic species (Table 4), and several small avian species. Although a cougar was confirmed in southern Illinois in 2000 (Heist et al. 2001) and despite the increasing likelihood of cougars recolonizing the Midwest (LaRue and Nielsen 2011, Henaux et al. 2011, LaRue et al. 2012), no cougars were photographed during our study.

Detectability

Estimated model-averaged detection probabilities (± SE) per week varied among species and scales of analysis ($\hat{p}_{\text{point}}$ vs. $\hat{p}_{\text{cluster}}$) (bobcat: $\hat{p}_{\text{point}} = 0.20 \pm 0.02$, $\hat{p}_{\text{cluster}} = 0.25 \pm 0.02$; coyote: $\hat{p}_{\text{point}} = 0.31 \pm 0.02$, $\hat{p}_{\text{cluster}} = 0.52 \pm 0.02$; gray fox: $\hat{p}_{\text{point}} = 0.32 \pm 0.03$, $\hat{p}_{\text{cluster}} = 0.37 \pm 0.03$; red fox: $\hat{p}_{\text{point}} = 0.28 \pm 0.04$, $\hat{p}_{\text{cluster}} = 0.30 \pm 0.04$; striped skunk: $\hat{p}_{\text{point}} = 0.30 \pm 0.02$, $\hat{p}_{\text{cluster}} = 0.58 \pm 0.03$). Only a few models in each species' *p* model set received substantial support (Appendix A). For bobcat, the null detection models were the third (camera cluster) and fourth (camera point) ranked models (ΔAIC = 0.83 and 2.05, respectively; Table 5). In the best-supported models, bobcat detection probability was negatively related to precipitation and temperature at the camera-cluster scale, and negatively related to precipitation and previous detection at the camera-point scale (Table 5). Model convergence failed for camera-cluster scale bobcat data with previous photographic survey covariate included, so these models were not considered.

The top-ranked detection models for the 3 canids and striped skunks received considerably more support than the null detection models at both point and cluster scales (ΔAIC ≥ 8.65; Table 5). Coyote and gray fox detection probabilities were negatively related to temperature and positively related to previous detection at the camera-cluster scale (Table 5). The camera-cluster-scale model with temperature and previous photograph was highly supported, with $w > 0.9$ for both coyotes and gray foxes. Coyote $\hat{p}_{\text{point}}$ was higher in February, but lower in March and April compared to January (Table 5). Red fox detectability differed by year (Table 5), being higher in 2010 ($\hat{p}_{\text{point}} = 0.38 \pm 0.06$, $\hat{p}_{\text{cluster}} = 0.47 \pm 0.07$) than in 2008 ($\hat{p}_{\text{point}} = 0.12 \pm 0.04$, $\hat{p}_{\text{cluster}} = 0.21 \pm 0.05$) or 2009 ($\hat{p}_{\text{point}} = 0.16 \pm 0.05$, $\hat{p}_{\text{cluster}} = 0.19 \pm 0.05$).

Striped skunk detectability was influenced by temperature, precipitation, previous detections, and month (Table 5). Detection probability was higher in January ($\hat{p}_{\text{point}} = 0.23 \pm 0.03$, $\hat{p}_{\text{cluster}} = 0.34 \pm 0.04$) and February ($\hat{p}_{\text{point}} = 0.43 \pm 0.03$, $\hat{p}_{\text{cluster}} = 0.56 \pm 0.03$) than March ($\hat{p}_{\text{point}} = 0.15 \pm 0.02$, $\hat{p}_{\text{cluster}} = 0.22 \pm 0.04$) and April ($\hat{p}_{\text{point}} = 0.08 \pm 0.01$, $\hat{p}_{\text{cluster}} = 0.16 \pm 0.03$). Temperature and precipitation individually had weak negative coefficient estimates, but when month was included in the model, their coefficients were positive. Detection probabilities were similar between 2008 ($\hat{p}_{\text{point}}$ = 0.26 ± 0.03, $\hat{p}_{\text{cluster}}$ = 0.40 ± 0.03), 2009 ($\hat{p}_{\text{point}}$ = 0.34 ± 0.03, $\hat{p}_{\text{cluster}}$ = 0.48 ± 0.05), and 2010 ($\hat{p}_{\text{point}}$ = 0.31 ± 0.03, $\hat{p}_{\text{cluster}}$ = 0.43 ± 0.04). We was more likely to record a striped skunk photograph if previous photographs were recorded (β_{point} = 1.97 ± 0.13, β_{cluster} = 1.39 ± 0.28).

Single-Species Occupancy

Model-averaged bobcat $\hat{\psi}_{\text{point}}$ = 0.24 ± 0.04 and $\hat{\psi}_{\text{cluster}}$ = 0.75 ± 0.06. Habitat models did not perform well in explaining bobcat ψ_{point}, and the top-ranked habitat model received similar support as the null model (Table 6). Explanatory power was greater at the camera-cluster scale than at the camera-point scale (Appendix B). Bobcat ψ_{cluster} was most strongly influenced by anthropogenic features within both buffer sizes (100% and 20% of home range; Table 6). Bobcat ψ_{cluster} decreased with increased anthropogenic features, primarily paved road density and human structures. The top-ranked model using habitat within the 100% home-range buffer was more supported than the top-ranked using habitat within the 20% of home-range buffer (ΔAIC = 2.69; Table 6). Mapping bobcat predicted occupancy (range $\hat{\psi}$ = 0.50 to 1.00) based on the top camera-cluster model indicated a wide distribution of high occupancy areas with moderate predicted occupancy in urban areas and near roads (Figure 3).

Coyote model-averaged $\hat{\psi}_{\text{point}}$ = 0.58 ± 0.03 and $\hat{\psi}_{\text{cluster}}$ = 0.95 ± 0.03. At the camera-point scale, the null model (ΔAIC = 1.55) received 2.15 times less support than the top-ranked habitat model (Table 7). Coyote ψ_{point} was higher with increasing slope (β = 0.56 ± 0.12) and percentage of hardwood (β = 0.38 ± 0.11), but decreased with stem density (β = -0.41 ± 0.14). Given that coyote $\hat{\psi}_{\text{cluster}}$ was near 1, many of the more complicated habitat models were over-fit (especially at the 100% home-range scale), so model convergence failed; we removed such models from the model set. The top-ranked model of habitat at the 20% of home-range scale received similar support (0.93 AIC values lower) as the top-ranked model at the 100% home-range scale (Table 7). All hypotheses were represented in the 90% confidence model set and model selection uncertainty was high at all scales of analysis (Table 7; Appendix B). However, there was slightly more support for avoidance of anthropogenic features than other hypotheses at the 100% home-range scale and a positive effect of landscape complexity at the 20% home-range scale. Mapping predicted occupancy of coyotes (range $\hat{\psi} = 0.55$ to 1) based on the top camera-cluster model resulted in a map with predicted high occupancy throughout much of the study area and moderate occupancy only near urban areas (Figure 4).

Model-averaged gray fox $\hat{\psi}_{\text{point}} = 0.13 \pm 0.01$ and $\hat{\psi}_{\text{cluster}} = 0.29 \pm 0.03$. The prey-availability hypothesis was the most supported hypothesis at the camera-point scale (Table 8), but the coefficient estimates were not consistent with our hypothesis that gray fox ψ would increase with covariates thought to be related to prey density (Table 2). Gray fox ψ_{point} was negatively affected by percentage of hardwood ($\beta = -0.20 \pm 0.06$), distance to human structures ($\beta = -0.23 \pm 0.10$), and was also lower on private land than public land ($\beta = -0.39 \pm 0.11$). Coarse woody debris ($\beta = 0.13 \pm 0.07$) and distance to streams ($\beta = 0.13 \pm 0.09$) had little effect on gray fox ψ_{point}.

For gray foxes there were more models in the 90% confidence set at the camera-point scale than at the camera-cluster scale (Table 8; Appendix B). Anthropogenic features were important, but the direction of effects of variables measured in the 100% home-range buffer was mixed. Gray fox ψ_{cluster} generally increased with higher density of minor paved roads ($\beta = 0.33 \pm 0.08$), but also increased with distance from minor paved roads ($\beta = 0.48 \pm 0.09$) and major roads ($\beta = 0.92 \pm 0.13$) within those areas. The density of streams ($\beta = -0.78 \pm 0.09$) and proportion of agriculture land cover ($\beta = -1.06 \pm 0.12$) within the 100% home-range buffers negatively influenced gray fox ψ_{cluster}. Landscape complexity and vegetative land cover within 20% of home-range buffers were more important than anthropogenic features for gray fox ψ_{cluster}. Edge density ($\beta = 1.00 \pm 0.18$) and proportion of forest cover ($\beta = 0.48 \pm 0.12$) positively influenced gray fox ψ_{cluster}. Conversely, gray fox ψ_{cluster} decreased with increased patch-type diversity ($\beta = -1.24 \pm 0.21$), forest proximity index ($\beta = -0.25 \pm 0.09$), and agriculture land cover ($\beta = -0.41 \pm 0.16$). The top-ranked model at the 100% home-range-buffer scale received slightly more support (2.45 AIC values lower) than the top-ranked model at the 20% of home-range-buffer scale (Table 8). Mapping predicted occupancy of gray fox (range $\hat{\psi} = 0.23$ to 0.41) based on top camera-cluster models indicated that the species likely occurred in more localized populations than bobcats and coyotes, the highest probability of occupancy being in the forested areas in the southern region of the study area (Figure 5). The lowest predicted occupancy was in agriculture land and near streams, but roads played only a small role in the prediction map (Figure 5).

The model-averaged red fox $\hat{\psi}_{\text{point}} = 0.12 \pm 0.02$ and $\hat{\psi}_{\text{cluster}} = 0.26 \pm 0.04$. Most models (range 68% to 76%) in all 3 red fox habitat ψ model sets (100%, 20% of home-range, and camera-point scale) received little or no support ($w < 0.01$; Appendix B). At the camera-point scale, the anthropogenic features/predator avoidance hypothesis received all model-weight support (Table 9, Appendix B). Red fox ψ_{point} decreased with distance to human structures ($\beta = -0.77 \pm 0.09$) and was higher on private land ($\beta = 0.54 \pm 0.12$). AF was the only hypothesis represented in the 90% confidence model set for red fox ψ_{cluster} (Table 9). The effect of AF was primarily positive: red fox ψ_{cluster} increased with density of human structures ($\beta = 0.67 \pm 0.16$), density of roads ($\beta = 0.95 \pm 0.21$), and proportion of urban land cover ($\beta = 0.55 \pm 0.11$); it decreased with distance to human structures ($\beta = -0.83 \pm 0.16$). Although red fox ψ_{cluster} was higher in areas with higher road density, it was higher further from roads in those areas. The top-ranked red fox $\psi_{cluster}$ model at the 100% home-range scale received much more support than the top-ranked model at the 20% home-range scale (9.45 AIC values lower; Table 9). Mapping red-fox-predicted occupancy (range $\hat{\psi}$ = 0.00 to 0.42) based on top camera-cluster habitat models indicated that the species had highest (moderate) predicted occupancy in areas where gray fox occupancy was predicted to be lowest, which was in the northern region of the study area (Figure 6).

The model-averaged striped skunk $\hat{\psi}_{point} = 0.47 \pm 0.01$ and $\hat{\psi}_{cluster} = 0.79 \pm 0.03$. An important predictor of occupancy was private property, especially at the camera-point scale (Table 10). Private property had higher levels of striped skunk occupancy than public land ($\hat{\psi}_{point} = 0.56 \pm 0.04$ private vs. 0.38 ± 0.04 public, $\hat{\psi}_{cluster} = 0.88 \pm 0.07$ private vs. 0.65 ± 0.06 public); resulting in wider distribution in the northern part of the study area with less public land. The most-supported model using habitat within 100% home-range buffer was slightly more supported than the top-ranked model at the 20% of home-range-buffer scale (1.62 AIC values lower; Table 10; Appendix B). AF was overall the most-supported hypothesis regarding striped skunk $\psi_{cluster}$, but percentage of agriculture ($\beta = 0.63 \pm 0.30$) and forest ($\beta = -0.41 \pm 0.20$) within 20% home-range buffers also influenced $\psi_{cluster}$ (Table 6; Appendix B). Generally, striped skunk $\psi_{cluster}$ was negatively related to anthropogenic features, but the effects were weak. For example, the density of roads and human structures had β estimates with confidence intervals that overlap 0 ($\beta = -0.08 \pm 0.21$ and $\beta = 0.00 \pm 0.18$, respectively). Distance to minor and major roads both had positive effects ($\beta = 0.69 \pm 0.30$, $\beta = 0.73 \pm 0.38$, respectively) on striped skunk $\psi_{cluster}$. Mapping striped skunk predicted occupancy (range $\hat{\psi}$ = 0.20 to 0.97) suggests the species was widely distributed throughout the study area with the highest levels of predicted occupancy in agricultural lands (Figure 7).

Species Co-occurrence

Focal species: gray fox.—The overall estimated levels of co-occurrence at a camera-point for gray foxes with bobcats, coyotes, and red foxes were $\hat{\varphi}$ = 1.06 ± 0.21, 1.08 ± 0.11, and 1.97 ± 0.50, respectively. According to the INTERACTING SPECIES-ONLY models, the probability of gray foxes occurring at a camera point did not differ based on the ψ of bobcats or coyotes (with bobcats: $\hat{\psi}_{\text{point}}$ = 0.14 ± 0.03; without bobcats: $\hat{\psi}_{\text{point}}$ = 0.13 ± 0.02; with coyotes: $\hat{\psi}_{\text{point}}$ = 0.14 ± 0.02; without coyotes: $\hat{\psi}_{\text{point}}$ = 0.12 ±0.02). Conversely, gray fox occupancy was higher with red foxes present ($\hat{\psi}$= 0.29 ± 0.07) than without red foxes ($\hat{\psi}$= 0.11 ± 0.02). Models for gray fox-bobcat co-occurrence with bobcat presence included had less support than gray fox habitat-only models and the bobcat-only model received 13 times less support than the gray fox habitat-only model (Figure 8A, Appendix C).

The gray fox HABITAT × INTERACTING SPECIES models indicated that coyote and red fox presence influenced gray fox ψ_{point}, albeit in different directions and ways (Figure 8A). Gray fox occupancy of camera points with higher percentage of hardwood changed based on the presence of coyotes, and this interactive effect was a strong enough signal to be 1 of the 2 top-ranked gray fox-coyote models (Appendix C). The hardwood coefficient estimate for gray fox ψ_{point} was near zero with coyotes present (β = 0.08 ± 0.18) and strongly negative with coyotes absent (β = -0.47 ± 0.15). The presence of red foxes at the camera-point scale was highly correlated with gray fox ψ (Figure 8A). Indeed, the top-ranked HABITAT + RED FOX model ranked above all HABITAT-ONLY models (≥24 times more support) and the RED FOX-ONLY model ranked higher than HABITAT-ONLY models, suggesting a positive association with red foxes (Figure 8A, Appendix C).

The raw levels of co-occurrence in a camera-cluster between gray foxes and bobcats, coyotes, and red foxes were $\hat{\varphi} = 1.02 \pm 0.10$, 1.00 ± 0.05, and 1.23 ± 0.20, respectively. After accounting for ψ of interacting species and imperfect detection of both species, the probability of gray foxes occurring in a camera-cluster was lower with the presence of coyotes ($\hat{\psi}_{\text{cluster}} = 0.27 \pm 0.03$ with coyote, $\hat{\psi}_{\text{cluster}} = 0.88 \pm 0.20$ without coyote) and higher with red foxes ($\hat{\psi}_{\text{cluster}} = 0.40 \pm 0.08$ with red fox, $\hat{\psi}_{\text{cluster}} = 0.25 \pm 0.03$ without red fox) (Figure 9). Conversely, there was no apparent difference in the level of gray fox occupancy in relation to the presence of bobcats ($\hat{\psi}_{\text{cluster}} = 0.29 \pm 0.04$ with bobcat, $\hat{\psi}_{\text{cluster}} = 0.27 \pm 0.08$ without bobcat). Although co-occurrence models with bobcat ψ_{cluster} included were among the most-supported models, gray fox ψ_{cluster} was more influenced by habitat features than the occurrence of bobcats (Figure 8B, Figure 9). Further, the BOBCAT-ONLY model received less support than the null model (Appendix D). Given the small influence of bobcat presence on the occupancy of gray foxes, the map of gray fox predicted occupancy with the effect of bobcats added (Figure 10A) was similar to the habitat-only gray fox occupancy map (Figure 5).

Unlike bobcats, coyotes appeared to strongly influence gray fox ψ_{cluster}, where all of the top-ranked gray fox co-occurrence models included the negative effect of coyote presence (Figure 8B, Appendix D). Because coyote ψ_{cluster} approached 1, there were few areas without coyote presence and these data suggested a high probability of gray foxes occupying coyote-free areas regardless of habitat. Unlike at the camera-point scale, the direction of effects of particular habitat variables on occupancy of gray foxes at the camera-cluster scale did not change based on coyote presence, as evidenced by the top HABITAT + COYOTE model being more supported than the top HABITAT × COYOTE model (separate slopes for habitat variables with and without coyotes present; Figure 8B, Appendix D). The strong influence of coyotes on gray fox occupancy was evident in the predicted gray fox occupancy map that included coyote occupancy (Figure 10B). The model predicts that gray fox occupancy was highest in or near urban areas and the forested areas of the study area.

Although the top gray fox HABITAT-ONLY model received more support than any other model that included red foxes, red fox presence may be an important factor in predicting gray fox ψ_{cluster}. Many of the most-supported gray fox-red fox co-occurrence models incorporated the presence of red foxes (Figure 8B). Adding the positive influence of red foxes to the predicted occupancy map for gray foxes suggested that gray foxes may be widespread throughout the study area albeit at relatively low levels (Figure 10C).

Focal species: red fox.—Overall, red foxes appeared to occur independently of bobcats at the camera-point scale ($\hat{\varphi} = 1.14 \pm 0.30$), but co-occurred more than expected with coyotes ($\hat{\varphi} = 1.40 \pm 0.15$). The probabilities of red foxes occurring at a camera-point with and without bobcats present were 0.12 ± 0.04 and 0.11 ± 0.02, respectively. Red fox $\hat{\psi}_{\text{point}} = 0.16 \pm 0.03$ with coyote presence, but 0.05 ± 0.03 without coyotes. Red fox ψ_{point} was also higher with gray fox presence ($\hat{\psi}_{\text{point}} = 0.23 \pm 0.07$ with gray fox, $\hat{\psi}_{\text{point}} = 0.10 \pm 0.02$ without gray fox). The red fox-bobcat co-occurrence models that included the effect of bobcat presence received less support than red fox habitat-only models. Furthermore, the BOBCAT-ONLY model ($w = 0.000$) received less support than the null model (2.10 AIC values higher) (Figure 11A, Appendix C). Conversely, at the camera-point scale, the top-ranked red fox models including both habitat and the effect of either coyotes or gray foxes received 20 or 12 times more support, respectively, than any red fox HABITAT-ONLY models (Figure 11A, Appendix C). In both circumstances, the presence of the interacting species had a positive influence on red fox camera-point occupancy (Figure 9). However, the COYOTE-ONLY and GRAY FOX-ONLY models received little support (Figure 11A, Appendix C), reiterating the importance of habitat in predicting red fox occurrence.

At the camera-cluster scale, the raw level of co-occurrence was lower between red foxes and bobcats ($\hat{\varphi} = 0.80 \pm 0.11$) than red foxes and coyotes ($\hat{\varphi} = 1.02 \pm 0.06$). Red fox $\psi_{cluster}$ was lower where bobcats were present ($\hat{\psi}_{cluster} = 0.20 \pm 0.04$ with bobcats, $\hat{\psi}_{cluster} = 0.45 \pm 0.11$ without bobcats), but was higher with gray foxes present ($\hat{\psi}_{cluster} = 0.38 \pm 0.08$ with gray foxes, $\hat{\psi}_{cluster} = 0.16 \pm 0.05$ without gray fox). Red fox $\psi_{cluster}$ did not appear to differ with the presence of coyotes ($\hat{\psi}_{cluster} = 0.26 \pm 0.04$ with coyotes, $\hat{\psi}_{cluster} = 0.29 \pm 0.21$ without coyotes). Although red fox occupancy differed in areas with and without other carnivores, all 3 red fox co-occurrence model sets (with bobcat, coyote, and gray fox) suggested habitat was a more important predictor of red fox occupancy than the presence of other carnivores at the camera-cluster scale (Figure 11A, Appendix D). Although red foxes had a higher probability of occupying a camera cluster without bobcats present, the 2 top-ranked red fox-bobcat co-occurrence models were HABITAT-ONLY models (Appendix D). Because of the small effect of bobcat presence, mapping red fox occupancy based on HABITAT + BOBCAT resulted in a map (Figure 12A) similar to the red fox HABITAT-ONLY map (Figure 6). Although coyote presence was not the most important factor, coyote occupancy did influence the map of predicted red fox occupancy (Figure 11B, Figure 12B). In urban areas where coyote occupancy was moderate, red fox occupancy was predicted to be highest although it was relatively low compared to predicted coyote occupancy (Figure 12B, Appendix D). Red fox occupancy was higher with gray foxes present, but habitat alone was a more-supported model (Figure 11B). The inclusion of gray fox occupancy resulted in a map that predicted a low level, but wide distribution of red foxes with the highest levels being in urban areas (Figure 12C).

Focal species: striped skunk.—Striped skunks co-occurred randomly at the camera-point scale with bobcats ($\hat{\varphi}$ = 1.10 ± 0.12), but at high levels with coyotes ($\hat{\varphi}$ = 1.68 ± 0.07), gray foxes ($\hat{\varphi}$ = 1.41 ± 0.18), and red foxes ($\hat{\varphi}$ = 1.77 ± 0.22). Co-occurrence modeling indicated that the probability of striped skunks occurring at a camera point was not apparently different based on the presence of bobcats ($\hat{\psi}_{\text{point}}$ = 0.48 ± 0.06 with bobcats, $\hat{\psi}_{\text{point}}$ = 0.45 ± 0.03 without bobcats). Estimates of striped skunk ψ were higher with coyotes ($\hat{\psi}_{\text{point}}$ = 0.72 ± 0.05 with coyotes, $\hat{\psi}_{\text{point}}$ = 0.07 ±0.05 without coyotes), gray foxes ($\hat{\psi}_{\text{point}}$ = 0.58 ± 0.08 with gray foxes, $\hat{\psi}_{\text{point}}$ = 0.45 ± 0.03 without gray foxes), and red foxes ($\hat{\psi}_{\text{point}}$ 0.75 ± 0.10 with red foxes, $\hat{\psi}_{\text{point}}$ = 0.42 ± 0.03 without red foxes). Although estimates of striped skunk occurrence differed with and without other species present at the camera-point scale, INTERACTING SPECIES-ONLY models received little support compared to models including habitat (Figure 13A). In most instances, models with main effects of habitat and interacting species were the most-supported models (Appendix C). The HABITAT × BOBCAT model had similar support as the top-ranked HABITAT-ONLY model. In areas with bobcats, distance to road had a weaker effect (DTRD β = -0.08 ± 0.04 vs. β = 0.30 ± 0.09 without bobcats) than the effects of distance to human structure (DTST β = 0.56 ± 0.08 with bobcats vs. β = -0.25 ± 0.06 without bobcats) and private land ownership (PVT β = 1.63 ± 0.20 with bobcats vs. β = 0.44 ± 0.14 without bobcats). The striped skunk HABITAT + COYOTE models were much more supported than either the HABITAT-ONLY or COYOTE-ONLY models, which received no support in the model set (Figure 13A). Adding the effect of gray fox to striped skunk habitat models also improved the support for those models (Figure 13A). Coefficient estimates suggest that camera-points where striped skunks and gray fox co-occurred were closer to human structures (DTST β = -1.22 ± 0.24), but less likely to be on private land (PVT β = -0.31 ± 0.14) than points where they did not co-occur (DTST $\beta = 0.01 \pm 0.05$, PVT $\beta = 0.80 \pm 0.20$). The top-ranked HABITAT + RED FOX model for striped skunks received 15 times more support than the HABITAT-ONLY model, but the RED FOX-ONLY model received no support (Figure 13A).

Estimated species interaction factors at the camera-cluster scale between striped skunks and bobcats ($\hat{\varphi} = 0.98 \pm 0.06$), coyotes ($\hat{\varphi} = 1.07 \pm 0.03$), and red foxes ($\hat{\varphi} = 1.12 \pm 0.12$) were all near 1 (co-occurrence similar to random expectation). Conversely, striped skunks were more likely to co-occur with gray foxes than expected ($\hat{\varphi} = 1.22 \pm 0.10$, Figure 9). For striped skunks the HABITAT-ONLY model at the camera-cluster scale was less supported than models that also include the effect of bobcats, coyotes, or gray foxes (Figure 13B). Striped skunk ψ_{cluster} was marginally lower in camera clusters occupied by bobcats than those without bobcats ($\hat{\psi}_{\text{cluster}} = 0.61 \pm 0.05$ vs. $\hat{\psi}_{\text{cluster}} = 0.78 \pm 0.11$); however, the estimates had overlapping confidence intervals. The most supported striped skunk-bobcat co-occurrence model had an interaction between agricultural landcover and bobcat presence (Figure 13B, Appendix D). Striped skunks were more likely to be detected in areas dominated by agriculture landcover with bobcats present ($\beta = 0.92 \pm 0.18$) than where bobcats were not present ($\beta = -0.36 \pm 0.14$). Although mapping striped skunk occupancy with the effect of bobcats suggests widespread distribution of skunks with relatively high occupancy throughout the study area (range $\hat{\psi} = 0.92$ to 0.70), the area of the highest predicted occupancy was smaller than in the HABITAT-ONLY map (Figure 7, Figure 14A). With bobcats present, predicted occupancy of striped skunks is predicted to be high in areas dominated by agriculture and moderate in forested areas (Figure 14A).

Occupancy of striped skunks was similar with and without coyotes present ($\hat{\psi} = 0.79 \pm 0.05$ and $\hat{\psi} = 0.77 \pm 0.06$, respectively). The striped skunk co-occurrence model that included only the effect of coyote received no model support, but habitat models with the effect of coyote presence included had more support than striped skunk HABITAT-ONLY models (Figure 13B). Although overall striped skunk occupancy was similar with and without coyotes present, the positive effects of agriculture and to a lesser degree urban areas on striped skunk occupancy were stronger where coyotes were present vs. absent (Figure 14B, Appendix C).

Striped skunk ψ_{cluster} was higher in camera clusters with than without gray foxes present ($\hat{\psi}_{\text{cluster}} = 0.97 \pm 0.09$ with gray foxes, $\hat{\psi}_{\text{cluster}} = 0.60 \pm 0.12$ without gray foxes) and the top-ranked HABITAT + GRAY FOX model received 11.5 times more support than any habitat-only models, although the GRAY FOX-ONLY model had similar support as the top-ranked habitat-only model (Figure 13B). The addition of gray foxes resulted in a map with slightly higher striped skunk predicted occupancy in the forest-dominated area of the study area than other co-occurrence maps (Figure 14C). Striped skunk ψ_{cluster} was slightly higher in camera-clusters occupied by red foxes compared to those without red foxes ($\hat{\psi}_{\text{cluster}} = 0.84 \pm 0.09$ with red foxes, $\hat{\psi}_{\text{cluster}} = 0.73 \pm 0.05$ without red foxes), but the estimates have overlapping confidence intervals and the species interaction factor is near 1. Models with the inclusion of red fox received similar support as the striped skunk HABITAT-ONLY models (Figure 13B). Additionally, adding red fox presence did not strongly influence the striped skunk predicted occupancy map, as the co-occurrence map (Figure 14D) was similar to the HABITAT-ONLY occupancy map (Figure 7).

Colonization and Extinction

I modeled factors that may influence bobcat colonization rather than extinction because colonization had a much higher probability of occurring ($\hat{\gamma} = 0.86 \pm 0.22$) than extinction ($\hat{\varepsilon} = 0.07 \pm 0.06$). Conversely, gray fox and red fox extinction probabilities ($\hat{\varepsilon} = 0.57 \pm 0.09$ and $\hat{\varepsilon} = 0.35 \pm 0.08$, respectively) were much higher than colonization probabilities ($\hat{\gamma} = 0.16 \pm 0.05$ and $\hat{\gamma} = 0.06 \pm 0.04$, respectively). Therefore, we fit models to elucidate factors influencing extinction events of the fox species (Appendix E). Striped skunk colonization ($\hat{\gamma} = 0.31 \pm 0.11$) and extinction ($\hat{\varepsilon} = 0.30 \pm 0.10$) had similar probabilities, thus we assumed the species was at or near equilibrium with respect to turnover rates of camera-cluster occupancy and did not model factors influencing those parameters. We could not include coyotes or raccoons in models to assess colonization and extinction because both species had occupancy estimates near 1 during the study.

Bobcat colonization was most strongly (and negatively) influenced by the proportion of agriculture on the landscape (Table 11; $\beta = -6.48 \pm 1.39$). Indeed, the model with agricultural landcover received 4 times the support as the next-ranked model, which was the null model (Table 11). Coefficient estimates suggest gray fox ε was lower in areas with higher densities of human structures (STHA $\beta = -2.38 \pm 0.34$) and higher with distance to human structures (DTST $\beta = 0.90 \pm 0.18$), but the STHA + DTST model received little more support than the null model (Table 11, Appendix E). Models of gray fox ε based on occupancy estimates of bobcat and red fox were not more supported than the null model. Red fox ε was positively related to agricultural landcover ($\beta = 2.43 \pm 0.25$) and density of minor paved roads ($\beta = 1.56 \pm 0.42$).

Activity

I used 15,092 photographs (34% of original photographs) in activity analyses, which represented photographs remaining after deleting duplicate photographs of a species detected within 2 hours at the same camera point. We only used 31% of raccoon and 34% of striped skunk photographs in analysis, but we used most of the bobcat (80%), coyote (79%), gray fox (53%), and red fox (83%) photographs recorded (Table 3). For all species recorded, far fewer photographs were recorded during the diurnal period than the crepuscular and nocturnal periods (Table 3).

Activity of all 6 focal species differed among diel periods (bobcat, $F_{2, 355} = 15.84$, $P < 0.01$; coyote, $F_{2, 355} = 53.47$, $P < 0.01$; gray fox, $F_{2, 355} = 12.66$, $P < 0.01$; raccoon, $F_{2, 355} = 168.06$, $P < 0.01$; red fox, $F_{2, 355} = 5.03$, $P < 0.01$; striped skunk, $F_{2, 355} = 11.52$, $P < 0.01$), primarily being lower during the day than crepuscular and nocturnal periods (Table 12). Coyotes, gray foxes, raccoons, and striped skunks were more active during the nocturnal period than the crepuscular period (Table 12). Indeed, nearly 70% of the gray fox, raccoon, and striped skunk photographs were recorded during the nocturnal period (Table 3). Conversely, bobcats were marginally more active during the crepuscular period, with approximately 50% of photographs recorded during this time. We recorded a similar number of red fox photographs in the crepuscular and nocturnal periods (Table 12). We recorded a similar percentage of bobcat, coyote, and red fox photographs during the diurnal period.

The mean number of bobcat photographs recorded in a camera cluster did not differ based on detection/non-detection of coyotes ($F_{1, 355} = 1.39$, $P = 0.24$), but increased with the number of coyote photographs recorded ($F_{1, 355} = 155.50$, $P < 0.01$, Figure 15). The mean number of gray fox ($F_{1, 355} = 6.67$, $P = 0.01$) and red fox ($F_{1, 355} = 7.93$, $P = 0.01$) photographs (overall activity) in a camera-cluster declined with increasing photographs of coyotes (Table 13, Figure 9, Figure 16). Conversely, total raccoon and striped skunk photographs increased ($F_{1, 355} = 96.84$ $P < 0.01$; $F_{1, 355} = 34.47$, $P < 0.01$, respectively) with increasing coyote total photographs (Table 13, Figure 17). With increasing bobcat photographs, red fox photographs decreased ($F_{1, 355} = 102.30$, $P < 0.01$), but raccoon photographs increased ($F_{1, 355} = 36.96$, $P < 0.01$; Figure 18). Gray fox and red fox total photographs were not influenced by the binary detection/non-detection of bobcats or coyotes (Table 13). The number of red fox photographs at a camera cluster was negatively related to probability of occupancy of bobcats ($F_{1, 355} = 6.57$, $P = 0.01$), but raccoon photographs increased with higher probabilities of bobcat occupancy ($F_{1, 355} = 6.33$, $P = 0.01$; Table 13, Figure 19). We recorded more raccoon and striped skunk photographs in camera-clusters with at least one bobcat and coyote detection (raccoon-bobcat: $F_{1, 355} = 49.02$, $P < 0.01$; raccoon-coyote: $F_{1, 355} = 17.01$, $P < 0.01$; striped skunk-bobcat: $F_{1, 355} = 7.03$, $P = 0.01$; striped skunk-coyote: $F_{1, 355} = 4.01$, $P = 0.05$; Figure 20).

I recorded a greater fraction of bobcat photographs at night at camera clusters where more nocturnal coyote photographs were recorded (Table 14). The fraction of gray fox photographs during the nocturnal period was apparently not affected by the number of nocturnal bobcat photographs. Conversely, with more nocturnal coyote photographs, gray foxes were detected less at night and more during crepuscular periods (Table 14). Further, a smaller fraction of gray fox photographs were recorded in specific diel periods with an increase in coyote photographs during the same time period (Figure 21). We observed an increase in the fraction of red fox photographs at night with more nocturnal coyote photographs (Table 14). Using the *a priori* designated α level, we was unable to reject the null hypothesis of no effect of the number of bobcat photographs on the fraction of raccoon photographs recorded during a time period ($F_{2, 708} = 3.40$, $P = 0.07$). However, we recorded a greater fraction of raccoon photographs during the nocturnal and crepuscular periods at camera clusters where ≥1 bobcat photograph was recorded (Figure 9); a similar pattern was observed where coyotes were detected (Figure 22). The number of raccoon photographs during each time period was positively associated with the number of coyote photographs ($F_{2, 708} = 19.14$, $P < 0.01$) and we observed a shift to more nocturnal and diurnal raccoon activity with an increase in coyote nocturnal photographs (Table 14). Red fox-bobcat models did not converge, so were not reported. More red fox nocturnal photographs were recorded with increases in nocturnal coyote photographs (Table 14). The number of period-specific bobcat photographs did not affect the number of striped skunk photographs ($F_{2,708} = 0.86$, $P = 0.35$). Striped skunks were more active during the diurnal period with more coyote activity during the nocturnal period (Table 14).

DISCUSSION

This research has quantified habitat occupancy and species interactions within a carnivore guild at much larger scale and encompassing more species than is typical for studies of wildlife, especially carnivores. The results provide novel insights regarding multiple scales of spatial and temporal structuring of a carnivore community that have implications beyond this guild to the broader ecosystem. Additionally, the results reiterate the importance of considering multiple spatial scales in ecological studies. Some species may demonstrate consistent resource selection at multiple scales, resulting in fairly consistent outcomes from occupancy analysis regardless of scale considered. For example, we found that anthropogenic feature models ranked highest for red fox occupancy regardless of scale. However, for many species, one scale of analysis may produce results quite different than results from another scale depending on a species' distribution, mobility, rarity, and the scale at which a species selects a particular habitat feature such as edge (Oehler and Litvaitis 1996, Gehring and Swihart 2003, He and Condit 2007). For example, our data suggested that gray foxes select areas near anthropogenic features at the landscape scale and areas with potential high prey density and enhanced predator avoidance at finer scales. Within the guild, patterns of occupancy and temporal activity emerged based on body size and expected diet; however, no 2 species shared the same patterns in all of the analyses included in this study.

Bobcat

The relatively low detection probability of bobcats that we observed suggests the species is wide-ranging in southern Illinois (Nielsen and Woolf 2001a), which is typical for a highly carnivorous mammal. In addition to influencing detectability, the wide-ranging behavior of bobcats likely also influenced their scale of habitat selection. We observed a gradient in importance of measured habitat features to bobcats from the largest to smallest spatial scales evaluated, where less model-selection uncertainty occurred at the camera-cluster scale than the camera-point scale. Although bobcats can exploit urban habitats (Riley et al. 2003), our data indicated that at the camera-cluster scale, bobcats were negatively impacted by anthropogenic features, especially at the largest buffer scale evaluated. This finding should be considered with the understanding that urbanization within the study area ranged from relatively low to moderate levels. Bobcats, especially adult females, appear to be negatively affected by increased urbanization through their reduced use of anthropogenic features (compared to natural habitat), which in turn reduces available habitats and space (Nielsen and Woolf 2001b, Riley et al. 2003, Riley 2006). Further, bobcats are sensitive to landscape complexity and may become locally extinct in highly fragmented areas (Crooks 2002). Unlike Kolowski and Woolf (2002), we found weak support for bobcats selecting sites based on microhabitat variables in southern Illinois. However, we deployed remote cameras only in forested areas, so our data do not provide information on the fine-scale use of non-forested habitat compared to forested habitat. Nevertheless, the stronger selection at the largest scale suggests bobcats establish home ranges in forested landscapes with the least anthropogenic influence available and are less selective regarding natural habitat within those areas.

Our data agree with Kennedy (1999) that bobcats are mostly crepuscular in southern Illinois. Bobcats may adjust activity to increase access to prey, but little evidence exists to suggest the species shifts spatial or temporal activity to avoid competitors, particularly coyotes (Witmer and deCalesta 1986, Neale and Sacks 2001b, Wilson et al. 2010). We also found no shift in activity by bobcats with regard to coyote activity. Indeed, our data suggested there may be an overall increase in bobcat activity, but not a shift in the diel period of activity, in areas with increased coyote activity. The reasons for this apparent association in activity remain unclear, but may be mediated by some unmeasured habitat factor or heterogeneous prey abundance.

Coyote

I observed heterogeneity in coyote detection probability, but found the species to have near-ubiquitous distribution within the study area. We found support at all scales for all hypotheses regarding coyote habitat occupancy. The overall camera-cluster occupancy of coyotes was near 1, suggesting that, like in other regions the species uses most available habitats (Person and Hirth 1991, Grinder and Krausman 2001). Despite coyotes being quite common throughout the study area, we found less use of anthropogenic features than natural habitats. Coyotes are remarkable in their behavioral plasticity and ability to exploit both natural and highly disturbed anthropogenic-dominated landscapes (Gese et al. 1988, Person and Hirth 1991, Chamberlain et al. 2000, Kays et al. 2008, Gehrt and Riley 2010). However, most studies of urban coyotes have found that although their territories can contain urban habitats, their core use areas typically contain forest patches (Grinder and Krausman 2001, Riley et al. 2003, Gehrt et al. 2009). Furthermore, coyote occupancy and abundance decline with size and isolation of natural habitat patches (Crooks 2002). We also found that coyotes had higher occupancy of areas with high levels of landscape complexity and densities of edge habitat. Selection for edge habitat has been repeatedly observed for coyotes and may enhance this highly mobile predator's success of cursorial hunting (Van Valkenburgh 1985, Bradley and Fagre 1988, Tigas et al. 2002, Thibault and Ouellet 2005, Gorini et al. 2012).

The estimated occupancy of coyotes at camera clusters ($\hat{\psi} = 0.95$) compared to the camera-point scale ($\hat{\psi} = 0.58$) suggests that although the species is generally ubiquitous, their distribution is somewhat patchy at small scales. At the camera-point scale, coyote distribution appeared to be influenced by the physical characteristics of forest habitat. Coyote occupancy was higher in open understory and hardwood forest stands. These hardwood stands likely had higher prey abundance and diversity than conifer stands (Healy and Brooks 1988, Willson and Comet 1996, Rosenblatt et al. 1999). The finding is consistent with the hypothesis that coyote diet and distribution is associated with prey abundance (Windberg and Mitchell 1990, Mills and Knowlton 1991, Patterson and Messier 2001, Wilson et al. 2010), open canopy forest, edge habitats, and landscapes devoid of larger canids (Person and Hirth 1991, Moorcroft et al. 2006, Kays et al. 2008). Analysis of a subset of our camera points ($n = 30$) indicated that coyote occurrence was negatively related to the percent basal area of a forest stand composed of hard-mast bearing trees (e.g., *Quercus* spp., *Carya* spp.; Gillen and Hellgren 2013), suggesting that the type of deciduous forest may be important to coyote occupancy patterns. The importance of having such a detailed and nuanced understanding of the role of forest structure has become increasingly clear for coyotes. For example, open canopy forest habitats may be preferred over other available habitats in winter and spring (Person and Hirth 1991, Kays et al. 2008).

Gray fox

Gray foxes were the only focal species in this study that had different hypotheses that were most-supported regarding camera-cluster occupancy between the 2 sizes of buffer areas.

