

Scale-dependent Factors Affecting North American River Otter Distribution in the Midwest

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ABSTRACT.—The North American river otter (*Lontra canadensis*) is recovering from near extirpation throughout much of its range. Although reintroductions, trapping regulations and habitat improvements have led to the reestablishment of river otters in the Midwest, little is known about how their distribution is influenced by local- and landscape-scale habitat. We conducted river otter sign surveys from Jan. to Apr. in 2008 and 2009 in eastern Kansas to assess how local- and landscape-scale habitat factors affect river otter occupancy. We surveyed three to nine 400-m stretches of stream and reservoir shorelines for 110 sites and measured local-scale variables (*e.g.*, stream order, land cover types) within a 100 m buffer of the survey site and landscape-scale variables (*e.g.*, road density, land cover types) for Hydrological Unit Code 14 watersheds. We then used occupancy models that account for the probability of detection to estimate occupancy as a function of these covariates using Program PRESENCE. The best-fitting model indicated river otter occupancy increased with the proportion of woodland cover and decreased with the proportion of cropland and grassland cover at the local scale. Occupancy also increased with decreased shoreline diversity, waterbody density and stream density at the landscape scale. Occupancy was not affected by land cover or human disturbance at the landscape scale. Understanding the factors and scale important to river otter occurrence will be useful in identifying areas for management and continued restoration.

INTRODUCTION

The North American river otter (*Lontra canadensis*) historically occupied most of North America (Toweill and Tabor, 1982), but by the early 1900s, overharvest, habitat loss and water pollution reduced river otter populations to less than 33% of their historic range in the contiguous 48 states (Nilsson and Vaughn, 1978; Toweill and Tabor, 1982; Larivière and

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Walton, 1998). Concerns about population declines and extirpation of a species with ecological, economic, cultural and aesthetic importance led many management agencies across the United States to initiate restoration programs in the 1980s (Raesly, 2001). Over the past 30 y, >800 otters from several regions have been released into Missouri, 159 in Nebraska, 14 in Oklahoma and 17 in Kansas (Fleharty, 1995; Shackelford and Whitaker, 1997; Gallagher, 1999; Bischof, 2003). Reintroductions, immigration from neighboring areas, habitat improvement and stringent harvest regulations are credited with the reestablishment of the species to 90% of their historic range in the U.S.; making for one of the most successful carnivore reintroductions in history (Raesly, 2001; Melquist *et al.*, 2003; Roberts *et al.*, 2008).

During the early 1800s river otters were believed to be common along all the major streams and rivers in Kansas during the early 1800s, but in 1904 the last reported otter was trapped near Manhattan in northeastern Kansas (Lantz, 1905; Bee *et al.*, 1981). Efforts to restore the river otter in Kansas began in 1983 to 1985 when Kansas Department of Wildlife and Parks released 17 river otters from Minnesota and Idaho into the South Fork of the Cottonwood River in Chase County, Kansas (Fleharty, 1995). River otters are classified as a furbearer in Kansas, but there is currently no open harvest. Incidental trappings, road kill carcasses, anecdotal sightings and results from limited sign surveys (Eccles, 1989; Ostroff, 2001) confirm river otter presence in Kansas, but little is known about their current distribution and how local- and landscape-level habitat factors affect their distribution.

The most common method to assess river otter presence and habitat associations is with sign surveys, which measure spatial patterns of animals based on the detection or non-detection of animal tracks, feces or other sign (Raesly, 2001; Heinemeyer *et al.*, 2008). The most common sign types for otters are tracks and scat, which is often found at communal latrine sites. Several latrines are typically found throughout a river otter's home range and visitation to these sites is high (Ben-David *et al.*, 1998). However, sign surveys often fail to account for false absences, which occur when a species is determined to be absent at a site although it was in fact present but went undetected (Ruiz-Olmo *et al.*, 2001; MacKenzie *et al.*, 2006; Evans *et al.*, 2009). These false absences may lead to an underestimation of true occupancy and consequently imprecise conclusions from wildlife-habitat models (MacKenzie *et al.*, 2002, 2006). Occupancy models have recently been developed to account for imperfect detection by incorporating estimates of detection probability and may improve inferences about species distributions and habitat relationships.

