

Habitat overlap among bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and Wild Turkeys (*Meleagris gallopavo*) in an agricultural landscape

C.K. Nielsen, C.R. Bottom, R.G. Tebo, and E. Greenspan

Abstract: Wild Turkey (*Meleagris gallopavo* Linnaeus, 1758) populations have grown considerably in the Midwestern U.S. alongside mesocarnivores, such as coyotes (*Canis latrans* Say, 1823) and bobcats (*Lynx rufus* (Schreber, 1777)). However, few studies have assessed habitat overlap between mesocarnivores and turkeys with a goal to understand potential impacts of mesocarnivores on turkeys. We captured and radiomarked bobcats, coyotes, and Wild Turkey hens in southern Illinois during 2011–2013 in an agricultural landscape and created single-species resource selection and overlap models. Wild Turkeys and bobcats demonstrated concentrated use in forested areas, whereas coyote use was highest in agricultural areas. We documented Wild Turkey nests ($n = 107$) and hen mortalities ($n = 28$), which were used to model the effect of bobcat, coyote, and Wild Turkey habitat use on turkey nest success and mortality. Increased coyote use was associated with higher nest success and increased turkey use was associated with higher probability of mortality. These findings suggest that top predators, such as coyotes, may be important and beneficial for ground-nesting avian species. With coyotes acting as the top predator throughout much of the Midwest, they are likely reducing densities of other important turkey nest predator species, thereby increasing nest success.

Key words: bobcat, *Canis latrans*, coyote, habitat modeling, Illinois, *Lynx rufus*, *Meleagris gallopavo*, mesocarnivore, predator–prey, species–habitat relationships, Wild Turkey.

Résumé : Les populations de dindons sauvages (*Meleagris gallopavo* Linnaeus, 1758) ont considérablement augmenté dans le Midwest des États-Unis parallèlement à celles de mésocarnivores, dont les coyotes (*Canis latrans* Say, 1823) et les lynx roux (*Lynx rufus* (Schreber, 1777)). Peu d'études ont toutefois évalué le chevauchement d'habitats entre les mésocarnivores et les dindons dans le but de comprendre les impacts potentiels des mésocarnivores sur les dindons sauvages. Nous avons capturé et radio-étiqueté des lynx roux, des coyotes et des dindons sauvages femelles dans le sud de l'Illinois de 2011 à 2013 dans un paysage agricole, et créé des modèles de sélection de ressources monospécifique et de chevauchement. Les dindons sauvages et les lynx roux présentaient une utilisation concentrée dans les zones boisées, alors que l'utilisation des coyotes était la plus forte dans les zones agricoles. Nous avons documenté des nids de dindons sauvages ($n = 107$) et des mortalités de dindons femelles ($n = 28$), qui ont été utilisés pour modéliser l'effet de l'utilisation de l'habitat par les lynx roux, les coyotes et les dindons sauvages sur le succès des nids et la mortalité des dindons. Une augmentation accrue par les coyotes est associée à un plus grand succès des nids et une utilisation accrue par les dindons est associée à une plus forte probabilité de mortalité. Ces constatations portent à croire que les prédateurs de niveau trophique supérieur, comme les coyotes, pourraient être importants et bénéfiques pour les espèces d'oiseaux nichant au sol. Étant donné le rôle de prédateurs de niveau trophique supérieur des coyotes dans une bonne partie du Midwest, ils réduisent probablement les densités d'autres importants prédateurs de nids de dindons, accroissant ainsi le succès des nids. [Traduit par la Rédaction]

Mots-clés : lynx roux, *Canis latrans*, coyote, modélisation de l'habitat, Illinois, *Lynx rufus*, *Meleagris gallopavo*, mésocarnivore, prédateur–proie, relations espèce–habitat, dindon sauvage.

Introduction

Historically, much of the Midwestern U.S. was home to several large carnivore species, including black bears (*Ursus americanus* Pallas, 1780), mountain lions (*Puma concolor* (Linnaeus, 1771)), and gray wolves (*Canis lupus* Linnaeus, 1758) (Feldhamer et al. 2003). Large-scale extirpation of these carnivores has likely resulted in a mesocarnivore release (Prugh et al. 2009), making mesocarnivores the de-facto apex predators in many ecosystems (Crooks and Soule 1999; Roemer et al. 2009). In much of the Midwestern U.S., this mesocarnivore release has produced an expansion of bobcat (*Lynx rufus* (Schreber, 1777)) and coyote (*Canis latrans* Say, 1823) popula-

tions (Neale and Sacks 2001; Woolf and Nielsen 2002; Nelson and Lloyd 2005; Roberts and Crimmins 2010). Bobcats and coyotes are sympatric throughout much of North America, exhibiting similarity in diet and habitat requirements, yet can co-exist through resource partitioning (Chamberlain and Leopold 1999; Neale and Sacks 2001; McDonald et al. 2008; Lesmeister et al. 2015).

Coincident with mesocarnivore increases, Wild Turkey (*Meleagris gallopavo* Linnaeus, 1758) populations have expanded substantially as the result of trap-and-transfer programs and harvest management (Kennamer et al. 1992; Tapley et al. 2005). Part of the success of these restoration programs can be attributed to the adaptability and generalist nature of the Wild Turkey (Porter 1992). Wild

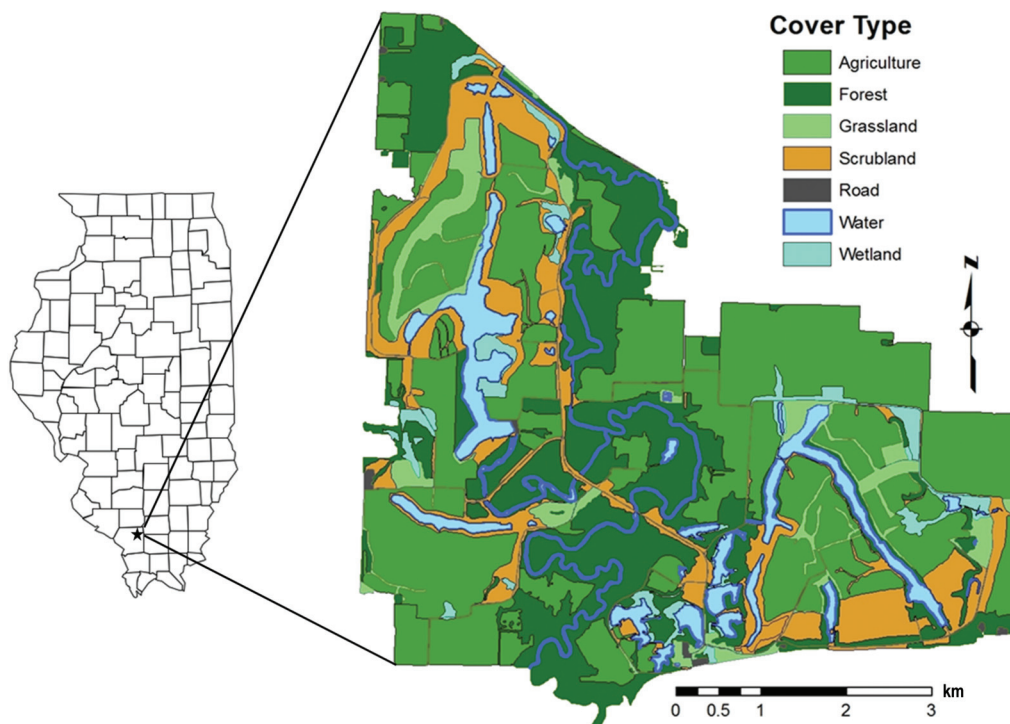
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Fig. 1. Cover type distribution for Burning Star No. 5 study area, southern Illinois, USA, 2011–2013. Color version online.