Most top-ranked occupancy models with variables measured in 100% home-range size buffers were associated with the AF hypothesis. Conversely, no models including anthropogenic features within smaller (20% of home range) buffers received support. At the 100% home-range buffer size, anthropogenic feature variables differed in their direction of effect. The mixed results and uncertainty associated with the model selection and suggests the need for a nuanced view of gray fox occupancy in semi-urban landscapes. The increase in occupancy with minor paved road density suggests gray foxes have the flexibility to use developed areas that may give them access to habitats not heavily exploited by larger sympatric carnivores, which has been observed in other gray fox populations. Riley (2006) observed gray fox core areas within natural habitats of protected areas, but the species regularly used urban landscapes despite the increased exposure to human-related mortality, which can be quite high in some populations (Temple et al. 2010). Therefore, use of developed areas should not be interpreted as ideal habitat, but rather preferred when better alternatives are not available. For example, a meta-analysis of multiple studies in southern California revealed a negative effect of urbanization on gray fox occurrence (Ordeñana et al. 2010).

Gray fox occupancy was highest in spatially complex areas within the 20% of home-range buffer, suggesting a higher degree of adaptation to fragmentation than other carnivores, which was observed statewide in Illinois (Cooper et al. 2012) and other landscapes (Crooks 2002). Although generally simplified in the diversity of habitats, urban landscapes have a high degree of fragmentation and juxtaposition of distinct habitats, which may offer increased foraging opportunities for omnivorous mesocarnivores like gray foxes (Goodrich and Buskirk 1995, Oehler and Litvaitis 1996, Adkins and Stott 1998, Ray 2000). Gray fox occupancy was negatively associated with grassland and agriculture land cover within the 20% of home-range buffer. Although not in the top 2 models at that scale, there was a strong positive coefficient estimate for forest cover. That gray foxes use forested habitats has been repeatedly reported (Chamberlain and Leopold 2000, Riley 2006, Kelly and Holub 2008, Temple et al. 2010, Cooper et al. 2012), but few studies assessed multiple scales of selection simultaneously.

At the camera-point scale, gray fox occupancy was lower in hardwood stands and near streams, but increased with coarse woody debris. Other studies have found that hardwood forest stands were selected by gray foxes when establishing core areas and were consistently used more than other habitats (Temple et al. 2010), suggesting a need for further investigation into factors beyond habitat that influence the use of hardwood stands. The analysis of co-occurrence with coyotes provides a possible explanation. Although intensity of forest management and decay stage of logs are important factors in the strength of effect, the abundance of coarse woody debris and small mammal abundance are positively correlated in many forest habitats (Loeb 1999, Bowman et al. 2000, McCay and Komoroski 2004, Davis et al. 2010a). However, Gillen (2011) did not observe a consistent positive relationship between these variables in our study area. Nevertheless, the positive association with coarse woody debris in this study suggests gray fox distribution at fine scales may be influenced by availability of small-mammal prey, which has also been reported for other gray fox populations (Chamberlain and Leopold 2000). Although gray foxes may readily use riparian corridors in highly developed landscapes (Hilty and Merenlender 2004), our findings suggest gray foxes select upland sites away from streams in more rural settings.

Our data indicated that gray fox distribution in southern Illinois decreased during the study, which is troubling because the species is of conservation concern due to declining populations and with limited distribution there is increased extirpation risk (Purvis et al. 2000).

One possible explanation for contracting gray fox distribution is the presence of competing species that may also kill gray foxes. Bobcats pose a predation risk for gray foxes and may influence space use of gray foxes in some landscapes (Fedriani et al. 2000, Farias et al. 2005). However, like Neale and Sacks (2001a), we found that bobcats did not appear to influence the spatial distribution, extinction patterns, or daily activity patterns of gray foxes. Habitat-only models were more-supported for gray fox occupancy than adding the effect of bobcat distribution. Further, gray foxes co-occurred randomly with bobcats at both the camera-point and camera-cluster scales, thus there was no apparent adjustment spatially, either positively or negatively, by gray foxes in relation to bobcat presence. Neither the presence nor the level of activity of bobcats appeared to affect the daily activity patterns or number of photographs recorded of gray foxes. Collectively these results suggest gray foxes can coexist with bobcats at the current population level of the felid.

Our data do not address abundance directly; however, results suggest that the abundance of gray foxes may be affected by the distribution and activity of coyotes. At minimum, coyotes appeared to influence the behavior of gray foxes. Although the effect differed by scale, coyote presence influenced gray fox occupancy at the camera-cluster and camera-point scales. Regardless of habitat, a camera-cluster was about 3 times more likely to be occupied by gray foxes if the area was unoccupied by coyotes, suggesting a strong effect of interference competition. Gray fox-coyote co-occurrence was more complicated to interpret at the camera-point scale than at the camera-cluster scale. Although habitat was very influential for gray fox occupancy at camera points, adding the effect of coyote presence revealed that gray foxes were more likely to co-occur with coyotes in hardwood stands compared to conifer stands. This finding suggests that fine-scale habitat features play an important role in mediating inference competition in possibly 2 ways, which are not necessarily mutually exclusive. First, hardwood trees may have morphology that makes climbing them easier for gray foxes. The tree-climbing behavior of gray foxes is an unusual behavior for canids and may serve as a mechanism to avoid predators by escaping to refugia relatively quickly (Yeager 1938, Sillero-Zubiri 2009). Trees are inaccessible by coyotes and if many trees that are suitable for climbing are nearby, gray foxes likely have a higher probability of escape from coyote predation. Second, mature hardwood stands can support small-mammal populations with high abundances (Mitchell et al. 1997, Miller et al. 2004, Ostfeld 2002). Therefore, hardwood stands may serve as coexistence habitats where high prey availability may mediate intraguild predation by coyotes killing fewer foxes or enhancing gray fox populations' ability to absorb losses caused by coyotes (Wilson et al. 2010).

Coyote activity also appeared to affect the timing and level of activity of gray foxes. We recorded fewer gray fox photographs at points and periods with more coyote photographs. The effect was observed both in a decrease in the total number of gray fox photographs and during time periods with more coyote photographs. The photographic results suggest gray foxes are less active, or densities are lower in areas and times with more coyote activity. Coyotes are approximately 200–400% heavier than gray foxes, suggesting coyotes will dominate in interspecific interactions. The ability of coyotes to affect the distribution of foxes through domination, and in many cases by killing foxes has been repeatedly observed (Major and Sherburne 1987, Sargeant and Allen 1989, Gese et al. 1996, Henke and Bryant 1999, Kitchen et al. 1999, Fedriani et al. 2000, Gosselink et al. 2003, Chamberlain and Leopold 2005). Therefore, the spatial and temporal activity shift of gray foxes away from coyotes in this study suggested gray foxes avoid areas of high predation risk when possible. However, it appears that gray foxes can persist and exploit resources in the few areas not occupied by coyotes, and can coexist in areas of the heterogeneous environment where predation risk is reduced.

Raccoon

I recorded more photographs of raccoons than any other species and most photographs were in sequence, suggesting they were highly attracted to the bait. They were also very common in the study area. Indeed, we recorded raccoons in all but 3 camera clusters (>99% of total). The ubiquity of raccoons made it impossible to assess spatial distribution using detection/non-detection data; however, we was able to quantify daily activity patterns and associations with other carnivores. There was no evidence for spatial or temporal avoidance by raccoons relative to the presence or amount of activity of any other carnivore. Indeed, we found a positive spatial association with bobcats and coyotes. Camera clusters with more raccoon photographs also had more bobcat, coyote, and striped skunk photographs. This shared higher activity was not associated with any particular cover type, suggesting coexistence was being facilitated by some other enhanced resource, such as food, which was not measured directly. The results underscore that raccoons are effective at living sympatrically with larger carnivores, and that carnivore relationships outside Canidae may not be dictated by body size alone (Gehrt and Prange 2007).

Reduced competition, thus enhanced coexistence, between the 2 larger carnivores (bobcats and coyotes) and raccoons may be because the larger carnivores are more carnivorous than raccoons. Further, raccoons are larger than the typical prey of either bobcats or coyotes and raccoons can effectively defend themselves and food. Indeed, remote camera studies have produced evidence that raccoons can effectively guard a deer carcass from bobcats and coyotes (D. Lesmeister, unpublished data). Rogers and Caro (1998) suggested that coyotes may be an effective tool for conserving ground-nesting birds by reducing the abundance of raccoons, an important nest predator. Our research provides additional support for Gehrt and Prange's (2007) assertion that coyotes are likely ineffective at suppressing raccoon populations, and in turn reducing raccoon nest predation.

Red fox

I recorded more red fox photographs in 2010 than the previous 2 years of the study. This pattern could reflect a trend in regional abundance or simply a random occurrence. It is unlikely that the red fox population increased from 2008 to 2010, especially when one considers the higher probability of extinction than colonization of camera-points surveyed in 2008 and 2010. Given that we detected red foxes far less often than the other species in this study, and their predicted occupancy is highly localized, this interannual pattern probably arose because we sampled more areas with red foxes in 2010 simply by chance.

Red fox distribution was most associated with anthropogenic features at each scale of analysis (Figure 9), which was expected because the species is increasingly common in urban areas of Australia, Japan, North America, and especially Europe (Willingham et al. 1996, Adkins and Stott 1998, Marks and Bloomfield 1999, Lewis et al. 1999, Tsukada et al. 2000, Gloor et al. 2001). Historically, urban red foxes were thought to be a British phenomenon, but now red foxes are the most abundant urban wild carnivore globally (Harris and Smith 1987, Coman et al. 1991, Gloor et al. 2001, Lavin et al. 2003). However, when considering extreme ends of an urbanization continuum, red foxes are most common in areas of intermediate urbanization (i.e., house densities of <20/ha; Randa and Yunger 2006, Soulsbury et al. 2010), which is typical for suburban development and rural communities in southern Illinois (Storm et al. 2007).

Several characteristics of red foxes allow them to be successful in urban habitats (McKinney 2002). They are a highly mobile, medium-sized carnivore without specific food or habitat requirements and have a high reproductive rate and gene flow between populations (Wandeler et al. 2003, Soulsbury et al. 2010). Furthermore, red foxes have well developed senses of hearing, sight, and smell, and have behavioral plasticity to exploit human-derived resources, primarily scavenged food, and avoid human-caused mortality (Harris 1981b, Doncaster et al. 1990, Saunders et al. 1993). The use of human-dominated landscapes by red foxes should not necessarily be considered ideal habitat for the species, but the habitat may provide mechanisms of coexistence with dominant predators in heterogeneous landscapes if mortality is lower in urban habitats than in more natural areas (Schmidt et al. 2000, Gosselink et al. 2003, Gosselink et al. 2007, Soulsbury et al. 2010). However, urban red fox distribution can be limited to areas where free-ranging dogs and urban coyotes are absent or rare (Harris 1981a, Gosselink et al. 2003). During this study, red fox occupancy was higher near anthropogenic developments, but those areas had few free-ranging dogs detected (D. Lesmeister, unpublished data).

Red fox populations can be regulated by food, social regulation, disease, and intraguild predation; hence, red foxes are influenced by both bottom-up and top-down forces (Sargeant et al. 1987, Lindström 1989, Lindström et al. 1994, Gese et al. 1996, Gosselink et al. 2007). Foxes may be limited by food supply when prey abundance is low, and those effects may be compounded if their diet overlaps highly with a dominant competitor. Given the large size difference, coyotes are expected to dominate red foxes in interference competition, and indeed, red foxes often have reduced use in areas with high coyote activity (Randa and Yunger 2006). Further, Lavin et al. (2003) found that coyotes were effective at competitively excluding red foxes and may be an important factor explaining the decline of red foxes in rural areas of Illinois. However, in our study, red foxes co-occurred randomly with coyotes at the camera-cluster scale, thus there was no apparent large-scale spatial adjustment by red foxes, either positively or negatively, regarding coyote presence. The higher use of urban habitats by red foxes may provide enough spatial partitioning to allow coexistence in the study area.

An unexpected finding was that occupancy by red foxes at the camera-point scale was higher with the presence of coyotes and gray foxes. However, as revealed by the low level of gray fox-coyote co-occurrence, the 3 species did not occur sympatrically at many camera points, thus red foxes are likely to occur with only 1 other canid. Red fox models combining of species interactions and habitat had 12–20 times more support than the top-ranked habitat-only model. Our results of red fox co-occurrence patterns are different from what is typically reported, especially with regard to coyotes (Sargeant et al. 1987, Major and Sherburne 1987, Harrison et al. 1989, Gosselink et al. 2003). We hypothesize red foxes coexist with coyotes in southern Illinois by staying near human structures and by balancing competitive abilities in prey acquisition by being more effective at hunting small prey. Additionally, it should be recognized that red foxes may coexist with coyotes through prey-mediated coexistence (Wilson et al. 2010), but our data were not able to elucidate that possibility.

Given body size difference, it can be expected that bobcats likely dominate red foxes in direct interactions, resulting in spatial or temporal adjustments by the fox. Fewer red foxes were recorded in areas with more bobcats photographed, and bobcats and red foxes co-occurred less than by chance. Initially, one may view this result as evidence of red foxes avoiding areas with higher bobcat activity, but integrating the results suggests the spatial partitioning is driven by other factors than interspecific interactions. Including bobcat presence resulted in models that ranked below red fox habitat-only models, suggesting that spatial segregation of the two species is driven by differences in selection of habitat, as hypothesized by McDonald et al. (2008). Major and Sherburne (1987) also reported that scant evidence existed for competitive relationship between bobcats and red foxes.

Striped skunk

The higher detection probability of striped skunks during January, and especially February, compared to March and April suggests a sharp increase in activity after winter dormancy (Sunquist 1974, Mutch and Aleksiuk 1977) and during the breeding season (Shirer and Fitch 1970, Bixler and Gittleman 2000). Striped skunk occupancy was highest in areas away from roads and in the privately owned and agriculturally dominated land in the northern region of the study area. Our results indicated striped skunks had higher occupancy near human structures (Figure 9), which supported the hypothesis that the species readily associates with human structures for denning and resting (Larivière and Messier 1998). In addition, urban areas with moderate housing density may provide ample food resources for opportunistic omnivores such as “urban-adapted” striped skunks (McKinney 2002, Rosatte et al. 2010). Furthermore, the evolved aposematic coloration of skunks, which is a well-known signal to humans that the animal can accurately spray noxious secretions from their anal glands, allows striped skunks to be avoided and less likely to be persecuted by humans (Stankowich et al. 2011).

Striped skunk occurrence was either unaffected by the presence of other carnivores, or was higher at camera points with other carnivores present, suggesting striped skunks can coexist with larger and potentially dangerous competitors. Although striped skunks may be primarily nocturnal to reduce predation risk (Neiswenter et al. 2010), we did not observe an adjustment in daily activity or space use in areas with intense carnivore activity; a finding also observed by

Prange and Gehrt (2007). On the contrary, the defensive mechanisms of striped skunks may influence the space use of larger carnivores. Their warning coloration elicits avoidance behavior in other carnivores, particularly those individuals that had learned about striped skunk noxiousness through experience (Hunter 2008). The high level of co-occurrence between striped skunks and other carnivores likely reflects an unmeasured shared resource.

Detection and Occupancy Patterns

As a community, the carnivores of southern Illinois had moderate detection probabilities and several survey covariates were important to explain the heterogeneity in photographic histories. The ability to detect carnivores primarily depended on month of survey, weather, and behavioral responses to baited camera points. The latter was true for coyotes and gray foxes, but especially so for raccoons and striped skunks, which were particularly drawn to the baited sites. Collectively, detection models reinforced the importance of accounting for imperfect detection of carnivores when modeling species distributions based on non-invasive survey methods (Gu and Swihart 2004, Field et al. 2005, MacKenzie et al. 2006, Rota et al. 2011).

The most influential habitat factors, as well as the scale with strongest selection, varied across this mesocarnivore guild. A common occupancy predictor for all species was that anthropogenic feature variables regularly occurred in top models. Density of or proximity to human structures and roads occurred in top models for most of the species, suggesting the importance of these variables to the structure of the carnivore community. Human structures and road density are the primary influences of urbanization, which dramatically alters natural communities and can strongly affect populations of carnivores of any body size (Sunquist and Sunquist 2001, Kerley et al. 2002, Riley et al. 2003, Grilo et al. 2009, Ordeñana et al. 2010). Occupancy responses to anthropogenic features were loosely associated with body size (Figure

9). The larger carnivores had lower occupancy rates in proximity to anthropogenic developments, whereas urban areas tended to have higher occupancy by smaller carnivores. Human-dominated areas are more fragmented than most natural habitats and have an altered prey base compared to natural habitats (Sauvajot et al. 1998, Schneider 2001). Body size and trophic position are strong indicators of space and prey abundance required for carnivores; hence, larger carnivores may be more negatively affected by small habitat fragments because of prey abundance and space use requirements (Crooks 2002). Alternatively, generalist species with high mobility are less affected by fragmentation because they can make more complete use of all habitats when moving through a fragmented landscape (Gehring and Swihart 2003). The decreased use of urban areas by larger carnivores in this study may be unrelated to fragmentation, but an avoidance of human persecution. Larger-bodied carnivores, especially canids, are less tolerated by humans and experience greater mortality risk in anthropogenic developments (Sillero-Zubiri and Laurenson 2001). Therefore, small carnivores may use urban areas to a greater extent because they experience less mortality risk in those areas than in areas with greater probability of occupancy by bobcats and coyotes.

Following anthropogenic features in importance to carnivore occupancy was landscape complexity, which was a positive influence for coyotes and gray foxes. This association between the canids and complex landscapes may be a reflection of their importance as predators along edges in fragmented landscapes (Donovan et al. 1997). In addition to both patterns and differences regarding habitat occupancy, we also observed some order in the strength of models at the various scales assessed.

Patterns of habitat occupancy within this guild were more strongly predicted by habitat features measured at the camera-cluster scale than the camera-point scale, which may reflect that mesocarnivores are driven more by second order selection than third order selection (Figure 9). Alternatively, data may be inherently noisier at the point scale, obscuring what could be a strong degree of selection for the features at camera points. Another possibility is that we selected variables that more accurately reflect large-scale patterns of occupancy rather than features influencing small-scale movements.

Co-occurrence Patterns

It is well documented that larger carnivores, especially coyotes, may limit fox population distribution and abundance. Indeed, among the most important influences of coyotes on the broader community is likely their impact on fox species. It seems plausible that the increase in coyotes is playing a role in the decline of foxes in southern Illinois. With suitable habitat, gray foxes are likely to occur in areas without coyotes; however, the effect is not universal because some studies have found no avoidance of coyotes by gray foxes. Our data suggest gray foxes are likely to use camera-cluster scale areas devoid of coyotes, but can coexist with the larger canid under certain conditions. Most canids are remarkable in their ability to perceive and adapt behaviorally to various threats, whether those dangers are direct human persecution, vehicle traffic, or intraguild predation. For example, in Montana, coyotes reduce aggressive interactions with wolves not by completely avoiding areas used by wolves, but rather by avoiding dangerous resources that are spatially and temporally discrete such as carrion (Atwood and Gese 2010). Similarly, gray foxes and red foxes reduce competitive asymmetry with coyotes by adapting their behavior to the fluctuating risks associated with coyotes (Linnell and Strand 2000). Foxes can reduce intraguild predation by being vigilant and avoid direct interactions without generalized spatial avoidance of coyotes. Further, we hypothesize that foxes can coexist with coyotes if there is an abundant shared resource available (e.g., prey-mediated coexistence). Even in a landscape where coyotes are ubiquitous, foxes can persist in areas that serve as refugia. Our data suggested that hardwood stands had the highest levels of gray fox-coyote coexistence, which we hypothesize is because the morphology of hardwood trees facilitate rapid escape of gray foxes from aggressive interactions with coyotes by climbing. Integrating results from occupancy modeling and activity analysis suggested that gray foxes and red foxes can coexist if the abundances of bobcats and coyotes are below some threshold level.

Many of the species-pairs in our study co-occurred more than expected by chance and their numbers of photographs were positively correlated among sites. For example, both occupancy and number of photographs of gray foxes and red foxes tended to be positively correlated. Although gray foxes and red foxes may compete for resources, their similar body size suggests that the species are not a real danger to each other, which was also found between other canid pairs of similar size (Mitchell and Banks 2005, Di Bitetti et al. 2009). The 2 fox species, which are smaller than bobcats and coyotes, but larger than striped skunks, were less active when and where the larger carnivores tended to be most active. Conversely, raccoons and striped skunks did not appear to be affected by the activity of the largest carnivores, thus intraguild interactions appeared to be body-size dependent. Carnivore species, especially canids, are most aggressive and display more interference behavior (including intraguild killing) toward the species that is the next size smaller (Crabtree and Sheldon 1999, Palomares and Caro 1999, Creel et al. 2001).

With the exception of the gray fox-coyote pair, we observed little evidence for spatial partitioning based on interspecific interactions within the southern Illinois carnivore guild and found that habitat preferences were more important in structuring the carnivore community (Figure 9). Given the widespread observation of strong interference competition among

Carnivora, often reaching extremes of intraguild predation (Palomares and Caro 1999), one might assume that this is a phenomenon playing a central role in structuring communities order-wide. Yet, most cases of documented strong interference competition among carnivores involve closely related species or species with similar foraging strategies and high dietary overlap (Donadio and Buskirk 2006). Our study differs from many others in that we took a community-wide perspective and assessed competitive dynamics between pairs of species at multiple scales within a large region with local-scale and landscape-scale heterogeneity incorporated. In almost all cases, we found that distributions of taxa were best predicted by measures of habitat variation alone rather than by models that only included patterns of co-occurrence of larger or potentially competing carnivore taxa.

Interactions among the 6 most abundant members of the carnivore community in southern Illinois can be collectively viewed as relatively unimportant in influencing distributions of individual species in comparison with the effects of natural habitat and human disturbances. Of the 20 possible interactions of taxa (10 at the camera-point scale and 10 at the camera-cluster scale), no interacting species-only (focal species habitat factors ignored) models received more than 0.03 model weight support and most received no support. Although 11 of the possible interactions had habitat plus interacting species models with the most support, only 2 (gray fox-coyote and striped skunk-bobcat at camera-cluster scale) interactions had occupancy estimates for focal species that were lower with interacting species present than without. Although not receiving the attention of studies showing strong space-use shifts as a result of intraguild interactions among pairs of carnivore species, a number of studies have failed to identify strong evidence of altered demography or habitat use among co-occurring carnivore species (Witmer and deCalesta 1986, Neale and Sacks 2001a, Wilson et al. 2010, Mattisson et al. 2011).

Considering this research in the context of the large body of carnivore ecology literature, it appears that carnivores use similar resources and thus have high niche overlap, with partitioning occurring along at least one other niche dimension than space or time, unless avoidance is fine-scaled. However, coexistence is possible even with broadly overlapping fundamental niches if asymmetric competition occurs along 2 or more realized niches, with each competitor being superior to the other in at least 1 dimension (Steinmetz et al. 2011). Although it appears to be relatively common, this model of the niche and balanced competition may be perceived as less dramatic than changes in space use and activity patterns of one carnivore caused by another carnivore, thus has received little attention in carnivore ecology. Given the ecological diversity of Carnivora, which includes foraging ecologies that range from frugivorous to strictly carnivorous, these results should not be surprising as the fitness advantage for strong and potentially risky interference competition is in many cases unclear. Indeed, our results suggest competitor-driven adjustments in space use among members of a carnivore community might be the exception rather than the norm.

Theory and empirical evidence suggest carnivores have evolved mechanisms of coexistence, even with asymmetrical competitive advantages when members of one species dominate individuals of another species (Persson 1985). In interference competition, larger animals are typically competitively superior, especially when competition takes the extreme form of intraguild predation. Smaller carnivores, on the other hand, may be superior in exploitative competition because of an enhanced ability to hunt specific prey (King 1989). These differing advantages should fortify the selective pressure leading to the evolution of hunting efficiency in smaller carnivores and interference behavior in larger members of carnivore guilds (Persson 1985). Additionally, coexistence within both predator-prey and intraguild predator-intraguild prey systems typically is enhanced in a heterogeneous environment with refugia from predation (Sergio et al. 2003, Matter and Mannan 2005, Berger 2010, Creswell et al. 2010, Wilson et al. 2010).

MANAGEMENT IMPLICATIONS

This study underscores the importance of accounting for and assessing the reasons for imperfect detection during surveys. For example, bobcat detection probability was negatively influenced by precipitation and temperature, suggesting the species' activity was reduced during inclement weather. Additionally, there was a strong negative effect of previous photographs on the probability that a bobcat would be detected during subsequent surveys at a camera-point, suggesting that bobcats likely avoided camera-points once the location of a remote camera was known. Although avoidance of remote cameras has been reported for other carnivores (Séquin et al. 2003, Wegge et al. 2004, Jackson et al. 2006, Schipper 2007), to our knowledge it has not been documented for bobcats.

Our ability to detect coyotes increased after ≥1 photograph was recorded, which suggests they were attracted to the bait or scent disks. We also found that detection probability decreased with increasing temperature. Gray foxes also appeared to be attracted to bait and detections increased in cold weather. Indeed, we recorded more than 3 times the number of gray fox photographs in January than in April. The apparent attraction of both coyotes and gray foxes to bait likely influenced the overall higher detection probabilities of those species compared to bobcats and red foxes. In addition to the importance to understanding factors influencing detection probabilities, this research underscores the necessity of considering multiple spatial scales over large landscapes when investigating carnivore ecology, particularly the effect of intraguild interactions.

The inferences drawn from this study would have been quite different had the spatial scale been smaller or if we considered only one scale in our analyses. For example, coyote occupancy was most affected by landscape complexity at large scales, but amount of hardwood forest at the local scale. Camera cluster occupancy of gray fox was best predicted by anthropogenic features within large buffered areas, but landscape complexity variables in smaller buffers. Additionally, the interaction between coyotes and habitat to negatively influence gray fox occupancy was most perceivable at the local scale. Therefore, our results highlight the need to consider multiple spatial scales in order to understand complex responses of individual species to habitat features and intraguild interactions among carnivores. Species likely perceive and respond to landscape fragmentation in part based on their mobility (Gehring and Swihart 2003). The distributions of larger and more mobile carnivores were best characterized by camera-cluster models; whereas, local habitat models were better for the smaller and less mobile species. Furthermore, detection probabilities for all species were similar between the camera-points and camera-clusters, but estimates of occupancy were very different between the scales. This finding emphasizes the advantage of deploying multiple remote cameras within the study unit because a single camera is unable to capture carnivore activity a relatively short distance away and multiple detection devices provide data at multiple scales.

In addition to multiple spatial scales, this research reinforces the need for multi-year studies of carnivores. For example, with the same effort expended per year, our results of red fox occupancy would have differed, either increased or decreased, if the study had been conducted at a smaller scale or for only 1 or 2 years. Although possible, it is unlikely that the red fox population increased from 2008 to 2010, especially when one considers the higher probability of extinction than colonization of camera-points surveyed in 2008 and 2010. Small-scale and short-term studies, especially those seeking to elucidate population distribution of multiple species, may have misleading results about the status and structure of populations.

During the study, a camera-cluster unoccupied by bobcats in 2008 was more likely to become occupied (colonization) in 2010 than an occupied camera-cluster was to become unoccupied (extinction). These results corroborate other research (Nielsen and Woolf 2002, Roberts and Crimmins 2010) and public surveys (Bluett 2011) that suggested bobcat populations had expanded their distribution over the past 2 decades in Illinois and other regions of the conterminous United States. The bobcat population may increase in its current range and may expand further into central and northern Illinois, but our data suggest the rate of expansion may be slower than it has been in southern Illinois, or the species may only expand into forested areas. We reason that north of the study area Illinois is dominated by agricultural and urban landcover. We observed that bobcat colonization was less likely in areas where agricultural land dominated. Further, the urban-dominated region of northern Illinois may be less suitable for bobcats than forest- and grassland-dominated southern Illinois, and agriculture-dominated central Illinois.

Our multi-year data suggest gray fox distribution in the study area contracted during the study because camera-cluster extinction was more likely than colonization. This pattern of contracted distribution provides further evidence to support public surveys (Bluett 2011), which suggest gray foxes are declining in Illinois. Taken together, these data indicate there should be concern for long-term persistence of the species in Illinois for 3 reasons. First, in southern Illinois, coyotes played a negative role in gray fox occupancy patterns at multiple scales. Coyotes were ubiquitous in the study area during this research and may have increased in abundance statewide since the early 1990s. Conversely, in the study area gray foxes had a localized and contracting distribution, which reinforced evidence that the species appears to have declined statewide during the time coyotes appeared to be increasing. Although we cannot definitively state that coyotes have been the sole cause of gray fox decline, our research provides additional evidence that coyotes are a factor. We found that gray foxes were much more likely to occupy a camera cluster without coyotes present and site-level coexistence may be facilitated by hardwood stands and enhanced resources, such as food. Second, gray foxes are not widely distributed throughout the state (i.e., most of the population occurs in southern Illinois), so population decline in its core area does not bode well for long-term persistence. Like most ecological challenges, extirpation does not have one cause; however, there is increased extirpation risk associated with small geographical range (Purvis et al. 2000). Third, gray foxes are already listed as a species in greatest need of conservation in Illinois (IDNR 2005), so a continued downward trend indicates current species recovery efforts are not effective and remedial action may be warranted. There was some evidence that areas with moderate densities of human structures had a slightly lower probability of extirpation than other areas, but was not clearly associated with the presence of other carnivores or specific habitats.

With the exception of coyote-gray fox, we found that habitat was a better predictor of carnivore occupancy than the presence of other species. Further, landscape-level cover types were better than site-level habitat factors for predicting occupancy. Therefore, management should focus on landscape-level patterns of habitat rather than fine-scale features of habitat. If occupancy surveys are to be conducted, we suggest the use of multiple cameras for each landscape-level sampling unit. Of those variables measured, we found that human structures and road density each occurred in top models for most of the species, reinforcing the importance of these variables for the carnivore community. Therefore, research and management of this carnivore community should consider the effect of anthropogenic features, whether that effect is positive or negative. Although in most cases not as impactful as habitat alone, species interactions did in some cases improve model ranking; therefore, should not be ignored in research and management of midwestern carnivores. Consequently, management plans that seek to perpetuate fox populations should consider the effect of coyotes and provide means to sustain high levels of fox-coyote shared resources. Further, promoting forest regeneration and management for hardwood stands should be an objective of gray fox management plans.

SUMMARY

- The detectability of each species was influenced by some measured survey covariate, which underscores the importance of accounting for factors that affect the imperfect detection of carnivores. Additionally, the varying results from different scales of analyses reinforce the understanding that ecological studies are highly affected by the scale of data.
- Bobcat occupancy was widespread in the study area, but was negatively influenced by anthropogenic features and infrastructure. Bobcats had high rates of colonization and low rates of extinction during the study, suggesting an expanding population, but agricultural land was less likely to be colonized. The presence of bobcats did not appear to influence the occupancy of any other carnivore.
- Nearly all camera clusters were occupied by coyotes, but at the camera-point scale, coyote occupancy was higher in hardwood forest stands.
- Gray foxes selected spatially-complex areas with anthropogenic features and high proportions of forest, and low proportions of grassland and agriculture land cover.
- Red foxes occupied a similar proportion of the study area as gray foxes, but were more closely associated with anthropogenic features. Indeed, at all three scales of red fox

occupancy analysis, anthropogenic feature models received more support than other hypotheses.

- Camera-cluster extinction probabilities were higher for both gray foxes and red foxes than their colonization rates, suggesting both species may be declining in southern Illinois.
- Striped skunks occupied a large portion of the study area and were associated primarily with anthropogenic features, especially if the features were surrounded by agricultural land and not forest.
- Raccoons were essentially ubiquitous within the study area, being photographed in 99% of camera clusters, and the level of raccoon activity in a camera cluster was positively correlated with the activity of bobcats and coyotes.
- In general, habitat models were more supported than co-occurrence models. An exception was that gray fox occupancy and level of activity were reduced in camera-clusters occupied by coyotes. Further, gray foxes were more likely to occupy camera points in hardwood stands than conifer stands if coyotes were also present. Hardwood stands may enhance gray fox-coyote coexistence because hardwood trees have structure that may be easier for tree-climbing gray foxes to escape coyote predation.
- The camera-point occupancy of red foxes was higher when coyotes were present, and the 2 fox species appeared to co-occur with each other more frequently than expected by chance alone or on the basis of their individual selection of habitat. These apparent canid associations may be a response to locally-high prey abundance or an unmeasured habitat variable.

- Efforts to manage gray foxes should focus on maintaining and increasing the amount of mature oak-hickory forest, which presumably provides a suitable prey base and refugia from intraguild predation.

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LITERATURE CITED

Adkins, C. A., and P. Stott. 1998. Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. Journal of Zoology 244:335–346.

Andren, H., J. D. C. Linnell, O. Liberg, R. Andersen, A. Danell, J. Karlsson, J. Odden, P. F. Moa, P. Ahlqvist, T. Kvam, R. Franzen, and P. Segerstrom. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23–32.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355.

Atwood, T. C., and E. M. Gese. 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. Journal of Mammalogy 91:490–499.

Atwood, T. C., H. P. Weeks, and T. M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000–1009.

Azevedo, F. C. C., V. Lester, W. Gorsuch, S. Larivière, A. J. Wirsing, and D. L. Murray. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. Journal of Zoology 269:127–135.

Barnhardt, M. L. 2010. Soils. Pages 373–384 *in* Kolata, D. R. and C. K. Nimz, editors. Geology of Illinois. University of Illinois at Urbana-Champaign and Illinois State Geological Survey, Champaign, Illinois, USA.

Berger, J. 2010. Fear-mediated food webs. Pages 241–253 *in* Terborgh, J., and J. A. Estes, editors. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, D. C., USA.

Bixler, A., and J. L. Gittleman. 2000. Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). Journal of Zoology 251:525–533.

Bluett, R D. 2011. 2010 archery deer hunter survey. Illinois Department of Natural Resources, Wildlife Diversity Program Note 11–3. Springfield, Illinois, USA.

Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79:1018–1028.

Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63:391–400.

Bowman, J. C., D. Sleep, G. J. Forbes, and M. Edwards. 2000. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management 129:119–124.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244–257.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–61 *in* Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger, editors. Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, D. C., USA.

Bradley, L. C., and D. B. Fagre. 1988. Coyote and bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322–327.

Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and conservation implications of mesopredator release. Pages 221–240 *in* Terborgh, J., and J. A. Estes, editors. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, D. C., USA.

Bunnell, F. L., and I. Houde. 2010. Down wood and biodiversity — implications to forest practices. Environmental Reviews 18:397–421.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York, New York, USA.

Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. Pages 165–188 *in* Clark, T. W., P. M. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in Ecosystems: The Yellowstone Experience. Yale University Press, New Haven, Connecticut, USA.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11:961–980.

Chamberlain, M. J., C. D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78:2087–2095.

Chamberlain, M. J., and B. D. Leopold. 2000. Spatial use patterns, seasonal habitat selection, and interactions among adult gray foxes in Mississippi. Journal of Wildlife Management 64:742–751.

Chamberlain, M. J., and B. D. Leopold. 2005. Overlap in space use among bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*). American Midland Naturalist 153:171–179.

Chen, B., and D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80:761–772.

Coman, B. J., J. Robinson, and C. Beaumont. 1991. Home range, dispersal and density of red foxes (*Vulpes vulpes* L.) in central Victoria. Wildlife Research 18:215–223.

Comer, C. E., M. E. Symmank, and J. C. Kroll. 2011. Bobcats do not exhibit rub response despite presence at hair collection stations. Wildlife Biology in Practice 7:116–122.

Constible, J. M., M. J. Chamberlain, and B. D. Leopold. 2006. Relationships between landscape pattern and space use of three mammalian carnivores in Central Mississippi. American Midland Naturalist 155:352–362.

Cooch, E., and G. C. White. 2005. Program Mark: a gentle introduction, 9th ed. http://www.phidot.org/software/mark/docs/book/ Accessed 10 November 2010.

Cooper, S. E., C. K. Nielsen, and P. T. McDonald. 2012. Landscape factors affecting relative abundance of gray foxes, *Urocyon cinereoargenteus*, at large scales in Illinois. Wildlife Biology 18:366–373.

Cooper, S. E. 2008. Surveying and habitat modeling for gray foxes in Illinois. Thesis, Department of Zoology, Southern Illinois University Carbondale, Illinois, USA.

Crabtree, R. L., and J. W. Sheldon. 1999. Coyotes and canid coexistence in Yellowstone. Pages 127–163 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in Ecosystems: The Yellowstone experience. Yale University Press. New Haven, Connecticut, USA.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526–538.

Creel, S., G. Spong, and N. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35–60 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press. Cambridge, United Kingdom.

Creswell W., J. Lind, and J. L. Quinn. 2010. Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. Journal of Animal Ecology 79:556–562.

Crimmins, S. M., N. M. Roberts, D. A. Hamilton, and A. R. Mynsberge. 2009. Seasonal detection rates of river otters (*Lontra canadensis*) using bridge-site and random-site surveys. Canadian Journal of Zoology 87:993–999.

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

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Cypher, B. L. 1993. Food item use by three sympatric canids in southern Illinois. Transactions of the Illinois State Academy of Science 86:139–144

Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204–214.

Davies, T. J., S. Meiri, T. G. Barraclough, and J. L. Gittleman. 2007. Species co-existence and character divergence across carnivores. Ecology Letters 10:146–152.

Davis, J. C., S. B. Castleberry, and J. C. Kilgo. 2010b. Influence of coarse woody debris on the soricid community in southeastern Coastal Plain pine stands. Journal of Mammalogy 91:993–999.

Davis, M. L., M. J. Kelly, and D. F. Stauffer. 2010a. Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Animal Conservation 14:56–65.

Dekker, D. 1983. Denning and foraging habits of red foxes, *Vulpes vulpes*, in their interaction with coyotes, *Canis latrans*, in central Alberta, 1972–1981. Canadian Field Naturalist 97:303–306.

Di Bitetti, M. S., Y. E. Di Blanco, J. A. Pereira, A. Paviolo, and I. J. Pérez. 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and pampas foxes (*Lycalopex gymnocercus*). Journal of Mammalogy 90:479–490.

Dijak, W. D., and F. R. Thompson, III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. The Journal of Wildlife Management 64:209–216.

Donadio, E., and S. W. Buskirk. 2006. Diet, morphology, and interspecific killing in Carnivora. American Naturalist 167:524–536.

Doncaster, C. P., C. R. Dickman, and D. W. Macdonald. 1990. Feeding ecology of red foxes (*Vulpes vulpes*) in the city of Oxford, England. Journal of Mammalogy 71:188–194.

Doncaster, C. P., and D. W. Macdonald. 1997. Activity patterns and interactions of red foxes (*Vulpes vulpes*) in Oxford city. Journal of Zoology 241:73–87.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecology Letters 10:197–206.

Eubanks, B. W., E. C. Hellgren, J. R. Nawrot, and R. D. Bluett. 2011. Habitat associations of the marsh rice rat (*Oryzomyspalustris*) in freshwater wetlands of southern Illinois. Journal of Mammalogy 92:552–560.

Farias, V., T. K. Fuller, R. K. Wayne, and R. M. Sauvajot. 2005. Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. Journal of Zoology 266:249–254.

Federal Highway Administration (FHWA). 2000. Road function classification. U.S. Department of Transportation, Federal Highway Administration. November, 2000. http://ntl.bts.gov/lib/23000/23100/23121/09RoadFunction.pdf. Accessed July 3, 2012.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fehrenbacher, J. B., J. D. Alexander, I. J. Jansen, R. G. Darmody, R. A. Pope, M. A. Flock, E. E. Voss, J. W. Scott, W. F. Andrews, and L. J. Bushue. 1984. Soils of Illinois. University of Illinois at Urbana-Champaign, Agricultural Experiment Station and U. S. Department of Agriculture, Soil Conservation Service. Bulletin 778. 85 pages.

Fehrenbacher, J. B., G. O. Walker, and H. L. Wascher. 1967. Soils of Illinois. University of Illinois at Urbana-Champaign, Agricultural Experiment Station and U. S. Department of Agriculture, Soil Conservation Service. Bulletin 725. 47 pages.

Feldhamer, G. A., B. C. Thompson, and J. A. Chapman, editors. 2003. Wild Mammals of North America: Biology, Management, and Conservation. The Johns Hopkins University Press. Baltimore, Maryland, USA.

Field, S. A., A J Tyre, K. H. Thorn, P. J. O'Connor, and H. P.Possingham. 2005. Improving the efficiency of wildlife monitoring by estimating detectability: A case study of foxes (*Vulpes vulpes*) on the Eyre Peninsula, South Australia. Wildlife Research 32:253–258.

Foresman, K. R., and D. E. Pearson. 1998. Comparison of proposed survey procedures for detection of forest carnivores. Journal of Wildlife Management 62:1217–1226.

Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, G. Johnson, S. Flemming, J. S. Gerrow, G. Forbes, and S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environmental Reviews 4:238–265.