A better understanding of how habitat affects river otter occurrence can help predict areas of current and future occupancy, evaluate population trends and identify areas for management focus and restoration. River otters tend to exhibit regional differences in their habitat requirements (Melquist *et al.*, 2003). Thus, a study that found conifers were important to river otter presence in Pennsylvania (Swimley *et al.*, 1998) or that river otters preferred coastal marshes in Texas (Foy, 1984) has limited applicability for determining river otter habitat in the Great Plains.

Additionally, the scale at which river otter occurrence is influenced by habitat is critical for proper recovery and management of the species. Johnson (1980) hypothesized that animals select resources at several hierarchical spatial scales, but studies of river otter habitat associations tend to evaluate only one habitat scale and often fail to adequately describe that scale. However, local-scale habitat may be important to river otter occurrence. For example, river otters are often associated with habitats that have beaver (*Castor canadensis*) denning structures (Melquist and Hornocker, 1983; Dubuc *et al.*, 1990; Waller, 1992; Newman and

Griffin, 1994; Boege-Tobin, 2005; Rosell *et al.*, 2005). However, stream channelization, water quality and land use practices can degrade aquatic food resources and reduce the availability of denning sites for river otters (Pitt *et al.*, 2003). Griess (1987) observed that river otters tend to use waterways that are not heavily polluted, and in Europe, activity of the closely-related Eurasian otter (*Lutra lutra*) increased with stream order and a surrounding riparian cover of woodland and semi-natural grassland vegetation (White *et al.*, 2003). In addition, a Kansas study found the percentage of woodland/riparian areas and the number of waterbodies within 300 m of the shoreline was positively associated with river otter presence (Ostroff, 2001).

Local populations of animals are also likely affected by regional scale processes. However, the effects of variables at broader spatial scales (*e.g.*, watersheds) have not been adequately addressed or contrasted with local-scale variables for river otters (Ricklefs, 1987; Levin, 1992; Barbosa *et al.*, 2001, 2003). For example, Eurasian otters were more common in areas with a higher percentage of forest cover measured at a national scale (Robitaille and Laurence, 2002). In Maine, river otter use was positively associated with watershed length and average shoreline diversity in a watershed, which can indicate an increased amount of shallow foraging habitat (Dubuc *et al.*, 1990). Finally, human disturbance as measured by human and road densities has been shown to have a negative relationship with otter presence at regional and national spatial scales (Robitaille and Laurence, 2002; Boege-Tobin, 2005; Gorman *et al.*, 2006). Therefore, river otter distribution may be affected by land use and human disturbance at larger, landscape scales.

A primary objective of this study was to determine the factors affecting river otter distribution in eastern Kansas at two spatial scales, a local scale and a landscape scale. One method for identifying important scale(s) is to model sign data using occupancy models incorporating the potential relationships at multiple scales and determine which models fit the data best (Holland *et al.*, 2004). Consequently, we developed and tested several hypotheses regarding factors such as land cover and use, geographic location, hydrologic features and human disturbance and their effects on the presence of river otters in eastern Kansas.

River otter occurrence has been linked to seasonal prey (*i.e.*, fish, crayfish) availability and abundance and riparian cover, which can be tied to the local landscape characteristics and water quality. Fishes are often more abundant in areas of woody debris (Angermeier and Karr, 1984), which is linked to the amount of riparian woodland cover. In contrast, areas with increased agriculture land tend to have lower water quality and biotic integrity (Wang *et al.*, 1997). Furthermore, the availability of cover and denning and resting sites, such as those created by beaver activity, provided by woodland riparian areas and influenced by the land use practices have all been correlated with river otter occurrence (Bradley, 1994; Newman and Griffin, 1994; Swimley *et al.*, 1998; Pitt *et al.*, 2003; Boege-Tobin, 2005; Gorman *et al.*, 2006; LeBlanc *et al.*, 2007; Gallant *et al.*, 2009). Therefore, we predicted the areas with predominant woodland and natural grassland cover type would have a higher probability of occupancy than sites that are mainly agricultural and urban land cover types. We also predicted that larger waterbodies and more sinuous and diverse shorelines would be indicative of reduced disturbance and higher prey availability and would be positively associated with river otter presence. Conversely, we predicted areas with high levels of human disturbance, such as high road density and polluted waterbodies, and areas located far from possible source populations, such as Missouri and Oklahoma, which have harvestable river otter populations would have lower probabilities of occupancy.