Turkeys are typically successful in forested landscapes containing interspersed open areas (Miller et al. 1999; Kiss et al. 2015a). Such areas (e.g., grasslands, forest openings, or abandoned fields) are important brood-rearing habitat and provide cover and abundant food sources (e.g., invertebrates) for turkeys. In agriculturally dominated landscapes, brooding hens use open areas with non-crop fields being preferred over crop fields (Wright et al. 1989). Successful turkey nests typically occur within spatially heterogeneous landscapes that contain larger forested tracts with a dense understory to provide visual obstructions from predators (Badyaev 1995; Delahunt 2011; Conley et al. 2015; Dreibelbis et al. 2015). High-quality nesting habitat is crucial to population growth, as nest success and poult survival are primary factors linked with population change (Hubbard et al. 1999; Hughes et al. 2005).

Despite the success of turkey restoration, many states in the Midwestern U.S. have reported declining population trends for Wild Turkeys, with mesocarnivores indicated as a possible limiting factor (Rolley et al. 1998; Hubbard et al. 1999; Thogmartin and Johnson 1999; Hughes et al. 2005; Eriksen et al. 2015). Nest success and survival rates of Wild Turkey adults and poults can be impacted greatly by mesocarnivores (Melville et al. 2014; Peyton et al. 2014; Pollentier et al. 2014; Kiss et al. 2015b; Little et al. 2016). Being a ground-nesting species with a relatively long incubation period of about 26 days (Healy 1992), Wild Turkeys are especially susceptible to predators with nest depredation rates ranging from 61% to 87% (Vangilder et al. 1987; Hughes et al. 2005; Melville et al. 2014). Raccoons (*Procyon lotor* (Linnaeus, 1758)) are the primary mammalian predator of Wild Turkey nests (Speake 1980; Williams and Austin 1988; Paisley et al. 1998; Melville et al. 2014), though many mesocarnivores and avian species may prey on Wild Turkey nests (Melville 2012; Martin et al. 2015). Mammalian predators, mainly canids, have been cited as the primary cause of Wild Turkey hen mortalities (Wright et al. 1996; Hubbard et al. 1999; Delahunt 2011; Niedzielski and Bowman 2014). Wild Turkey poults also are vulnerable to high levels of mortality (60%–90%) within 4 weeks of hatching (Everett et al. 1980; Speake et al. 1985; Peoples et al. 1995). Poults mortalities can occur due to starvation or extended periods

of rain, but the majority of poult mortalities (70%) are attributable to mammalian depredation (Speake et al. 1985; Vangilder and Kurzejeski 1995; Peoples et al. 1995). In southern Illinois, predation accounted for 78% of Wild Turkey nest failures, >90% of hen mortalities, and poult survival was estimated to be 25% at 4 weeks after hatch (Delahunt 2011).

Due to possible high levels of predation for Wild Turkeys at all life stages and the increase in mesopredators (Prugh et al. 2009), it is important to understand interactions between Wild Turkeys and mesocarnivores. Most studies that investigate turkey nest success or survival rates focus on the habitat attributes associated with successful and unsuccessful nests or locations of mortalities and only report rates of depredation (Thogmartin and Schaeffer 2000; Delahunt 2011; Melville 2012; Fleming and Porter 2015); few studies have simultaneously monitored habitat use of both Wild Turkeys and mesocarnivores (Lovell et al. 1995; Melville 2012). Although several models of habitat use exist for bobcats and coyotes (Nielsen and Woolf 2002; Woolf et al. 2002; McDonald et al. 2008; Lesmeister et al. 2015) in the Midwestern U.S., no studies have modeled habitat use for turkeys in the region. Melville (2012) investigated habitat use and overlap of mesocarnivores and Wild Turkeys, but did not directly investigate potential mesocarnivore impacts on Wild Turkey nest success and spatial location of turkey mortalities. To address these gaps in the literature, our objectives were to (i) create single-species models of habitat use for bobcats, coyotes, and Wild Turkeys; (ii) model habitat overlap among species; and (iii) determine the influence of mesocarnivore presence on Wild Turkey nest success and mortality.

Study area

We conducted research at Burning Star No. 5 mine (BS5), a 3400 ha wildlife area located in southern Illinois (37°50'21"N, 89°10'56"W). Formerly a coal mine owned and operated by Consolidation Coal Company, reclamation practices began in 1976 and continued through 2001, transforming the area into a successional diverse landscape (Fig. 1). Land cover during our study was about 50% agriculture; 25% forest; and a 25% interspersed of scrubland, grassland, wetlands, rivers, and lakes. Unmined bottom-

land hardwood areas were primarily characterized by mature oak (species of the genus *Quercus* L.), hickory (species of the genus *Carya* Nutt.), sycamore (*Platanus occidentalis* L.), maple (species of the genus *Acer* L.), and ash (species of the genus *Fraxinus* L.) stands. Grasslands comprised a variety of species including tall fescue (species of the genus *Festuca* L.), switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), Indiangrass (*Sorghastrum nutans* (L.) Nash), reedtop (*Agrostis gigantea* Roth), broom sedge (*Andropogon virginicus* L.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), multiflora rose (*Rosa multiflora* Thunb.), milkweed (species of the genus *Asclepias* L.), and goldenrod (species of the genus *Solidago* L.). Autumn olive (*Elaeagnus umbellata* Thunb.) was introduced in several reclamation areas. Other shrub species have increased over time, including eastern redcedar (*Juniperus virginiana* L.), hawthorn (species of the genus *Crataegus* L.), and smooth sumac (*Rhus glabra* L.). The property was managed under a partnership among the Illinois Department of Natural Resources, National Wild Turkey Federation, and the Cooperative Wildlife Research Laboratory of Southern Illinois University. The site was open to the public for archery and firearm white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) hunting in the fall and Wild Turkey hunting in spring.