Fretwell, S.D. 1987. Food chain dynamics: the central theory of ecology? Oikos 50:291–301.

Gehring, T. M., and R. K. Swihart. 2003. Body size, niche breadth, and ecological scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109: 283–295

Gehrt, S. D., C. Anchor, and L. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: Conflict or coexistence? Journal of Mammalogy 90:1045–1057.

Gehrt, S. D., and S. Prange. 2007. Interference competition between coyotes and raccoons: A test of the mesopredator release hypothesis. Behavioral Ecology 18:204–214.

Gehrt, S. D., and S. P. D. Riley. 2010. Coyotes (*Canis latrans*). Pages 79–96 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. The Journal of Wildlife Management 52:640–646.

Gese, E. M., T. E. Stotts, and S. Grothe. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. Journal of Mammalogy 77:377–382.

Gese, E. M. 2001. Monitoring of terrestrial carnivore populations.Pages 372–396 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, London, United Kingdom.

Gillen, C. A. 2011. Effects of forest composition on trophic relationships among mast production and mammals in southern Illinois.Thesis, Southern Illinois University, Carbondale, Illinois, USA.

Gillen, C.A., and E. C. Hellgren. 2013. Effects of forest composition on trophic relationships among mast production and mammals in central hardwood forest. Journal of Mammalogy. *In press*.

Gloor, S., F. Bontadina, D. Hegglin, P. Deplazes, and U. Breitenmoser. 2001. The rise of urban fox populations in Switzerland. Mammalian Biology 66:155–164.

Gompper, M. E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by coyotes. BioScience 52:185–190.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia 87:343–348.

Goodrich, J. M., and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9:1357–1364.

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. B. Nilsen. 2012. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Review, 42:55–77.

Gosselink, T. E., T. R. Van Deelen, M. G. Joselyn, and R. E. Warner. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 67:90–103.

Gosselink, T., T. Van Deelen, R. Warner, and P. Mankin. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. Journal of Wildlife Management 71:1862–1873.

Greenwood, R. J., A. B. Sargeant, J. L. Piehl, D. A. Buhl, and B. A. Hanson. 1999. Foods and foraging of prairie striped skunks during the avian nesting season. Wildlife Society Bulletin 27:823–832.

Grilo, C., J. A. Bissonette, and M. Santos-Reis. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. Biological Conservation 142:301–313.

Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. The Journal of Wildlife Management 65:887–898.

Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biological Conservation 116:195–203.

Hackett, H. M. 2008. Occupancy modeling of forest carnivores in Missouri. PhD. dissertation. Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, USA. 194 pp.

Hackett, H. M., D. B. Lesmeister, J. Desanty-Combes, W. G. Montague, J. J. Millspaugh, and M. E. Gompper. 2007. Detection rates of eastern spotted skunks (*Spilogale putorius*) in Missouri and Arkansas using live-capture and non-invasive techniques. American Midland Naturalist 158:123–131.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. The American Naturalist 94:421–425.

Haroldson, K. J., and E. K. Fritzell. 1984. Home ranges, activity, and habitat use by gray foxes in an oak-hickory forest. Journal of Wildlife Management 48:222–227.

Harris, S. 1981a. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol and some possible factors affecting their distribution. Journal of Applied Ecology 18:455–465.

Harris, S. 1981b. The food of suburban foxes (*Vulpes vulpes*), with special reference to London. Mammal Review 11:151–168.

Harris, S, and G. C. Smith. 1987. Demography of two urban fox (*Vulpes vulpes*) populations. Journal of Applied Ecology 24:75–86.

Harrison, D. J., J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53:181–185.

He, F., and R. Condit. 2007. The distribution of species: occupancy, scale, and rarity. Pages 32–50 *in* D. Storch, P. A. Marquet, and J. H. Brown, editors. Scaling Biodiversity. Cambridge University Press, Cambridge, United Kingdom.

Healy, W. M., and R. T. Brooks. 1988. Small mammal abundance in northern hardwood stands in West Virginia. Journal of Wildlife Management 52:491–496.

Heist, E. J., J. R. Bowles, and A. Woolf. 2001. Record of a North American cougar (*Puma concolor*) from southern Illinois. Transactions of the Illinois State Academy of Science 94:227–229.

Henaux, V., L. A. Powell, K. A. Hobson, C. K. Nielsen, and M. A. LaRue. 2011. Tracking large carnivore dispersal using isotopic clues in claws: an application to cougars across the Great Plains. Methods in Ecology and Evolution 2:489–499.

Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

Hilty, J. A. and A. M. Merenlender. 2004. Use of riparian corridors and vineyards by mammalian predators in northern California. Conservation Biology 18:126–135.

Hines, J. E. 2006. PRESENCE2- Software to estimate patch occupancy and related parameters. United States Geological Survey, Patuxent Wildlife Research Center.http://www.mbr-pwrc.usgs.gov/software/presence.html

Holt, R. D., and M. Loreau. 2001. Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. Pages 246–262 *in* Kinziz, A. P., S. W. Pacala, and D. Tilman, editors. The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Princeton University Press. Princeton, New Jersey, USA.

Hunter, J. S. 2008. Adaptations to intraguild competition in meoscarnivores. PhD dissertation. University of California Davis, California, USA.

Illinois Department of Natural Resources (IDNR). 1994. Streams and shorelines in Illinois. Illinois State Geological Survey Geographic Information System Database, Champaign, Illinois. http://www.isgs.illinois.edu/ Accessed November 3, 2007.

Illinois Department of Natural Resources (IDNR). 1996. Digital data set of Illinois. Springfield, Illinois.

Illinois Department of Natural Resources (IDNR). 2005. The Illinois Comprehensive Wildlife Conservation Plan and Strategy. Illinois Department of Natural Resources, Springfield, Illinois, USA.

Illinois State Geological Survey (ISGS). 2004a. Political townships in Illinois. Illinois State Geological Survey Geographic Information System Database, Champaign, Illinois. http://www.isgs.illinois.edu/ Accessed November 3, 2007.

Illinois State Geological Survey (ISGS). 2004b. Illinois Roads from USGS 1:100,000-scale digital line graphs. Illinois State Geological Survey Geographic Information System Database, Champaign, Illinois. http://www.isgs.illinois.edu/ Accessed November 3, 2007.

Illinois State Geological Survey (ISGS). 2005. Illinois digital orthophotography quarter quadrangle data. Illinois State Geological Survey Geographic Information System Database, Champaign, Illinois. http://www.isgs.uiuc.edu/nsdihome/webdocs/doq05/ Accessed November 3, 2007.

Illinois State Geological Survey (ISGS). 2006. Municipal boundaries in Illinois: incorporated places, 2000 U.S. Census. Illinois State Geological Survey Geographic Information System Database, Champaign, Illinois. http://www.isgs.illinois.edu/ Accessed November 3, 2007.

Jackson, R. M., J. D. Roe, R. Wangchuk, and D. O. Hunter. 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildlife Society Bulletin 34:772–781.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, D. M., and J. B. Theberge. 1982. Summer home range and habitat utilisation of the red fox (*Vulpes vulpes*) in a tundra habitat, northwest British Columbia. Canadian Journal of Zoology 60:807–812.

Kamler, J. F., W. B. Ballard, P. R. Lemons, R. L. Gilliland, and K. Mote. 2003. Impacts of coyotes on swift foxes in northwestern Texas. Journal of Wildlife Management 67:317–323.

Karanth, K. U., A. M. Gopalaswamy, N. S. Kumar, S. Vaidyanathan, J. D. Nichols, and D. I. MacKenzie. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. Journal of Applied Ecology 48:1048–1056.

Kays, R. W., and K. M. Slauson. 2008. Remote cameras. Pages 110–140 *in* Long, R. A., P. Mackay, W. J. Zielinski, and J. C. Ray, editors. Noninvasive survey methods for carnivores Island Press, Washington, D. C., USA.

Kays, R., M. Gompper, and J. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications 18:1014–1027.

Kelly, M. J., and E. L. Holub. 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15:249–262.

Kennedy, D. E. 1999. Daily movement patterns of bobcats in southern Illinois. Thesis, Southern Illinois University, Carbondale, Illinois, USA.

Kerley, L. L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16:97–108.

King, C. M. 1989. The advantages and disadvantages of small size to weasels, *Mustela* species. Pages 302–334 *in* Gittleman, J. L., editor. Carnivore Behavior, Ecology, and Evolution, Vol. 1. Cornell University Press, Ithaca, New York, USA.

Kitchen, A. M., E. R. Schauster, and E. M. Gese. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77:1645–1656.

Kolowski, J. M., and A. Woolf. 2002. Microhabitat use by bobcats in southern Illinois. Journal of Wildlife Management 66:822–832.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

Kurki, S., A. Nikula, P. Helle, and H. Linden. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. Journal of Animal Ecology 67:874–886.

Larivière, S., and F. Messier. 1997. Seasonal and daily activity patterns of striped skunks (*Mephitis mephitis*) in the Canadian prairies. Journal of Zoology 243:255–262.

Larivière, S., and F. Messier. 1998. Denning ecology of the striped skunk in the Canadian prairies: implications for waterfowl nest predation. Journal of Applied Ecology 35:207–213.

LaRue, M. A., and C. K. Nielsen. 2011. Modelling potential habitat for cougars in midwestern North America. Ecological Modelling 222:897–900.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson, Jr. 2012. Cougars are recolonizing the Midwest: Analysis of cougar confirmations during 1990–2008. Journal of Wildlife Management 76:1364–1369.

Lavin, S. R., T. R. Van Deelen, P. W. Brown, R. E. Warner, and S. H. Ambrose. 2003. Prey use by red foxes (*Vulpes vulpes*) in urban and rural areas of Illinois. Canadian Journal of Zoology 81:1070–1082.

Lesmeister, D. B., R. S. Crowhurst, M. E. Gompper, and J. J. Millspaugh. 2013. Landscape ecology of eastern spotted skunks in habitats restored for red-cockaded woodpeckers. Restoration Ecology 21:267–275.

Lesmeister, D. B., M. E. Gompper, and J. J. Millspaugh. 2008. Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in the Ouachita Mountains, Arkansas. Journal of Mammalogy 89:1512–1520.

Lesmeister, D. B., and C. K. Nielsen. 2011. Protocol for large-scale monitoring of riparian mammals. Wildlife Biology in Practice 7:55–70.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Science 109:10942–10947.

Lewis, J. C., K. L. Sallee, and R. T. Golightly. 1999. Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. American Midland Naturalist 142:372–381.

Lindström, E. R. 1989. Food limitation and social regulation in a red fox population. Holarctic Ecology 12:70–79.

Lindström, E. R., H. Andrén, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P. Lemnell, B. Martinsson, K. Sköld, and J. E. Swenson. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75:1042–1049.

Linkie, M., I. Haidir, A. Nugroho, and Y. Dinata. 2008. Conserving tigers *Panthera tigris* in selectively logged Sumatran forests. Biological Conservation 141:2410–2415.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

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

Litvaitis, J. A., J A Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110–117.

Litvaitis, J. A., and J. H. Shaw. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. Journal of Wildlife Management 44:62–68.

Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460–471.

Loomis, D., D. B. Richardson, and L. Elliott. 2005. Poisson regression analysis of ungrouped data. Occupational and Environmental Medicine 62:325–329.

Luman, D., M. Joselyn, and L. Suloway. 1996. Critical trends assessment project: landcover database. Illinois Natural History Survey, Champaign, Illinois, USA.

Ma, J., and K. G. Goulias. 1999. Application of Poisson regression models to activity frequency analysis and prediction. Transportation Research Record 1676:86–94.

MacKenzie, D. I., L. L. Bailey, and J. D. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology 73:546–555.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, New York, New York, USA.

Maffei, L., E. Cuellar, and A. Noss. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. Journal of Zoology 262:295–304.

Major, J. T., and J.A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. The Journal of Wildlife Management 51:606–616.

Marks, C. A., and T. E. Bloomfield. 1999. Distribution and density estimates for urban foxes (*Vulpes vulpes*) in Melbourne: implications for rabies control. Wildlife Research 26:777–787.

Martin, T. G., B. A.Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. Ecology Letters 8:1235–1246.

Mattisson, J., J. Persson, H. Andrén, H., P. Segerström. 2011. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoolology 89:79–89.

Mayntz, D., and S. Toft. 2001. Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. Oecologia 127:207–213.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McCann, K. S. 2012. Food Webs. Levin, S. A., and H. S. Horn, editors. Monographs in Population Biology. Princeton University Press. Princeton, New Jersey.

McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. Ecology Letters 8:513–523.

McCay, T. S., and M. J. Komoroski. 2004. Demographic responses of shrews to removal of coarse woody debris in a managed pine forest. Forest Ecology and Management 189:387–395.

McDonald, P., C. K. Nielsen, T. Oyana, and W. Sun. 2008. Modelling habitat overlap among sympatric mesocarnivores in southern Illinois, USA. Ecological Modeling 215:276–286.

McGarigal, K., S. A. Cushman, N. C. Neel, and E. Erie. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257–289

Mills, S. L., and F. F. Knowlton. 1991. Coyote space use in relation to prey abundance. Canadian Journal of Zoology 69:1516–1521.

Miller, D., R. Thill, M. Melchiors, T. Wigley, and P. Tappe. 2004. Small mammal communities of streamside management zones in intensively managed pine forests of Arkansas. Forest Ecology and Management 203:381–393.

Mitchell, B. D., and P. B. Banks. 2005. Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. Austral Ecology 30:581–591.

Mitchell, J. C., S. C. Rinehart, J. F. Pagels, K. A. Buhlmann, and C. A. Pague. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management 96:65–76.

Moorcroft, P. R., M. A. Lewis, and R. L. Crabtree. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. Proceedings of the Royal Society Series B Biological Sciences 273:1651–1659.

Mutch, G. R. P., and M. Aleksiuk. 1977. Ecological aspects of winter dormancy in the striped skunk (*Mephitis mephitis*). Canadian Journal of Zoology 55:607–615.

National Oceanic and Atmospheric Administration (NOAA). 2010. National Climate Data Center: world’s largest archive of climate data. http://www.ncdc.noaa.gov/oa/ncdc.html. Accessed 10 November 2010.

Neale, J. C. C., and B. N. Sacks. 2001a. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. Canadian Journal of Zoology 79:1794–1800.

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

Neely, R. D., and C. G. Heister. 1987. The natural resources of Illinois: introduction and guide. special publication 6. Illinois Natural History Survey, Champaign, Illinois, USA.

Neiswenter, S. A., R. C. Dowler, and J. H. Young. 2010. Activity patterns of two sympatric species of skunks (*Mephitis mephitis* and *Spilogale gracilis*) in Texas. The Southwestern Naturalist 55:16–21.

Nielsen, C. K., and S. E. Cooper. 2012. Comparison of methods to detect mesocarnivores in southern Illinois. Transactions of Illinois State Academy of Science *In Press.*

Nielsen, C. K., and M. A. McCollough. 2009. Considerations on the use of remote cameras to detect Canada lynx in northern Maine. Northeastern Naturalist 16:153–157.

Nielsen, C. K., and A. Woolf. 2001a. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. American Midland Naturalist 146:43–52.

Nielsen, C. K., and A. Woolf. 2001b. Bobcat habitat use relative to human dwellings in southern Illinois. Pages 40–44 *in* A. Woolf, C. K. Nielsen, and R. D. Bluett, editors. Proceedings of a symposium on current bobcat research and implications for management.The Wildlife Society 2000 Conference, Nashville, Tennessee, USA.

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

O'Connell, A. F., N. W. Talancy, L. L. Bailey, J. R. Sauer, R. Cook, and A. T. Gilbert. 2006. Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. Journal of Wildlife Management 70:1625–1633.

O'Connell, A. F., and L. L. Bailey. 2010. Inference for occupancy and occupancy dynamics. Pages 191–205 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology: methods and analyses. Springer, New York, New York.

Oehler, J. D., and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070–2079.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management 69:918–932.

Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.

Ostfeld, R. S. 2002. Ecological webs involving acorns and mice: basic research and its management implications. Pages 196–214 *in* Oak forest ecosystems: ecology and management for wildlife. W. J. McShea and W. M. Healy, editors. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. 2008. Predator diversity and identity driven interaction strength and tropic cascades in a food web. Ecology 89:134–144.

Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. Journal of Animal Ecology 49:667–685.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

Patterson, B. R., S. Bondrup-Nielsen, and F. Messier. 1999. Activity patterns and daily movements of the eastern coyote, *Canis latrans*, in Nova Scotia. Canadian Field Naturalist 113:251–257.

Patterson, B. R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463–477.

Pearson, D. E., and L. F. Ruggiero. 2001. Test of the prey-base hypothesis to explain use of red squirrel midden sites by American martens. Canadian Journal of Zoology 79:1372–1379.

Pereira, J. A. 2010. Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. Journal of Arid Environments 74:1106–1109.

Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. The Journal of Wildlife Management 55:433–441.

Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? The American Naturalist 126:261–266.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press. New York, USA.

Powell, R. A., and W. J. Zielinski. 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica 174:223–227.

Prange, S., and S. D. Gehrt. 2007. Response of skunks to a simulated increase in coyote activity. Journal of Mammalogy 88:1040–1049.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. The Journal of Wildlife Management 67:324–333.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences 267:1947–1952.

Ralls, K., and L. L. Eberhardt. 1997. Assessment of abundance of San Joaquin kit foxes by spotlight surveys. Journal of Mammalogy 78:65–73.

Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban-rural gradient: a landscape-level analysis. Journal of Mammalogy 87:1154–1164.

Ray, J. C. 2000. Mesocarnivores of Northeastern North America: Status and Conservation Issues. Wildlife Conservation Society Working Papers No. 15.

Reed, S. E. 2011. Non-invasive methods to assess co-occurrence of mammalian carnivores. The Southwestern Naturalist 56:231–240.

Riley, S. P. D. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. Journal of Wildlife Management 70:1425–1435.

Riley, S. P. D., R. M. Sauvajot, E. C. York, D. A. Kamradt, C. Bromley, T. K. Fuller, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Roberts, N. M., and S. M. Crimmins. 2010. Bobcat population status and management in North America: Evidence of large-scale population increase. Journal of Fish and Wildlife Management 1:169–174.

Rogers, C. M., and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. Oecologia 116:227–233.

Rosatte, R., K. Sobey, J. W. Dragoo, and S. D. Gehrt. 2010. Striped skunks and allies (*Mephitis* spp.). Pages 97–106 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: islands or habitat patches for mammals? The American Midland Naturalist 141:115–123.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47:602–612.

Rota, C. T., R. J. J. Fletcher, J. M. Evans, and R. L. Hutto. 2011. Does accounting for imperfect detection improve species distribution models? Ecography 34:659–670.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84:777–790.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. The Journal of Wildlife Management 51:285–293.

Sargeant, A. B., and S. H. Allen. 1989. Observed interactions between coyotes and red foxes. Journal of Mammalogy 70:631–633.

Saunders, G., P. C. L. White, S. Harris, and J. M. V. Rayner. 1993. Urban foxes (*Vulpes vulpes*): food acquisition, time and energy budgeting of a generalized predator. Symposia of the Zoological Society of London 65:215–234.

Sauvajot, R. M., M. Buechner, D. A. Kamradt, and C. M. Schonewald. 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. Urban Ecosystems 2:279–297.

Scheffer, M. 2010. Alternative states in ecosystems. Pages 287–298 in J. Terborgh and J. A. Estes, editors. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press. Washington, D. C., USA

Schipper, J. 2007. Camera-trap avoidance by kinkajous *Potos flavus*: rethinking the “non-invasive” paradigm. Small Carnivore Conservation 36:38–41.

Schmidt, K. A., J. M. Earnhardt, J. S. Brown, and R. D. Holt. 2000. Habitat selection under temporal heterogeneity: exorcizing the ghost of competition past. Ecology 81:2622–2630.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. Ecology 88:2415–2426.

Schmitz, O. J. 2010. Resolving ecosystem complexity. S. A. Levin and H. S. Horn, editors. Monographs in Population Biology 47. Princeton University Press, Princeton, New Jersey, USA.

Schneider, M. F. 2001. Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. Journal of Applied Ecology 38:720–735.

Schoonover, L. J., and W. H. Marshall. 1951. Food habits of the raccoon (*Procyon lotor hirtus*) in north-central Minnesota. Journal of Mammalogy 32:422–428.

Schwegman, J. E. 1973. Comprehensive Plan for the Illinois Nature Preserves System, Part 2: the Natural Divisions of Illinois. Commission, Rockford, Illinois, USA.

Séquin, E. S., P. F. Brussard, M. M. Jaeger, and R. H. Barrett. 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. Canadian Journal of Zoology 81:2015–2025.

Sergio. F., L. Marchesi, and P. Pedrini. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. Journal of Animal Ecology 72:232–245.

Shirer, H. W., and H. S. Fitch. 1970. Comparison from radiotracking of movements and denning habits of the raccoon, striped skunk, and opossum in northeastern Kansas. Journal of Mammalogy 51:491–503.

Sillero-Zubiri, C., and M. K. Laurenson. 2001. Interactions between carnivores and local communities: conflict or coexistence? Pages 282–314 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge, United Kingdom.

Sillero-Zubiri, C. 2009. Family Canidae (Northern gray fox *Urocyon cinereoargenteus*). Pages 432–433 *in* D. E. Wilson and R. A. Mittermeier, editors Handbook of The Mammals of The World.Vol. 1. Carnivores. Lynx Edicions, Barcelona.

Silveira, L., A. T. A. Jácomo, and J. A. F. Diniz-Filho. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation 114:351–355.

Sollmann, R., M. M. Furtado, H. Hofer, A. T. A. Jácomob, N. M. Tôrres, and L. Silveira. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammalian Biology 77:41–46.

Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238–1250.

Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2010. Red foxes (*Vulpes vulpes*). Pages 63–78 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland.

Stankowich, T., T. Caro, and M. Cox. 2011. Bold coloration and the evolution of aposematism in terrestrial carnivores. Evolution 65:3090–3099.

Steinmetz R., D. L. Garshelis, W. Chutipong, N. Seuaturien. 2011. The shared preference niche of sympatric Asiatic black bears and sun bears in a tropical forest mosaic. PLoS ONE 6: e14509. doi:10.1371/journal.pone.0014509

Storm, G. L. 1972. Daytime retreats and movements of skunks on farmlands in Illinois. The Journal of Wildlife Management 36:31–45.

Storm, D. J., C. K. Nielsen, E. M. Schauber, and A. Woolf. 2007. Space use and survival of white-tailed deer in an exurban landscape. Journal of Wildlife Management 71:1170–1176.

Sunquist, M. E. 1974. Winter activity of striped skunks (*Mephitis mephitis*) in east-central Minnesota. American Midland Naturalist 92:434–446.

Sunquist, M. E., and F. Sunquist. 2001. Changing landscapes: consequences for carnivores. Pages 399–418 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press. Cambridge, United Kingdom.

Temple, D. L., M. J. Chamberlain, and L. M. Conner. 2010. Spatial ecology, survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in a longleaf pine ecosystem. American Midland Naturalist 163:413–422.

Terborgh, J., R. D. Holt, and J. A. Estes. 2010. Trophic cascades: what they are, how they work, and why they matter. Pages 1–18 *in* J. Terborgh and J. A. Estes, editors. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington D. C.

Thibault, I., and J. P. Ouellet. 2005. Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. Ecoscience 12:466–475.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. Journal of Mammalogy 85:973–982.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108:299–306.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2003. Carnivore persistence in fragmented habitats in urban southern California. Pacific Conservation Biology 9:144–151.

Toft, S., and D. H. Wise. 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. Oecologia 119:191–197.

Toweill, D. E., and R. G. Anthony. 1988a. Annual diet of bobcats in Oregon's Cascade Range. Northwest Science 62:99–103.

Toweill, D. E., and R. G. Anthony. 1988b. Coyote foods in a coniferous forest in Oregon. The Journal of Wildlife Management 52:507–512.

Tsukada, H., Y. Morishima, N. Nonaka, Y. Oku, and M. Kamiya. 2000. Preliminary study of the role of red foxes in *Echinococcus multilocularis* transmission in the urban area of Sapporo, Japan. Parasitology 120:423–428.

Tucker, S., W. Clark, and T. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. Journal of Wildlife Management 72:1114–1124.

United States Department of the Interior (USDOI). 2008. The Public Land Survey System (PLSS). http://www.nationalatlas.gov/articles/boundaries/a_plss.html. Accessed 21 August 2008.

United States Geological Survey (USGS). 2007. National land cover database 2001. Multi-resolution land characteristics consortium.http://www.mrlc.gov/index.php.Accessed 10 November 2010.

Van Etten, K. W., K. R. Wilson, and R. L. Crabtree. 2007. Habitat use of red foxes in Yellowstone National Park based on snow tracking and telemetry. Journal of Mammalogy 88:1498–1507.

Van Valkenburgh, B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. Paleobiology 11:406–428.

Van Valkenburgh, B. 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. Pages 410–436 *in* Gittleman, J. L., editor. Carnivore Behavior, Ecology, and Evolution, Vol. 1. Cornell University Press, Ithaca, New York.

Vine, S., M. Crowther, S. Lapidge, C. Dickman, N. Mooney, M. Piggott, and A. English. 2009. Comparison of methods to detect rare and cryptic species: a case study using the red fox (*Vulpes vulpes*). Wildlife Research 36:436–446.

Wandeler, P., S. M. Funk, C. R. Largiadér, S. Gloor, and U. Breitenmoser. 2003. The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. Molecular Ecology 12:647–656.

Ware, D. M. and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. Science 308:1280–1284.

Wegge, P., C. P. Pokheral, and S. R. Jnawali. 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Animal Conservation 7:251–256.

White, T. R. C. 1978. The importance of relative shortage of food in animal ecology. Oecologia 33:233–242.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Willingham, A. L., N. W. Ockens, C. M. O. Kapel, and J. Monrad. 1996. A helminthological survey of wild red foxes (*Vulpes vulpes*) from the metropolitan area of Copenhagen. Journal of Helminthology 70:259–263.

Willson, M. F., and T. A. Comet. 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. The Condor 98:350–362.

Wilson, D. E., and R. A. Mittermeier, editors. 2009. Handbook of the Mammals of the World. Volume 1. Carnivores. Lynx Edicions, Barcelona.

Wilson, R. R., T. L. Blankenship, M. B. Hooten, and J. A. Shivik. 2010. Prey-mediated avoidance of an intraguild predator by its intraguild prey. Oecologia 164:921–929.

Wilson, S. E., and C. K. Nielsen. 2007. Habitat characteristics of raccoon daytime resting sites in southern Illinois. American Midland Naturalist 157:175–186.

Windberg, L. A., and C. D. Mitchell. 1990. Winter diets of coyotes in relation to prey abundance in southern Texas. Journal of Mammalogy 71:439–447.

Wise, D. H., and B. Chen. 1999. Impact of intraguild predators on survival of a forest-floor wolf spider. Oecologia 121:129–137.

Witmer, G. W., and D. S. deCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology 64:2333–2338.

Woolf, A., C. K. Nielsen, T. Weber, and T. J. Gibbs-Kieninger. 2002. Statewide modeling of bobcat, *Lynx rufus*, habitat in Illinois, USA. Biological Conservation 104:191–198.

Yeager, L. E. 1938. Tree-climbing by a gray fox. Journal of Mammalogy 19:376.

Zielinski, W. J., R. L. Truex, F. V. Schlexer, L. A. Campbell, and C. Carroll. 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. Journal of Biogeography 32:1385–1407.

Figure Captions

Figure 1. Landcover classifications of the study area (expanded) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010.

Figure 2. Sections (2.6 km^2) surveyed using remote cameras in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. Sixty sections were surveyed in 2008 and 2010 and 297 sections were surveyed once.

Figure 3. Predicted probability of bobcat occupancy (range $\hat{\psi}$ = 0.5 to 1) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results in the 90% confidence set of camera-cluster scale (100% home range) analysis. Model-averaged coefficients of density of human structures and minor roads, and distance to human structures and roads (minor and major) were used for populating the prediction model.

Figure 4. Predicted probability of coyote occupancy (range $\hat{\psi}$ = 0.55 to 1) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results in the 90% confidence set of camera-cluster scale analysis. Model-averaged coefficients of forest, grassland, urban, and distance to municipality boundary were used for prediction.

Figure 5. Predicted probability of gray fox occupancy (range $\hat{\psi}$ = 0.23 to 0.41) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results in the 90% confidence set of camera-cluster scale analysis. To populate the predictive model, we used

model-averaged coefficients of minor road density, distance to human structures and major roads, stream density, agriculture, and forest landcover.

Figure 6. Predicted probability of red fox occupancy (range $\hat{\psi}$ = 0.00 to 0.42) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results in the 90% confidence set of camera-cluster scale analysis. We used model-averaged coefficients of human structure and minor road density, and distance to human structures for prediction.

Figure 7. Predicted probability of striped skunk occupancy (range $\hat{\psi}$ = 0.20 to 0.97) in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results in the 90% confidence set of camera-cluster scale analysis. To populate the predictive model, we used model-averaged coefficients of anthropogenic features (human structure density, minor road density, distance to human structures, distance to minor and major roads), agriculture landcover, and private land ownership.

Figure 8. Model weights for most-supported (A) camera-point scale and (B) camera-cluster scale co-occurrence models within 4 model categories for gray fox-bobcat, gray fox-coyote, and gray fox-red fox. For each candidate model set, we fit encounter-history data from surveys at 1188 camera points and 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. Combined effect models were parameterized by adding the effect of interacting species to habitat variables or the interaction between habitat and the interacting species. The most supported detection and occupancy models of interacting species were

included to account for heterogeneity in detection and occupancy probabilities of those species. See Appendices C and D for full model sets.

Figure 9. Positive (solid line) and negative (dashed line) associations within the carnivore guild in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on modeling results from camera-cluster scale habitat occupancy, co-occurrence, and activity analysis.

Figure 10. Predicted probability of gray fox occupancy in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on modeling results from camera-cluster scale habitat occupancy and co-occurrence with (A) bobcats (range $\hat{\psi}$ = 0.22 to 0.44), (C) coyotes (range $\hat{\psi}$ = 0.20 to 0.45), and (C) red foxes (range $\hat{\psi}$ = 0.20 to 0.45).

Figure 11. Model weights for most-supported (A) camera-point scale and (B) camera-cluster scale co-occurrence models within 4 model categories for red fox-bobcat, red fox-coyote, and red fox-gray fox. For each candidate model set we fit encounter-history data from surveys at 1188 camera points and 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. Combined effect models were parameterized by adding the effect of interacting species to habitat variables or the interaction between habitat and the interacting species. The most supported detection and occupancy models of interacting species were included to account for heterogeneity in detection and occupancy probabilities of those species. See Appendices C and D for full model sets.

Figure 12. Predicted probability of red fox occupancy in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results from camera-cluster scale habitat occupancy and co-occurrence with (A) bobcats (range $\hat{\psi}$ = 0.18 to 0.50), (B) coyotes (range $\hat{\psi}$ = 0.12 to 0.38), and (C) gray foxes (range $\hat{\psi}$ = 0.15 to 0.45).

Figure 13. Model weights for most-supported (A) camera-point scale and (B) camera-cluster scale co-occurrence models within 4 model categories for striped skunk-bobcat, striped skunk-coyote, and striped skunk-red fox. For each candidate model set we fit encounter-history data from surveys at 1188 camera points and 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. Combined effect models were parameterized by adding the effect of interacting species to habitat variables or the interaction between habitat and the interacting species. The most supported detection and occupancy models of interacting species were included to account for heterogeneity in detection and occupancy probabilities of those species. See Appendices C and D for full model sets.

Figure 14. Predicted probability of striped skunk occupancy in the 16 southernmost counties of Illinois, USA, January–April 2008–2010, based on results from camera-cluster scale habitat occupancy and co-occurrence with (A) bobcats (range $\hat{\psi}$ = 0.70 to 0.92), (B) coyotes (range $\hat{\psi}$ = 0.65 to 0.95), (C) gray foxes (range $\hat{\psi}$ = 0.65 to 0.95), and (D) red foxes (range $\hat{\psi}$ = 0.65 to 0.95).

Figure 15. Relationship of the total number of bobcat photographs recorded with the total number of coyote photographs recorded during remote camera surveys at 1188 camera points in

357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 16. Relationship of the total number of gray fox (open circles, solid regression line) and red fox (triangles, dashed regression line) photographs recorded with the total number of coyote photographs recorded during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 17. Relationship of the total number of raccoon (open circles, solid regression line) and striped skunk (triangles, dashed regression line) photographs recorded with the total number of coyote photographs recorded during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 18. Relationship between the total number of raccoon (open circles, solid regression line) and red fox (triangles, dashed regression line) photographs recorded with the total number of bobcat photographs recorded during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 19. Relationship of the total number of raccoon (open circles, solid regression line) and red fox (triangles, dashed regression line) photographs recorded in a camera cluster with the estimated bobcat camera-cluster occupancy based on occupancy models. Data were collected during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 20. Relationship of the total number of raccoon (open bars) and striped skunk (gray bars) photographs (with standard error bars) recorded in camera clusters with and without bobcat and coyote photographs. Ndet = no photographs for bobcat or coyote recorded. Det = at least one photograph recorded for bobcat or coyote recorded. Data were collected during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 21. Relationship between the number of gray fox (open circles, solid regression line) and red fox (triangles, dashed regression line) photographs recorded during diel period (crepuscular, diurnal, or nocturnal) with the number of coyote photographs recorded during the same time period. Data were collected during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA during January–April 2008–2010.

Figure 22. Relationship between the number of raccoon photographs (with standard error bars) recorded during crepuscular, diurnal, and nocturnal time periods in camera clusters with and without bobcat and coyote photographs. Data were collected during remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA, during January–April 2008–2010.

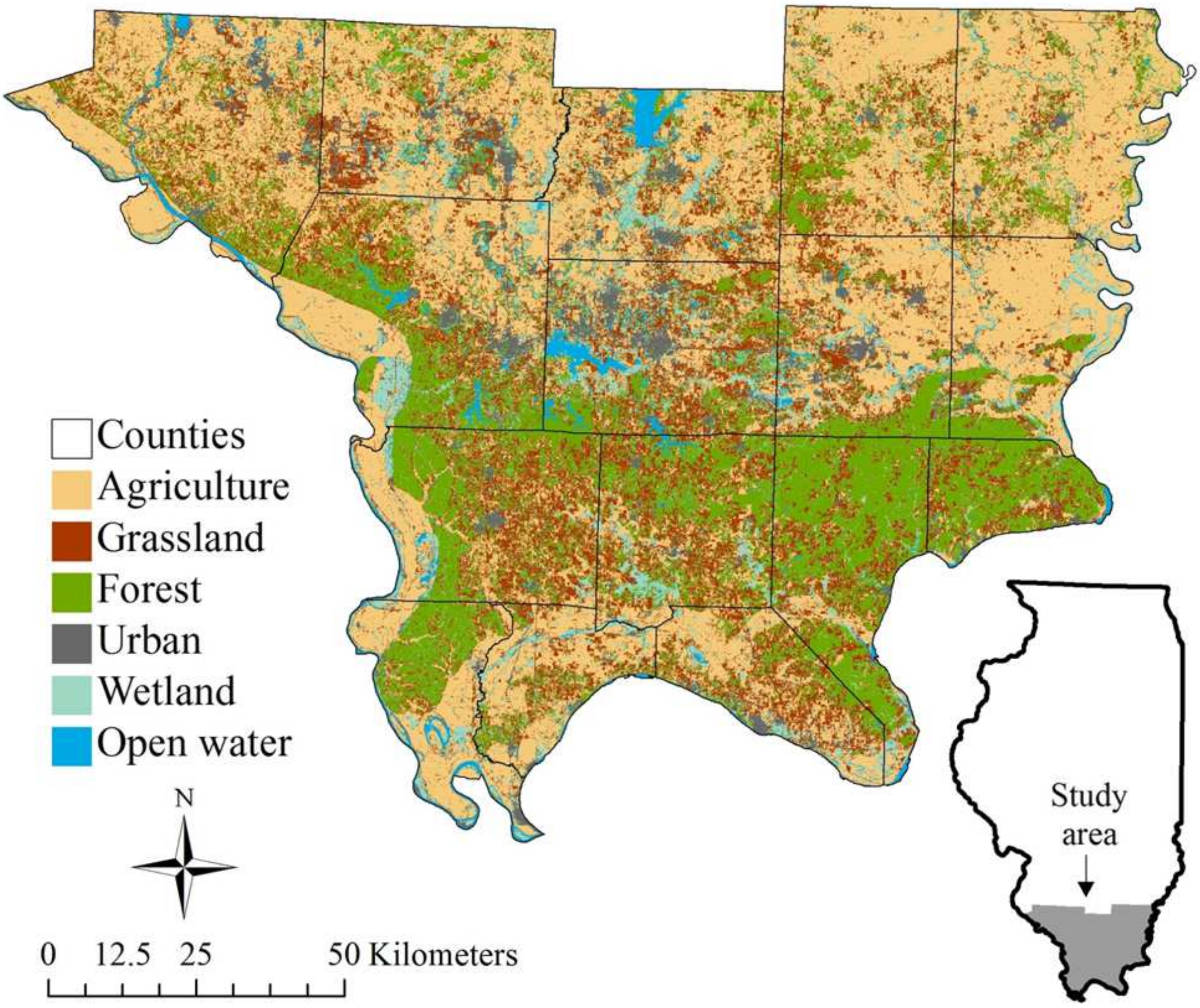
Counties
Agriculture
Grassland
Forest
Urban
Wetland
Open water
N
0
12.5
25
50 Kilometers
Study area

Figure 1.

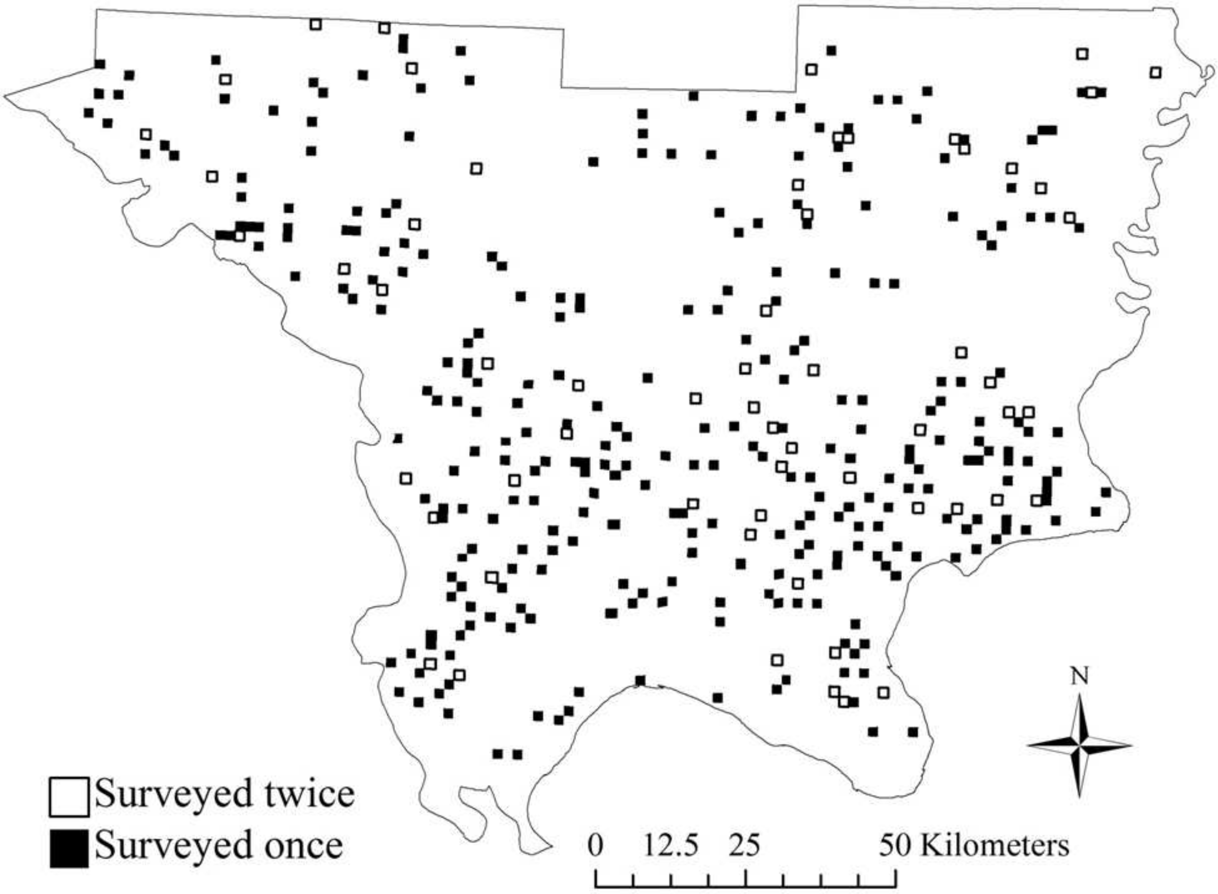

Figure 2.