Our study area has a temperate climate characterized by hot summers and mild winters with a seasonal mean winter temperature of 2 °C and a mean summer temperature of 25 °C. Precipitation is relatively consistent throughout the year with a slight increase in spring and 1200 mm of annual rainfall (NOAA 2010).

Materials and methods

Trapping

We captured Wild Turkeys during January–March 2012–2013 using updated rocket-netting techniques (Delahunt et al. 2011) at edges of agricultural fields where turkeys had been detected previously. Wild Turkey captures occurred from dawn to mid-day using a 9 m × 18 m net with 5 cm × 5 cm nylon 27 kg test mesh net, with three rocket leads and five anchor leads. Upon capture, female Wild Turkeys were weighed, aged as adults or juveniles using plumage characteristics, and fitted with a 105 g backpack-style radio transmitter with a 4 h mortality sensor (Vangilder et al. 1987; Wildlife Materials, Murphysboro, Illinois, USA). Turkeys were released at the original capture location within 45 min.

Bobcats and coyotes were captured along game trails in forest, grassland, and edge habitats during December–March 2011–2012 and 2012–2013. Bobcats were captured using cage and foot-hold traps, whereas coyotes were captured using cable restraints and foot-hold traps. Cage traps were 38 cm × 38 cm × 90 cm in size and constructed of wire mesh. Duke #3 and Bridger #3 rubber jawed, foot-hold traps were modified with 35 cm chains with an inline shock spring and swivels at the trap base, shock spring, and anchor (F and T Fur Harvesters Trading Post, Alpena, Michigan, USA). Cable restraints used were Professional Live Catch Coyote Snare constructed with 214 cm of 0.28 cm diameter, 7 × 7 galvanized aircraft cable. All cable restraints were built with a relaxing, bent-washer style lock, two wire-snare swivels (one inline and one at the anchor) and an 8.9 cm diameter minimum loop stop (Snare Shop, Lidderdale, Iowa, USA). Captured animals were restrained and a 9:1 ketamine:xylazine solution was administered intramuscularly either by hand or with a pole syringe at a dose of 13 mg/kg of estimated body mass. Each carnivore captured was weighed and aged (juvenile: <1.5 years; adult: >1.5 years) based on body size, mass, and tooth wear (Gier 1968; Crowe 1975). Adults were fitted with a 165 g radio transmitter collar with an 8 h mortality sensor (model HLP-2140; Wildlife Materials, Murphysboro, Illinois, USA). After handling, individuals were placed in a crate measuring 92 cm × 64 cm × 69 cm (Model 700 Series, Petco Classic Kennel) near the trap site and allowed to fully recover without further disturbance. Animals were released when they were fully

alert. All capture and handling procedures were conducted in accordance with a protocol approved by the Southern Illinois University at Carbondale Institutional Animal Care and Use Committee (SIUC Animal Assurance A-3078-01).

Radiotelemetry

Standard ground radiotelemetry techniques were used to relocate radiomarked individuals (White and Garrott 1990). Individuals were located 3–5 times/week during April–September (i.e., during the Wild Turkey breeding season) 2012 and 2013 using a handheld three-element Yagi antenna, GPS receiver, and compass. We estimated locations and associated error polygons using ≥3 bearings and the maximum likelihood estimator as described in Lenth (1981). All bearings were obtained within 15 min to reduce error associated with animal movement. Locations with associated error polygons <0.5 ha were used for analysis.

Habitat variables

We used a GIS (ArcView version 10.1; ESRI, Redlands, California, USA) and personal knowledge of the study area to hand digitize aerial photos into seven cover types: forest, agriculture, grassland, scrubland, wetland, road, and water. The resulting polygon layer was reclassified into a raster layer with 3 m × 3 m pixel size (Fig. 1). Forested areas consisted mostly of mature bottomland hardwoods. Agricultural areas contained row crops and were typically bordered by forests. The scrubland cover type was defined by dense vegetation with high levels of horizontal obstruction, occurring mostly along road ways and the edges of grasslands. Wetlands (mostly reclaimed strip-mine cuts) were abundant on the property relative to the surrounding landscape. The road system was gravel roads and dirt farm lanes; although roads were well represented on the study site, vehicle traffic was minimal due to the area being closed to the public. Open water bodies were abundant and ranged in size from <1 to >10 ha.

We created a nonoverlapping grid composed of 4507 hexagons (100 m diameter) and overlaid it on the land-cover raster of the study area. We believe that the 100 m diameter hexagons to be an appropriate size for considering the influence of surrounding habitat characteristics on an animal's decision to occupy a discrete location, especially given radiotelemetry error. Within each hexagon, we calculated 42 habitat variables at the class and landscape scales, from eight metric groups representing edge, shape, area, interspersed, and diversity metrics, using the program FRAGSTATS version 4.0 (McGarigal et al. 2012). The term landscape refers to variables that are computed for the entire patch mosaic within each hexagon; class variables are computed for every patch type or class in the landscape (McGarigal et al. 2012). To reduce the initial set of 42 habitat variables, we used a multivariate cluster analysis (PROC VARCLUS; SAS Institute, Inc. 2011). Cluster analysis is similar to principal component analysis and factor analysis in that it forms groups of variables which are highly correlated among themselves while being uncorrelated with variables in other groups. This technique is ideal for reducing the dimensionality of a data set with little loss of information (Nelson 2001; Pasta and Suhr 2004) and has been used in similar habitat research (Anderson et al. 2011; Cooper et al. 2012; Urbanek and Nielsen 2013). The most representative variable of each cluster was chosen based on the 1 – R² ratio (SAS Institute, Inc. 2011); this resulted in 10 variables being selected for habitat modeling (Table 1).

Modeling habitat use and overlap

Resource selection functions (RSF) were estimated using logistic regression to reflect the probability of use throughout the study area for all three focal species separately (i.e., single-species models) and for overlap of species pairs (i.e., overlap models). RSF models are a type of generalized linear model, similar to logistic regression models, except that RSF models use an exponential link function (McDonald 2013). We used a Design 2 approach

Table 1. Variables (McGarigal et al. 2012) used to model habitat overlap among Wild Turkeys (*Meleagris gallopavo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in southern Illinois, USA, 2011–2013.

Variable	Unit	Description
Percentage of landscape (PLAND) ^a	%	The sum of the areas (m^2) of all patches of the corresponding patch type divided by the total landscape area (m^2), then multiplied by 100 (to convert to a percentage)
Mean patch area (AREA_MN) ^b	ha	The sum of the areas (m^2) of all patches of the corresponding patch type divided by the number of patches of the same type, then divided by 10 000 (to convert to hectares)
Mean proximity index (PROX_MN) ^c	None	The sum of patch area (m^2) divided by the nearest edge-to-edge distance squared (m^2) between the patch and the focal patch of all patches of the corresponding patch type whose edges are within a specified distance (m^2) of the focal patch, summed across all patches of the same type, then divided by the total number of patches in the class

^aCalculated for forest, agriculture, water, wetland, grassland, and scrubland cover types.

^bCalculated for the road cover type.

^cCalculated for forest and agriculture cover types.

(Manly et al. 2002) at the landscape scale, as the entire study area was assumed to be occupied by all three species. In this design, data from individual animals were pooled and habitat variables were calculated at each location (i.e., used cell). All other nonused cells on the study area were classified as available cells. We used the log-linear equation to calculate the influence of habitat variables on the probability of species use:

$$\omega(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_p x_p)$$

where β_i are selection coefficients for each habitat variable (x_i) for $i = 1, 2, 3, \dots, p$, estimated using logistic regression.

We randomly selected a training data set composed of 75% of the relocation data to build each habitat distribution model and a validation set of the remaining 25% of relocation data (Capen et al. 1986). Validation points were overlaid on each single-species model and categorized into the appropriate habitat-use class in which they occurred. A χ^2 test was then used to compare the observed versus expected distribution of the validation points (Neu et al. 1974). The χ^2 test assumes a null hypothesis of validation points being randomly distributed. Rejection of the null hypothesis indicates a significant difference between expected and observed frequencies of validation points. Models were considered validated if test points occurred more than expected in habitat with $\geq 75\%$ probability of species use (Neu et al. 1974; Preuss and Gehring 2007).

We used Kruskal–Wallis ANOVA ($\alpha = 0.05$) to determine which variables differed among species (McDonald et al. 2008). If the ANOVA identified a significant overall difference, then we again used a Kruskal–Wallis ANOVA to determine pairwise differences among species. Because there were multiple comparisons among three species, we used a Bonferroni correction to obtain a more conservative P value of 0.017 (i.e., $\alpha = 0.05/3$) to indicate significance (Shaw et al. 1998; deMaynadier and Hunter 1999).

Turkey nest and mortality locations

Locations of Wild Turkey nests with known fates were obtained from radiomarked hens on our study area during breeding seasons of 2008–2010 (Delahunt 2011) and the current study. We considered hens to have initiated incubation of a nest when three consecutive daily locations were in close proximity (10 m) to previous locations, or if we used close-range (i.e., homing) radiotelemetry (Miller et al. 1998) to directly observe the nesting hen. If the transmitter emitted a mortality signal for a nesting hen, then we assumed a hen was incubating and visually marked the nest site by circling the nest from 20 m (Vangilder and Kurzejeski 1995). When a hen left a suspected nest site or was emitting a mortality signal for >24 h, we located the nest and determined its fate by examining evidence at the nest site (e.g., egg shell characteristics, egg count). Nests were considered successful if ≥ 1 poult fledged (Thogmartin and Schaeffer 2000).

Using RSF probabilities for mesocarnivores and Wild Turkeys, we developed four logistic regression models to determine whether habitat use of bobcats, coyotes, Wild Turkeys, or a combination of species were associated with nest success or failure within the appropriate cell. To rank and select candidate models, we used Akaike's information criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002; Fields et al. 2006). Models $< 2 \Delta AIC_c$ units from the top models were considered equally parsimonious. If there were ≥ 2 competing models, then we used model averaging to calculate variable coefficients.

Mortality locations also were recorded from radiomarked Wild Turkeys during the breeding season as they occurred; all deceased radiomarked hens were found within 72 h of their death (Delahunt 2011). Mesocarnivore and Wild Turkey use were compared between known turkey mortality locations and a separate sample of random locations with unknown presence of mortalities. We generated 100 random locations using Geospatial Modeling Environment (Beyer 2012) that were weighted by high Wild Turkey RSF values (i.e., high turkey use areas). An RSF model was used to compare locations of known mortalities with the “pseudo-absence” random locations, which have an unknown presence of mortalities (McDonald 2013; McDonald et al. 2013; Warton and Aarts 2013). Using seven RSF models, we estimated the relative probability of a mortality occurring in a given cell by comparing probability of species use at locations where mortalities occurred versus probability of species use at random locations with unknown presence of mortalities. Model selection techniques were the same as for analyses of nest success.