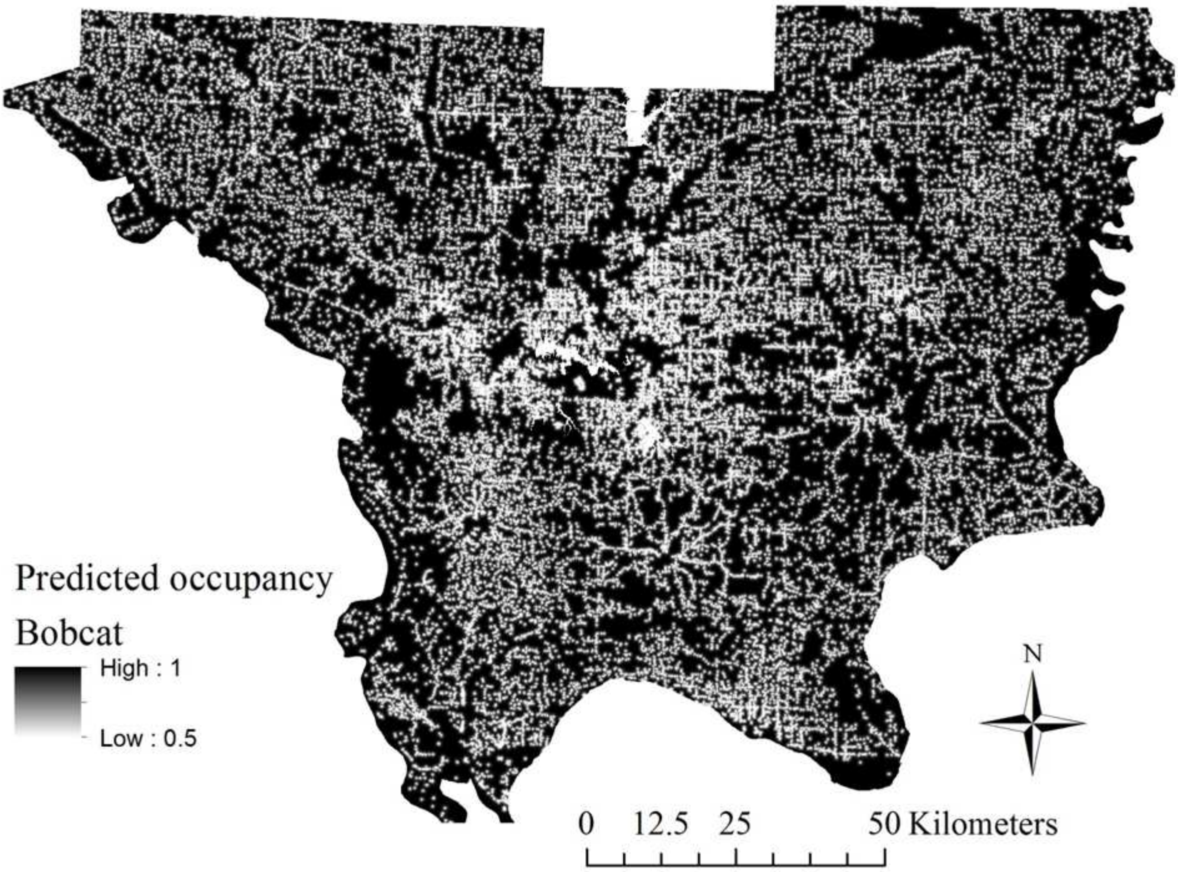
Predicted occupancy
Bobcat
High : 1
Low : 0.5
N
0
12.5
25
50 Kilometers

Figure 3.

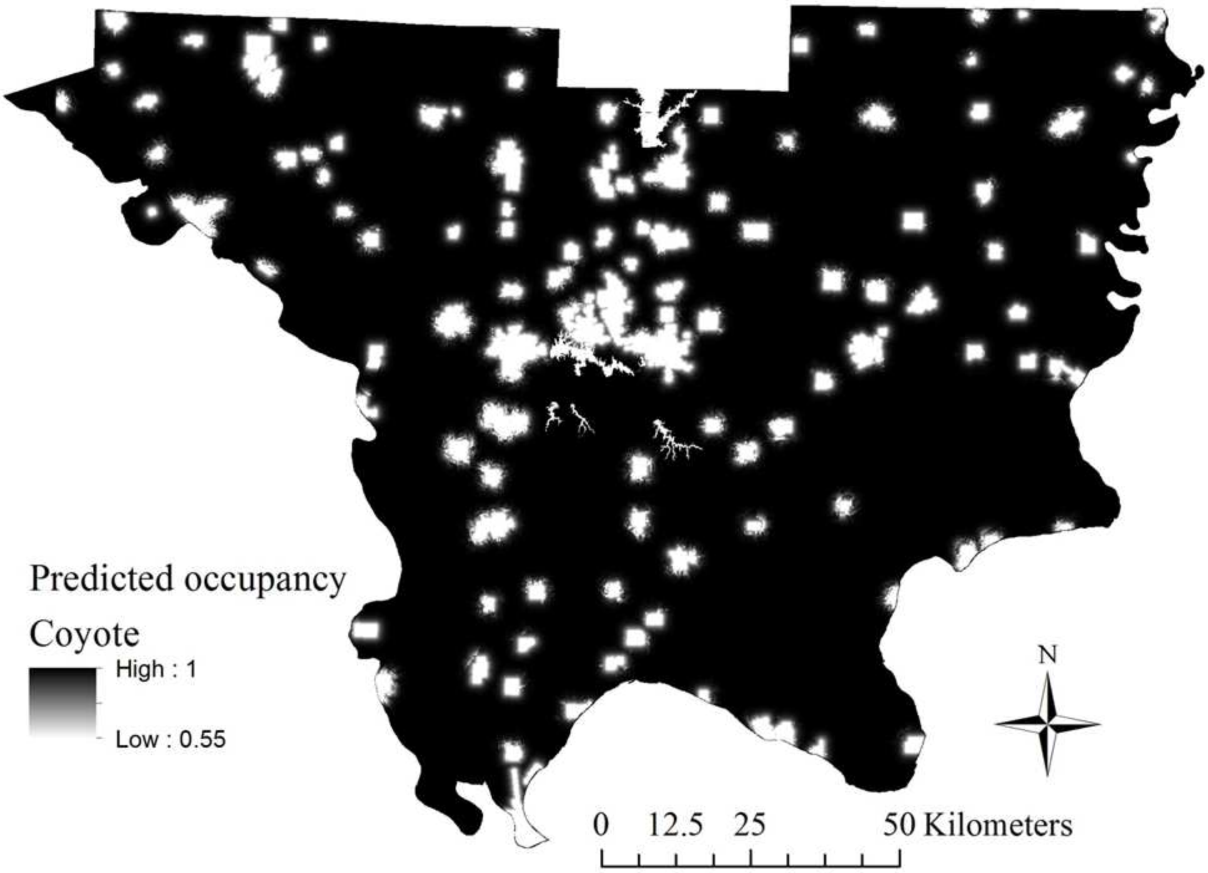
Predicted occupancy
Coyote
High : 1
Low : 0.55
N
0 12.5 25 50 Kilometers

Figure 4.

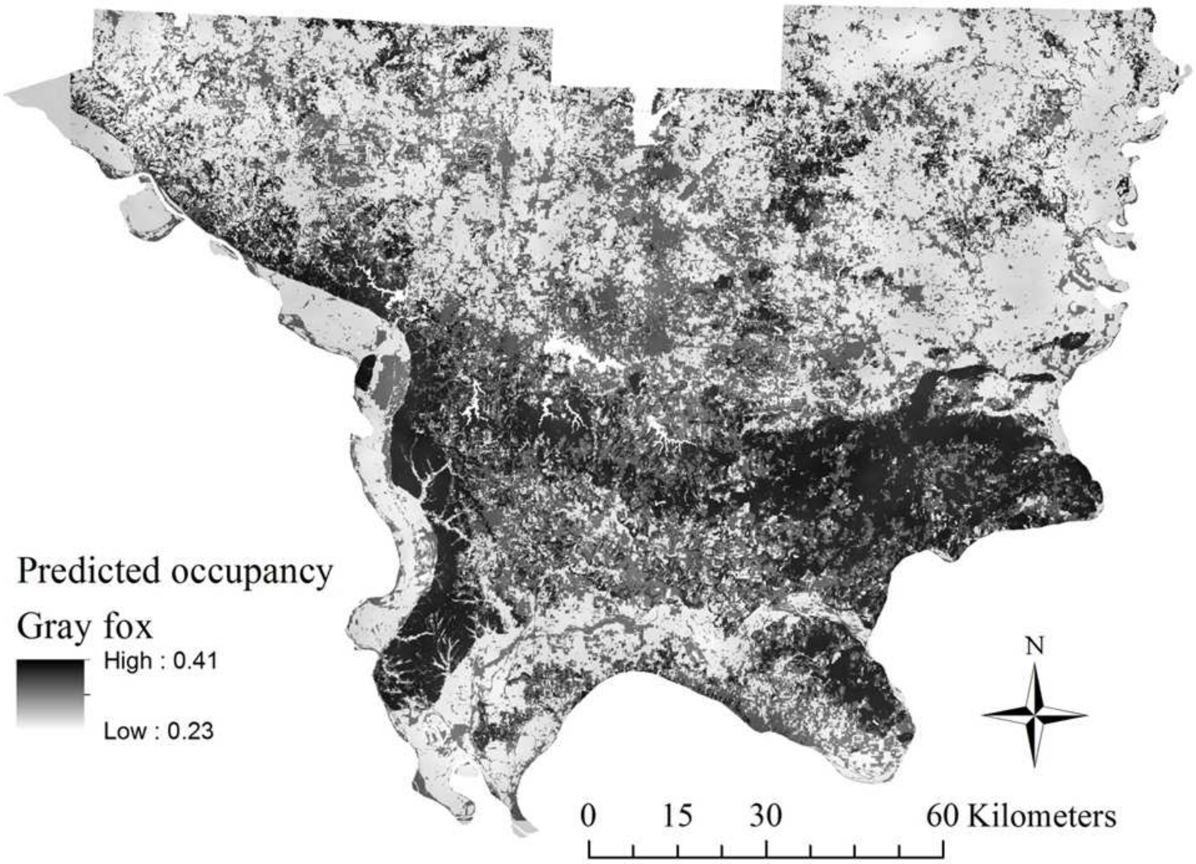
Predicted occupancy
Gray fox
High : 0.41
Low : 0.23
N
0
15
30
60 Kilometers

Figure 5.

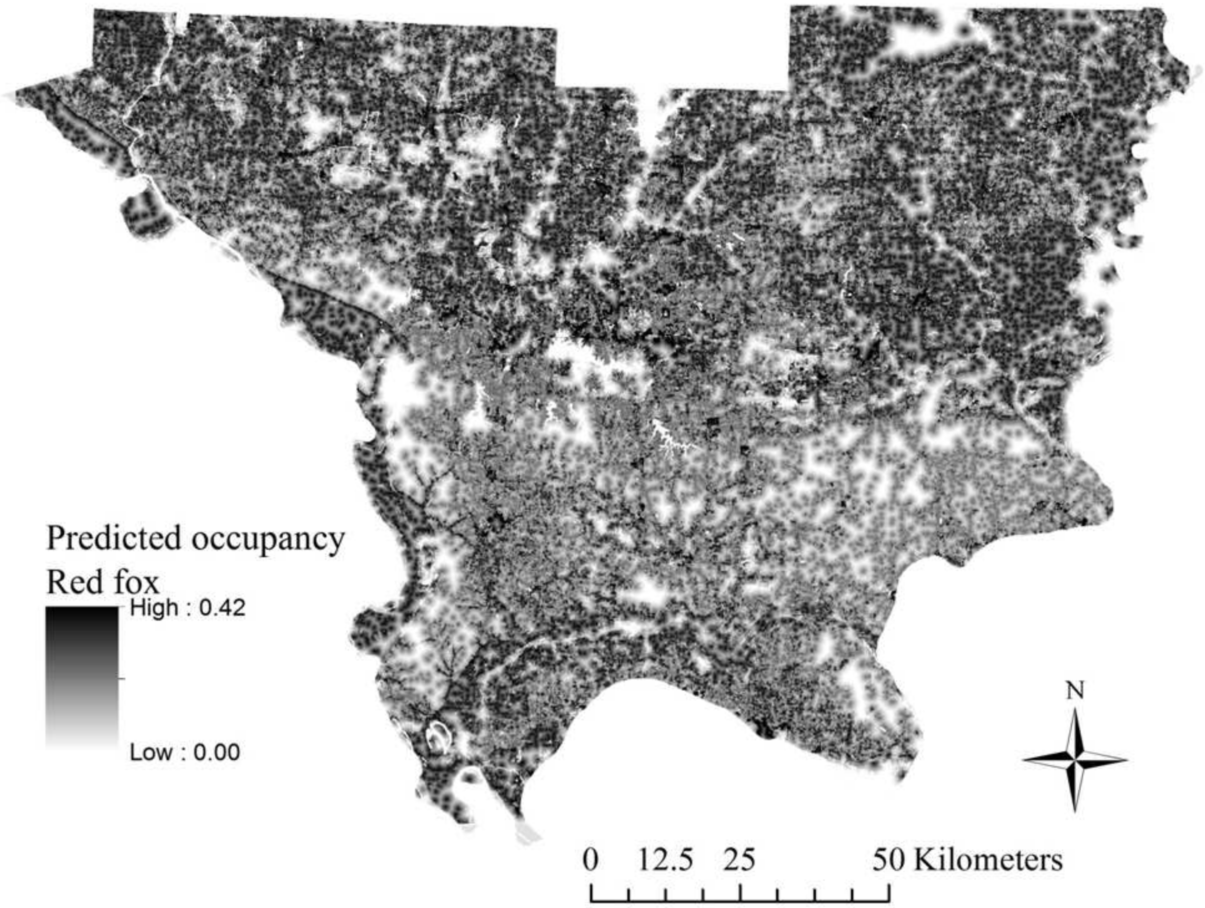
Predicted occupancy
Red fox
High : 0.42
Low : 0.00
N
0 12.5 25 50 Kilometers

Figure 6.

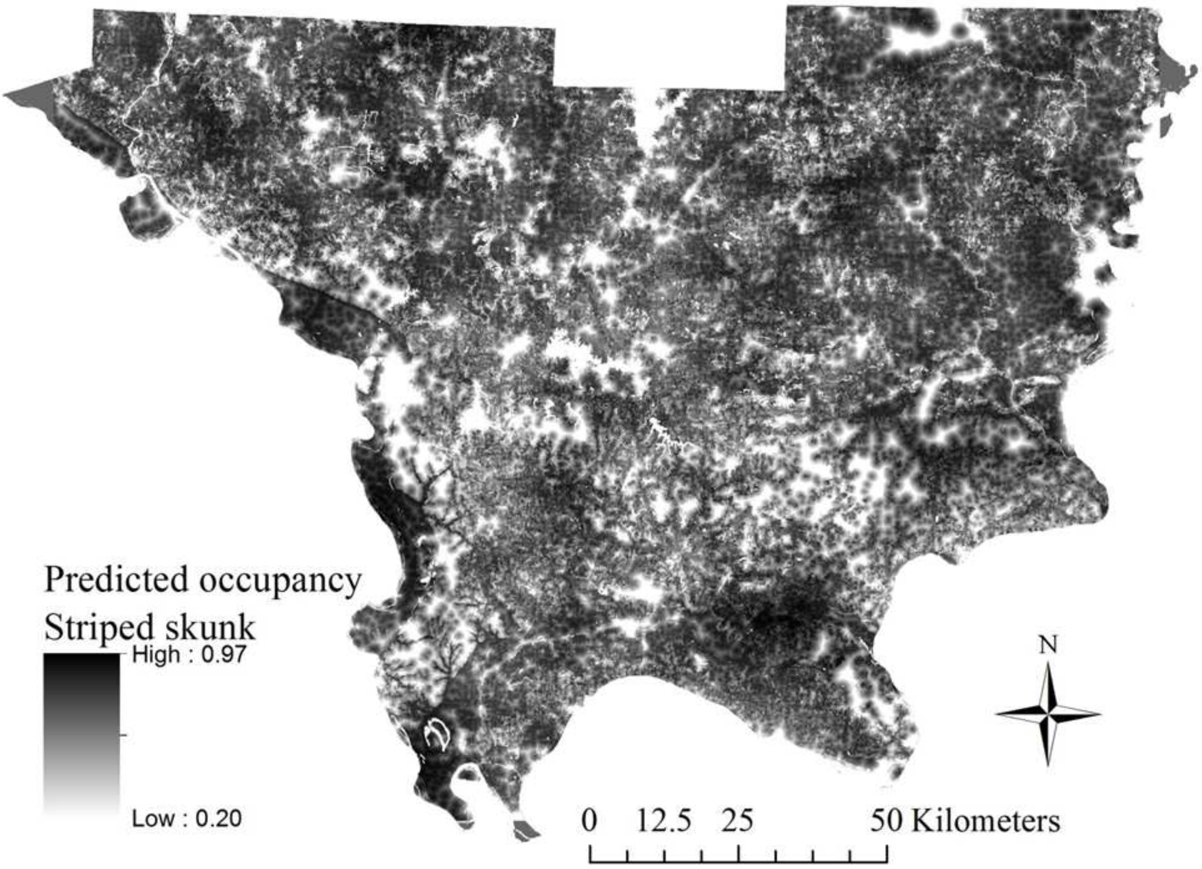
Predicted occupancy
Striped skunk
High : 0.97
Low : 0.20
N
0 12.5 25 50 Kilometers

Figure 7.

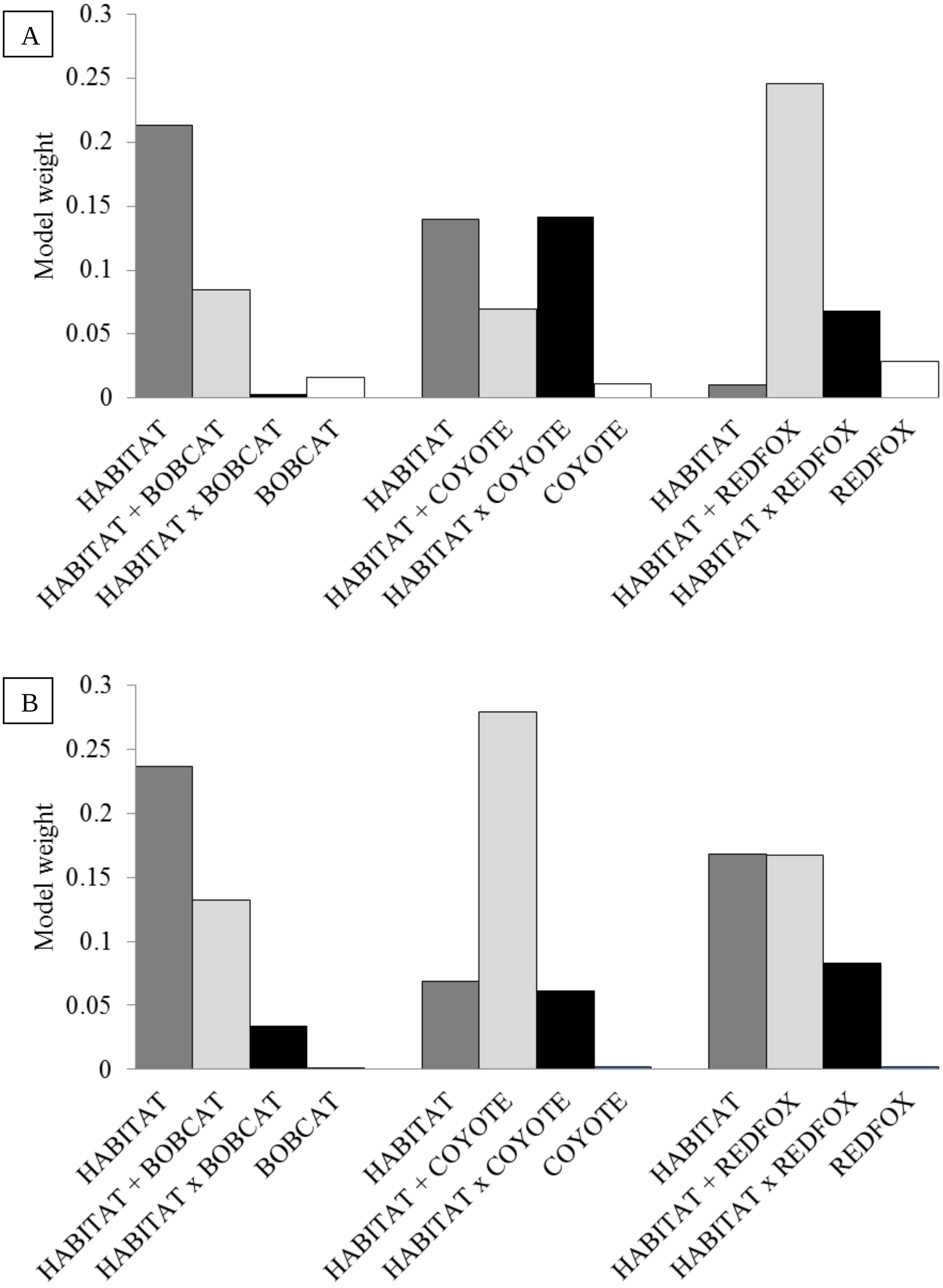
A
0.3
0.25
0.2
0.15
0.1
0.05
0
Model weight
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABITAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT + REDFOX
HABITAT x REDFOX
REDFOX
B
0.3
0.25
0.2
0.15
0.1
0.05
0
Model weight
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABITAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT + REDFOX
HABITAT x REDFOX
REDFOX

Figure 8.

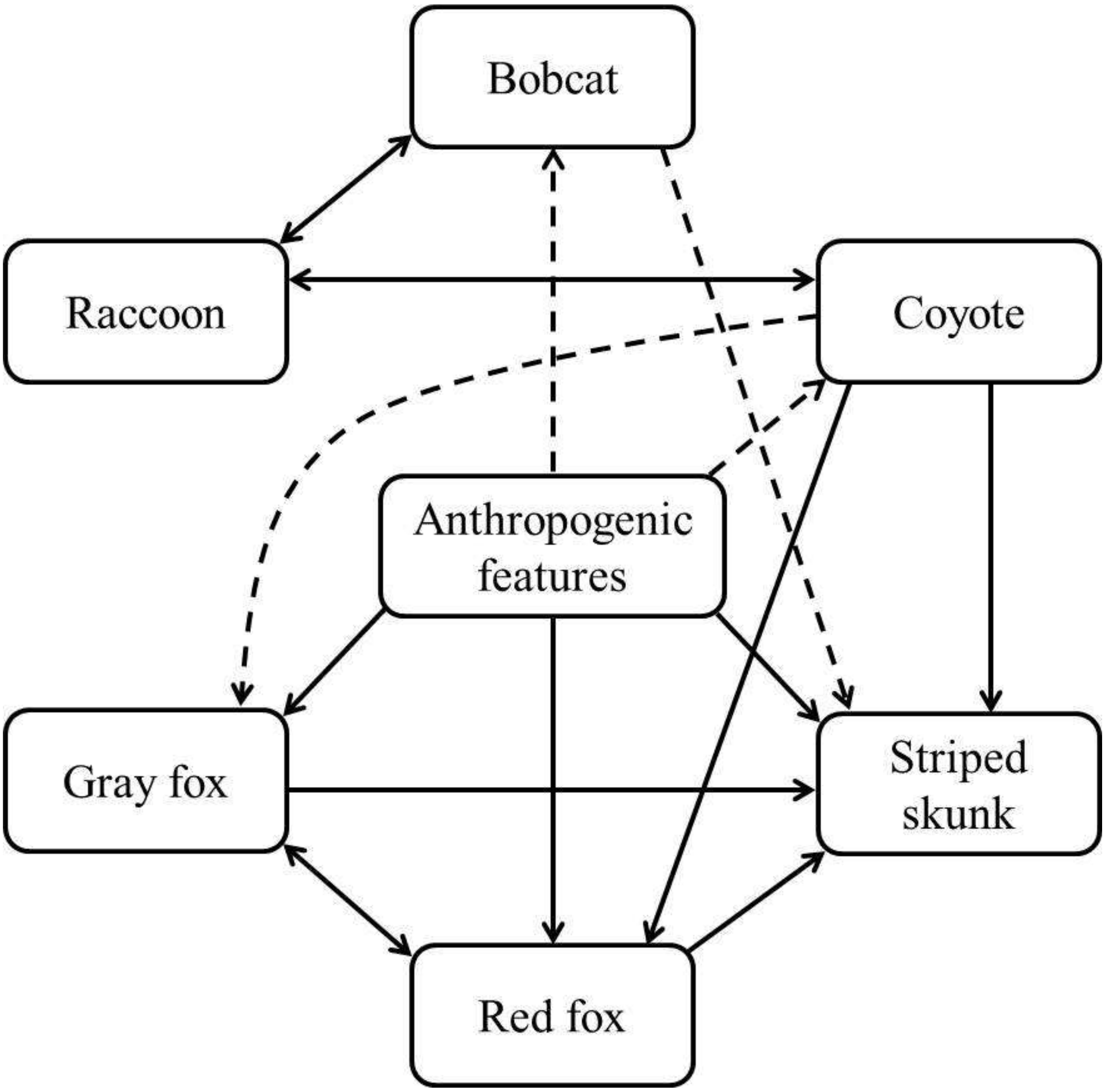
Bobcat
Raccoon
Coyote
Anthropogenic features
Gray fox
Striped skunk
Red fox

Figure 9.

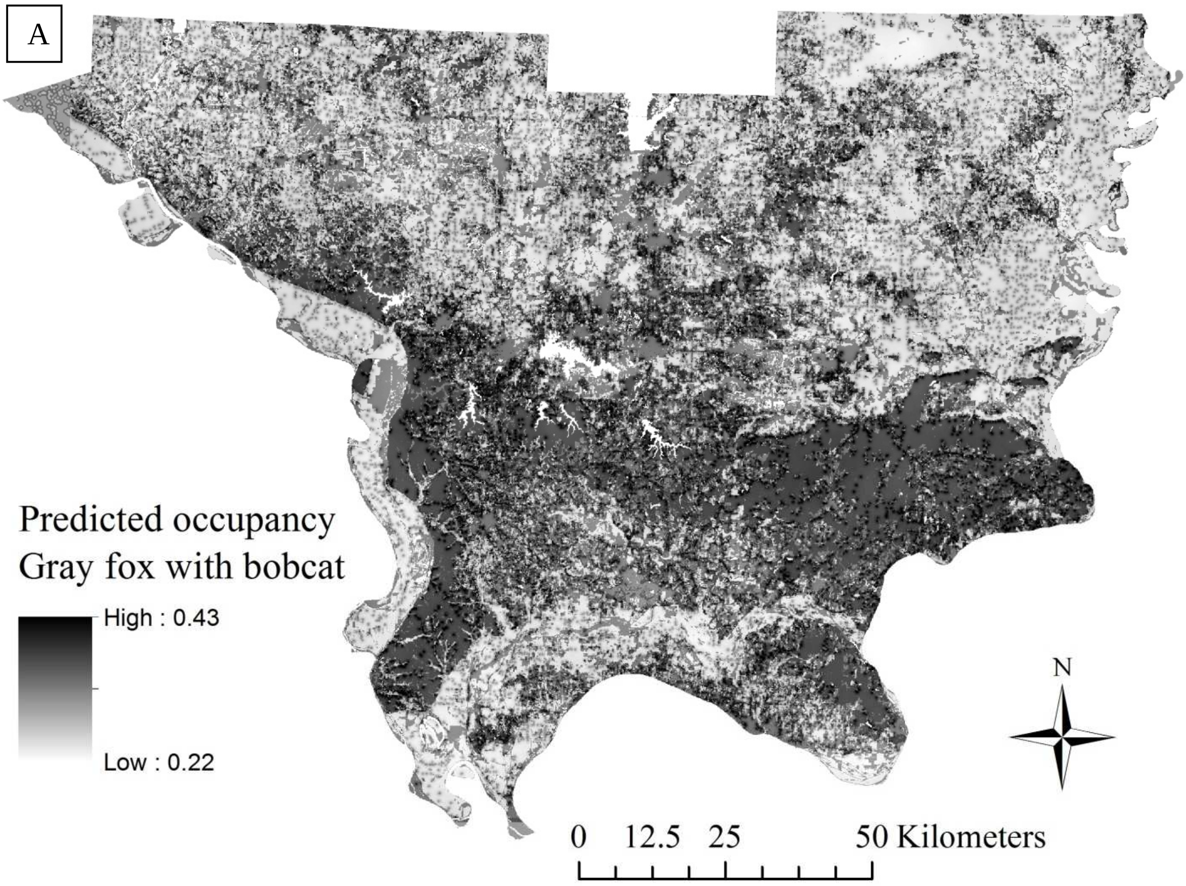
A
Predicted occupancy
Gray fox with bobcat
High : 0.43
Low : 0.22
N
0
12.5
25
50 Kilometers

Figure 10A.

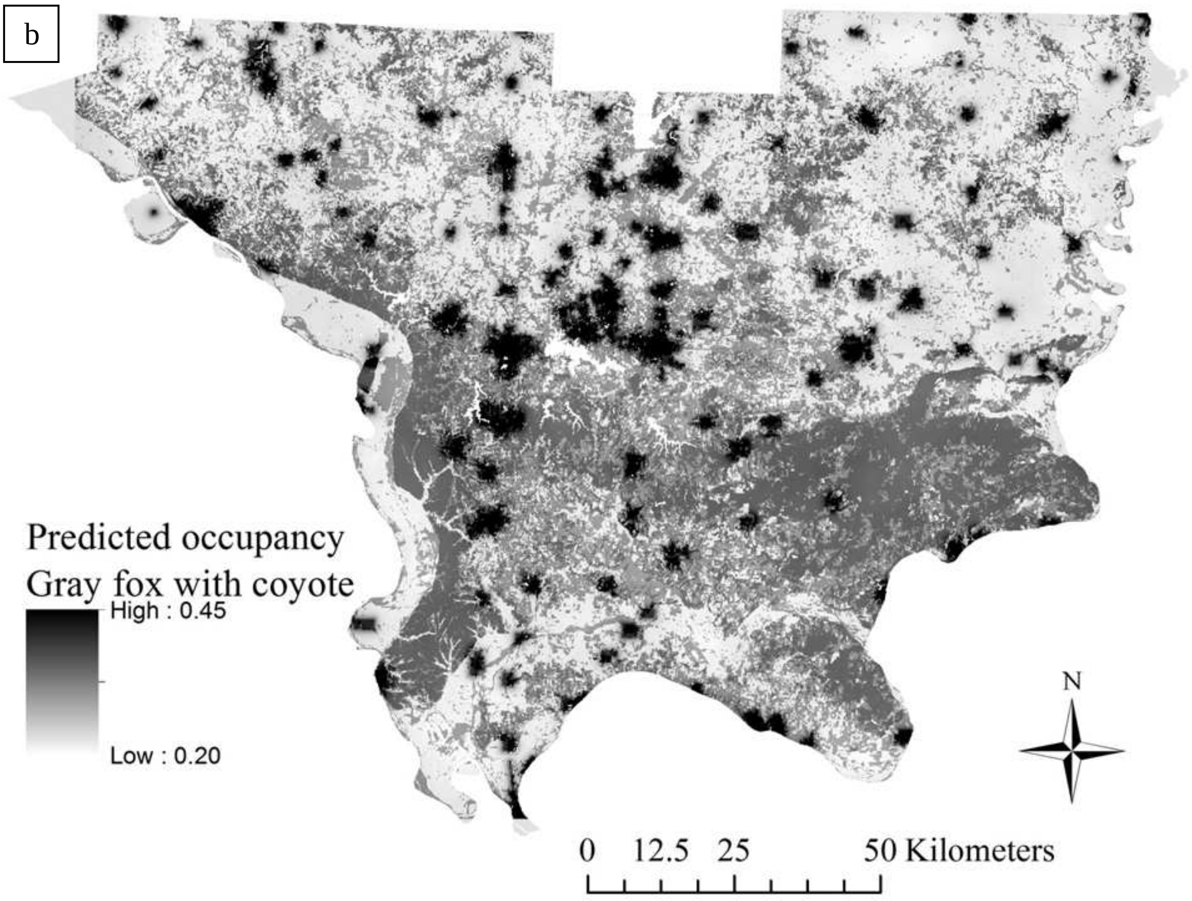
b
Predicted occupancy
Gray fox with coyote
High : 0.45
Low : 0.20
N
0 12.5 25 50 Kilometers

Figure 10B.

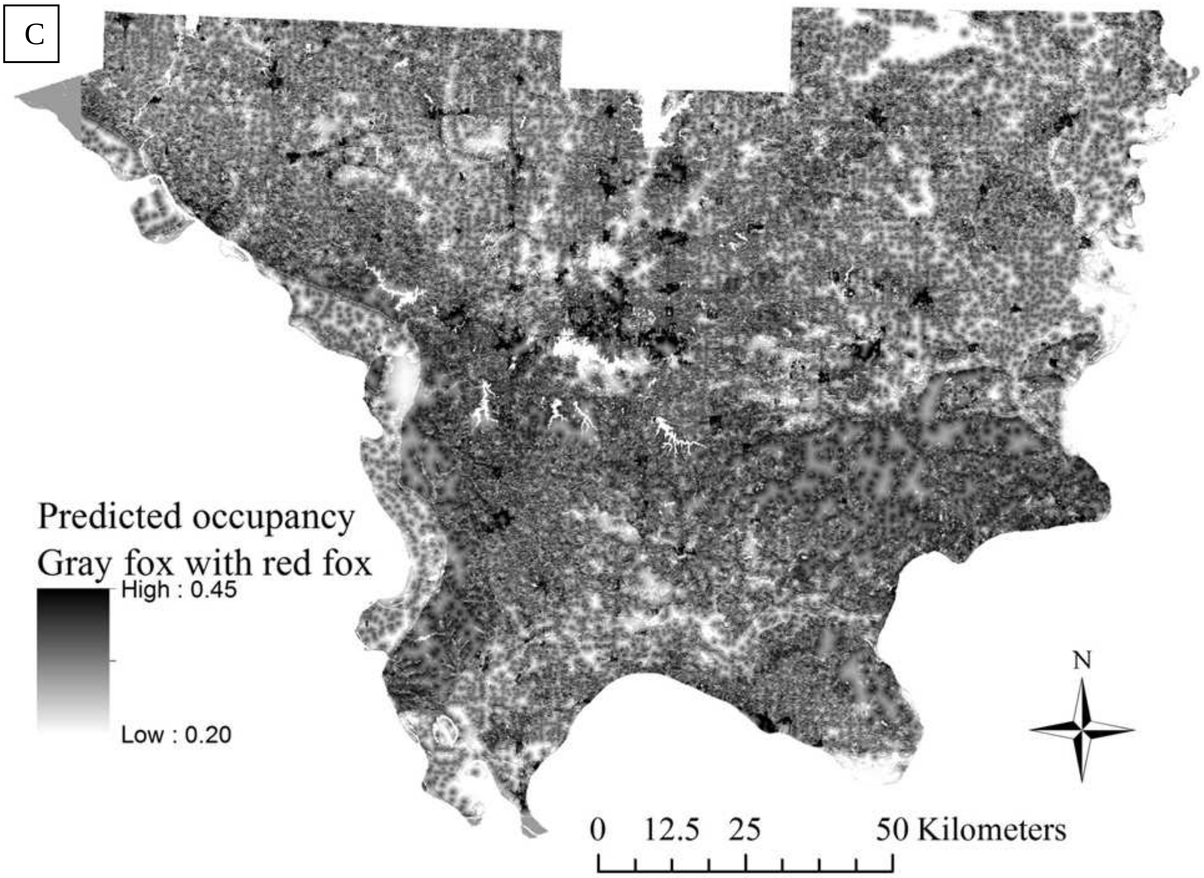

Figure 10C.

Figure 10.

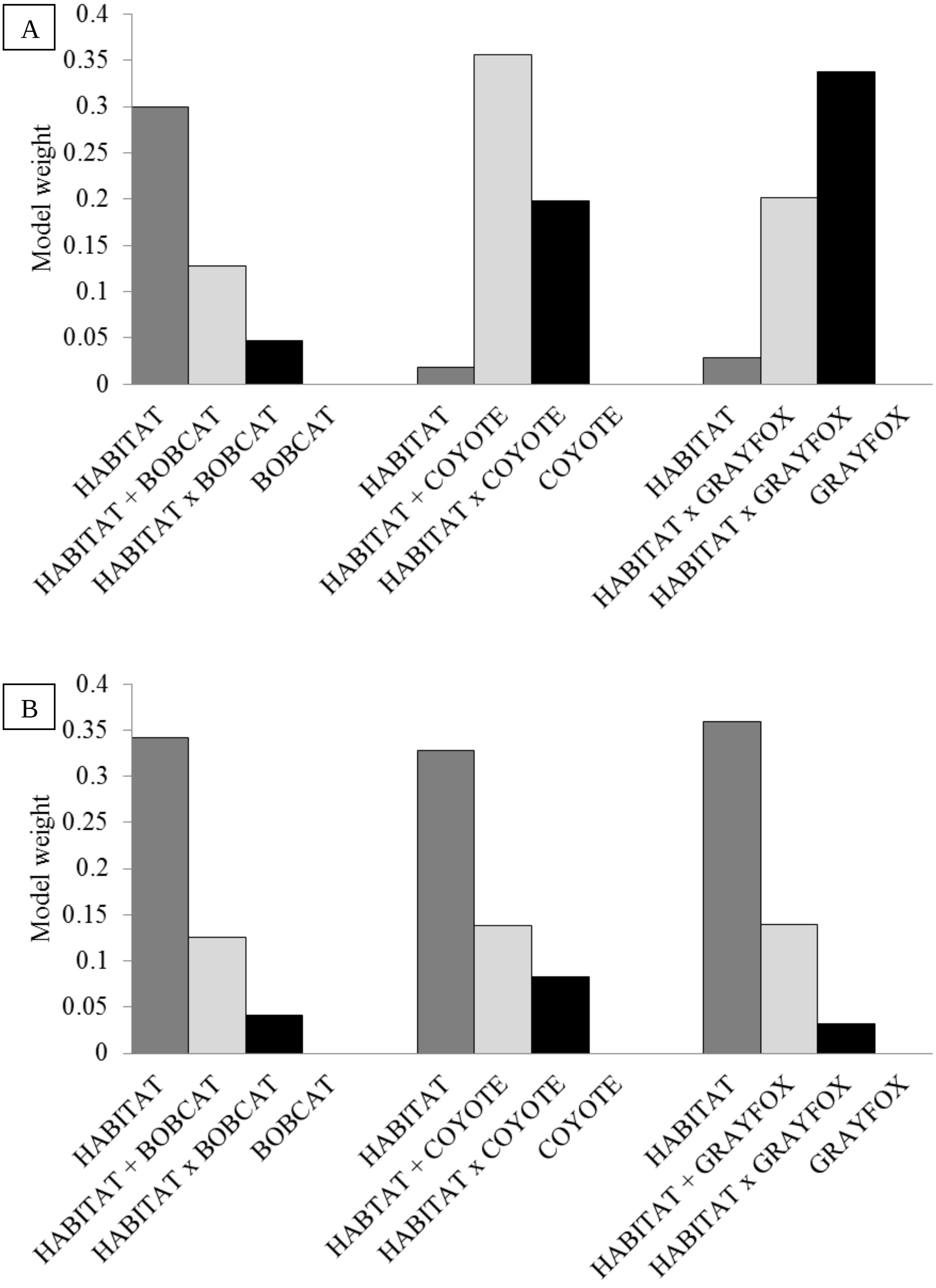
A
Model weight
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABITAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT x GRAYFOX
HABITAT x GRAYFOX
GRAYFOX
B
Model weight
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABTAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT + GRAYFOX
HABITAT x GRAYFOX
GRAYFOX

Figure 11.