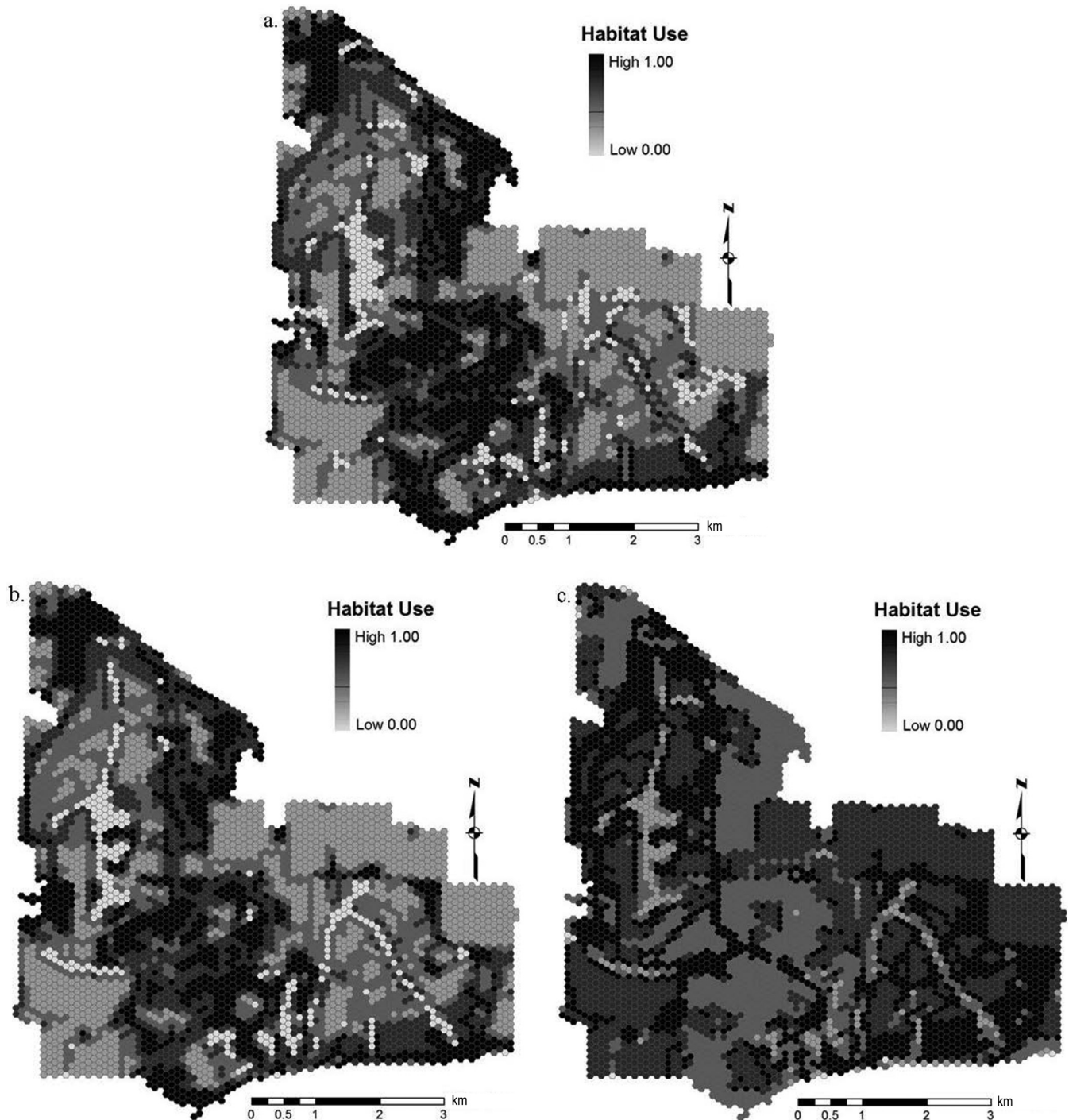
Results

Habitat models

We captured and radiomarked 44 Wild Turkey hens (10 juveniles, 34 adults), 14 adult bobcats (10 males, 4 females), and 19 adult coyotes (11 males, 8 females), and collected 400 bobcat, 550 coyote, and 1229 turkey radiolocations. Single-species habitat-use models (Figs. 2a–2c) were very accurate, with the majority of validation locations occurring more than expected in habitat with $\geq 75\%$ probability of areas used by bobcats ($\chi^2_{[4]} = 38.22$, $P < 0.001$), coyotes ($\chi^2_{[4]} = 14.34$, $P < 0.010$), and Wild Turkeys ($\chi^2_{[4]} = 175.19$, $P < 0.001$).

The three focal species differed most in their use of forest and agriculture cover types (Table 2). Bobcat habitat use was highly similar to Wild Turkeys, with only 3 of the 10 variables assessed differing between species (Table 2). Due to these similarities, the bobcat – Wild Turkey overlap model (Fig. 3a) closely resembled the original habitat model for each species; overlap between bobcats and Wild Turkeys did not occur in agricultural areas. Areas used by Wild Turkeys and coyotes (Table 2, Fig. 3b) differed in mean percentage of water, wetland, and grassland cover, as well as mean area of roads. Bobcat habitat use differed from coyotes (Table 2, Fig. 3c) in mean percentage of water, forest, and grass-

Fig. 2. Resource selection function (RSF) single-species models of habitat use for (a) Wild Turkeys (*Meleagris gallopavo*), (b) bobcats (*Lynx rufus*), and (c) coyotes (*Canis latrans*) in southern Illinois, USA, 2011–2013. High RSF values indicate areas with higher probability of use by each species.



land cover. Coyote habitat use varied the most from Wild Turkeys, with 7 of the 10 variables assessed different between species (Table 2). Wild Turkeys favored forested areas and did not highly use agricultural areas, which were occupied consistently by coyotes. Because coyotes used forested areas to an extent, overlap between coyotes and Wild Turkeys occurred primarily in forests, although less than in the overlap observed between bobcats and Wild Turkeys. Overlap between bobcats and coyotes occurred mostly in forested areas, though to a lesser extent than all other overlap models; this model was the only model that showed overlap occurring in agricultural cover (Fig. 3c).

Nest success

We obtained location and nest fate data for 78 nests from 42 hens during 2008–2010 (Delahunt 2011) and 29 nests from 23 hens during 2011–2013. Of the 107 total nests, 23 were successful and 84 failed. The top model indicated that nest success was positively influenced by coyote use ($\beta = 0.30 \pm 0.20$; Table 3).

Turkey mortality locations

We used 108 radiomarked turkey hens for models of habitat associated with mortality locations ($n = 64$ during 2008–2010 (Delahunt 2011) and $n = 44$ during 2011–2013); 28 mortalities oc-

Table 2. Habitat differences among Wild Turkeys (*Meleagris gallopavo*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in southern Illinois, USA, 2011–2013.

Variable	Species	Mean ± SD	χ^2	P
PLAND Forest	Turkey	55.622±39.703 A	213.210	<0.0001
	Bobcat	42.442±41.900 B		
	Coyote	21.057±34.506 C		
PLAND Agriculture	Turkey	13.327±28.116 A	165.522	<0.0001
	Bobcat	21.097±35.415 B		
	Coyote	40.931±43.020 C		
PLAND Water	Turkey	4.848±13.136 A	19.069	<0.0001
	Bobcat	4.156±12.140 A		
	Coyote	3.858±13.456 B		
PLAND Wetland	Turkey	0.757±5.803 A	43.722	<0.0001
	Bobcat	6.339±19.131 B		
	Coyote	4.565±15.880 B		
PLAND Grassland	Turkey	4.528±19.177 A	80.741	<0.0001
	Bobcat	5.024±17.703 A		
	Coyote	10.088±24.114 B		
PLAND Scrubland	Turkey	19.287±32.493	1.316	0.518
	Bobcat	19.209±34.292		
	Coyote	18.319±33.494		
AREA_MN Roads	Turkey	0.014±0.037 A	13.207	0.0014
	Bobcat	0.015±0.061 AB		
	Coyote	0.010±0.043 B		
PROX_MN Forest	Turkey	1.743±9.491 A	10.108	0.0064
	Bobcat	0.916±6.592 AB		
	Coyote	0.375±4.907 B		
PROX_MN Agriculture	Turkey	0.239±3.515	0.076	0.9627
	Bobcat	0.457±6.611		
	Coyote	0.404±5.013		
SHDI	Turkey	0.380±0.356	1.571	0.4506
	Bobcat	0.367±0.356		
	Coyote	0.365±0.369		

Note: Mean ± SD values with different letters were significantly different based on a Kruskal-Wallis ANOVA with a Bonferroni-corrected P value. For variable definitions see Table 1.

curred. For mortality locations, all single-species models were ranked above the null with Wild Turkey use being the only variable in the top model (Table 4). The Wild Turkey – coyote and Wild Turkey – bobcat models were competitive with the top model (Table 4). For Wild Turkeys ($\beta = -0.60 \pm 0.49$), bobcats ($\beta = -0.16 \pm 1.07$), and coyotes ($\beta = -0.40 \pm 0.77$), habitat use was negatively associated with mortality locations.

Discussion

Our study presents small-scale habitat distribution models for three common species that co-occur throughout much of the U.S. (Porter 1992; Feldhamer et al. 2003) and is the first to our knowledge to simultaneously monitor bobcats, coyotes, and Wild Turkeys to investigate habitat overlap among these species. Bobcats and Wild Turkeys largely used forested areas and coyote use was concentrated in agricultural areas; however, overlap among species was common. Our results provide insight into how a heterogeneous agricultural landscape can affect areas of potential interactions between bobcats and coyotes and provide hypotheses into how mesocarnivores may impact their prey. For example, we found evidence of higher levels of spatial segregation between bobcats and coyotes than have been previously reported in more homogenous, forested landscapes (Litvaitis 1981; Major and Sherburne 1987; Litvaitis and Harrison 1989; Chamberlain and Leopold 2005). We also provide information regarding the possible role of top predators in affecting nest success and survival of Wild Turkeys, the results of which are likely applicable to many systems, especially those with other ground-nesting bird species (e.g., songbirds and waterfowl; Sargeant et al. 1995; Sovada et al. 1995; Rogers and Caro 1998). We found areas used by coyotes were associated with higher Wild Turkey nest success, and habitat use for all three focal species was associated with locations of Wild

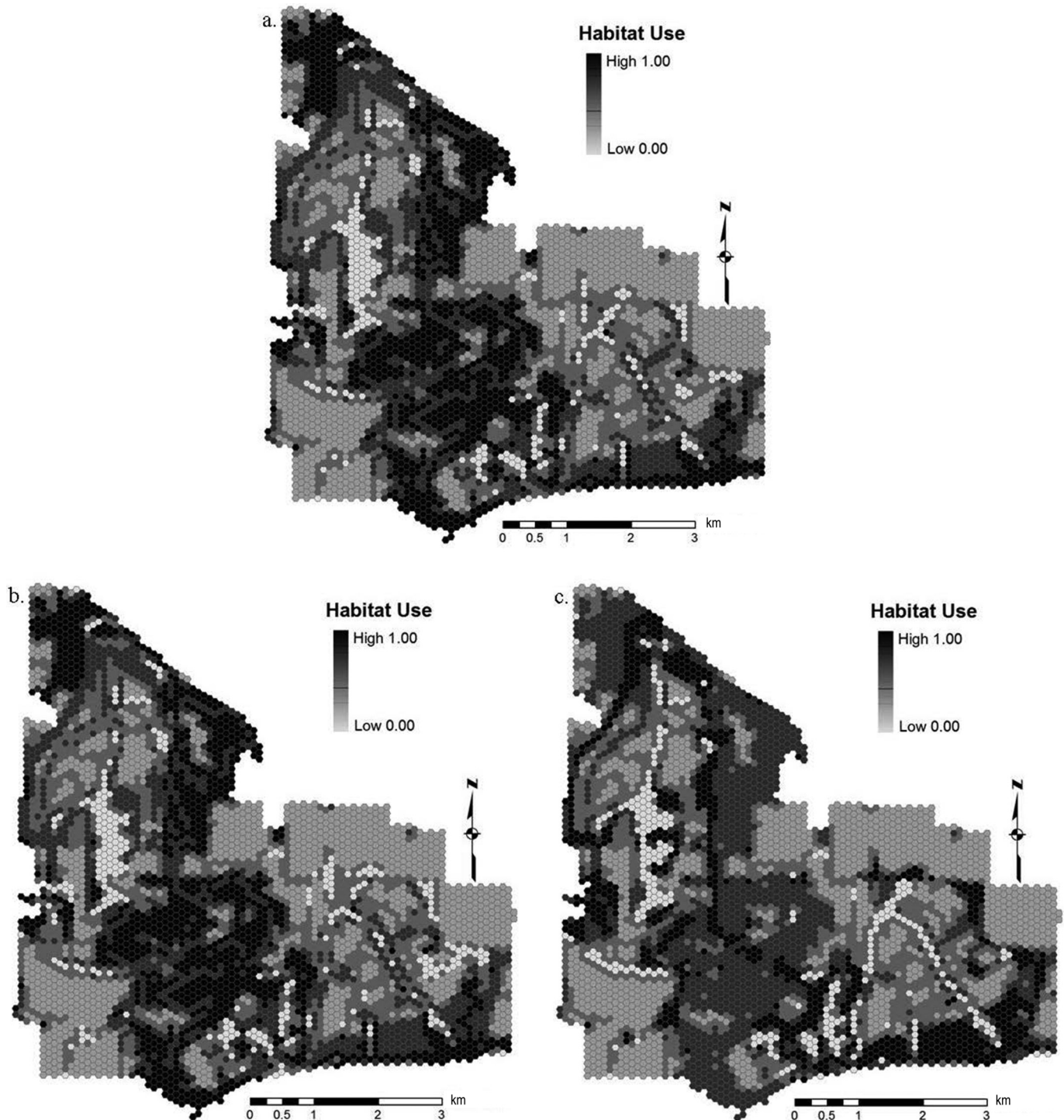
Turkey mortalities with Wild Turkey use being the most strongly supported variable.

Single-species models

Of the three focal species investigated, coyotes were the only species that highly used agricultural areas and did not heavily use forests. Because of the timing of the study (April–September), row crops were present for the majority of the investigation period. When row crops are present, coyotes are able to use agricultural areas for both feeding and cover because they provide straight-line pathways for travel and lend themselves well to coyotes' cursorial style of hunting (Van Deelen and Gosselink 2006). Coyote use of grassland and scrubland cover types on our study area also is consistent with previous studies in Illinois (Gosselink et al. 2003; McDonald et al. 2008; Lesmeister et al. 2015), but this association with grasslands is likely due to shared edges with agricultural cover. Grasslands typically contain higher densities of prey relative to agricultural cover types but also are characterized by lower prey detection and capture rates for predators (Gese et al. 1996a; Laundre et al. 2009). For coyotes, agricultural areas provide ample cover once crops reach a sufficient height (Gosselink et al. 2003; VanDeelen and Gosselink 2006), but cover at ground level is sparse making prey (e.g., small mammals) more vulnerable and thereby increasing detection and capture rates (Laundre et al. 2009).