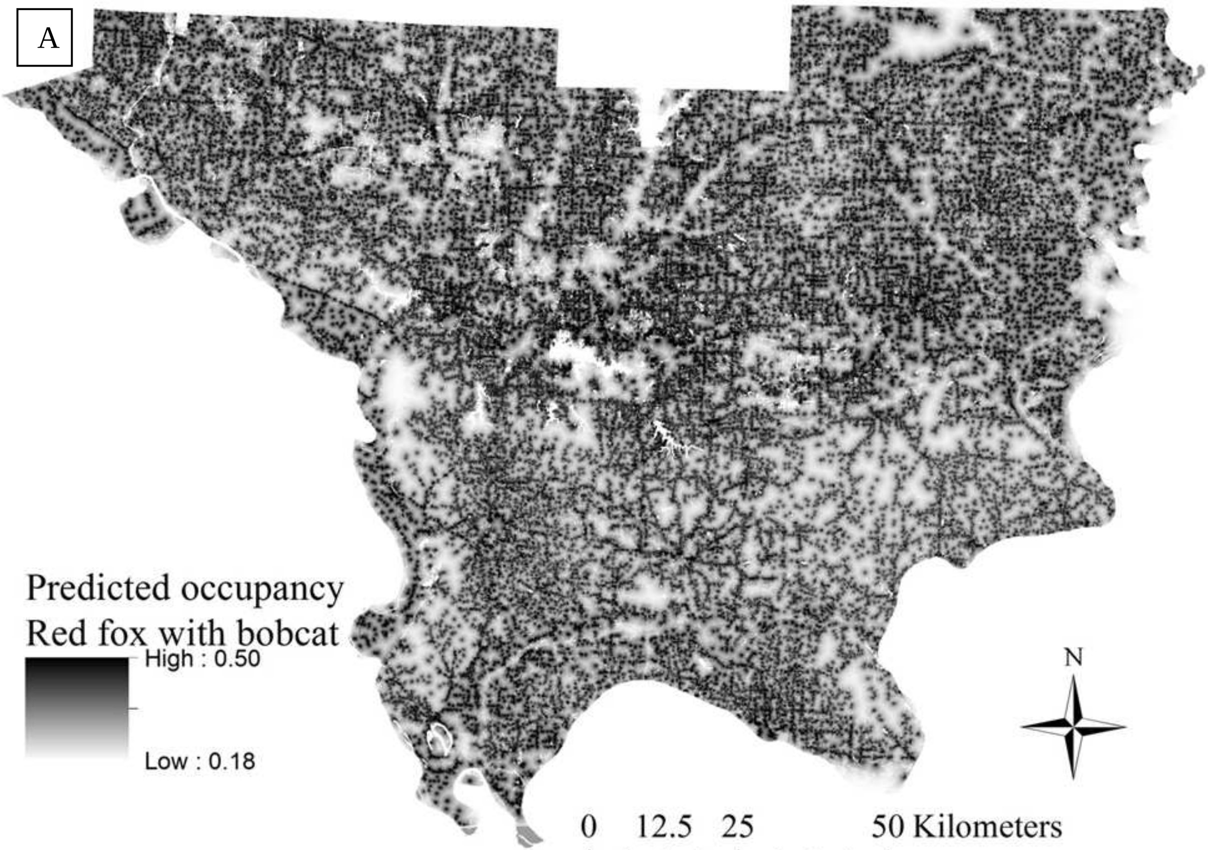
A
Predicted occupancy
Red fox with bobcat
High : 0.50
Low : 0.18
N
0
12.5
25
50 Kilometers

Figure 12A.

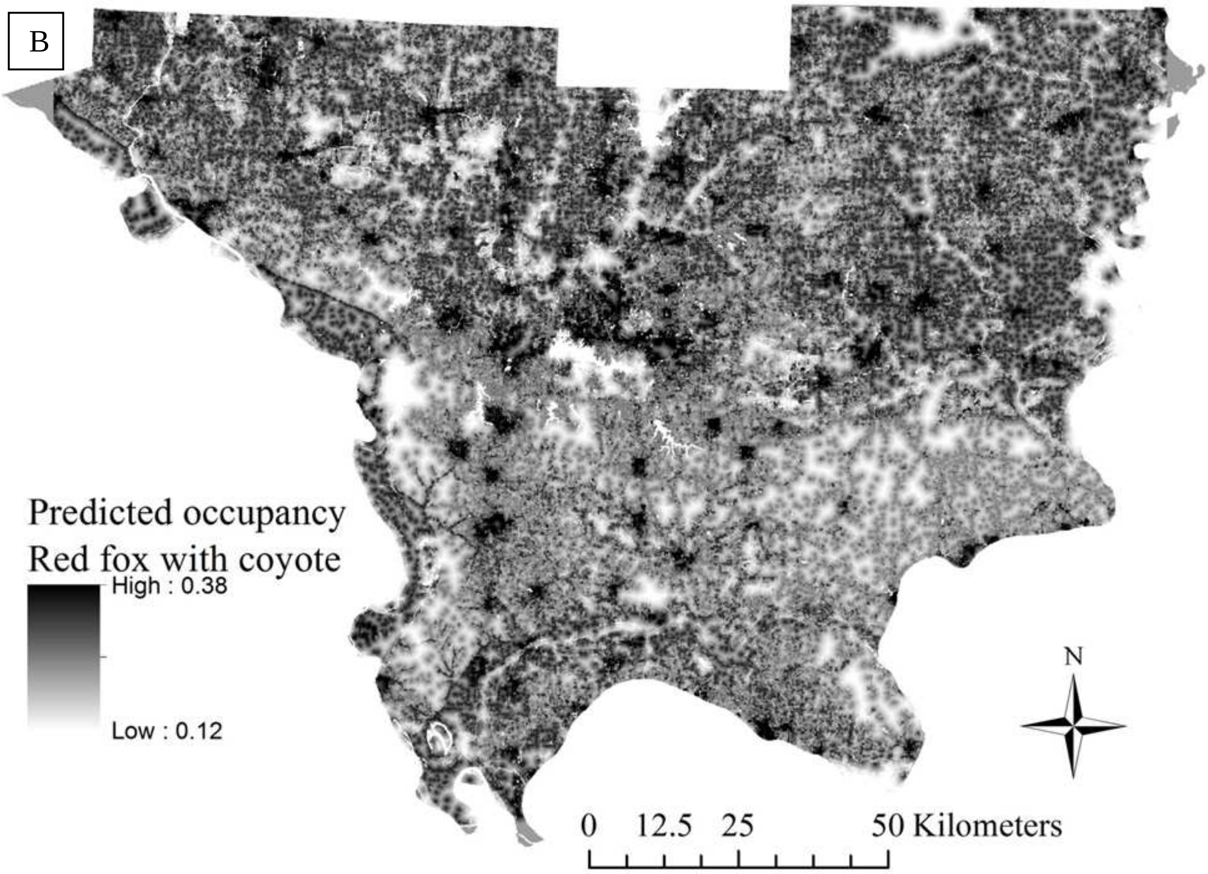
B
Predicted occupancy
Red fox with coyote
High : 0.38
Low : 0.12
N
0 12.5 25 50 Kilometers

Figure 12B.

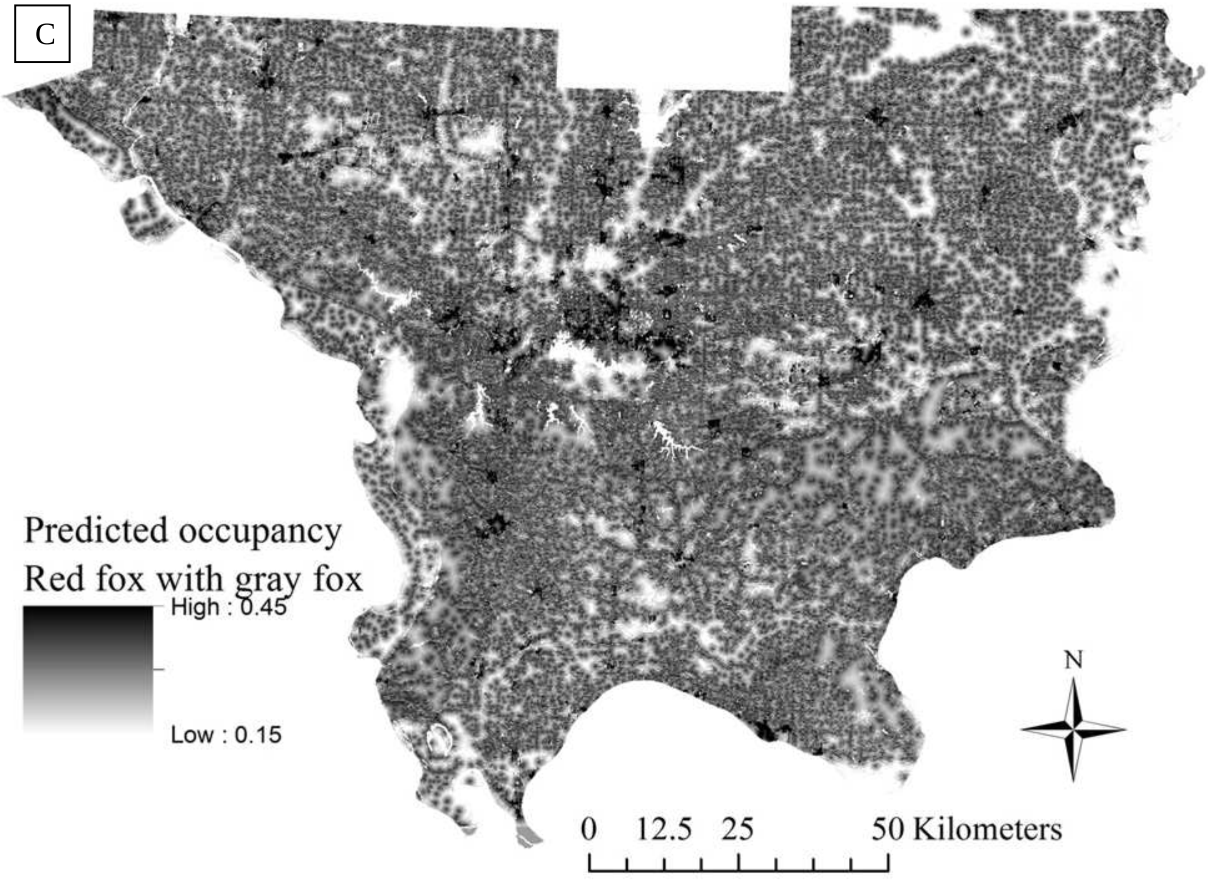

Figure 12C.

Figure 12.

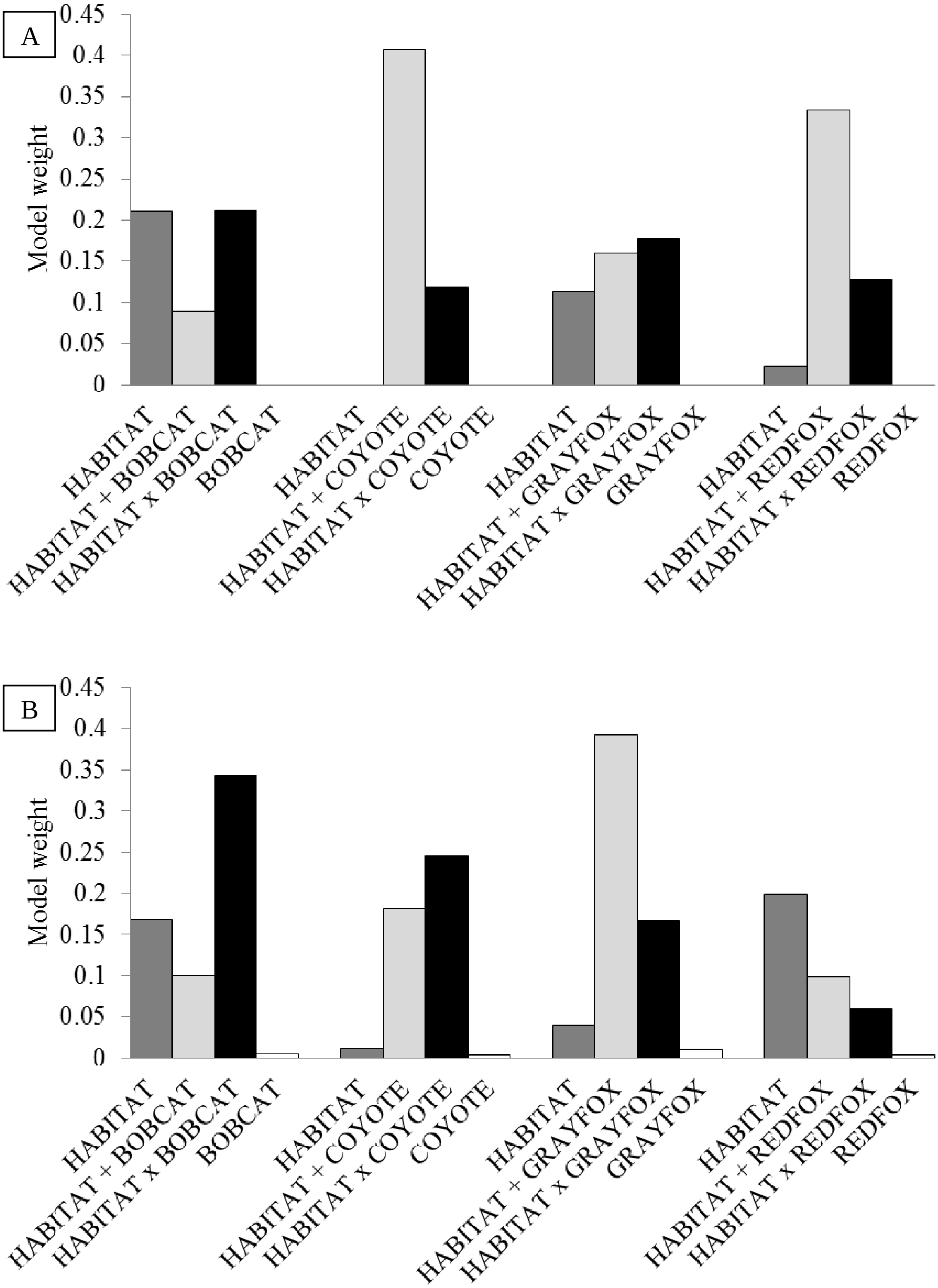
A
Model weight
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABITAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT + GRAYFOX
HABITAT x GRAYFOX
GRAYFOX
HABITAT
HABITAT + REDFOX
HABITAT x REDFOX
REDFOX
B
Model weight
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
HABITAT
HABITAT + BOBCAT
HABITAT x BOBCAT
BOBCAT
HABITAT
HABITAT + COYOTE
HABITAT x COYOTE
COYOTE
HABITAT
HABITAT + GRAYFOX
HABITAT x GRAYFOX
GRAYFOX
HABITAT
HABITAT + REDFOX
HABITAT x REDFOX
REDFOX

Figure 13.

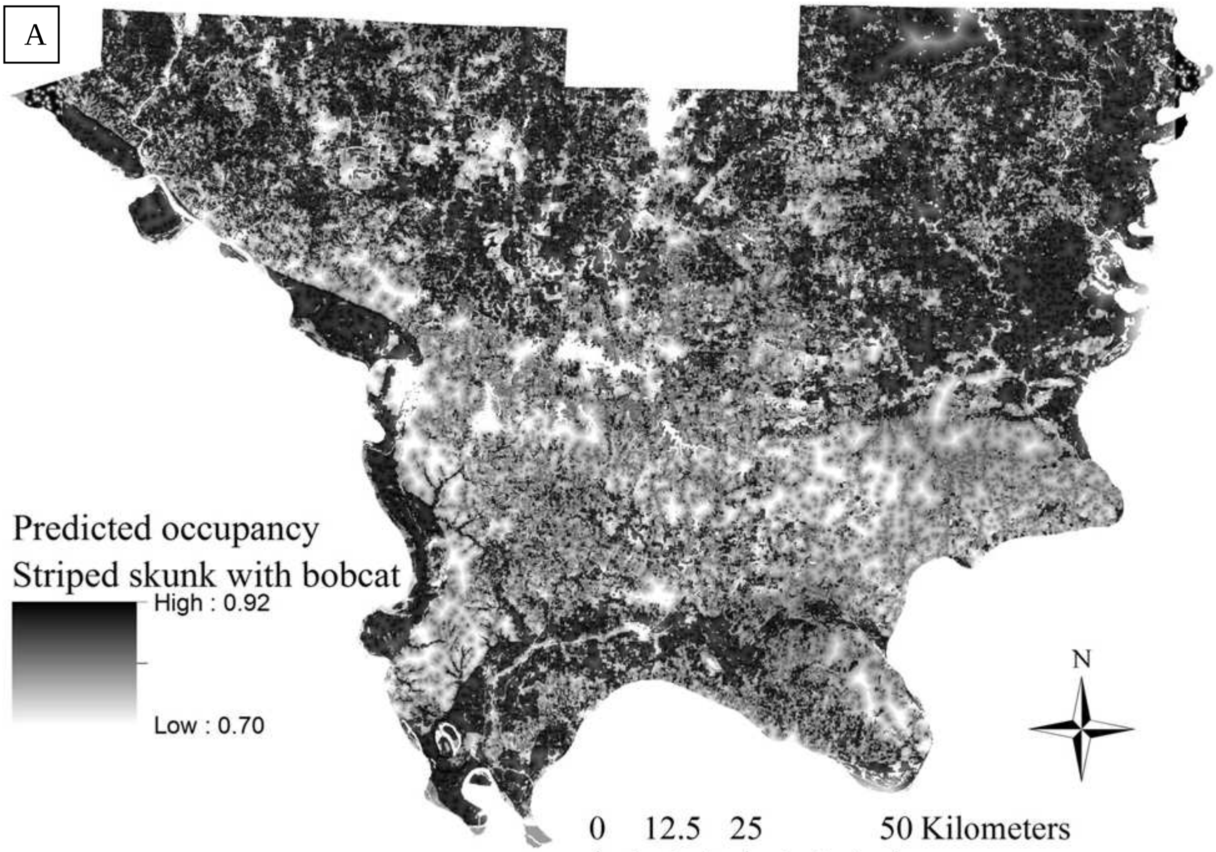
A
Predicted occupancy
Striped skunk with bobcat
High : 0.92
Low : 0.70
N
0 12.5 25 50 Kilometers

Figure 14A.

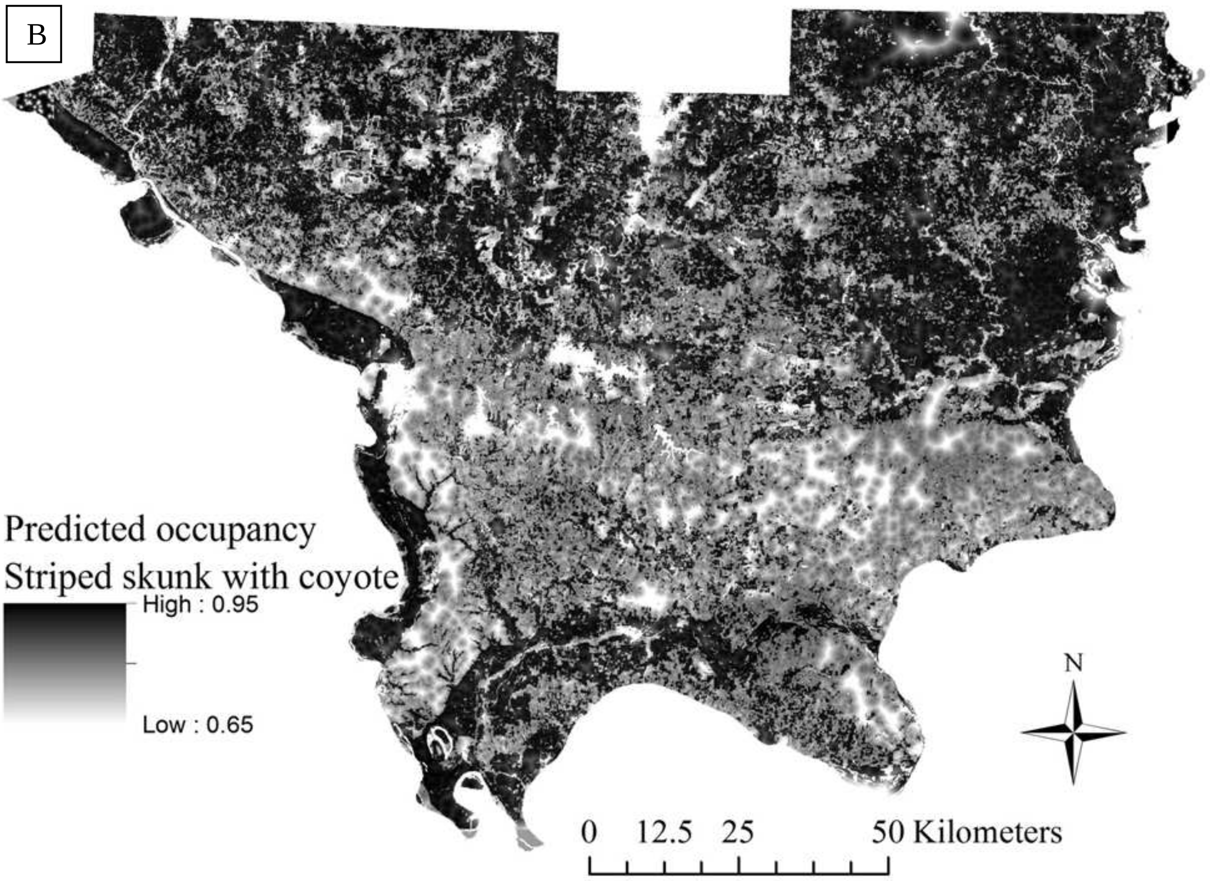
B
Predicted occupancy
Striped skunk with coyote
High : 0.95
Low : 0.65
N
0 12.5 25 50 Kilometers

Figure 14B.

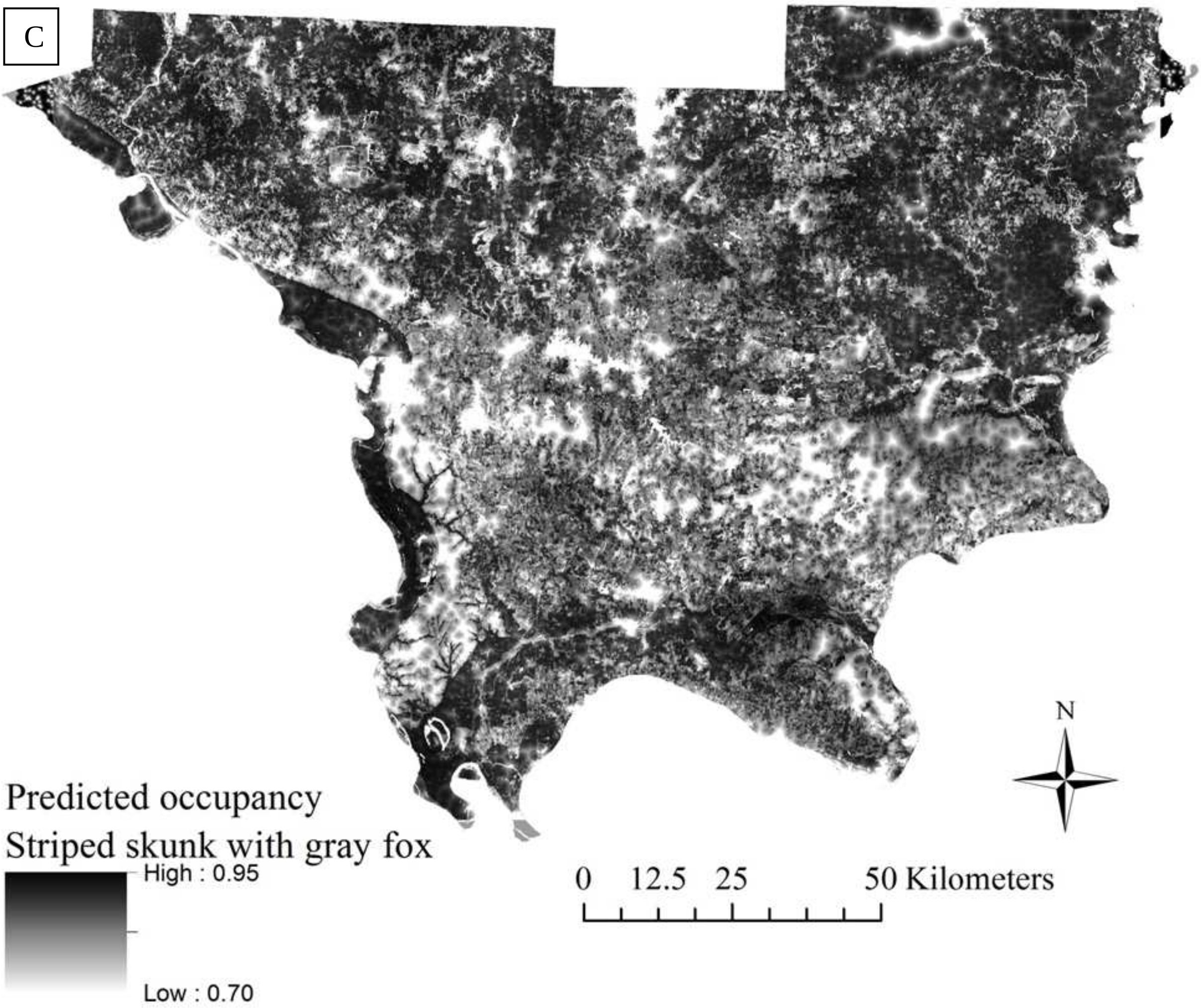
C
Predicted occupancy
Striped skunk with gray fox
High : 0.95
Low : 0.70
0 12.5 25 50 Kilometers
N

Figure 14C.

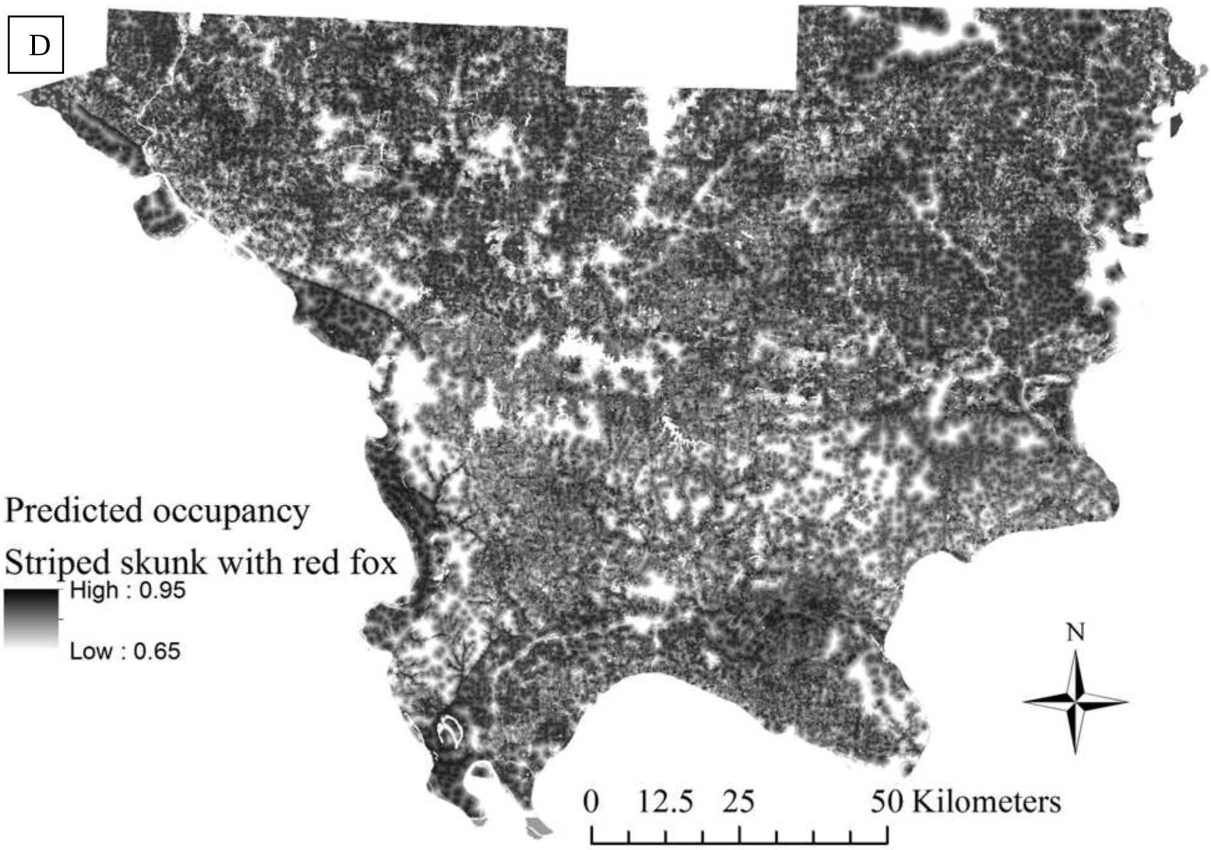

Figure 14D.

Figure 14.

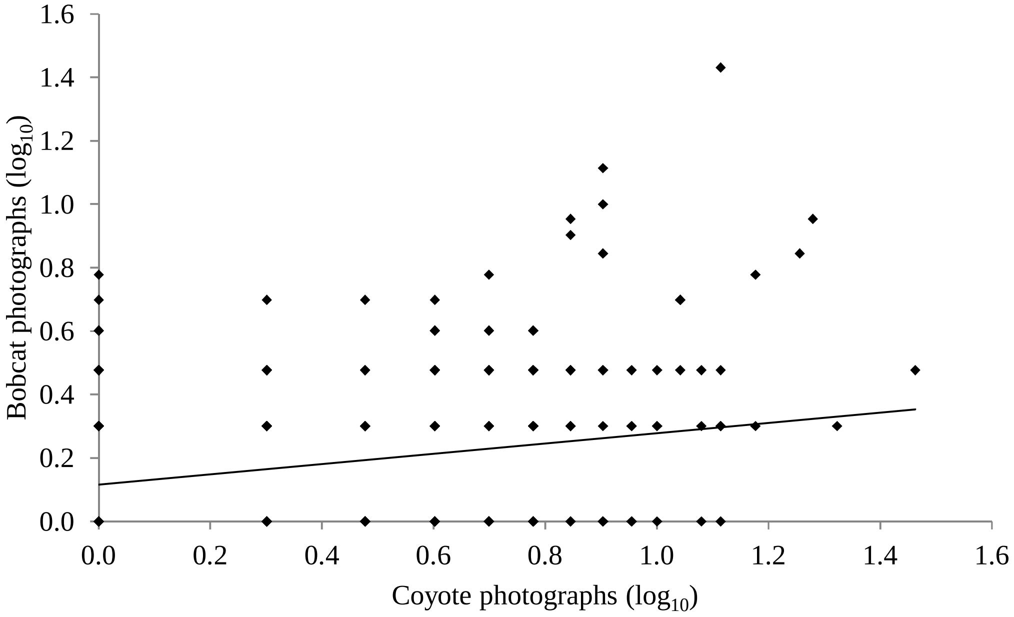
Bobcat photographs ($\log_{10}$)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Coyote photographs ($\log_{10}$)

Figure 15.

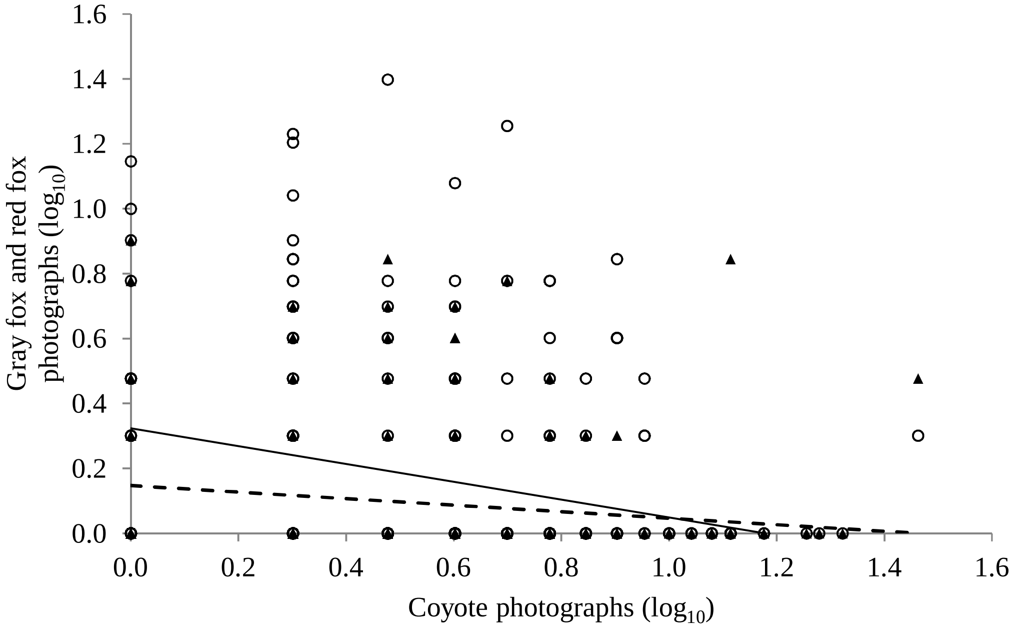
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Gray fox and red fox photographs ($\log_{10}$)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Coyote photographs ($\log_{10}$)

Figure 16.

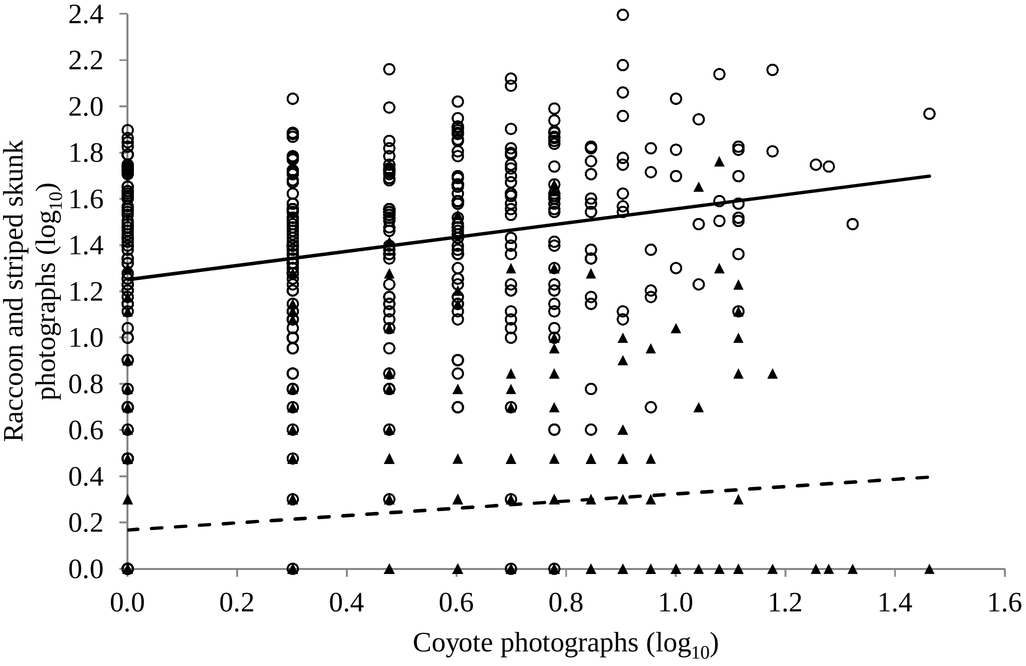
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Raccoon and striped skunk photographs ($\log_{10}$)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Coyote photographs ($\log_{10}$)

Figure 17.

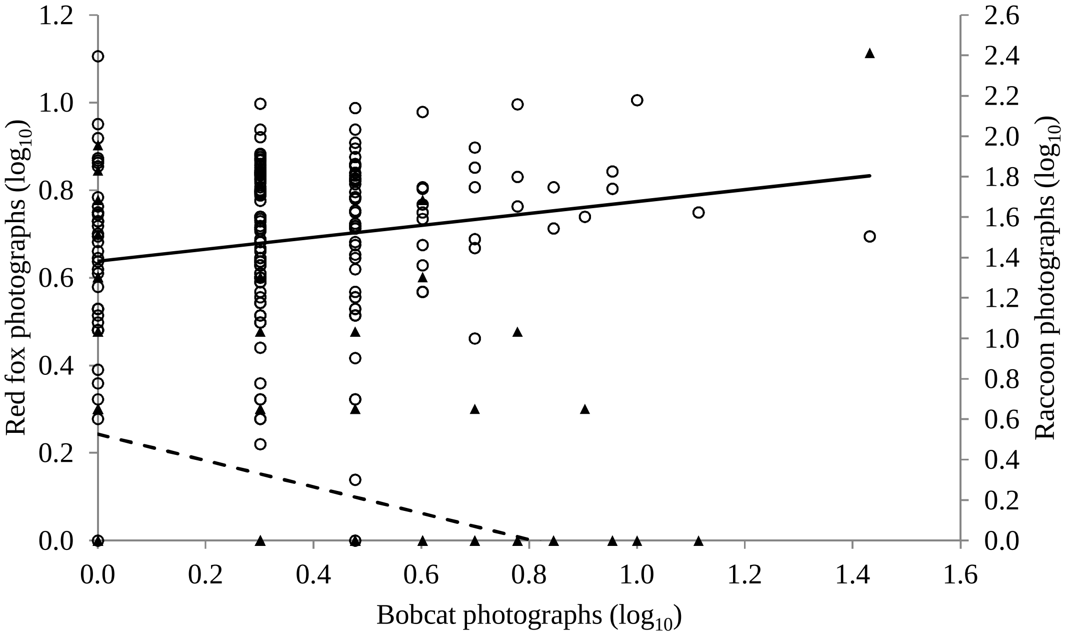
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Red fox photographs ($\log_{10}$)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Raccoon photographs ($\log_{10}$)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Bobcat photographs ($\log_{10}$)

Figure 18.

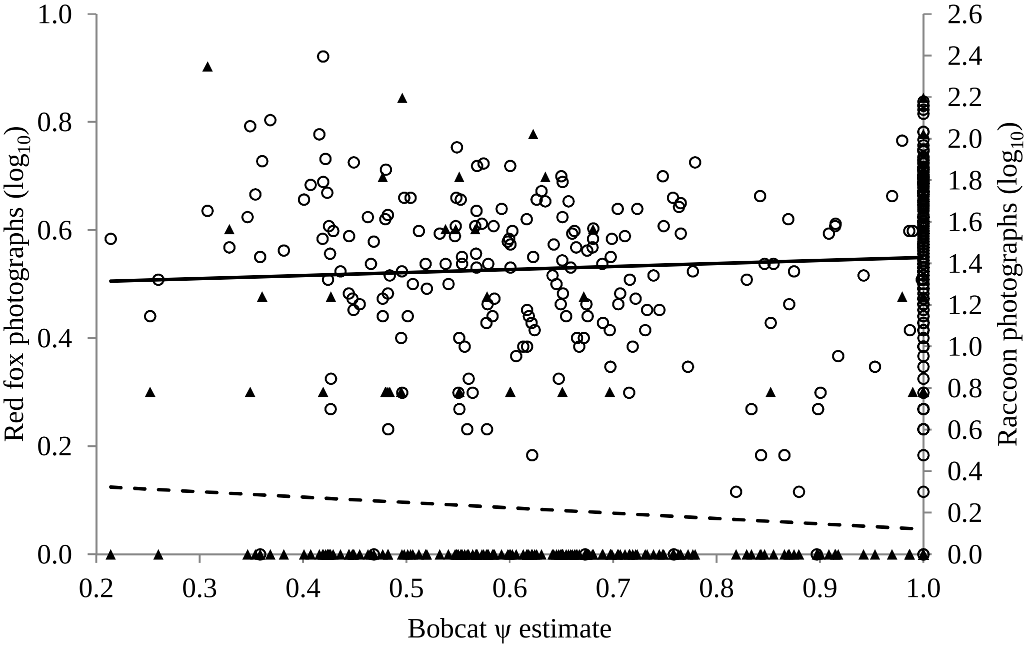
Red fox photographs ($\log_{10}$)
Raccoon photographs ($\log_{10}$)
Bobcat ψ estimate
1.0
0.8
0.6
0.4
0.2
0.0
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 19.