Bobcat and Wild Turkey habitat use was very similar, with both species strongly using forested areas and avoiding large agricultural patches. A high level of forest use for both species is consistent with previous studies. Bobcats require relatively large and contiguous forest tracts and typically avoid open cover types, favoring dense understories (e.g., scrubland) for hunting (Nielsen and Woolf 2002; Preuss and Gehring 2007; McDonald et al. 2008;

Fig. 3. Resource selection function (RSF) overlap models of habitat use for (a) Wild Turkeys (*Meleagris gallopavo*) and bobcats (*Lynx rufus*), (b) Wild Turkeys and coyotes (*Canis latrans*), and (c) bobcats and coyotes in southern Illinois, USA, 2011–2013. High RSF values indicate areas with higher probability of overlap between species.



Lesmeister et al. 2015). Wild Turkey populations typically thrive in forested landscapes containing interspersed open areas, often selecting for forested bottomlands and dense shrubby areas (Miller et al. 1999; Cohen et al. 2015) such as those on our study area.

Wild Turkey hens do use open areas (e.g., agriculture, grasslands) for brooding and poult success is largely dependent on time spent foraging for insects produced in these areas (Healy 1985). However, agricultural areas offer limited forage value for brooding turkeys, so noncrop fields are typically preferred over crop

fields (Wright et al. 1989). In our study, Wild Turkey preference for brooding in nonagricultural open areas likely accounted for grasslands having the largest impact on Wild Turkey habitat use rather than bobcat or coyote presence. Scrubland also was important in determining Wild Turkey use and they were the only species for which mean area of roads influenced habitat use. Both of these variables were likely important for Wild Turkeys as nesting habitat. Successful Wild Turkey nests on the study area typically occurred in areas characterized by high levels of horizontal

Table 3. Competing models used to examine the influence of species' habitat use on Wild Turkey (*Meleagris gallopavo*) nest success in southern Illinois, USA, 2008–2010 and 2011–2013.

Model ^a	<i>k</i>	AIC _c	ΔAIC _c	ω _i
Coyote	2	110.29	0.00	0.63
(.) ^b	1	112.93	2.64	0.17
Bobcat	2	113.24	2.95	0.14
Turkey	2	114.99	4.70	0.06

Note: AIC_c, Akaike's information criterion adjusted for small sample size; ΔAIC_c, change in AIC_c value from top model; ω_i, Akaike weight; *k*, number of parameters estimated.

^aValues obtained from habitat models related to single-species resource-selection functions.

^bNull model indicates validation points being randomly distributed.

obstruction (e.g., scrubland), especially within 1 m of the nest (Delahunt 2011). Roads had a positive impact on Wild Turkey habitat use because scrubland areas typically occurred along road edges throughout the study area.

Overlap models

Coyote – Wild Turkey overlap occurred mostly in forested areas and in areas with high cover-type diversity. Wild Turkeys did use agricultural areas preferred by coyotes, but likely only as travel corridors (Porter et al. 1980). Coyotes are a remarkable generalist species capable of using most available habitat types (Person and Hirth 1991; Grinder and Krausman 2001; Gehrt et al. 2009). When in forests, coyotes tend to select hardwood stands and open understories (Lesmeister et al. 2015), which were abundant in our study area and largely used by Wild Turkey hens (Delahunt 2011). Thus, the limited use of crop fields by Wild Turkeys and the ability of coyotes to use forested areas led to coyote – Wild Turkey overlap occurring largely in forested areas. Overlap also occurred in scrubland and grassland cover types and roads; these areas provided habitat for Wild Turkey nesting and brooding (Delahunt 2011) and hunting opportunities for coyotes (Gese et al. 1996b).

In the coyote–bobcat model, overlap occurred mostly in forested areas, though to a lesser extent than for coyotes and Wild Turkeys. Previous studies of sympatry between bobcats and coyotes reported similarities in habitat use and activity patterns (Major and Sherburne 1987; Litvaitis and Harrison 1989; Chamberlain and Leopold 2005; McDonald et al. 2008). However, our models showed strong spatial segregations between species, with coyote use of agricultural cover being contrasted by bobcats' relatively low agricultural use and high use of forested areas. Differences in these findings from previous studies are likely attributed to the seasonal timing of our study and high levels (48%) of agricultural cover types on our study area. Many of the previous studies (e.g., Litvaitis 1981; Major and Sherburne 1987; Litvaitis and Harrison 1989; Chamberlain and Leopold 2005) were conducted year-round, in areas dominated by forest cover types, or during times when row crops were not usually present (McDonald et al. 2008). Conversely, our study was conducted primarily during the growing season when row crops were abundant, thereby increasing the cover available to coyotes.

Differences in habitat patterns between bobcats and coyotes are likely also explained by differences in food habits and, ultimately, as a way of avoiding interspecific competition. Bobcats have a more specialized diet as obligate carnivores compared with more generalist omnivorous coyotes. Diets of bobcats in southern Illinois are composed mostly (75%) of small mammals (e.g., Muridae, rabbits, squirrels; Woolf and Nielsen 2002), whereas coyotes consume mammals and fruits and insects when abundant (Andelt et al. 1987). Most fruit species in our study area (e.g., blackberries

Table 4. Competing models used to examine the influence of species' habitat use on locations of Wild Turkey (*Meleagris gallopavo*) mortalities in southern Illinois, USA, 2008–2010 and 2011–2013.

Model ^a	<i>k</i>	AIC _c	ΔAIC _c	ω _i
Turkey	3	47.51	0.00	0.42
Turkey + coyote	4	48.31	0.80	0.28
Turkey + bobcat	4	49.39	1.87	0.17
Turkey + coyote + bobcat	5	49.95	2.44	0.13
Bobcat	3	63.03	15.52	0.00
Coyote	3	80.17	32.66	0.00
(.) ^b	2	82.13	34.62	0.00

Note: AIC_c, Akaike's information criterion adjusted for small sample size; ΔAIC_c, change in AIC_c value from top model; ω_i, Akaike weight; *k*, number of parameters estimated.

^aValues obtained from habitat models related to single-species resource-selection functions.

^bNull model indicates validation points being randomly distributed.

(species of the genus *Rubus* L.) and persimmon (*Diospyros virginia* L.) were highly available during the study season and were abundant on edges, especially agricultural edges. In addition to dietary differences, the likely high abundance of food resources in the study area may be allowing bobcats to spatially segregate themselves from coyotes. Wilson et al. (2010) found that given sufficient resources, bobcats will spatially avoid coyote core areas, which they attributed as a way to reduce interspecific competition. However, when resources became limited, Wilson et al. (2010) reported bobcat home ranges were more likely to occur within coyote core areas. In areas characterized by a mosaic of agriculture and forest patches such as southern Illinois, bobcats may avoid agricultural areas and increase use of forested areas to limit the chances of agonistic encounters with coyotes. Forested areas also provide bobcats with dense cover that facilitates their stalk-and-ambush style of predation (Litvaitis and Harrison 1989; Anderson and Lavallo 2003; Preuss and Gehring 2007). Although some interspecific competition may have occurred between bobcats and coyotes, the spatial segregation that we observed may simply be a result of differing habitat preferences (McDonald et al. 2008; Lesmeister et al. 2015), and an abundance of resources may be allowing bobcats to spatially avoid high coyote use areas (Wilson et al. 2010).