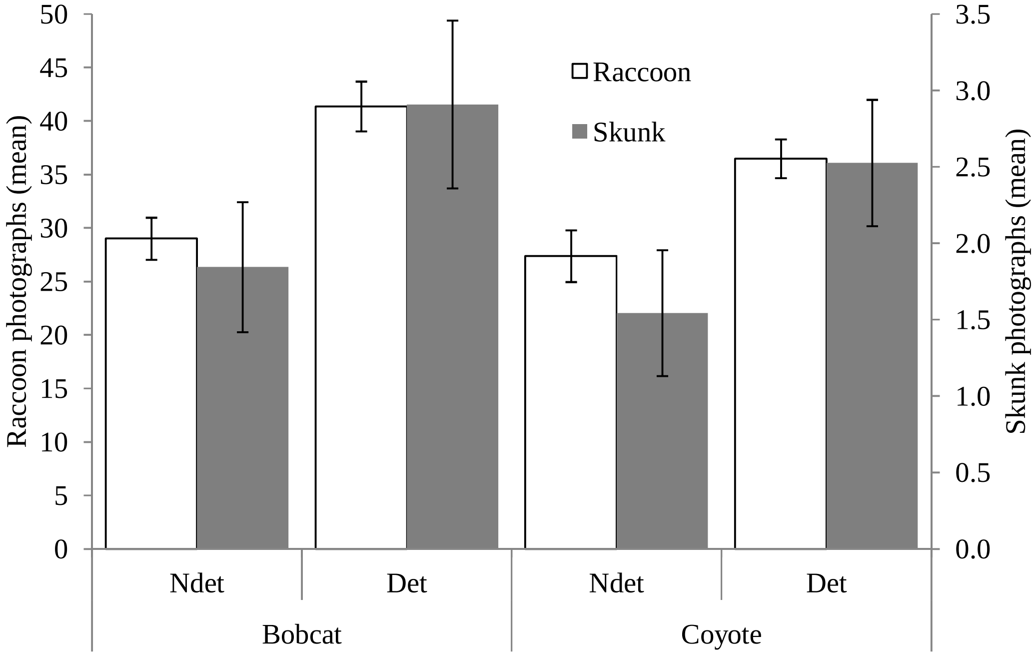
50
45
40
35
30
25
20
15
10
5
0
Raccoon photographs (mean)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Skunk photographs (mean)
☐ Raccoon
■ Skunk
Ndet
Det
Ndet
Det
Bobcat
Coyote

Figure 20.

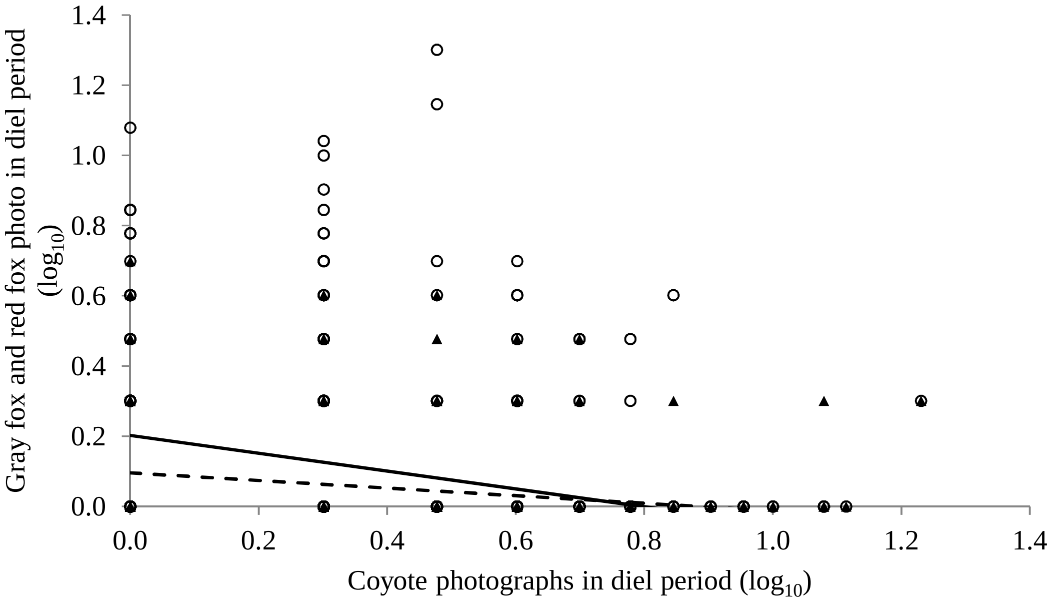
Gray fox and red fox photo in diel period (log10)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Coyote photographs in diel period (log10)

Figure 21.

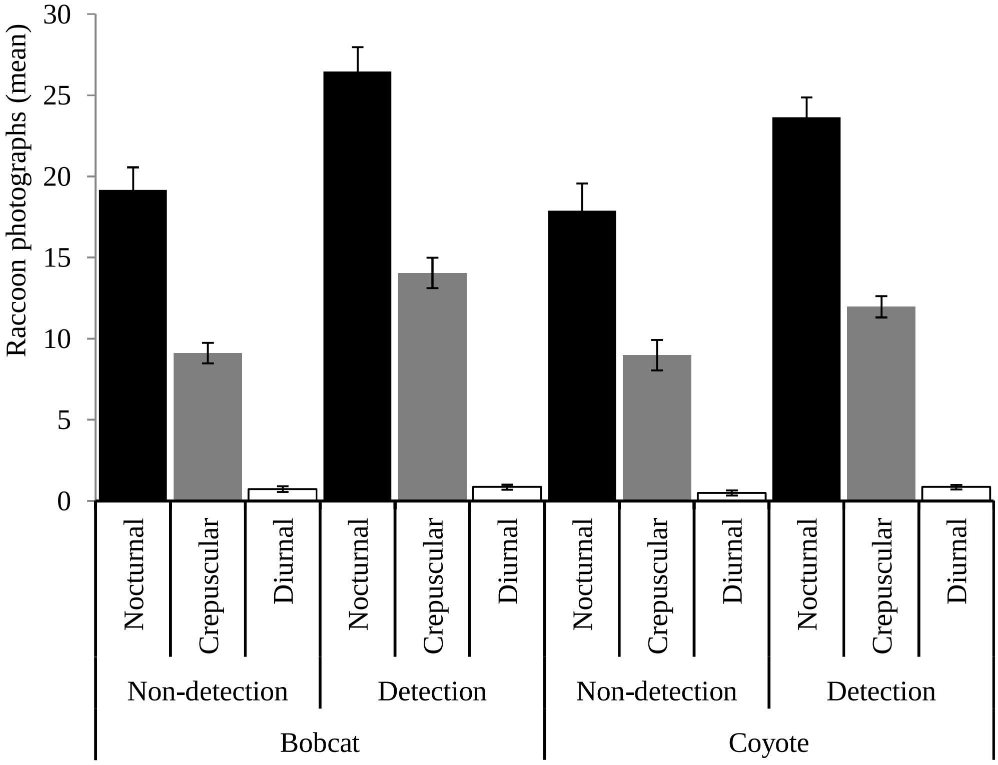
Raccoon photographs (mean)
30
25
20
15
10
5
0
Nocturnal
Crepuscular
Diurnal
Nocturnal
Crepuscular
Diurnal
Nocturnal
Crepuscular
Diurnal
Nocturnal
Crepuscular
Diurnal
Non-detection
Detection
Non-detection
Detection
Bobcat
Coyote

Figure 22.

Table 1. Survey, camera-point, and camera-cluster explanatory variable codes, descriptions, and expected direction of effect (positive +, negative -, no effect 0, not applicable n/a) on bobcat, coyote, gray fox, red fox, and striped skunk populations during January–April 2008–2010 in the 16 southernmost counties of Illinois, USA. Included are survey variables to inform detection probability (p) models, and camera-point and camera-cluster occupancy (ψ) models. Camera-cluster scale parameters were averaged across 3–4 camera-points distributed within camera-clusters and derived from ArcGIS-based measurements using 2 buffer sizes for each species: 100% estimated home-range size and 20% of the estimated home-range size.

		Expected result				
Variable	Description	Bobcat	Coyote	Gray fox	Red fox	Skunk
PPT[a]	Sum of precipitation recorded during survey week at nearest National Weather Service station	-	-	-	-	-
TMP[a]	Average temperature recorded during survey week at nearest National Weather Service station	-	-	-	-	-
TMP*PPT[a]	Interaction of average Temperature and sum of precipitation recorded during survey week at nearest National Weather Service station	-	-	-	-	-
INT[a]	Survey week-specific intercept; detection probability calculated	n/a	n/a	n/a	n/a	n/a

	for each week of survey					
PREVDET[a]	Previous photograph recorded at a camera-point during a previous survey	-	-	+	+	+
MONTH[a]	Month survey was conducted (Jan was reference); months for comparison: Feb, Mar, Apr	-	-	-	-	-
YEAR[a]	Year survey was conducted (2008 was reference); years for comparison: 2009, 2010	+	+	+	+	+
BA[b]	Tree basal area measured in m^2/ha at remote camera	+	-	+	-	-
HW[b]	Percentage of basal area at remote camera that were hardwood trees	+	+	+	+	+
CWD[b]	Number of coarse woody debris ≥10-cm diameter counted within 1-m of 4 10-m cardinal direction transects from remote camera	+	+	+	+	+
SLP[b]	Degree (°) slope measured at remote camera-point	+	-	+	-	-
STEM[b]	Number of woody stems ≥1.5-m tall counted within 1-m of 4 10-	-	-	+	+	-

	m cardinal direction transects from remote camera					
DTSTRM	Distance (m) to nearest linear water feature (streams and rivers)	-	-	-	-	-
DTMU	Distance (m) to nearest municipality	+	+	0	-	-
DTMJRD[c]	Distance (m) to nearest major road (interstate highways and arterials)	+	+	0	-	-
DTRD[c]	Distance (m) to nearest minor paved road (collectors and local roads)	+	+	0	-	-
DTST	Distance (m) to nearest human structure	+	+	0	-	-
MJRDHA[c]	Length (m) of major road (interstate highways and arterials) per hectare	-	-	0	+	+
RDHA[c]	Length (m) of minor paved road (collectors and local roads) per hectare	-	-	0	+	+
STHA	Number of human structures per hectare	-	-	0	+	+
PVT	Ownership (public or private) of	-	-	0	+	+

	remote camera-point (reference is public ownership)					
URPD	Number of urban patches per hectare	-	-	0	+	+
URPL	Percentage camera-cluster comprised of urban patches	-	-	0	+	+
ARCV	Patch area coefficient of variation: standard deviation/mean patch size (ha)	-	+	-	+	+
ED	Total length (m) of patch edge per hectare	-	+	-	+	+
SID	Simpson’s diversity index, proportional abundance of each patch type	-	+	-	-	+
FORSI	Forest shape index, mean perimeter-to-area ratio of patch, increases as patch becomes less compact	-	+	-	+	+
GRSI	Grassland shape index, mean perimeter-to-area ratio of patch, increases as patch becomes less compact	-	+	-	+	+
STRMHA	Length (m) of stream per hectare	+	+	+	+	+

WASI	Water shape index, mean perimeter-to-area ratio of patch, increases as patch becomes less compact	+	+	+	+	+
WESI	Wetland shape index, mean perimeter-to-area ratio of patch, increases as patch becomes less compact	+	+	+	+	+
AGCL	Agriculture clumpiness (fragmentation) index,range-1 (patch maximally disaggregated) to 1 (patch maximally clumped)	+	+	+	+	-
AGPL	Percentage camera-cluster comprised of agriculture patches	-	+	-	+	+
FORPI	Forest proximity index, mean sum of forest patch size (ha) divided by the squared distance (m) from focal patch	+	+	+	+	-
FORPL	Percentage camera-cluster comprised of forest patches	+	-	+	-	-
GRPI	Grassland proximity index, mean sum of forest patch size (ha) divided by the squared distance	-	+	-	+	-

	(m) from focal patch					
GRPL	Percentage camera-cluster comprised of grassland patches	-	+	-	+	+

[a] Survey-specific variable used in detection probability models.

[b] Field-measured habitat variable for camera-point occupancy models.

[c] U.S. Department of Transportation road classifications (FHWA 2000).

Table 2. Structure of *a priori* habitat models used to evaluate camera-point and camera-cluster scale occupancy by bobcats, coyotes, gray foxes, red foxes, and striped skunks during January–April 2008–2010 in the 16 southernmost counties of Illinois, USA. Models are arranged by the scale of analysis and the primary hypotheses regarding the influence of habitat attributes on carnivore occupancy. See Table 1 for measured parameter codes, descriptions, and expected direction of variable effect on species-specific habitat occupancy.

Hypothesis (scale)	Model[a]
AF-PRED[b] (camera-point)	1. $\beta_0 + \beta_1$(STEM) + β_2(SLP) + β_3(DTRD) + β_4(DTST) + β_5(PVT)
AF-PRED (camera-point)	2. $\beta_0 + \beta_1$(STEM) + β_2(DTRD) + β_3(DTST)
AF-PRED (camera-point)	3. $\beta_0 + \beta_1$(STEM) + β_2(SLP) + β_3(DTRD)
AF-PRED (camera-point)	4. $\beta_0 + \beta_1$(STEM) + β_2(DTST) + β_3(PVT)
AF-PRED (camera-point)	5. $\beta_0 + \beta_1$(DTRD) + β_2(DTST) + β_3(PVT)
AF-PRED (camera-point)	6. $\beta_0 + \beta_1$(STEM) + β_2(SLP)
AF-PRED (camera-point)	7. $\beta_0 + \beta_1$(DTST) + β_2(PVT)
AF-PRED (camera-point)	8. $\beta_0 + \beta_1$(DTRD) + β_2(DTST)
AF-PRED (camera-point)	9. $\beta_0 + \beta_1$(STEM)
AF-PRED (camera-point)	10. $\beta_0 + \beta_1$(DTRD)
AF-PRED (camera-point)	11. $\beta_0 + \beta_1$(DTST)
AF-PRED (camera-point)	12. $\beta_0 + \beta_1$(PVT)
PREY[c] (camera-point)	13. $\beta_0 + \beta_1$(BA) + β_2(HW) + β_3(CWD) + β_4(DTSTRM)
PREY (camera-point)	14. $\beta_0 + \beta_1$(BA) + β_2(HW) + β_3(CWD)
PREY (camera-point)	15. $\beta_0 + \beta_1$(HW) + β_2(CWD) + β_3(DTSTRM)

PREY (camera-point)	16. $\beta_0 + \beta_1(BA) + \beta_2(HW)$
PREY (camera-point)	17. $\beta_0 + \beta_1(BA) + \beta_2(CWD)$
PREY (camera-point)	18. $\beta_0 + \beta_1(CWD) + \beta_2(DTSTRM)$
PREY (camera-point)	19. $\beta_0 + \beta_1(HW) + \beta_2(CWD)$
PREY (camera-point)	20. $\beta_0 + \beta_1(HW)$
PREY (camera-point)	21. $\beta_0 + \beta_1(CWD)$
AF[d] (camera-cluster)	22. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA) + \beta_3(MJRDHA) + \beta_4(URPL) + \beta_5(URPD) + \beta_6(DTMJRD) + \beta_7(DTST) + \beta_8(DTRD) + \beta_9(DTMU) + \beta_{10}(PVT)$
AF (camera-cluster)	23. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA) + \beta_3(URPL) + \beta_4(URPD) + \beta_5(DTST) + \beta_6(DTRD) + \beta_7(DTMU) + \beta_8(PVT)$
AF (camera-cluster)	24. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA) + \beta_3(URPL) + \beta_4(DTMJRD) + \beta_5(DTST) + \beta_6(DTRD) + \beta_7(DTMU)$
AF (camera-cluster)	25. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA) + \beta_3(DTMJRD) + \beta_4(DTST) + \beta_5(DTRD)$
AF (camera-cluster)	26. $\beta_0 + \beta_1(RDHA) + \beta_2(DTRD) + \beta_3(DTMJRD) + \beta_4(MJRDHA)$
AF (camera-cluster)	27. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA) + \beta_3(DTST)$
AF (camera-cluster)	28. $\beta_0 + \beta_1(URPL) + \beta_2(URPD) + \beta_3(DTMU)$
AF (camera-cluster)	29. $\beta_0 + \beta_1(RDHA) + \beta_2(DTRD) + \beta_3(DTMJRD)$
AF (camera-cluster)	30. $\beta_0 + \beta_1(STHA) + \beta_2(RDHA)$
AF (camera-cluster)	31. $\beta_0 + \beta_1(STHA) + \beta_2(DTST)$
AF (camera-cluster)	32. $\beta_0 + \beta_1(RDHA) + \beta_2(DTRD)$

AF (camera-cluster)	33. $\beta_0 + \beta_1(\text{STHA}) + \beta_2(\text{PVT})$
AF (camera-cluster)	34. $\beta_0 + \beta_1(\text{URPL}) + \beta_2(\text{URPD})$
AF (camera-cluster)	35. $\beta_0 + \beta_1(\text{RDHA})$
AF (camera-cluster)	36. $\beta_0 + \beta_1(\text{STHA})$
AF (camera-cluster)	37. $\beta_0 + \beta_1(\text{URPL})$
LC[e] (camera-cluster)	38. $\beta_0 + \beta_1(\text{ED}) + \beta_2(\text{ARCV}) + \beta_3(\text{SID}) + \beta_4(\text{FORSI}) + \beta_5(\text{GRSI}) + \beta_6(\text{WASI}) + \beta_7(\text{WESI}) + \beta_8(\text{STRMHA})$
LC (camera-cluster)	39. $\beta_0 + \beta_1(\text{ARCV}) + \beta_2(\text{SID}) + \beta_3(\text{FORSI}) + \beta_4(\text{GRSI})$
LC (camera-cluster)	40. $\beta_0 + \beta_1(\text{ED}) + \beta_2(\text{GRSI}) + \beta_3(\text{FORSI}) + \beta_4(\text{ARCV})$
LC (camera-cluster)	41. $\beta_0 + \beta_1(\text{WASI}) + \beta_2(\text{WESI}) + \beta_3(\text{STRMHA})$
LC (camera-cluster)	42. $\beta_0 + \beta_1(\text{ED}) + \beta_2(\text{ARCV}) + \beta_3(\text{SID})$
LC (camera-cluster)	43. $\beta_0 + \beta_1(\text{GRSI}) + \beta_2(\text{FORSI})$
LC (camera-cluster)	44. $\beta_0 + \beta_1(\text{ED}) + \beta_2(\text{ARCV})$
LC (camera-cluster)	45. $\beta_0 + \beta_1(\text{ED}) + \beta_2(\text{SID})$
LC (camera-cluster)	46. $\beta_0 + \beta_1(\text{ED})$
LC (camera-cluster)	47. $\beta_0 + \beta_1(\text{STRMHA})$
VEG[f] (camera-cluster)	48. $\beta_0 + \beta_1(\text{AGCL}) + \beta_2(\text{FORPL}) + \beta_3(\text{FORPI}) + \beta_4(\text{GRPL}) + \beta_5(\text{GRPI})$
VEG (camera-cluster)	49. $\beta_0 + \beta_1(\text{FORPL}) + \beta_2(\text{FORPI}) + \beta_3(\text{GRPL}) + \beta_4(\text{GRPI})$
VEG (camera-cluster)	50. $\beta_0 + \beta_1(\text{FORPL}) + \beta_2(\text{FORPI}) + \beta_3(\text{GRPL})$
VEG (camera-cluster)	51. $\beta_0 + \beta_1(\text{FORPL}) + \beta_2(\text{GRPL})$
VEG (camera-cluster)	52. $\beta_0 + \beta_1(\text{FORPL}) + \beta_2(\text{FORPI})$
VEG (camera-cluster)	53. $\beta_0 + \beta_1(\text{GRPL}) + \beta_2(\text{GRPI})$

VEG (camera-cluster)	54. $\beta_0 + \beta_1$(AGPL)
VEG (camera-cluster)	55. $\beta_0 + \beta_1$(FORPL)
VEG (camera-cluster)	56. $\beta_0 + \beta_1$(GRPL)

---

[a] The structure of each model followed the logit function:

$\hat{\psi} = (\exp(\beta_0 + \beta_1 + ... + \beta_k))/(1 + \exp(\beta_0 + \beta_1 + ... + \beta_k))$, where $\hat{\psi}$ = estimated occupancy and k = number of model covariates.

[b] Anthropogenic features and larger predator avoidance.

[c] Prey availability.

[d] Anthropogenic features.

[e] Landscape complexity.

[f] Vegetative landcover.

Table 3. The total number of bobcat, coyote, gray fox, raccoon, red fox, and striped skunk photographs recorded within each month and diel time period during a remote camera survey in a 3-week period for carnivores in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. Also included are the number of photographs recorded per camera day and the species-specific total number of photographs used in analyses.

	Bobcat	Coyote	Gray fox	Raccoon	Red fox	Striped skunk
Month						
January	97	319	105	2740	44	188
February	80	324	89	2668	25	533
March	81	256	67	3581	19	77
April	73	211	31	3412	36	36
Diel period						
Crepuscular	170	425	83	4072	48	246
Diurnal	28	86	8	280	11	27
Nocturnal	133	599	201	8049	65	561
Total 1[a]	412	1397	546	40029	149	2467
Total 2[b]	331	1110	292	12401	124	834
Total photographs/ camera day	0.014	0.047	0.018	1.335	0.005	0.082

[a] Total number of photographs (detections) recorded of each species.

[b] Total number of photographs (detections) used in activity analysis for each species after removing photographs taken within 2 hours of another photo at the same camera-point.

Table 4. Non-target species detected during a remote camera survey for upland carnivores in the 16 southernmost counties of Illinois, USA, January–April 2008–2010.

Common name	Species name
American mink	*Neovison vison*
Barred owl	*Strix varia*
Beaver	*Castor canadensis*
Domestic cat	*Felis catus*
Domestic cattle	*Bos primigenius*
Domestic dog	*Canis lupus familiaris*
Eastern cottontail	*Sylvilagus floridanus*
Eastern gray squirrel	*Sciurus carolinensis*
Fox squirrel	*Sciurus niger*
Great blue heron	*Ardea herodias*
Great horned owl	*Bubo virginianus*
Human	*Homo sapiens*
Long-tailed weasel	*Mustela frenata*
Mouse	*Peromyscus spp*
Nine-banded armadillo	*Dasypus novemcinctus*
River otter	*Lontra canadensis*
Red-tailed hawk	*Buteo jamaicensis*
Southern flying squirrel	*Glaucomys volans*
Turkey vulture	*Cathartes aura*
Virginia opossum	*Didelphis virginiana*

White-tailed deer	*Odocoileus virginianus*
Wild turkey	*Meleagris gallopavo*
Woodchuck	*Marmota monax*

Table 5. Most supported (≤ 2 AIC of top model) models (plus the null model (.)) related to detection probabilities (*p*) for bobcats, coyotes, gray foxes, red foxes, and striped skunks in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. To estimate *p* for each species we held occupancy constant [ψ(.)] and fit encounter history data from 3 week surveys at 1188 remote camera-points (camera-point scale analyses) and 357 camera-clusters (camera-cluster scale analyses) in to the candidate model set. See Table 1 for measured parameter codes and descriptions and Appendix A for full model sets.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]
Bobcat (camera point)				
PPT + PREVDET	1947.52	0.00	0.258	4
PPT	1948.10	0.58	0.193	3
TMP*PPT	1948.42	0.90	0.165	3
(.)	1949.57	2.05	0.093	2
Bobcat (camera cluster)				
PPT	1239.47	0.00	0.281	3
TMP*PPT	1239.84	0.37	0.234	3
(.)	1240.30	0.83	0.186	2
TMP + PPT	1241.45	1.98	0.105	4
Coyote (camera point)				
TMP + MONTH	3922.97	0.00	0.281	6
TMP	3923.52	0.55	0.213	3
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	3923.73	0.76	0.192	11

(.)	3936.58	13.61	0.000	2
Coyote (camera cluster)				
TMP + PREVDET	1681.02	0.00	0.975	4
(.)	1706.51	25.49	0.000	2
Gray fox (camera point)				
TMP	1264.53	0.00	0.371	3
TMP + PREVDET	1265.58	1.05	0.219	4
TMP + PPT	1266.36	1.83	0.149	4
(.)	1276.03	11.50	0.001	2
Gray fox (camera cluster)				
TMP + PREVDET	738.07	0.00	0.931	4
(.)	751.70	13.63	0.001	2
Red fox (camera point)				
YEAR	809.34	0.00	0.984	4
(.)	821.53	12.19	0.002	2
Red fox (camera cluster)				
YEAR	553.22	0.00	0.952	4
(.)	561.87	8.65	0.013	2
Striped skunk (camera point)				
TMP + PPT + TMP*PPT + MONTH + YEAR	2539.61	0.00	0.784	10
(.)	2666.89	127.46	0.000	2
Striped skunk (camera cluster)				
TMP + PREVDET	1251.32	0.00	0.412	4

TMP + PPT + TMP*PPT + MONTH + YEAR	1251.60	0.28	0.358	10
(.)	1312.99	61.67	0.000	2

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[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

Table 6. Habitat occupancy results in the 90% confidence model set (cumulative *w* ≥ 0.90) for bobcats at three spatial scales in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. We fit encounter-history data from 3-week surveys at 1188 camera points (camera-point scale analyses) and 357 camera clusters (100% estimated home-range size and 20% of the estimated home-range size) to the candidate model set at each spatial scale. For all models, the probability of detection (*p*) was the most parsimonious scale-specific model from detectability modeling process for each species (Table 5). The null (.) model (occupancy held constant across all camera points) is included to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions and Appendix B for full model sets.

Model	Hypothesis	AIC[a]	ΔAIC	*w*[b]	K[c]
Camera point					
STEM + SLP	AF-PRED[d]	1946.88	0.00	0.119	6
STEM + SLP + DTRD	AF-PRED	1947.04	0.16	0.110	7
(.)	NULL	1947.52	0.64	0.086	4
DTRD	AF-PRED	1947.67	0.79	0.080	5
HW	PREY[e]	1947.92	1.04	0.071	5
BA + CWD	PREY	1948.11	1.23	0.064	6
BA + HW	PREY	1948.30	1.42	0.058	6
STEM	AF-PRED	1948.38	1.50	0.056	5
CWD	PREY	1948.70	1.82	0.048	5
DTST	AF-PRED	1948.73	1.85	0.047	5
HW + CWD	PREY	1949.08	2.20	0.040	6
DTRD + DTST	AF-PRED	1949.33	2.45	0.035	6

PVT	AF-PRED	1949.52	2.64	0.032	5
BA + HW + CWD	PREY	1949.65	2.77	0.030	7
STEM + DTRD + DTST	AF-PRED	1950.14	3.26	0.023	7
DTST + PVT	AF-PRED	1950.64	3.76	0.018	6
Camera cluster (20% of home range: 3.63-km^2 buffer)					
STHA + RDHA + DTST	AF[f]	1230.29	0.00	0.607	6
STHA + RDHA + DTMJRD + DTST + DTRD	AF	1232.66	2.37	0.186	8
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	AF	1235.04	4.75	0.056	10
(.)	NULL	1239.47	9.18	0.006	3
Camera cluster (100% home range: 18.15-km^2 buffer)					
STHA + RDHA + DTST	AF	1227.60	0.00	0.525	6
STHA + RDHA + DTST + DTRD + DTMJRD	AF	1228.70	1.10	0.303	8
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	AF	1230.83	3.23	0.105	10
(.)	NULL	1239.47	11.87	0.001	3

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[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

[d] Anthropogenic features and predator avoidance.

[e] Prey availability.

[f] Anthropogenic features.

Table 7. Habitat occupancy results in the 90% confidence model set (cumulative *w* ≥ 0.90) for coyotes at three spatial scales in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. We fit encounter-history data from 3-week surveys at 1188 camera points (camera-point scale analyses) and 357 camera clusters (100% estimated home-range size and 20% of the estimated home-range size) to the candidate model set at each spatial scale. For all models, the probability of detection (*p*) was the most parsimonious scale-specific model from detectability modeling process for each species (Table 5). The null (.) model (occupancy held constant across all camera-points) is included to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions and Appendix B for full model sets.

Model	Hypothesis	AIC[a]	ΔAIC	*w*[b]	K[c]
Camera point					
STEM + SLP	AF-PRED[d]	3921.42	0.00	0.127	8
HW	PREY[e]	3921.61	0.19	0.116	7
STEM	AF-PRED	3921.66	0.24	0.113	7
STEM + SLP + DTRD	AF-PRED	3922.02	0.60	0.094	9
HW + CWD	PREY	3922.46	1.04	0.076	8
(.)	NULL	3922.97	1.55	0.059	6
DTRD	AF-PRED	3923.32	1.90	0.049	7
BA + HW	PREY	3923.47	2.05	0.046	8
CWD	PREY	3923.68	2.26	0.041	7
PVT	AF-PRED	3923.96	2.54	0.036	7
STEM + DTRD + DTST	AF-PRED	3924.22	2.80	0.031	9
HW + CWD + DTSTRM	PREY	3924.23	2.81	0.031	9

BA + HW + CWD	PREY	3924.38	2.96	0.029	9
STEM + DTST + PVT	AF-PRED	3924.78	3.36	0.024	9
DTST	AF-PRED	3924.88	3.46	0.023	7
DTRD + DTST	AF-PRED	3925.32	3.90	0.018	8
Camera cluster (20% of home range: 4.38-km^2 buffer)					
ARCV + SID + FORSI + GRSI	LC[f]	1673.64	0.00	0.303	8
FORSI + GRSI	LC	1675.12	1.48	0.145	6
ED + FORSI + GRSI + ARCV	LC	1675.83	2.19	0.102	8
WASI + WESI + STRMHA	LC	1677.11	3.47	0.054	7
URPL + URPD + DTMU	AF[g]	1677.40	3.76	0.046	7
FORPL + FORPI	VEG[h]	1677.46	3.82	0.045	6
RDHA + DTRD	AF	1677.89	4.25	0.036	6
FORPL	VEG	1678.05	4.41	0.033	5
RDHA	AF	1678.55	4.91	0.026	5
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	AF	1678.61	4.97	0.025	12
FORPL + FORPI + GRPL	VEG	1678.85	5.21	0.022	7
ED + ARCV + SID	LC	1679.12	5.48	0.020	7
RDHA + DTRD + DTMJRD	AF	1679.79	6.15	0.014	7
FORPL + GRPL	VEG	1680.00	6.36	0.013	6
STHA + RDHA	AF	1680.07	6.43	0.012	6
STHA + RDHA + URPL + URPD + DTMJRD DTST + DTRD + DTMU +	AF	1680.34	6.70	0.011	13

PVT					
FORPL + FORPI + GRPL + GRPI	VEG	1680.62	6.98	0.009	8
(.)	NULL	1681.02	7.38	0.008	4
Camera cluster (100% home range: 21.90-km^2 buffer)					
URPL + URPD + DTMU	AF	1674.57	0.00	0.515	7
AGCL + FORPL + FORPI + GRPL + GRPI	VEG	1677.14	2.57	0.142	9
ED	LC	1680.12	5.55	0.032	5
ED + ARCV	LC	1680.49	5.92	0.027	6
RDHA	AF	1680.59	6.02	0.025	5
STHA + RDHA	AF	1680.80	6.23	0.023	6
ED + SID	LC	1680.87	6.3	0.022	6
FORPL + FORPI	VEG	1680.97	6.4	0.021	6
(.)	NULL	1681.02	6.45	0.021	4
ARCV + SID + FORSI + GRSI	LC	1681.77	7.2	0.014	8
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	AF	1681.83	7.26	0.014	12
STRMHA	LC	1681.85	7.28	0.014	5
WASI + WESI + STRMHA	LC	1682.18	7.61	0.012	7
ED + ARCV + SID	LC	1682.37	7.8	0.010	7
STHA	AF	1682.40	7.83	0.010	5
RDHA + DTRD	AF	1682.54	7.97	0.010	6

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[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

[d] Anthropogenic features and predator avoidance.

[e] Prey availability.

[f] Landscape complexity.

[g] Anthropogenic features.

[h] Vegetative landcover.

Table 8. Habitat occupancy results in the 90% confidence model set (cumulative $w \geq 0.90$) for gray foxes at three spatial scales in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. We fit encounter-history data from 3-week surveys at 1188 camera points (camera-point scale analyses) and 357 camera clusters (100% estimated home-range size and 20% of the estimated home-range size) to the candidate model set at each spatial scale. For all models, the probability of detection (p) was the most parsimonious scale-specific model from detectability modeling process for each species (Table 5). The null (.) model (occupancy held constant across all camera points) is included to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions and Appendix B for full model sets.

Model	Hypothesis	AIC[a]	ΔAIC	*w*[b]	K[c]
Camera point					
HW + CWD + DTSTRM	PREY[d]	1261.23	0.00	0.145	6
HW + CWD	PREY	1261.28	0.05	0.142	5
HW	PREY	1261.69	0.46	0.115	4
DTST + PVT	AF-PRED[e]	1262.55	1.32	0.075	5
BA + HW + CWD	PREY	1262.59	1.36	0.074	6
BA + HW + CWD + DTSTRM	PREY	1262.67	1.44	0.071	7
BA + HW	PREY	1262.71	1.48	0.069	5
CWD + DTSTRM	PREY	1263.61	2.38	0.044	5
DTST	AF-PRED	1263.98	2.75	0.037	4
CWD	PREY	1264.08	2.85	0.035	4
DTRD + DTST + PVT	AF-PRED	1264.30	3.07	0.031	6
STEM + DTST + PVT	AF-PRED	1264.33	3.10	0.031	6

(.)	NULL	1264.53	3.30	0.028	3
PVT	AF-PRED	1264.81	3.58	0.024	4
Camera cluster (20% of home range: 0.55-km^2 buffer)					
ED + SID	LC[f]	731.06	0.00	0.343	6
ED + ARCV + SID	LC	733.05	1.99	0.127	7
FORPL + FORPI	VEG[g]	733.53	2.47	0.100	6
AGPL	VEG	733.67	2.61	0.093	5
FORPL	VEG	733.70	2.64	0.092	5
FORPL + FORPI + GRPL	VEG	735.48	4.42	0.038	7
ED	LC	735.55	4.49	0.036	5
FORPL + GRPL	VEG	735.69	4.63	0.034	6
FORPL + FORPI + GRPL + GRPI	VEG	736.43	5.37	0.023	8
GRPL	VEG	737.41	6.35	0.014	5
AGCL + FORPL + FORPI + GRPL + GRPI	VEG	737.49	6.43	0.014	9
(.)	NULL	738.07	7.01	0.010	4
Camera cluster (100% home range: 2.75-km^2 buffer)					
RDHA + DTRD + DTMJRD	AF[h]	728.61	0.00	0.252	7
STRMHA	LC	730.07	1.46	0.121	5
AGPL	VEG	730.16	1.55	0.116	5
RDHA + DTRD + DTMJRD + MJRDHA	AF	730.52	1.91	0.097	8
RDHA	AF	731.04	2.43	0.075	5

RDHA + DTRD	AF	731.25	2.64	0.067	6
STHA + RDHA + DTMJRD + DTST + DTRD	AF	732.10	3.49	0.044	9
ED + SID	LC	732.41	3.80	0.038	6
STHA + RDHA	AF	732.93	4.32	0.029	6
WASI + WESI + STRMHA	LC	733.22	4.61	0.025	7
STHA + RDHA + DTST	AF	733.48	4.87	0.022	7
FORPL	VEG	733.53	4.92	0.022	5
(.)	NULL	738.07	9.46	0.002	4

[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

[d] Prey availability.

[e] Anthropogenic features and predator avoidance.

[f] Landscape complexity.

[g] Vegetative landcover.

[h] Anthropogenic features.

Table 9. Habitat occupancy results in the 90% confidence model set (cumulative $w \geq 0.90$) for red foxes at three spatial scales in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. We fit encounter-history data from 3-week surveys at 1188 camera points (camera-point scale analyses) and 357 camera clusters (100% estimated home-range size and 20% of the estimated home-range size) to the candidate model set at each spatial scale. For all models, the probability of detection (p) was the most parsimonious scale-specific model from detectability modeling process for each species (Table 5). The null (.) model (occupancy held constant across all camera points) is included to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions and Appendix B for full model sets.

Model	Hypothesis	AIC[a]	ΔAIC	w[b]	K[c]
Camera point					
DTST	AF-PRED[d]	793.67	0.00	0.382	5
DTST + PVT	AF-PRED	794.91	1.24	0.206	6
DTRD + DTST	AF-PRED	795.48	1.81	0.155	6
STEM + DTST + PVT	AF-PRED	796.70	3.03	0.084	7
DTRD + DTST + PVT	AF-PRED	796.86	3.19	0.078	7
(.)	NULL	809.34	15.67	0.000	4
Camera cluster (20% of home range: 1.42-km^2 buffer)					
STHA + RDHA + DTMJRD + DTST + DTRD	AF[e]	536.59	0.00	0.231	9
STHA + RDHA + DTST	AF	536.73	0.14	0.216	7
RDHA + DTRD + DTMJRD	AF	536.95	0.36	0.193	7
RDHA + DTRD + DTMJRD +	AF	538.29	1.70	0.099	8

MJRDHA					
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	AF	538.59	2.00	0.085	11
STHA + RDHA	AF	540.28	3.69	0.037	6
RDHA + DTRD	AF	540.30	3.71	0.036	6
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	AF	540.32	3.73	0.036	12
(.)	NULL	553.22	16.63	0.000	4
Camera cluster (100% home range: 7.09-km^2 buffer)					
STHA + RDHA + DTST	AF	527.14	0.00	0.462	7
RDHA	AF	529.00	1.86	0.182	5
STHA + RDHA + DTMJRD + DTST + DTRD	AF	529.47	2.33	0.144	9
RDHA + DTRD	AF	530.01	2.87	0.110	6
RDHA + DTRD + DTMJRD	AF	531.93	4.79	0.042	7
(.)	NULL	553.22	26.08	0.000	4

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[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

[d] Anthropogenic features and predator avoidance.

[e] Anthropogenic features.

Table 10. Habitat occupancy results in the 90% confidence model set (cumulative $w \geq 0.90$) for striped skunks at three spatial scales in the 16 southernmost counties of Illinois, USA, January–April 2008–2010. We fit encounter-history data from 3-week surveys at 1188 camera points (camera-point scale analyses) and 357 camera clusters (100% estimated home-range size and 20% of the estimated home-range size) to the candidate model set at each spatial scale. For all models, the probability of detection (*p*) was the most parsimonious scale-specific model from detectability modeling process for each species (Table 5). The null (.) model (occupancy held constant across all camera points) is included to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions and Appendix B for full model sets.

Model	Hypothesis	AIC[a]	ΔAIC	*w*[b]	K[c]
Camera point					
PVT	AF-PRED[d]	2524.80	0.00	0.382	11
DTRD + DTST + PVT	AF-PRED	2525.11	0.31	0.327	13
DTST + PVT	AF-PRED	2526.76	1.96	0.143	12
STEM + SLP + DTRD + DTST + PVT	AF-PRED	2528.42	3.62	0.063	15
(.)	NULL	2539.61	14.81	0.000	10
Camera cluster (20% of home range: 0.55-km^2 buffer)					
STHA + PVT	AF[e]	1243.41	0.00	0.266	9
AGPL	VEG[f]	1243.93	0.52	0.205	8
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	AF	1245.57	2.16	0.090	17
RDHA + DTRD + DTMJRD	AF	1246.20	2.79	0.066	10

STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	AF	1246.51	3.10	0.057	15
STHA + RDHA + DTMJRD + DTST + DTRD	AF	1246.58	3.17	0.055	12
FORPL	VEG	1247.25	3.74	0.041	8
RDHA + DTRD	AF	1247.25	3.84	0.039	9
RDHA + DTRD + DTMJRD + MJRDHA	AF	1247.75	4.34	0.030	11
FORPL + FORPI	VEG	1248.68	5.27	0.019	9
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	AF	1248.72	5.31	0.019	14
FORPL + GRPL	VEG	1249.15	5.74	0.015	9
(.)	NULL	1249.28	5.87	0.014	7
Camera cluster (100% home range: 2.75-km^2 buffer)					
STHA + RDHA + DTMJRD + DTST + DTRD	AF	1241.79	0.00	0.211	12
AGPL	VEG	1241.98	0.19	0.192	8
STHA + PVT	AF	1242.89	1.10	0.122	9
RDHA + DTRD + DTMJRD	AF	1243.13	1.34	0.108	10
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	AF	1243.29	1.50	0.100	17
STHA + RDHA + URPL + DTMJRD +	AF	1243.57	1.78	0.090	14

DTST + DTRD + DTMU					
RDHA + DTRD + DTMJRD + MJRDHA	AF	1244.84	3.05	0.046	11
RDHA + DTRD	AF	1245.46	3.67	0.034	9
(.)	NULL	1249.28	7.49	0.005	7

[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

[d] Anthropogenic features and predator avoidance.

[e] Anthropogenic features.

[f] Vegetative landcover.