We found considerable habitat overlap between Wild Turkeys and bobcats. High forest and low agricultural use by both species is consistent with previous studies (Nielsen and Woolf 2002; McDonald et al. 2008; Delahunt 2011; Lesmeister et al. 2015). Scrubland and grassland cover types and roads were areas used by turkeys for nesting and brooding and likely by bobcats for hunting.

Nest success

We recognize that our analyses of potential mesocarnivore effects on nest success and mortality locations of turkeys are correlative in nature and therefore best for developing hypotheses for future research. Coyote use had a positive influence on Wild Turkey nest success and coyotes were identified as the most important species in predicting nest success. Coyotes are known to depredate Wild Turkey nests (Wright et al. 1996; Hubbard et al. 1999; Delahunt 2011; Martin et al. 2015), but also are acting as the top predator in Midwestern ecosystems and are therefore capable of reducing the local abundance of many other mesocarnivore species (e.g., bobcats, raccoons, red foxes (*Vulpes vulpes* Linnaeus, 1758)), skunks (*Mephitis mephitis* Schreber, 1776)) that are responsible for the majority of nest depredate events (Sovada et al. 1995; Rogers and Caro 1998; Miller et al. 2001). This is especially important in the case of coyote–raccoon interactions, as raccoons represent the top nest predator of ground-nesting birds (Sargeant et al. 1993; Rogers and Caro 1998). Coyotes are known to prey upon

raccoons at rates that can limit raccoon abundance (Andrews and Boggess 1978; Clark et al. 1989), creating a significant inverse relationship between coyote and raccoon abundance (Sargeant et al. 1993). Coyotes' ability to reduce abundance of smaller mesocarnivore species leads to an overall lower density of nest predators in a given area, which has been shown to increase nest success, particularly for ground-nesting birds (Sargeant et al. 1995; Sovada et al. 1995; Rogers and Caro 1998), such as the Wild Turkey. This positive relationship between top predator habitat use and nest success has been observed extensively in canine guilds in the prairie pothole region of the U.S. and Canada where coyotes reduced red fox abundance, thereby increasing waterfowl nest success (Sargeant et al. 1993; Sovada et al. 1995); this relationship also has been observed in systems with avian top predators. Arctic waterfowl (e.g., Red-breasted Geese (*Branta ruficollis* (Pallas, 1769)), Steller's Eiders (*Polysticta stelleri* (Pallas, 1769)), Brant Geese (*Branta bernicla* (Linnaeus, 1758))) often nest in close proximity to top avian predators that are aggressive towards other major nest predators such as the Arctic fox (*Vulpes lagopus* (Linnaeus, 1758)). This aggression can reduce local Arctic fox abundance in the nesting colonies, thereby increasing nest success for avian species (Summers et al. 1994; Quinn et al. 2003; Quakenbush et al. 2004).

We hypothesize bobcats were likely not included in the top nest success models for two reasons. First, bobcats, similar to raccoons, are subordinate to coyotes and can be displaced spatially (Wilson et al. 2010) or, in rare cases, preyed upon by coyotes (Litvaitis and Harrison 1989). In our study area, bobcat use and coyote use showed a strong negative correlation ($r = -0.79$, $P < 0.001$); therefore, areas associated with high bobcat use were likely areas of low coyote use, and vice versa. We suggest that low coyote use may lead to higher localized densities of other mesocarnivore species which can negatively impact Wild Turkey nest success rates. Second, bobcats are solitary and wide ranging, and usually exist at lower densities than coyotes (Nielsen and Woolf 2002; Lesmeister et al. 2015). Even assuming that bobcats had the same per capita impact as coyotes in reducing densities of smaller mesocarnivores, due to relatively low densities of bobcats, we hypothesize that their overall impact on reducing mesocarnivore densities would likely be less than that of coyotes. Rather than using habitat models, we suggest that future research assess the relationship between mesocarnivore behavior and turkey nesting ecology to provide a more comprehensive assessment of nest depredation relationships in this system.

Turkey mortality locations

Habitat use by all three species predicted the location of Wild Turkey hen mortalities, though Wild Turkey use was the only variable for which the coefficient did not overlap with 0 ($\beta = 0.60 \pm 0.49$). Although bobcats and coyotes were the two main predators of Wild Turkey hens in our study area (Delahunt 2011), it is important to note that Wild Turkeys do not constitute a significant portion of either species' diet (Chamberlain and Leopold 1999; Neale and Sacks 2001; Woolf and Nielsen 2002). Hen survival is lowest during the Wild Turkey breeding season (Vangilder and Kurzejeski 1995; Delahunt 2011), but bobcats and coyotes are likely not having significant impacts because adult hen survival was relatively high (>70%) in our study area (Delahunt 2011). Given that their main food sources (e.g., small mammals, fruits) are likely increasing or peaking in abundance during the Wild Turkey breeding season (Melville 2012), bobcats and coyotes are likely focusing on more abundant or easier to capture food sources and are primarily consuming Wild Turkeys opportunistically.

Conclusions

We provide single-species and overlap habitat-use models for Wild Turkeys, coyotes, and bobcats to better understand how predators may be impacting Wild Turkey populations in diverse Midwestern landscapes. High levels of habitat overlap among coy-

otes, bobcats, and Wild Turkeys may result in an increase of both direct and indirect predator-prey interactions, particularly between coyotes and Wild Turkeys. These interactions may impact prey species either through direct predation events resulting in an individual being removed from the population or in behavioral changes made by the prey in an effort to avoid predation (Lima 1998; Berger et al. 2001; Miller et al. 2001; Orrock et al. 2010; Wilson et al. 2010). Both bobcats and Wild Turkeys will alter their behavior (e.g., feeding locations, time spent vigilant) in response to changes in coyote use (Wilson et al. 2010; Melville 2012), which may result in decreased nest success and survival for Wild Turkeys. Given the abundance of prey and cover resources on our study area, bobcats may be successfully avoiding coyotes through spatial segregation (Wilson et al. 2010). The high contrast in habitat use between bobcats and coyotes means that Wild Turkeys are almost always in areas which overlap with known predators. The more time a Wild Turkey spends in overlap areas increases their chances of having an encounter and a potentially negative interaction with mesocarnivores.

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