Table 11. Results from multi-year model selection at the camera-cluster scale in the 90% confidence set for bobcat, gray fox, and red fox. We modeled habitat factors potentially influencing bobcat colonization (γ); and effects of habitat and presence of other carnivores on gray fox and red fox extinction (ε). We fit encounter-history data from surveys at 357 camera-clusters over a 3-week period in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. All models were fit using the most supported detection model (Table 5) for each species. The null (.) model is included for each species to assess relative support for habitat and species interaction covariates. See Table 1 for habitat variable codes and descriptions and Appendix E for full model sets.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]
a) Bobcat (γ)				
AGPL	1217.58	0.00	0.495	8
(.)	1220.37	2.79	0.123	7
STHA	1220.95	3.37	0.092	8
GRPL	1221.70	4.12	0.063	8
RDHA	1221.98	4.40	0.055	8
FORPL	1222.35	4.77	0.046	8
STHA + DTST	1222.67	5.09	0.039	9
b) Gray fox (ε)				
STHA	724.85	0.00	0.116	10
STHA + DTST	725.15	0.30	0.100	11
(.)	725.24	0.39	0.095	9
STHA + RDHA	725.48	0.63	0.085	11

STHA + BOBCAT	725.61	0.76	0.079	11
STHA + REDFOX	725.73	0.88	0.075	11
AGPL + BOBCAT	726.25	1.40	0.058	11
BOBCAT	726.26	1.41	0.057	10
FORPL	726.77	1.92	0.044	10
STHA + DTST + BOBCAT	726.96	2.11	0.040	12
AGPL	727.07	2.22	0.038	10
REDFOX	727.13	2.28	0.037	10
RDHA	727.14	2.29	0.037	10
GRPL	727.20	2.35	0.036	10
STHA + RDHA + BOBCAT	727.41	2.56	0.032	12
c) Red fox (ε)				
AGPL	522.65	0.00	0.252	9
AGPL + GRAYFOX	523.33	0.68	0.180	10
RDHA + DTRD	523.66	1.01	0.152	10
AGPL + BOBCAT	524.70	2.05	0.091	10
FORPL + GRAYFOX	526.26	3.61	0.042	10
BOBCAT	526.72	4.07	0.033	9
RDHA + BOBCAT	526.79	4.14	0.032	10
GRAYFOX + BOBCAT	526.83	4.18	0.031	10
FORPL + GRPL + GRAYFOX	527.10	4.45	0.027	11
RDHA	527.43	4.78	0.023	9
STHA + DTST + GRAYFOX	527.56	4.91	0.022	11

(.)	527.64	4.99	0.021	8

[a] Akaike Information Criterion.

[b] Model weight; the probability of that model being the best approximating model among those evaluated.

[c] Number of model parameters.

Table 12. Poisson regression results for diel time period of activity comparisons for bobcat, coyote, gray fox, red fox, and striped skunk. We fitted models to data from remote camera surveys at 357 camera clusters over a 3-week period in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. We used the Tukey-Kramer multiple comparison procedure to adjust *P*-values.

	Crepuscular[a] – Diurnal[b]		Crepuscular – Nocturnal[c]		Diurnal - Nocturnal	
Species	*t*	*P*	*t*	*P*	*t*	*P*
Bobcat	5.57	<0.01	2.02	0.11	-4.10	<0.01
Coyote	9.01	<0.01	-2.30	0.06	-10.32	<0.01
Gray fox	3.68	<0.01	-2.44	0.04	-4.71	<0.01
Raccoon	12.98	<0.01	-10.23	<0.01	-16.40	<0.01
Red fox	3.05	0.01	-0.61	0.81	-3.41	<0.01
Skunk	3.83	<0.01	-1.81	0.07	-4.69	<0.01

[a] The diel time period 2 hours before and after sunrise and sunset. Adjusted during study to account for changing times of sunrise and sunset.

[b] Diel time period between 2 hours after sunrise and 2 hours before sunset.

[c] Diel time period between 2 hours after sunset and 2 hours before sunrise.

Table 13. Poisson regression results for the total number of gray fox, raccoon, red fox, and striped skunk photographs recorded (level of activity) in a camera cluster based on spatial and temporal activity of bobcats and coyotes. Coefficient estimates (β) with 95% confidence interval (LCI: lower confidence interval limit; UCI: upper confidence interval limit) not overlapping 0 were considered significant (*). We fitted models to data from remote camera surveys at 1188 camera points in 357 camera clusters over a 3-week period in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. We used the Tukey-Kramer least squares means adjustment procedure for multiple comparisons to adjust estimates.

Model	Gray fox			Red fox			Raccoon			Striped skunk		
	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI
Bobcat												
Detection[a]	-0.21	-0.58	0.16	-0.23	-0.64	0.18	*0.36	0.25	0.45	*0.46	0.12	0.79
ψ[b]	-0.36	-0.84	0.26	*-1.12	-1.98	-0.26	*0.29	0.06	0.52	*1.82	0.99	2.64
Photographs[c]	-0.11	-0.26	0.04	*-0.14	-0.11	-0.16	*0.05	0.03	0.07	0.05	-0.01	0.11
Coyote												
Detection[d]	0.24	-0.26	0.74	0.30	-0.25	0.85	*0.29	0.15	0.42	*0.49	0.01	0.98
Photographs[e]	*-0.09	-0.17	-0.02	*-0.06	-0.02	-0.10	*0.05	0.04	0.06	*0.08	0.06	0.11

[a] Binary covariate based on the detection or non-detection of bobcats in a camera-cluster.

[b] Model-averaged estimated probability of camera-cluster occupancy of bobcats.

[c] Total number of photographs of bobcats recorded in a camera-cluster after removing photographs taken of the species within 2 hours of another bobcat photo at the same camera-point.

[d] Binary covariate based on the detection or non-detection of coyotes in a camera-cluster.

[e] Total number of photographs of coyotes recorded in a camera-cluster after removing photographs taken of the species within 2 hours of another coyote photo at the same camera-point.

Table 14. Mixed-model logistic regression results for the variation in diel period activity (crepuscular, diurnal, nocturnal) of bobcats, gray foxes, raccoons, red foxes, and striped skunks based on the number of bobcat and coyote photographs recorded during the nocturnal period at a camera cluster. Coefficient estimates (β) with 95% confidence interval (LCI: lower confidence interval limit; UCI: upper confidence interval limit) not overlapping 0 were considered significant (*). Red fox-bobcat models did not converge. We fitted models to data from remote camera surveys at 1188 camera points in 357 camera clusters in the 16 southernmost counties of Illinois, USA, during January–April 2008–2010.

Species	Diel period[a]	Bobcat[b]			Coyote[b]		
		β	LCI	UCI	β	LCI	UCI
Bobcat	Nocturnal				*0.18	0.10	0.26
Bobcat	Crepuscular				-0.03	-0.13	0.08
Bobcat	Diurnal				0.24	-0.16	0.65
Gray fox	Nocturnal	-0.26	-0.68	0.15	*-0.27	-0.44	-0.10
Gray fox	Crepuscular	0.29	-0.16	0.73	*0.30	0.06	0.52
Gray fox	Diurnal	0.85	-0.54	2.24	-0.10	-2.12	1.92
Raccoon	Nocturnal	0.02	-0.18	0.21	*0.18	0.04	0.33
Raccoon	Crepuscular	0.04	-0.25	0.33	0.03	-0.15	0.20
Raccoon	Diurnal	0.70	-0.02	1.42	*0.53	0.10	0.95
Red fox	Nocturnal				*0.22	0.10	0.34
Red fox	Crepuscular				-0.12	-0.29	0.06
Red fox	Diurnal				-0.07	-1.34	1.19
Striped skunk	Nocturnal	0.11	-0.02	0.25	0.11	0.01	0.21

Striped skunk	Crepuscular	-0.03	-0.25	0.20	0.01	-0.13	0.15
Striped skunk	Diurnal	-1.24	-3.17	0.69	*0.82	0.10	1.54

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[a] Ratio of the maximum possible photographs during a diel time period and the number of photographs of the species during the period.

[b] Predictor variables; the number of bobcat or coyote photographs recorded during the nocturnal time period at a camera-cluster.

APPENDIX A. DETECTION MODELS

Evaluation of survey covariates related to detection probabilities (*p*) for bobcats, coyotes, gray foxes, and red foxes in the 16 southernmost counties of Illinois, USA. To estimate *p* for each species we held occupancy constant [ψ(.)] and fit encounter history data from surveys at 1188 remote camera sites in 357 camera-clusters during January–April 2008–2010 to the candidate model set. The null (.) model (*p* held constant across all surveys) was included for each species for assessment of relative strength of survey covariates to explain heterogeneity in detection probabilities. See Table 1 for measured parameter codes and descriptions.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]	Deviance[d]
Bobcat (camera point)					
PPT + PREVDET	1947.52	0.00	0.257	4	1939.52
PPT	1948.10	0.58	0.192	3	1942.10
TMP*PPT	1948.42	0.90	0.164	3	1942.42
(.)	1949.57	2.05	0.092	2	1945.57
PREVDET	1949.67	2.15	0.088	3	1943.67
TMP + PPT	1950.10	2.58	0.071	4	1942.10
TMP	1951.47	3.95	0.036	3	1945.47
TMP + PREVDET	1951.64	4.12	0.033	4	1943.64
INT	1952.19	4.67	0.025	4	1944.19
YEAR	1952.88	5.36	0.018	4	1944.88
PPT + MONTH	1953.81	6.29	0.011	6	1941.81
MONTH	1954.96	7.44	0.006	5	1944.96
TMP + MONTH	1956.73	9.21	0.003	6	1944.73

TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	1958.97	11.45	0.001	11	1936.97
Bobcat (camera cluster)					
PPT	1239.47	0.00	0.278	3	1233.47
TMP*PPT	1239.84	0.37	0.231	3	1233.84
(.)	1240.30	0.83	0.184	2	1236.30
TMP + PPT	1241.45	1.98	0.103	4	1233.45
TMP	1242.26	2.79	0.069	3	1236.26
INT	1243.26	3.79	0.042	4	1235.26
YEAR	1243.59	4.12	0.035	4	1235.59
PPT + MONTH	1244.87	5.40	0.019	6	1232.87
MONTH	1245.08	5.61	0.017	5	1235.08
TMP + PPT + MONTH	1245.90	6.43	0.011	7	1231.90
TMP + MONTH	1246.27	6.80	0.009	6	1234.27
TMP + PPT + TMP*PPT + MONTH + YEAR	1249.56	10.09	0.002	10	1229.56
Coyote (camera point)					
TMP + MONTH	3922.97	0.00	0.254	6	3910.97
TMP	3923.52	0.55	0.193	3	3917.52
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	3923.73	0.76	0.174	11	3901.73
TMP + PREVDET	3925.08	2.11	0.088	4	3917.08
MONTH	3925.10	2.13	0.088	5	3915.10
TMP + PPT	3925.50	2.53	0.072	4	3917.50

PPT + MONTH	3926.93	3.96	0.035	6	3914.93
TMP*PPT	3936.26	13.29	0.000	3	3930.26
(.)	3936.58	13.61	0.000	2	3932.58
YEAR	3937.53	14.56	0.000	4	3929.53
PPT	3937.81	14.84	0.000	3	3931.81
PREVDET	3938.51	15.54	0.000	3	3932.51
PPT + PREVDET	3939.73	16.76	0.000	4	3931.73
INT	3939.88	16.91	0.000	4	3931.88
Coyote (camera cluster)					
TMP + PREVDET	1681.02	0.00	0.929	4	1673.02
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	1686.29	5.27	0.067	11	1664.29
TMP	1693.47	12.45	0.002	3	1687.47
PREVDET	1695.15	14.13	0.001	3	1689.15
TMP + PPT	1695.35	14.33	0.001	4	1687.35
TMP + MONTH	1696.92	15.90	0.000	6	1684.92
PPT + PREVDET	1697.11	16.09	0.000	4	1689.11
TMP + PPT + MONTH	1698.83	17.81	0.000	7	1684.83
MONTH	1700.38	19.36	0.000	5	1690.38
PPT + MONTH	1702.35	21.33	0.000	6	1690.35
(.)	1706.51	25.49	0.000	2	1702.51
TMP*PPT	1707.73	26.71	0.000	3	1701.73
YEAR	1708.23	27.21	0.000	4	1700.23

PPT	1708.38	27.36	0.000	3	1702.38
INT	1708.81	27.79	0.000	4	1700.81
Gray fox (camera point)					
TMP	1264.53	0.00	0.355	3	1258.53
TMP + PREVDET	1265.58	1.05	0.210	4	1257.58
TMP + PPT	1266.36	1.83	0.142	4	1258.36
TMP + MONTH	1266.87	2.34	0.110	6	1254.87
MONTH	1267.11	2.58	0.098	5	1257.11
TMP + PPT + MONTH	1268.76	4.23	0.043	7	1254.76
PPT + MONTH	1269.10	4.57	0.036	6	1257.10
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	1274.92	10.39	0.002	11	1252.92
(.)	1276.03	11.50	0.001	2	1272.03
INT	1276.38	11.85	0.001	4	1268.38
TMP*PPT	1277.43	12.90	0.001	3	1271.43
PREVDET	1277.48	12.95	0.001	3	1271.48
PPT	1277.68	13.15	0.001	3	1271.68
YEAR	1278.51	13.98	0.000	4	1270.51
PPT + PREVDET	1279.31	14.78	0.000	4	1271.31
Gray fox (camera cluster)					
TMP + PREVDET	738.07	0.00	0.909	4	730.07
PREVDET	743.74	5.67	0.053	3	737.74
PPT + PREVDET	745.52	7.45	0.022	4	737.52

TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	748.43	10.36	0.005	11	726.43
TMP	749.20	11.13	0.004	3	743.20
TMP + PPT	750.52	12.45	0.002	4	742.52
(.)	751.70	13.63	0.001	2	747.70
MONTH	752.17	14.10	0.001	5	742.17
TMP + MONTH	752.41	14.34	0.001	6	740.41
YEAR	752.92	14.85	0.001	4	744.92
INT	753.23	15.16	0.001	4	745.23
PPT	753.64	15.57	0.000	3	747.64
TMP*PPT	753.67	15.60	0.000	3	747.67
PPT + MONTH	753.90	15.83	0.000	6	741.90
TMP + PPT + MONTH	753.92	15.85	0.000	7	739.92
Red fox (camera point)					
YEAR	809.34	0.00	0.983	4	801.34
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	819.34	10.00	0.007	11	797.34
(.)	821.53	12.19	0.002	2	817.53
PREVDET	821.90	12.56	0.002	3	815.90
INT	823.34	14.00	0.001	4	815.34
PPT	823.42	14.08	0.001	3	817.42
TMP	823.42	14.08	0.001	3	817.42
TMP*PPT	823.46	14.12	0.001	3	817.46

PPT + PREVDET	823.77	14.43	0.001	4	815.77
TMP + PREVDET	823.89	14.55	0.001	4	815.89
TMP + PPT	825.25	15.91	0.000	4	817.25
MONTH	825.30	15.96	0.000	5	815.30
TMP + MONTH	826.62	17.28	0.000	6	814.62
PPT + MONTH	827.28	17.94	0.000	6	815.28
TMP + PPT + MONTH	828.59	19.25	0.000	7	814.59
Red fox (camera cluster)					
YEAR	553.22	0.00	0.950	4	545.22
(.)	561.87	8.65	0.013	2	557.87
PREVDET	563.30	10.08	0.006	3	557.30
TMP*PPT	563.80	10.58	0.005	3	557.80
PPT	563.80	10.58	0.005	3	557.80
TMP + PPT + TMP*PPT + PREVDET + MONTH + YEAR	563.84	10.62	0.005	11	541.84
TMP	563.86	10.64	0.005	3	557.86
INT	565.16	11.94	0.003	4	557.16
PPT + PREVDET	565.20	11.98	0.002	4	557.20
TMP + PREVDET	565.29	12.07	0.002	4	557.29
TMP + PPT	565.79	12.57	0.002	4	557.79
MONTH	566.07	12.85	0.002	5	556.07
TMP + MONTH	567.27	14.05	0.001	6	555.27
PPT + MONTH	567.77	14.55	0.001	6	555.77

TMP + PPT + MONTH	569.02	15.80	0.000	7	555.02
Striped skunk (camera point)					
TMP + PPT + TMP*PPT + MONTH + YEAR	2539.61	0.00	0.577	10	2519.61
TMP + PPT + MONTH	2541.17	1.56	0.264	7	2527.17
PPT + MONTH	2542.27	2.66	0.153	6	2530.27
MONTH	2549.79	10.18	0.004	5	2539.79
TMP + MONTH	2550.00	10.39	0.003	6	2538.00
TMP + PREVDET	2585.59	45.98	0.000	4	2577.59
INT	2605.96	66.35	0.000	4	2597.96
PPT + PREVDET	2616.56	76.95	0.000	4	2608.56
TMP + PPT	2629.25	89.64	0.000	4	2621.25
PREVDET	2630.04	90.43	0.000	3	2624.04
TMP	2633.98	94.37	0.000	3	2627.98
TMP*PPT	2649.53	109.92	0.000	3	2643.53
PPT	2657.45	117.84	0.000	3	2651.45
YEAR	2665.42	125.81	0.000	4	2657.42
(.)	2666.89	127.28	0.000	2	2662.89
Striped skunk (camera cluster)					
TMP + PPT + MONTH	1249.28	0.00	0.533	7	1235.28
TMP + PREVDET	1251.32	2.04	0.192	4	1243.32
TMP + PPT + TMP*PPT + MONTH + YEAR	1251.60	2.32	0.167	10	1231.60
TMP + MONTH	1253.73	4.45	0.058	6	1241.73
PPT + MONTH	1254.40	5.12	0.041	6	1242.40

MONTH	1257.62	8.34	0.008	5	1247.62
PPT + PREVDET	1267.91	18.63	0.000	4	1259.91
PREVDET	1273.47	24.19	0.000	3	1267.47
INT	1278.37	29.09	0.000	4	1270.37
TMP + PPT	1303.56	54.28	0.000	4	1295.56
TMP	1306.06	56.78	0.000	3	1300.06
TMP*PPT	1306.82	57.54	0.000	3	1300.82
PPT	1308.74	59.46	0.000	3	1302.74
(.)	1312.99	63.71	0.000	2	1308.99
YEAR	1314.87	65.59	0.000	4	1306.87

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[a] Akaike Information Criterion.

[b] Model probability.

[c] Number of model parameters.

[d] Difference in -2Log(Likelihood) of the current model and -2log(Likelihood) of the saturated model as a measure of model fit.

APPENDIX B. SINGLE-SPECIES OCCUPANCY MODELS

Habitat occupancy results for bobcats, coyotes, gray foxes, and red foxes at three spatial scales (100% home range size, 20% of estimated home range size derived from literature, and camera-point level) in the 16 southernmost counties of Illinois, USA. We fit encounter history data from 3-week surveys at 1188 remote camera points in 357 camera clusters during January–April 2008–2010 to the candidate model set at each spatial scale for each species. For all models, the probability of detection (*p*) was the most supported model from scale-specific detectability modeling process for each species (Appendix A). The null (.) model (occupancy held constant across all sites) is included for each species at each scale to assess relative support for habitat covariates. See Table 1 for measured parameter codes and descriptions.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]	Deviance[d]
Bobcat (camera point)					
STEM + SLP	1946.88	0.00	0.119	6	1934.88
STEM + SLP + DTRD	1947.04	0.16	0.110	7	1933.04
(.)	1947.52	0.64	0.086	4	1939.52
DTRD	1947.67	0.79	0.080	5	1937.67
HW	1947.92	1.04	0.071	5	1937.92
BA + CWD	1948.11	1.23	0.064	6	1936.11
BA + HW	1948.30	1.42	0.058	6	1936.30
STEM	1948.38	1.50	0.056	5	1938.38
CWD	1948.70	1.82	0.048	5	1938.70
DTST	1948.73	1.85	0.047	5	1938.73
HW + CWD	1949.08	2.20	0.040	6	1937.08

DTRD + DTST	1949.33	2.45	0.035	6	1937.33
PVT	1949.52	2.64	0.032	5	1939.52
BA + HW + CWD	1949.65	2.77	0.030	7	1935.65
STEM + DTRD + DTST	1950.14	3.26	0.023	7	1936.14
DTST + PVT	1950.64	3.76	0.018	6	1938.64
CWD + DTSTRM	1950.69	3.81	0.018	6	1938.69
STEM + SLP + DTRD + DTST + PVT	1950.81	3.93	0.017	9	1932.81
HW + CWD + DTSTRM	1951.08	4.20	0.015	7	1937.08
DTRD + DTST + PVT	1951.33	4.45	0.013	7	1937.33
STEM + DTST + PVT	1951.51	4.63	0.012	7	1937.51
BA + HW + CWD + DTSTRM	1951.64	4.76	0.011	8	1935.64
STHA + RDHA + DTST	1227.60	0.00	0.525	6	1215.60
Bobcat (camera cluster: 20% of home range: 3.63-km^2 buffer)					
STHA + RDHA + DTST	1230.29	0.00	0.607	6	1218.29
STHA + RDHA + DTMJRD + DTST + DTRD	1232.66	2.37	0.186	8	1216.66
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	1235.04	4.75	0.056	10	1215.04
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1236.88	6.59	0.023	11	1214.88
STHA + DTST	1237.90	7.61	0.014	5	1227.90
AGPL	1238.16	7.87	0.012	4	1230.16
RDHA	1238.53	8.24	0.010	4	1230.53
DTST	1238.64	8.35	0.009	4	1230.64

STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	1238.65	8.36	0.009	13	1212.65
STRMHA	1239.20	8.91	0.007	4	1231.20
STHA + RDHA	1239.22	8.93	0.007	5	1229.22
(.)	1239.47	9.18	0.006	3	1233.47
ED + ARCV	1239.51	9.22	0.006	5	1229.51
FORPL	1240.18	9.89	0.004	4	1232.18
RDHA + DTRD	1240.24	9.95	0.004	5	1230.24
DTMJRD	1241.03	10.74	0.003	4	1233.03
ED	1241.06	10.77	0.003	4	1233.06
URPL	1241.12	10.83	0.003	4	1233.12
STHA	1241.41	11.12	0.002	4	1233.41
URPL + URPD + DTMU	1241.45	11.16	0.002	6	1229.45
GRPL	1241.46	11.17	0.002	4	1233.46
ED + ARCV + SID	1241.49	11.20	0.002	6	1229.49
RDHA + DTRD + DTMJRD	1241.78	11.49	0.002	6	1229.78
FORPL + GRPL	1241.83	11.54	0.002	5	1231.83
ED + SID	1242.16	11.87	0.002	5	1232.16
FORPL + FORPI	1242.18	11.89	0.002	5	1232.18
GRPL + GRPI	1242.29	12.00	0.002	5	1232.29
STHA + PVT	1242.32	12.03	0.002	5	1232.32
URPL + URPD	1242.55	12.26	0.001	5	1232.55
ED + GRSI + FORSI + ARCV	1242.56	12.27	0.001	7	1228.56

WASI + WESI + STRMHA	1242.61	12.32	0.001	6	1230.61
GRSI + FORSI	1243.24	12.95	0.001	5	1233.24
RDHA + DTRD + DTMJRD + MJRDHA	1243.29	13.00	0.001	7	1229.29
FORPL + FORPI + GRPL	1243.83	13.54	0.001	6	1231.83
AGCL + FORPL + FORPI + GRPL + GRPI	1243.96	13.67	0.001	8	1227.96
ARCV + SID + FORSI + GRSI	1244.08	13.79	0.001	7	1230.08
FORPL + FORPI + GRPL + GRPI	1244.09	13.80	0.001	7	1230.09
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	1246.75	16.46	0.000	11	1224.75
Bobcat (camera cluster:100% home range: 18.15-km^2 buffer)					
STHA + RDHA + DTST + DTRD + DTMJRD	1228.70	1.10	0.303	8	1212.70
STHA + RDHA + URPL + DTST + DTRD + DTMU + DTMJRD	1230.83	3.23	0.105	10	1210.83
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1233.86	6.26	0.023	11	1211.86
STHA + DTST	1235.22	7.62	0.012	5	1225.22
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	1236.30	8.70	0.007	13	1210.30
RDHA	1238.04	10.44	0.003	4	1230.04
AGPL	1238.54	10.94	0.002	4	1230.54
DTST	1238.64	11.04	0.002	4	1230.64
RDHA + DTRD	1239.05	11.45	0.002	5	1229.05
STHA	1239.16	11.56	0.002	4	1231.16

STHA + PVT	1239.29	11.69	0.002	5	1229.29
(.)	1239.47	11.87	0.001	3	1233.47
URPL	1239.97	12.37	0.001	4	1231.97
STRMHA	1240.03	12.43	0.001	4	1232.03
DTRD	1240.21	12.61	0.001	4	1232.21
URPD	1240.48	12.88	0.001	4	1232.48
RDHA + DTMJRD + DTRD	1240.73	13.13	0.001	6	1228.73
FORSI + GRSI	1240.90	13.30	0.001	5	1230.90
DTMJRD	1241.03	13.43	0.001	4	1233.03
FORPL + GRPL	1241.04	13.44	0.001	5	1231.04
GRPL	1241.05	13.45	0.001	4	1233.05
WASI + WESI + STRMHA	1241.38	13.78	0.001	6	1229.38
ED	1241.42	13.82	0.001	4	1233.42
ARCV + SID + FORSI + GRSI	1241.57	13.97	0.001	7	1227.57
URPL + URPD	1241.59	13.99	0.001	5	1231.59
URPL + URPD + DTMU	1241.67	14.07	0.001	6	1229.67
FORPL + FORPI	1241.93	14.33	0.000	5	1231.93
ED + ARCV	1242.08	14.48	0.000	5	1232.08
ED + ARCV + FORSI + GRSI	1242.08	14.48	0.000	7	1228.08
RDHA + MJRDHA + DTMJRD + DTRD	1242.65	15.05	0.000	7	1228.65
FORPL + FORPI + GRPL	1242.84	15.24	0.000	6	1230.84
GRPL + GRPI	1243.04	15.44	0.000	5	1233.04
ED + SID	1243.34	15.74	0.000	5	1233.34

ED + ARCV + SID	1243.70	16.10	0.000	6	1231.70
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	1244.75	17.15	0.000	11	1222.75
FORPL + FORPI + GRPL + GRPI	1244.79	17.19	0.000	7	1230.79
AGCL + FORPL + FORPI + GRPL + GRPI	1246.78	19.18	0.000	8	1230.78
Coyote (camera point)					
STEM + SLP	3921.42	0.00	0.127	8	3905.42
HW	3921.61	0.19	0.116	7	3907.61
STEM	3921.66	0.24	0.113	7	3907.66
STEM + DTRD + SLP	3922.02	0.60	0.094	9	3904.02
HW + CWD	3922.46	1.04	0.076	8	3906.46
(.)	3922.97	1.55	0.059	6	3910.97
DTRD	3923.32	1.90	0.049	7	3909.32
BA + HW	3923.47	2.05	0.046	8	3907.47
CWD	3923.68	2.26	0.041	7	3909.68
PVT	3923.96	2.54	0.036	7	3909.96
STEM + DTRD + DTST	3924.22	2.80	0.031	9	3906.22
HW + CWD + DTSTRM	3924.23	2.81	0.031	9	3906.23
BA + HW + CWD	3924.38	2.96	0.029	9	3906.38
STEM + DTST + PVT	3924.78	3.36	0.024	9	3906.78
DTST	3924.88	3.46	0.023	7	3910.88
DTRD + DTST	3925.32	3.90	0.018	8	3909.32
CWD + DTSTRM	3925.39	3.97	0.017	8	3909.39

BA + CWD	3925.39	3.97	0.017	8	3909.39
DTST + PVT	3925.49	4.07	0.017	8	3909.49
STEM + SLP + DTRD + DTST + PVT	3925.55	4.13	0.016	11	3903.55
BA + HW + CWD + DTSTRM	3926.17	4.75	0.012	10	3906.17
DTRD + DTST + PVT	3926.43	5.01	0.010	9	3908.43
Coyote (camera cluster: 20% of home range: 4.38-km^2 buffer)					
ARCV + SID + FORSI + GRSI	1673.64	0.00	0.303	8	1657.64
FORSI + GRSI	1675.12	1.48	0.145	6	1663.12
ED + ARCV + FORSI + GRSI	1675.83	2.19	0.102	8	1659.83
WASI + WESI + STRMHA	1677.11	3.47	0.054	7	1663.11
URPL + URPD + DTMU	1677.40	3.76	0.046	7	1663.40
FORPL + FORPI	1677.46	3.82	0.045	6	1665.46
RDHA + DTRD	1677.89	4.25	0.036	6	1665.89
FORPL	1678.05	4.41	0.033	5	1668.05
RDHA	1678.55	4.91	0.026	5	1668.55
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1678.61	4.97	0.025	12	1654.61
FORPL + FORPI + GRPL	1678.85	5.21	0.022	7	1664.85
ED + ARCV + SID	1679.12	5.48	0.020	7	1665.12
RDHA + DTRD + DTMJRD	1679.79	6.15	0.014	7	1665.79
FORPL + GRPL	1680.00	6.36	0.013	6	1668.00
STHA + RDHA	1680.07	6.43	0.012	6	1668.07
STHA + RDHA + URPL + URPD + DTMJRD	1680.34	6.70	0.011	13	1654.34

DTST + DTRD + DTMU + PVT					
FORPL + FORPI + GRPL + GRPI	1680.62	6.98	0.009	8	1664.62
URPL	1680.79	7.15	0.009	5	1670.79
(.)	1681.02	7.38	0.008	4	1673.02
STRMHA	1681.18	7.54	0.007	5	1671.18
AGCL + FORPL + FORPI + GRPL + GRPI	1681.28	7.64	0.007	9	1663.28
STHA	1681.63	7.99	0.006	5	1671.63
STHA + RDHA + DTST	1682.05	8.41	0.005	7	1668.05
GRPL	1682.17	8.53	0.004	5	1672.17
URPL + URPD	1682.19	8.55	0.004	6	1670.19
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	1682.38	8.74	0.004	12	1658.38
ED	1682.55	8.91	0.004	5	1672.55
MJRDHA	1682.59	8.95	0.004	5	1672.59
AGPL	1682.92	9.28	0.003	5	1672.92
STHA + PVT	1683.14	9.50	0.003	6	1671.14
ED + SID	1683.35	9.71	0.002	6	1671.35
STHA + RDHA + DTMJRD + MJRDHA	1683.36	9.72	0.002	8	1667.36
STHA + DTST	1683.42	9.78	0.002	6	1671.42
GRPL + GRPI	1683.83	10.19	0.002	6	1671.83
STHA + RDHA + DTMJRD + DTST + DTRD	1683.86	10.22	0.002	9	1665.86
ED + ARCV	1683.89	10.25	0.002	6	1671.89
Coyote (camera cluster: 100% home range: 21.90-km^2 buffer)					

URPL + URPD + DTMU	1674.57	0	0.5148	7	1660.57
AGCL + FORPL + FORPI + GRPL + GRPI	1677.14	2.57	0.1424	9	1659.14
ED	1680.12	5.55	0.0321	5	1670.12
ED + ARCV	1680.49	5.92	0.0267	6	1668.49
RDHA	1680.59	6.02	0.0254	5	1670.59
STHA + RDHA	1680.8	6.23	0.0228	6	1668.8
ED + SID	1680.87	6.3	0.0221	6	1668.87
FORPL + FORPI	1680.97	6.4	0.021	6	1668.97
(.)	1681.02	6.45	0.0205	4	1673.02
ARCV + SID + FORSI + GRSI	1681.77	7.2	0.0141	8	1665.77
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1681.83	7.26	0.0136	12	1657.83
STRMHA	1681.85	7.28	0.0135	5	1671.85
WASI + WESI + STRMHA	1682.18	7.61	0.0115	7	1668.18
ED + ARCV + SID	1682.37	7.8	0.0104	7	1668.37
DTRD	1682.4	7.83	0.0103	5	1672.4
RDHA + DTRD	1682.54	7.97	0.0096	6	1670.54
STHA	1682.68	8.11	0.0089	5	1672.68
DTST	1682.69	8.12	0.0089	5	1672.69
GRPL	1682.8	8.23	0.0084	5	1672.8
URPL	1682.93	8.36	0.0079	5	1672.93
FORPL + FORPI + GRPL	1682.93	8.36	0.0079	7	1668.93
AGPL	1683.02	8.45	0.0075	5	1673.02

FORPL	1683.02	8.45	0.0075	5	1673.02
URPL + URPD	1683.09	8.52	0.0073	6	1671.09
GRPL + GRPI	1684.37	9.8	0.0038	6	1672.37
RDHA + DTMJRD + DTRD	1684.48	9.91	0.0036	7	1670.48
STHA + DTST	1684.55	9.98	0.0035	6	1672.55
FORPL + FORPI + GRPL + GRPI	1684.64	10.07	0.0033	8	1668.64
STHA + PVT	1684.65	10.08	0.0033	6	1672.65
FORSI + GRSI	1684.83	10.26	0.003	6	1672.83
FORPL + GRPL	1685.02	10.45	0.0028	6	1673.02
RDHA + DTRD + DTMJRD + MJRDHA	1686.07	11.5	0.0016	8	1670.07
Gray fox (camera point)					
HW + CWD + DTSTRM	1261.23	0.00	0.145	6	1249.23
HW + CWD	1261.28	0.05	0.142	5	1251.28
HW	1261.69	0.46	0.115	4	1253.69
DTST + PVT	1262.55	1.32	0.075	5	1252.55
BA + HW + CWD	1262.59	1.36	0.074	6	1250.59
BA + HW + CWD + DTSTRM	1262.67	1.44	0.071	7	1248.67
BA + HW	1262.71	1.48	0.069	5	1252.71
CWD + DTSTRM	1263.61	2.38	0.044	5	1253.61
DTST	1263.98	2.75	0.037	4	1255.98
CWD	1264.08	2.85	0.035	4	1256.08
DTRD + DTST + PVT	1264.30	3.07	0.031	6	1252.30
STEM + DTST + PVT	1264.33	3.10	0.031	6	1252.33

(.)	1264.53	3.30	0.028	3	1258.53
PVT	1264.81	3.58	0.024	4	1256.81
DTRD + DTST	1265.98	4.75	0.014	5	1255.98
BA + CWD	1266.03	4.80	0.013	5	1256.03
STEM	1266.12	4.89	0.013	4	1258.12
DTRD	1266.42	5.19	0.011	4	1258.42
STEM + SLP	1266.71	5.48	0.009	5	1256.71
STEM + SLP + DTRD + DTST + PVT	1266.83	5.60	0.009	8	1250.83
STEM + DTRD + DTST	1267.41	6.18	0.007	6	1255.41
STEM + SLP + DTRD	1268.62	7.39	0.004	6	1256.62
Gray fox (camera cluster: 20% of home range: 0.55-km^2 buffer)					
ED + SID	731.06	0.00	0.343	6	719.06
ED + ARCV + SID	733.05	1.99	0.127	7	719.05
FORPL + FORPI	733.53	2.47	0.100	6	721.53
AGPL	733.67	2.61	0.093	5	723.67
FORPL	733.70	2.64	0.092	5	723.70
FORPL + FORPI + GRPL	735.48	4.42	0.038	7	721.48
SID	735.55	4.49	0.036	5	725.55
FORPL + GRPL	735.69	4.63	0.034	6	723.69
FORPL + FORPI + GRPL + GRPI	736.43	5.37	0.023	8	720.43
GRPL	737.41	6.35	0.014	5	727.41
AGCL + FORPL + FORPI + GRPL + GRPI	737.49	6.43	0.014	9	719.49
(.)	738.07	7.01	0.010	4	730.07

ARCV	738.91	7.85	0.007	5	728.91
GRPL + GRPI	738.96	7.90	0.007	6	726.96
FORPI	739.14	8.08	0.006	5	729.14
ED	739.27	8.21	0.006	5	729.27
STRMHA	739.47	8.41	0.005	5	729.47
URPL	739.60	8.54	0.005	5	729.60
RDHA	739.86	8.80	0.004	5	729.86
STHA	739.90	8.84	0.004	5	729.90
ED + ARCV	740.35	9.29	0.003	6	728.35
STHA + PVT	740.54	9.48	0.003	6	728.54
ARCV + SID + FORSI + GRSI	740.77	9.71	0.003	8	724.77
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	741.13	10.07	0.002	12	717.13
URPL + URPD	741.56	10.50	0.002	6	729.56
GRSI + FORSI	741.57	10.51	0.002	6	729.57
RDHA + DTRD	741.64	10.58	0.002	6	729.64
STHA + RDHA	741.74	10.68	0.002	6	729.74
STHA + DTST	741.89	10.83	0.002	6	729.89
RDHA + DTRD + DTMJRD	741.91	10.85	0.002	7	727.91
WASI + WESI + STRMHA	742.34	11.28	0.001	7	728.34
RDHA + DTRD + DTMJRD + MJRDHA	743.31	12.25	0.001	8	727.31
URPL + URPD + DTMU	743.54	12.48	0.001	7	729.54
ED + ARCV + FORSI + GRSI	743.72	12.66	0.001	8	727.72

STHA + RDHA + DTST	743.73	12.67	0.001	7	729.73
STHA + RDHA + DTMJRD + DTST + DTRD	745.57	14.51	0.000	9	727.57
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	748.87	17.81	0.000	11	726.87
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	751.74	20.68	0.000	12	727.74
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	752.37	21.31	0.000	14	724.37
Gray fox (camera cluster:100% home range: 2.75-km^2 buffer)					
RDHA + DTRD + DTMJRD	728.61	0.00	0.252	7	714.61
STRMHA	730.07	1.46	0.121	5	720.07
AGPL	730.16	1.55	0.116	5	720.16
RDHA + DTRD + DTMJRD + MJRDHA	730.52	1.91	0.097	8	714.52
RDHA	731.04	2.43	0.075	5	721.04
RDHA + DTRD	731.25	2.64	0.067	6	719.25
STHA + RDHA + DTMJRD + DTST + DTRD	732.10	3.49	0.044	9	714.10
ED + SID	732.41	3.80	0.038	6	720.41
STHA + RDHA	732.93	4.32	0.029	6	720.93
WASI + WESI + STRMHA	733.22	4.61	0.025	7	719.22
STHA + RDHA + DTST	733.48	4.87	0.022	7	719.48
FORPL	733.53	4.92	0.022	5	723.53
ED + ARCV + SID	734.38	5.77	0.014	7	720.38
FORPL + FORPI	735.16	6.55	0.010	6	723.16

ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	735.21	6.60	0.009	12	711.21
FORPL + GRPL	735.40	6.79	0.008	6	723.40
AGCL + FORPL + FORPI + GRPL + GRPI	735.80	7.19	0.007	9	717.80
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	735.99	7.38	0.006	11	713.99
FORSI + GRSI	736.31	7.70	0.005	6	724.31
STHA + PVT	736.98	8.37	0.004	6	724.98
FORPL + FORPI + GRPL	736.99	8.38	0.004	7	722.99
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	737.63	9.02	0.003	12	713.63
STHA	737.80	9.19	0.003	5	727.80
(.)	738.07	9.46	0.002	4	730.07
GRPL	738.24	9.63	0.002	5	728.24
FORPL + FORPI + GRPL + GRPI	738.25	9.64	0.002	8	722.25
DTMJRD	738.41	9.80	0.002	5	728.41
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	738.63	10.02	0.002	14	710.63
ED + ARCV	738.77	10.16	0.002	6	726.77
URPL	739.00	10.39	0.001	5	729.00
ED + ARCV + FORSI + GRSI	739.38	10.77	0.001	8	723.38
STHA + DTST	739.43	10.82	0.001	6	727.43
ARCV + SID + FORSI + GRSI	739.56	10.95	0.001	8	723.56

ED	739.75	11.14	0.001	5	729.75
DTRD	739.76	11.15	0.001	5	729.76
GRPL + GRPI	740.23	11.62	0.001	6	728.23
URPL + URPD	740.99	12.38	0.001	6	728.99
URPL + URPD + DTMU	742.99	14.38	0.000	7	728.99
Red fox (camera point)					
DTST	793.67	0.00	0.382	5	783.67
DTST + PVT	794.91	1.24	0.206	6	782.91
DTRD + DTST	795.48	1.81	0.155	6	783.48
STEM + DTST + PVT	796.70	3.03	0.084	7	782.70
DTRD + DTST + PVT	796.86	3.19	0.078	7	782.86
STEM + DTRD + DTST	797.22	3.55	0.065	7	783.22
STEM + SLP + DTRD + DTST + PVT	798.75	5.08	0.030	9	780.75
PVT	807.40	13.73	0.000	5	797.40
(.)	809.34	15.67	0.000	4	801.34
HW	810.28	16.61	0.000	5	800.28
DTRD	810.56	16.89	0.000	5	800.56
STEM + SLP	811.05	17.38	0.000	6	799.05
STEM	811.08	17.41	0.000	5	801.08
CWD	811.08	17.41	0.000	5	801.08
HW + CWD	812.01	18.34	0.000	6	800.01
BA + HW	812.28	18.61	0.000	6	800.28
STEM + SLP + DTRD	812.32	18.65	0.000	7	798.32

CWD + DTSTRM	812.63	18.96	0.000	6	800.63
BA + CWD	812.89	19.22	0.000	6	800.89
HW + CWD + DTSTRM	813.45	19.78	0.000	7	799.45
BA + HW + CWD	814.01	20.34	0.000	7	800.01
BA + HW + CWD + DTSTRM	815.45	21.78	0.000	8	799.45
Red fox (camera cluster: 20% of home range: 1.42-km^2 buffer)					
STHA + RDHA + DTMJRD + DTST + DTRD	536.59	0.00	0.231	9	518.59
STHA + RDHA + DTST	536.73	0.14	0.216	7	522.73
RDHA + DTRD + DTMJRD	536.95	0.36	0.193	7	522.95
RDHA + DTRD + DTMJRD + MJRDHA	538.29	1.70	0.099	8	522.29
STHA + RDHA + URPL + DTMJRD + DTST + DTMU + DTRD	538.59	2.00	0.085	11	516.59
STHA + RDHA	540.28	3.69	0.037	6	528.28
RDHA + DTRD	540.30	3.71	0.036	6	528.30
STHA + RDHA + URPL + URPD + DTST + DTMU + DTRD + PVT	540.32	3.73	0.036	12	516.32
STHA + DTST	540.70	4.11	0.030	6	528.70
RDHA	541.74	5.15	0.018	5	531.74
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTMU + DTRD + PVT	543.87	7.28	0.006	14	515.87
STHA	544.85	8.26	0.004	5	534.85
URPL	545.33	8.74	0.003	5	535.33
STHA + PVT	546.45	9.86	0.002	6	534.45

URPL + URPD + DTMU	546.83	10.24	0.001	7	532.83
URPL + URPD	547.08	10.49	0.001	6	535.08
ED	547.66	11.07	0.001	5	537.66
ED + ARCV	549.41	12.82	0.000	6	537.41
ED + SID	549.45	12.86	0.000	6	537.45
ARCV + SID + ED	550.65	14.06	0.000	7	536.65
FORPL + FORPI	550.73	14.14	0.000	6	538.73
ARCV + SID + FORSI + GRSI	552.28	15.69	0.000	8	536.28
FORPL + FORPI + GRPL	552.72	16.13	0.000	7	538.72
FORPL	552.86	16.27	0.000	5	542.86
ED + ARCV + FORSI + GRSI	552.98	16.39	0.000	8	536.98
(.)	553.22	16.63	0.000	4	545.22
GRPL	554.20	17.61	0.000	5	544.20
AGCL + FORPL + FORPI + GRPL + GRPI	554.38	17.79	0.000	9	536.38
FORPL + FORPI + GRPL + GRPI	554.40	17.81	0.000	8	538.40
FORPL + GRPL	554.85	18.26	0.000	6	542.85
STRMHA	554.99	18.40	0.000	5	544.99
AGPL	555.02	18.43	0.000	5	545.02
ED + ARCV + SID + FORSI + GRSI + WESI + WASI + STRMHA	555.98	19.39	0.000	12	531.98
GRPL + GRPI	556.19	19.60	0.000	6	544.19
FORSI + GRSI	556.69	20.10	0.000	6	544.69
WASI + WESI + STRMHA	558.24	21.65	0.000	7	544.24

Red fox (camera cluster:100% home range: 7.09-km^2 buffer)					
STHA + RDHA + DTST	527.14	0.00	0.462	7	513.14
RDHA	529.00	1.86	0.182	5	519.00
STHA + RDHA + DTMJRD + DTST + DTRD	529.47	2.33	0.144	9	511.47
RDHA + DTRD	530.01	2.87	0.110	6	518.01
RDHA + DTRD + DTMJRD	531.93	4.79	0.042	7	517.93
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	533.22	6.08	0.022	11	511.22
STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	533.73	6.59	0.017	12	509.73
RDHA + MJRDHA + DTMJRD + DTRD	533.83	6.69	0.016	8	517.83
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	537.67	10.53	0.002	14	509.67
STHA + DTST	540.80	13.66	0.001	6	528.80
DTST	540.97	13.83	0.001	5	530.97
URPL	544.86	17.72	0.000	5	534.86
URPL + URPD	546.86	19.72	0.000	6	534.86
STHA	546.93	19.79	0.000	5	536.93
URPL + URPD + DTMU	547.31	20.17	0.000	7	533.31
STHA + PVT	548.28	21.14	0.000	6	536.28
ED	548.84	21.70	0.000	5	538.84
ED + SID	550.33	23.19	0.000	6	538.33
ED + ARCV	550.66	23.52	0.000	6	538.66

ED + ARCV + SID	551.14	24.00	0.000	7	537.14
ARCV + SID + FORSI + GRSI	551.92	24.78	0.000	8	535.92
FORPL	552.48	25.34	0.000	5	542.48
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	552.83	25.69	0.000	12	528.83
(.)	553.22	26.08	0.000	4	545.22
STRMHA	553.39	26.25	0.000	5	543.39
GRPL	554.28	27.14	0.000	5	544.28
FORPL + FORPI	554.30	27.16	0.000	6	542.30
ED + ARCV + FORSI + GRSI	554.36	27.22	0.000	8	538.36
AGPL	555.11	27.97	0.000	5	545.11
GRPL + GRPI	555.50	28.36	0.000	6	543.50
WASI + WESI + STRMHA	555.62	28.48	0.000	7	541.62
FORSI + GRSI	555.72	28.58	0.000	6	543.72
FORPL + FORPI + GRPL + GRPI	556.86	29.72	0.000	8	540.86
AGCL + FORPL + FORPI + GRPL + GRPI	558.19	31.05	0.000	9	540.19
Striped skunk (camera point)					
PVT	2524.80	0.00	0.382	11	2502.80
DTRD + DTST + PVT	2525.11	0.31	0.327	13	2499.11
DTST + PVT	2526.76	1.96	0.143	12	2502.76
STEM + SLP + DTRD + DTST + PVT	2528.42	3.62	0.063	15	2498.42
STEM + DTST + PVT	2528.57	3.77	0.058	13	2502.57

HW + CWD	2533.16	8.36	0.006	12	2509.16
HW	2533.20	8.40	0.006	11	2511.20
HW + CWD + DTSTRM	2533.26	8.46	0.006	13	2507.26
BA + HW	2535.03	10.23	0.002	12	2511.03
BA + HW + CWD	2535.07	10.27	0.002	13	2509.07
BA + HW + CWD + DTSTRM	2535.11	10.31	0.002	14	2507.11
DTRD + DTST	2535.79	10.99	0.002	12	2511.79
STEM + DTRD + DTST	2537.72	12.92	0.001	13	2511.72
DTRD	2537.86	13.06	0.001	11	2515.86
CWD	2539.59	14.79	0.000	11	2517.59
(.)	2539.61	14.81	0.000	10	2519.61
DTST	2539.68	14.88	0.000	11	2517.68
CWD + DTSTRM	2539.92	15.12	0.000	12	2515.92
STEM + SLP + DTRD	2541.01	16.21	0.000	13	2515.01
BA + CWD	2541.04	16.24	0.000	12	2517.04
STEM	2541.52	16.72	0.000	11	2519.52
STEM + SLP	2542.70	17.90	0.000	12	2518.70
Striped skunk (camera cluster: 20% of home range: 0.55-km^2 buffer)					
STHA + PVT	1243.41	0.00	0.266	9	1225.41
AGPL	1243.93	0.52	0.205	8	1227.93
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	1245.57	2.16	0.090	17	1211.57
RDHA + DTRD + DTMJRD	1246.20	2.79	0.066	10	1226.20

STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1246.51	3.10	0.057	15	1216.51
STHA + RDHA + DTMJRD + DTST + DTRD	1246.58	3.17	0.055	12	1222.58
FORPL	1247.15	3.74	0.041	8	1231.15
RDHA + DTRD	1247.25	3.84	0.039	9	1229.25
RDHA + DTRD + DTMJRD + MJRDHA	1247.75	4.34	0.030	11	1225.75
FORPL + FORPI	1248.68	5.27	0.019	9	1230.68
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	1248.72	5.31	0.019	14	1220.72
FORPL + GRPL	1249.15	5.74	0.015	9	1231.15
(.)	1249.28	5.87	0.014	7	1235.28
GRPL	1249.66	6.25	0.012	8	1233.66
FORSI + GRSI	1250.50	7.09	0.008	9	1232.50
FORPL + FORPI + GRPL	1250.67	7.26	0.007	10	1230.67
STRMHA	1250.98	7.57	0.006	8	1234.98
RDHA	1251.12	7.71	0.006	8	1235.12
ED	1251.20	7.79	0.005	8	1235.20
URPL	1251.25	7.84	0.005	8	1235.25
STHA	1251.28	7.87	0.005	8	1235.28
STHA + DTST	1251.58	8.17	0.005	9	1233.58
GRPL + GRPI	1251.60	8.19	0.004	9	1233.60
ED + ARCV	1252.25	8.84	0.003	9	1234.25
FORPL + FORPI + GRPL + GRPI	1252.67	9.26	0.003	11	1230.67

STHA + RDHA	1253.12	9.71	0.002	9	1235.12
ARCV + SID + FORSI + GRSI	1253.12	9.71	0.002	11	1231.12
URPL + URPD	1253.14	9.73	0.002	9	1235.14
ED + ARCV + FORSI + GRSI	1253.16	9.75	0.002	11	1231.16
ED + SID	1253.20	9.79	0.002	9	1235.20
STHA + RDHA + DTST	1253.40	9.99	0.002	10	1233.40
ED + ARCV + SID	1254.22	10.81	0.001	10	1234.22
AGCL + FORPL + FORPI + GRPL + GRPI	1254.28	10.87	0.001	12	1230.28
URPL + URPD + DTMU	1254.77	11.36	0.001	10	1234.77
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	1260.37	16.96	0.000	15	1230.37
WASI + WESI + STRMHA	1300.11	56.70	0.000	10	1280.11
Striped skunk (camera cluster:100% home range: 2.75-km^2 buffer)					
STHA + RDHA + DTMJRD + DTST + DTRD	1241.79	0.00	0.211	12	1217.79
AGPL	1241.98	0.19	0.192	8	1225.98
STHA + PVT	1242.89	1.10	0.122	9	1224.89
RDHA + DTRD + DTMJRD	1243.13	1.34	0.108	10	1223.13
STHA + RDHA + MJRDHA + URPL + URPD + DTMJRD + DTST + DTRD + DTMU + PVT	1243.29	1.50	0.100	17	1209.29
STHA + RDHA + URPL + DTMJRD + DTST + DTRD + DTMU	1243.57	1.78	0.087	14	1215.57
RDHA + DTMJRD + MJRDHA + DTRD	1244.84	3.05	0.046	11	1222.84
RDHA + DTRD	1245.46	3.67	0.034	9	1227.46

STHA + RDHA + URPL + URPD + DTST + DTRD + DTMU + PVT	1246.10	4.31	0.025	15	1216.10
FORPL	1247.03	5.24	0.015	8	1231.03
FORPL + GRPL	1248.69	6.90	0.007	9	1230.69
FORPL + FORPI	1248.82	7.03	0.006	9	1230.82
ED	1248.94	7.15	0.006	8	1232.94
(.)	1249.28	7.49	0.005	7	1235.28
AGCL + FORPL + FORPI + GRPL + GRPI	1249.46	7.67	0.005	12	1225.46
URPL	1250.12	8.33	0.003	8	1234.12
FORPL + FORPI + GRPL	1250.36	8.57	0.003	10	1230.36
GRPL	1250.37	8.58	0.003	8	1234.37
ED + SID	1250.90	9.11	0.002	9	1232.90
ED + ARCV	1250.91	9.12	0.002	9	1232.91
STHA + DTST	1251.01	9.22	0.002	9	1233.01
STRMHA	1251.15	9.36	0.002	8	1235.15
STHA	1251.24	9.45	0.002	8	1235.24
RDHA	1251.25	9.46	0.002	8	1235.25
FORSI + GRSI	1251.32	9.53	0.002	9	1233.32
GRPL + GRPI	1251.96	10.17	0.001	9	1233.96
URPL + URPD	1252.00	10.21	0.001	9	1234.00
FORPL + FORPI + GRPL + GRPI	1252.19	10.40	0.001	11	1230.19
ED + ARCV + SID	1252.89	11.10	0.001	10	1232.89
WASI + WESI + STRMHA	1253.00	11.21	0.001	10	1233.00

STHA + RDHA + DTST	1253.01	11.22	0.001	10	1233.01
STHA + RDHA	1253.14	11.35	0.001	9	1235.14
ED + ARCV + FORSI + GRSI	1253.84	12.05	0.001	11	1231.84
ARCV + SID + FORSI + GRSI	1254.64	12.85	0.000	11	1232.64
RDHA + URPD + DTMU	1254.69	12.90	0.000	10	1234.69
ED + ARCV + SID + FORSI + GRSI + WASI + WESI + STRMHA	1259.42	17.63	0.000	15	1229.42

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[a] Akaike Information Criterion.

[b] Model probability.

[c] Number of model parameters.

[d] Difference in -2Log(Likelihood) of the current model and -2log(Likelihood) of the saturated model as a measure of model fit.

APPENDIX C. CAMERA-POINT CO-OCCURRENCE MODELS

Camera-point co-occurrence model selection results for gray fox-bobcat (a), gray fox-coyote (b), gray fox-red fox (c), red fox-bobcat (d), red fox-coyote (e), red fox-gray fox (f), striped skunk-bobcat (g), striped skunk-coyote (h), striped skunk-gray fox (i), and striped skunk-red fox (j). To each candidate model set we fit encounter history data from surveys at 1188 camera points in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. Co-occurrence models were fit using the most supported detection model (Appendix A) and the top 3–4 occupancy models for gray foxes and red foxes (Appendix B). Combined models of habitat and interacting species were parameterized in two ways: (1) added effect of interacting species and (2) interaction between habitat and interacting species (separate intercept and separate β coefficient estimate for each habitat covariate based on presence of interacting species). The most supported detection and occupancy models of interacting species were included to account for heterogeneity in detection and occupancy probabilities of those species (Appendix B). See Table 1 for habitat variable codes and descriptions.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]	Deviance[d]
a) Gray fox with bobcat					
HW + CWD + DTSTRM	3208.38	0.00	0.213	12	3184.38
HW + CWD	3208.43	0.05	0.208	11	3186.43
HW	3208.83	0.45	0.170	10	3188.83
HW + CWD + DTSTRM + BOBCAT	3210.21	1.83	0.085	13	3184.21
HW + CWD + BOBCAT	3210.24	1.86	0.084	12	3186.24
HW + BOBCAT	3210.61	2.23	0.070	11	3188.61

DTST + PVT	3211.43	3.05	0.046	11	3189.43
(.)	3211.68	3.30	0.041	9	3193.68
DTST + PVT + BOBCAT	3213.30	4.92	0.018	12	3189.30
BOBCAT	3213.54	5.16	0.016	10	3193.54
DTST + PVT × BOBCAT	3217.05	8.67	0.003	14	3189.05
HW + CWD × BOBCAT	3217.76	9.38	0.002	14	3189.76
HW × BOBCAT	3217.90	9.52	0.002	12	3193.90
HW + CWD + DTSTRM × BOBCAT	3219.52	11.14	0.001	16	3187.52
b) Gray fox with coyote					
HW × COYOTE	5183.22	0.00	0.142	14	5155.22
HW + CWD + DTSTRM	5183.25	0.03	0.140	14	5155.25
HW + CWD	5183.30	0.08	0.137	13	5157.30
HW	5183.71	0.49	0.111	12	5159.71
HW + CWD × COYOTE	5184.43	1.21	0.078	16	5152.43
DTST + PVT	5184.56	1.34	0.073	13	5158.56
HW + CWD + DTSTRM + COYOTE	5184.63	1.41	0.070	15	5154.63
HW + CWD + COYOTE	5184.69	1.47	0.068	14	5156.69
HW + COYOTE	5185.25	2.03	0.052	13	5159.25
HW + CWD + DTSTRM × COYOTE	5185.94	2.72	0.037	18	5149.94
DTST + PVT + COYOTE	5186.19	2.97	0.032	14	5158.19
(.)	5186.56	3.34	0.027	11	5164.56
COYOTE	5188.30	5.08	0.011	12	5164.30
DTST + PVT × COYOTE	5189.64	6.42	0.006	16	5157.64

c) Gray fox with red fox					
HW + CWD + REDFOX	2048.71	0.00	0.246	11	2026.71
HW + CWD + DTSTRM + REDFOX	2048.82	0.11	0.233	12	2024.82
HW + REDFOX	2049.36	0.65	0.178	10	2029.36
HW × REDFOX	2051.27	2.56	0.068	11	2029.27
DTST × REDFOX	2051.45	2.74	0.063	11	2029.45
DTST + PVT × REDFOX	2051.59	2.88	0.058	13	2025.59
DTST + PVT + REDFOX	2052.50	3.79	0.037	11	2030.50
HW + CWD × REDFOX	2052.61	3.90	0.035	13	2026.61
REDFOX	2053.00	4.29	0.029	9	2035.00
HW + CWD + DTSTRM × REDFOX	2053.96	5.25	0.018	15	2023.96
HW + CWD + DTSTRM	2055.08	6.37	0.010	11	2033.08
HW + CWD	2055.13	6.42	0.010	10	2035.13
HW	2055.53	6.82	0.008	9	2037.53
DTST + PVT	2056.38	7.67	0.005	10	2036.38
(.)	2058.38	9.67	0.002	8	2042.38
d) Red fox with bobcat					
DTST	2740.76	0.00	0.300	11	2718.76
DTST + PVT	2742.02	1.26	0.160	12	2718.02
DTST + BOBCAT	2742.46	1.70	0.128	12	2718.46
DTRD + DTST	2742.58	1.82	0.121	12	2718.58
DTST + PVT + BOBCAT	2743.71	2.95	0.069	13	2717.71
STEM + DTST + PVT	2743.80	3.04	0.066	13	2717.80

DTRD + DTST + BOBCAT	2744.30	3.54	0.051	13	2718.30
DTST × BOBCAT	2744.46	3.70	0.047	13	2718.46
STEM + DTST + PVT + BOBCAT	2745.47	4.71	0.029	14	2717.47
STEM + DTST + PVT × BOBCAT	2747.12	6.36	0.013	17	2713.12
DTST + PVT × BOBCAT	2747.48	6.72	0.010	15	2717.48
DTRD + DTST × BOBCAT	2748.28	7.52	0.007	15	2718.28
(.)	2756.48	15.72	0.000	10	2736.48
BOBCAT	2758.38	17.62	0.000	11	2736.38
e) Red fox with coyote					
DTST + COYOTE	4709.62	0.00	0.356	14	4681.62
DTST × COYOTE	4710.80	1.18	0.198	15	4680.80
DTST + PVT + COYOTE	4711.05	1.43	0.174	15	4681.05
DTRD + DTST + COYOTE	4711.53	1.91	0.137	15	4681.53
DTRD + DTST × COYOTE	4713.17	3.55	0.060	17	4679.17
DTST + PVT × COYOTE	4713.98	4.36	0.040	17	4679.98
DTST	4715.64	6.02	0.018	13	4689.64
DTST + PVT	4716.89	7.27	0.009	14	4688.89
DTRD + DTST	4717.46	7.84	0.007	14	4689.46
COYOTE	4726.23	16.61	0.000	13	4700.23
(.)	4731.36	21.74	0.000	12	4707.36
f) Red fox with gray fox					
DTST × GRAYFOX	2050.18	0.00	0.338	13	2024.18
DTST + GRAYFOX	2051.22	1.04	0.201	12	2027.22

DTST + PVT + GRAYFOX	2052.03	1.85	0.134	13	2026.03
DTRD + DTST × GRAYFOX	2052.64	2.46	0.099	15	2022.64
DTST + PVT × GRAYFOX	2052.88	2.70	0.088	15	2022.88
DTRD + DTST + GRAYFOX	2053.02	2.84	0.082	13	2027.02
DTST	2055.08	4.90	0.029	11	2033.08
DTST + PVT	2056.33	6.15	0.016	12	2032.33
DTRD + DTST	2056.68	6.50	0.013	12	2032.68
GRAYFOX	2066.94	16.76	0.000	11	2044.94
(.)	2070.79	20.61	0.000	10	2050.79
g) Striped skunk with bobcat					
DTRD + DTST + PVT × BOBCAT	4471.20	0.00	0.211	20	4431.20
DTRD + DTST + PVT	4471.21	0.01	0.210	16	4439.21
PVT	4471.39	0.19	0.192	14	4443.39
DTRD + DTST + PVT + BOBCAT	4472.95	1.75	0.088	17	4438.95
PVT + BOBCAT	4473.18	1.98	0.079	15	4443.18
DTST + PVT	4473.28	2.08	0.075	15	4443.28
PVT × BOBCAT	4473.79	2.59	0.058	16	4441.79
DTST + PVT × BOBCAT	4473.84	2.64	0.056	18	4437.84
DTST + PVT + BOBCAT	4475.04	3.84	0.031	16	4443.04
(.)	4488.20	17.00	0.000	13	4462.20
BOBCAT	4490.02	18.82	0.000	14	4462.02
h) Striped skunk with coyote					
DTRD + DTST + PVT + COYOTE	6341.50	0.00	0.407	19	6303.50

PVT + COYOTE	6342.76	1.26	0.217	17	6308.76
DTRD + DTST + PVT × COYOTE	6343.97	2.47	0.118	22	6299.97
DTST + PVT + COYOTE	6344.07	2.57	0.113	18	6308.07
PVT × COYOTE	6344.34	2.84	0.098	18	6308.34
DTST + PVT × COYOTE	6345.85	4.35	0.046	20	6305.85
COYOTE	6361.38	19.88	0.000	16	6329.38
DTRD + DTST + PVT	6446.09	104.59	0.000	18	6410.09
PVT	6446.27	104.77	0.000	16	6414.27
DTST + PVT	6448.15	106.65	0.000	17	6414.15
(.)	6449.36	107.86	0.000	15	6419.36
i) Striped skunk with gray fox					
DTRD + DTST + PVT × GRAYFOX	3784.64	0.00	0.177	20	3744.64
PVT + GRAYFOX	3784.84	0.20	0.160	15	3754.84
DTRD + DTST + PVT + GRAYFOX	3784.86	0.22	0.158	17	3750.86
DTST + PVT × GRAYFOX	3785.28	0.64	0.128	18	3749.28
DTRD + DTST + PVT	3785.53	0.89	0.113	16	3753.53
PVT	3785.70	1.06	0.104	14	3757.70
DTST + PVT + GRAYFOX	3786.82	2.18	0.059	16	3754.82
PVT × GRAYFOX	3786.82	2.18	0.059	16	3754.82
DTST + PVT	3787.59	2.95	0.040	15	3757.59
GRAYFOX	3801.75	17.11	0.000	14	3773.75
(.)	3802.51	17.87	0.000	13	3776.51
j) Striped skunk with red fox					

PVT + REDFOX	3312.48	0.00	0.333	14	3284.48
DTRD + DTST + PVT + REDFOX	3312.90	0.42	0.270	16	3280.90
PVT × REDFOX	3314.41	1.93	0.127	15	3284.41
DTST + PVT + REDFOX	3314.43	1.95	0.126	15	3284.43
DTRD + DTST + PVT × REDFOX	3315.70	3.22	0.067	19	3277.70
DTST + PVT × REDFOX	3317.46	4.98	0.028	17	3283.46
DTRD + DTST + PVT	3317.91	5.43	0.022	15	3287.91
PVT	3318.09	5.61	0.020	13	3292.09
DTST + PVT	3319.97	7.49	0.008	14	3291.97
REDFOX	3327.82	15.34	0.000	13	3301.82
(.)	3334.90	22.42	0.000	12	3310.90

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[a] Akaike Information Criterion.

[b] Model probability.

[c] Number of model parameters.

[d] Difference in -2Log(Likelihood) of the current model and -2log(Likelihood) of the saturated model as a measure of model fit.

APPENDIX D. CAMERA-CLUSTER CO-OCCURRENCE MODELS

Camera-cluster co-occurrence model selection results for gray fox-bobcat (a), gray fox-coyote (b), gray fox-red fox (c), red fox-bobcat (d), red fox-coyote (e), red fox-gray fox (f), striped skunk-bobcat (g), striped skunk-coyote (h), striped skunk-gray fox (i), and striped skunk-red fox (j). To each candidate model we fit encounter history data from surveys at 357 camera clusters (3–4 cameras per cluster) in the 16 southernmost counties of Illinois, USA during January–April 2008–2010. Combined models of habitat and interacting species were parameterized in two ways: (1) added effect of interacting species and (2) interaction between habitat and interacting species (separate intercept and separate β coefficient estimate for each habitat covariate based on presence of interacting species). The most supported detection and occupancy models of interacting species were included to account for heterogeneity in detection and occupancy probabilities of those species (Appendix B). See Table 1 for habitat variable codes and descriptions.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]	Deviance[d]
a) Gray fox with bobcat					
RDHA + DTRD + DTMJRD	1967.95	0.00	0.236	13	1941.95
RDHA + DTRD + DTMJRD + BOBCAT	1969.11	1.16	0.132	14	1941.11
RDHA + DTRD + DTMJRD + MJRDHA	1969.74	1.79	0.096	14	1941.74
AGPL	1969.74	1.79	0.096	11	1947.74
STRMHA	1969.95	2.00	0.087	11	1947.95
RDHA	1970.34	2.39	0.071	11	1948.34
RDHA + DTRD + DTMJRD + MJRDHA + BOBCAT	1970.83	2.88	0.056	15	1940.83

RDHA + BOBCAT	1971.02	3.07	0.051	12	1947.02
AGPL + BOBCAT	1971.27	3.32	0.045	12	1947.27
RDHA × BOBCAT	1971.80	3.85	0.034	13	1945.8
STRMHA + BOBCAT	1971.87	3.92	0.033	12	1947.87
STRMHA × BOBCAT	1972.01	4.06	0.031	13	1946.01
AGPL × BOBCAT	1973.20	5.25	0.017	13	1947.2
RDHA + DTRD + DTMJRD × BOBCAT	1973.95	6.00	0.012	17	1939.95
(.)	1977.51	9.56	0.002	10	1957.51
BOBCAT	1979.46	11.51	0.001	11	1957.46
b) Gray fox with coyote					
RDHA + DTRD + DTMJRD + COYOTE	2413.8	0	0.2785	14	2385.82
RDHA + DTRD + DTMJRD + MJRDHA + COYOTE	2415.4	1.56	0.1277	15	2385.38
AGPL + COYOTE	2415.9	2.05	0.0999	12	2391.87
RDHA + COYOTE	2416	2.2	0.0927	12	2392.02
RDHA + DTRD + DTMJRD	2416.6	2.78	0.0694	13	2390.6
STRMHA + COYOTE	2416.7	2.9	0.0653	12	2392.72
RDHA + DTRD + DTMJRD × COYOTE	2416.9	3.05	0.0606	17	2382.87
AGPL × COYOTE	2417	3.17	0.0571	13	2390.99
RDHA × COYOTE	2417.6	3.78	0.0421	13	2391.6
RDHA + DTRD + DTMJRD + MJRDHA	2418.4	4.54	0.0288	14	2390.36
STRMHA	2418.4	4.55	0.0286	11	2396.37
AGPL	2418.7	4.83	0.0249	11	2396.65

RDHA	2418.9	5.12	0.0215	11	2396.94
COYOTE	2423.4	9.62	0.0023	11	2401.44
(.)	2426.4	12.53	0.0005	10	2406.35
c) Gray fox with red fox					
RDHA + DTRD + DTMJRD	1268.59	0	0.1675	14	1240.59
AGPL + REDFOX	1268.6	0.01	0.1667	13	1242.6
STRMHA + REDFOX	1269.26	0.67	0.1198	13	1243.26
AGPL × REDFOX	1270	1.41	0.0828	14	1242
STRMHA × REDFOX	1270.19	1.6	0.0753	14	1242.19
STRMHA	1270.34	1.75	0.0698	12	1246.34
AGPL	1270.37	1.78	0.0688	12	1246.37
RDHA + DTRD + DTMJRD + MJRDHA	1270.37	1.78	0.0688	15	1240.37
RDHA + DTRD + DTMJRD + REDFOX	1270.53	1.94	0.0635	15	1240.53
RDHA	1270.86	2.27	0.0539	12	1246.86
RDHA + DTRD + DTMJRD + MJRDHA + REDFOX	1272.3	3.71	0.0262	16	1240.3
RDHA + REDFOX	1272.78	4.19	0.0206	13	1246.78
RDHA × REDFOX	1273.72	5.13	0.0129	14	1245.72
REDFOX	1277.58	8.99	0.0019	12	1253.58
(.)	1278.07	9.48	0.0015	11	1256.07
d) Red fox with bobcat					
STHA + RDHA + DTST	1754.7	0	0.3416	13	1728.74
RDHA	1756.6	1.87	0.1341	11	1734.61

STHA + RDHA + DTST + BOBCAT	1756.7	2	0.1257	14	1728.74
STHA + RDHA + DTMJRD + DTST + DTRD	1757.1	2.33	0.1065	15	1727.07
RDHA + DTRD	1757.6	2.87	0.0813	12	1733.61
RDHA + BOBCAT	1758.4	3.61	0.0562	12	1734.35
STHA + RDHA + DTST × BOBCAT	1759	4.22	0.0414	17	1724.96
STHA + RDHA + DTMJRD + DTST + DTRD + BOBCAT	1759.1	4.33	0.0392	16	1727.07
RDHA + DTRD + BOBCAT	1759.2	4.47	0.0365	13	1733.21
RDHA × BOBCAT	1759.9	5.16	0.0259	13	1733.9
RDHA + DTRD × BOBCAT	1761.9	7.13	0.0097	15	1731.87
BOBCAT	1778.1	23.32	0	11	1756.06
(.)	1780.8	26.09	0	10	1760.83
e) Red fox with coyote					
STAH + RDHA + DTST	2200.8	0	0.3282	15	2170.78
STAH + RDHA + DTST + COYOTE	2202.5	1.74	0.1375	16	2170.52
RDHA	2202.6	1.86	0.1295	13	2176.64
STAH + RDHA + DTMJRD + DTST + DTRD	2203.1	2.33	0.1024	17	2169.11
STAH + RDHA + DTST +COYOTE(2)	2203.5	2.75	0.083	19	2165.53
RDHA + DTRD	2203.6	2.86	0.0786	14	2175.64
RDHA + COYOTE	2204.6	3.83	0.0484	14	2176.61
STAH + RDHA + DTMJRD + DTST + DTRD + COYOTE	2204.8	3.98	0.0449	18	2168.76
RDHA + DTRD + COYOTE	2205.6	4.8	0.0298	15	2175.58

RDHA × COYOTE	2206.6	5.83	0.0178	15	2176.61
(.)	2226.9	26.08	0	12	2202.86
COYOTE	2228.9	28.07	0	13	2202.85
f) Red fox with gray fox					
STHA + RDHA + DTST	1255.8	0	0.3597	14	1227.75
RDHA	1257.6	1.86	0.1419	12	1233.61
STHA + RDHA + DTST + GRAYFOX	1257.6	1.89	0.1398	15	1227.64
STHA + RDHA + DTMJRD + DTST + DTRD	1258.1	2.33	0.1122	16	1226.08
RDHA + DTRD	1258.6	2.86	0.0861	13	1232.61
RDHA + GRAYFOX	1259.6	3.86	0.0522	13	1233.61
STHA + RDHA + DTMJRD + DTST + DTRD + GRAYFOX	1260	4.23	0.0434	17	1225.98
RDHA × GRAYFOX	1260.6	4.84	0.032	14	1232.59
RDHA + DTRD + GRAYFOX	1260.6	4.86	0.0317	14	1232.61
RDHA + DTRD × GRAYFOX	1267.6	11.8	0.001	16	1235.55
GRAYFOX	1279.5	23.74	0	12	1255.49
(.)	1281.8	26.08	0	11	1259.83
g) Striped skunk with bobcat					
AGPL × BOBCAT	2505.44	0.00	0.343	15	2475.44
AGPL	2506.87	1.43	0.168	13	2480.87
AGPL + BOBCAT	2507.91	2.47	0.100	14	2479.91
RDHA + DTMJRD + DTRD × BOBCAT	2508.11	2.67	0.090	19	2470.11
STHA + RDHA + DTMJRD + DTST + DTRD	2508.66	3.22	0.069	17	2474.66

RDHA + DTMJRD + DTRD	2508.82	3.38	0.063	15	2478.82
RDHA + DTMJRD + DTRD + BOBCAT	2509.21	3.77	0.052	16	2477.21
STHA + PVT	2509.70	4.26	0.041	14	2481.70
STHA + RDHA + DTMJRD + DTST + DTRD + BOBCAT	2510.41	4.97	0.029	18	2474.41
STHA + PVT + BOBCAT	2510.74	5.30	0.024	15	2480.74
STHA + RDHA + DTMJRD + DTST + DTRD × BOBCAT	2513.16	7.72	0.007	23	2467.16
(.)	2513.65	8.21	0.006	12	2489.65
BOBCAT	2513.75	8.31	0.005	13	2487.75
STHA + PVT × BOBCAT	2514.41	8.97	0.004	17	2480.41
h) Striped skunk with coyote					
AGPL × COYOTE	2916.79	0.00	0.245	14	2888.79
STHA + PVT × COYOTE	2917.28	0.49	0.192	16	2885.28
STHA + RDHA + DTMJRD + DTST + DTRD × COYOTE	2917.29	0.50	0.191	22	2873.29
STHA + RDHA + DTMJRD + DTST + DTRD + COYOTE	2917.41	0.62	0.180	17	2883.41
AGPL + COYOTE	2918.67	1.88	0.096	13	2892.67
STHA + PVT + COYOTE	2919.22	2.43	0.073	14	2891.22
AGPL	2923.00	6.21	0.011	12	2899.00
STHA + PVT	2923.91	7.12	0.007	13	2897.91
COYOTE	2925.41	8.62	0.003	12	2901.41

STHA + RDHA + DTMJRD + DTST + DTRD	2926.65	9.86	0.002	16	2894.65
(.)	2930.30	13.51	0.000	11	2908.30
i) Striped skunk with gray fox					
AGPL + GRAYFOX	1965.70	0.00	0.392	16	1933.70
AGPL × GRAYFOX	1967.42	1.72	0.166	17	1933.42
STHA + PVT + GRAYFOX	1967.99	2.29	0.125	17	1933.99
STHA + RDHA + DTMJRD + DTST + DTRD × GRAYFOX	1968.77	3.07	0.084	25	1918.77
STHA + RDHA + DTMJRD + DTST + DTRD + GRAYFOX	1968.88	3.18	0.080	20	1928.88
STHA + PVT × GRAYFOX	1969.83	4.13	0.050	19	1931.83
STHA + RDHA + DTMJRD + DTST + DTRD	1970.39	4.69	0.038	19	1932.39
AGPL	1970.59	4.89	0.034	15	1940.59
STHA + PVT	1971.50	5.80	0.022	16	1939.50
GRAYFOX	1972.96	7.26	0.010	15	1942.96
(.)	1977.89	12.19	0.001	14	1949.89
j) Striped skunk with red fox					
STHA + RDHA + DTMJRD + DTST + DTRD	1768.93	0.00	0.198	19	1730.93
AGPL	1769.12	0.19	0.181	15	1739.12
STHA + PVT	1770.03	1.10	0.115	16	1738.03
RDHA + DTMJRD + DTRD	1770.27	1.34	0.102	17	1736.27
AGPL + REDFOX	1770.33	1.40	0.099	16	1738.33
STHA + RDHA + DTMJRD + DTST + DTRD +	1770.90	1.97	0.074	20	1730.90

REDFOX					
STHA + PVT + REDFOX	1770.95	2.02	0.072	17	1736.95
AGPL × REDFOX	1771.37	2.44	0.059	17	1737.37
RDHA + DTMJRD + DTRD + REDFOX	1772.27	3.34	0.037	18	1736.27
RDHA + DTMJRD + DTRD × REDFOX	1772.47	3.54	0.034	21	1730.47
STHA + PVT × REDFOX	1774.62	5.69	0.012	19	1736.62
STHA + RDHA + DTMJRD + DTST + DTRD × REDFOX	1774.64	5.71	0.011	25	1724.64
(.)	1776.42	7.49	0.005	14	1748.42
REDFOX	1777.48	8.55	0.003	15	1747.48

[a] Akaike Information Criterion.

[b] Model probability.

[c] Number of model parameters.

[d] Difference in -2Log(Likelihood) of the current model and -2log(Likelihood) of the saturated model as a measure of model fit.

APPENDIX E. COLONIZATION AND EXTINCTION MODELS

Camera-cluster multi-year model selection results for bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*). For bobcats we modeled 100% home range scale habitat factors potentially influencing site colonization (γ). We modeled factors that may influence site extinction (ε) of gray foxes and red foxes with combinations of 100% home range scale habitat (Appendix B) and carnivore (bobcat, gray fox, and red fox) occupancy estimates. We fit encounter history data from surveys at 357 camera clusters (3–4 cameras per cluster) in the 16 southernmost counties of Illinois, USA during January–April 2008–2010, to each candidate model set. All models were fit using the most supported detection model (Appendix A) for each species. The null (.) extinction model is included for each species to assess relative support for habitat and species interaction covariates. See Table 1 for habitat variable codes and descriptions.

Model	AIC[a]	ΔAIC	*w*[b]	K[c]	Deviance[d]
a) Bobcat (γ)					
AGPL	1217.58	0.00	0.495	8	1201.58
(.)	1220.37	2.79	0.123	7	1206.37
STHA	1220.95	3.37	0.092	8	1204.95
GRPL	1221.70	4.12	0.063	8	1205.70
RDHA	1221.98	4.40	0.055	8	1205.98
FORPL	1222.35	4.77	0.046	8	1206.35
STHA + DTST	1222.67	5.09	0.039	9	1204.67
RDHA + DTRD	1222.73	5.15	0.038	9	1204.73
STHA + RDHA	1222.91	5.33	0.034	9	1204.91

STHA + RDHA + DTST	1224.65	7.07	0.014	10	1204.65
STHA + RDHA + DTST + DTRD + DTMJRD	1228.55	10.97	0.002	12	1204.55
b) Gray fox (ε)					
STHA	724.85	0.00	0.116	10	704.85
STHA + DTST	725.15	0.30	0.100	11	703.15
(.)	725.24	0.39	0.095	9	707.24
STHA + RDHA	725.48	0.63	0.085	11	703.48
STHA + BOBCAT	725.61	0.76	0.079	11	703.61
STHA + REDFOX	725.73	0.88	0.075	11	703.73
AGPL + BOBCAT	726.25	1.40	0.058	11	704.25
BOBCAT	726.26	1.41	0.057	10	706.26
FORPL	726.77	1.92	0.044	10	706.77
STHA + DTST + BOBCAT	726.96	2.11	0.040	12	702.96
AGPL	727.07	2.22	0.038	10	707.07
REDFOX	727.13	2.28	0.037	10	707.13
RDHA	727.14	2.29	0.037	10	707.14
GRPL	727.20	2.35	0.036	10	707.20
STHA + RDHA + BOBCAT	727.41	2.56	0.032	12	703.41
BOBCAT + REDFOX	727.47	2.62	0.031	11	705.47
FORPL + GRPL	728.30	3.45	0.021	11	706.30
RDHA + DTRD	729.13	4.28	0.014	11	707.13
RDHA + DTRD + DTMJRD	730.98	6.13	0.005	12	706.98
c) Red fox (ε)					

AGPL	522.65	0.00	0.252	9	504.65
AGPL + GRAYFOX	523.33	0.68	0.180	10	503.33
RDHA + DTRD	523.66	1.01	0.152	10	503.66
AGPL + BOBCAT	524.70	2.05	0.091	10	504.70
FORPL + GRAYFOX	526.26	3.61	0.042	10	506.26
BOBCAT	526.72	4.07	0.033	9	508.72
RDHA + BOBCAT	526.79	4.14	0.032	10	506.79
GRAYFOX + BOBCAT	526.83	4.18	0.031	10	506.83
FORPL + GRPL + GRAYFOX	527.10	4.45	0.027	11	505.10
RDHA	527.43	4.78	0.023	9	509.43
STHA + DTST + GRAYFOX	527.56	4.91	0.022	11	505.56
(.)	527.64	4.99	0.021	8	511.64
STHA + DTST	528.10	5.45	0.017	10	508.10
GRPL + GRAYFOX	528.50	5.85	0.014	10	508.50
STHA	528.55	5.90	0.013	9	510.55
STHA + BOBCAT	528.64	5.99	0.013	10	508.64
RDHA + GRAYFOX	529.00	6.35	0.011	10	509.00
FORPL + GRPL	529.37	6.72	0.009	10	509.37
GRAYFOX	529.63	6.98	0.008	9	511.63
FORPL + GRPL + BOBCAT	529.85	7.20	0.007	11	507.85
STHA + GRAYFOX	530.40	7.75	0.005	10	510.40
STHA + DTST + BOBCAT	547.53	24.88	0.000	11	525.53

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[a] Akaike Information Criterion.

[b] Model probability.

[c] Number of model parameters.

[d] Difference in -2Log(Likelihood) of the current model and -2log(Likelihood) of the saturated model as a measure of model fit.