METHODS

STUDY AREA

Our study area covered the eastern third of Kansas (about 54,000 km²) from the Missouri border west to approximately Manhattan, KS (96.6°W), and from Nebraska south to Oklahoma. Major rivers included the Kansas River, Caney River, Little Caney Creek, Verdigris River, Neosho River, Marais Des Cygnes River, Little Osage River and Marmaton River. The highest elevations are in the northwest portion of the study area (510 m) and the lowest elevations in the southeast (204 m). The area is predominately rural (>95%) with the Kansas City and Topeka metro areas being the largest urban areas (>100,000 people; U.S. Census Bureau, 2007). The dominant land cover is grassland (56.3%) followed by cropland (25.4%) and woodland (11.1%).

SURVEY METHODS AND DESIGN

Sampling effort was stratified into seven watershed regions, which we refer to as otter units, to allow us to compare occupancy probabilities in different regions of the state. The otter units were further delineated into 14-digit U.S. Geological Survey Hydrological Unit Codes (HUC 14) watersheds that ranged in size from 4000 to 16,000 ha. There were 21 to 154 HUC 14 watersheds in each otter unit. Since river otter home ranges follow stream drainage patterns (Melquist and Hornocker, 1983), watersheds were considered appropriate sample units and we assumed otter sign located at a site within a watershed indicated that river otters were using the watershed. Five hundred twenty-nine watersheds containing at least one third order or higher stream or reservoirs with shorelines ≥ 3600 m were available for surveying. We then randomly selected watersheds for river otter sign surveys. We did not survey first and second order streams due to their small size and low likelihood of river otter use (Prenda *et al.*, 2001; Kiesow and Dieter, 2005; Barrett, 2008).

Surveys began at bridges, low-water crossings or locations where water was adjacent to a roadway or access point (*e.g.*, boat launch; Lodé, 1993; Romanowski *et al.*, 1996; Shackelford and Whitaker, 1997; Barrett, 2008). Sites with public land access were given preference to reduce the amount of time obtaining landowner permission and when only multiple private sites were available, we randomly selected access points until permission was obtained. We assumed there was no difference in river otter use between public and private sites. We conducted sign surveys between 9 Feb. and 13 Apr. 2008 (30 d) and between 28 Jan. and 8 Apr. 2009 (44 d). The late winter/early spring months were chosen for multiple reasons. First, it is the breeding season of otters and scent-marking at latrines is likely to be at its highest (Gallagher, 1999). We also expected differences in diets between river otters and raccoons (*Procyon lotor*) during this time, potentially making their scat easier to differentiate (Swimley *et al.*, 1998; McElwee, 2008). Furthermore, vegetation at this time is less dense than in other months, expectedly making sign easier to find (Swimley *et al.*, 1998; Ostroff, 2001). Sites sampled within the same year were ≥ 16 stream km apart while different year sites were ≥ 8 stream km apart to ensure spatial independence. This was based on average river otter home range sizes and distances used in past otter surveys (Melquist and Hornocker, 1983; Clark *et al.*, 1987; Shackelford and Whitaker, 1997; Barrett, 2008). Sites were not sampled within 2 d of precipitation (>0.2 cm) to avoid sign degradation (Clark *et al.*, 1987; Shackelford and Whitaker, 1997; Barrett, 2008). However, we expected that sign degraded quickly, with most scat and tracks well degraded within 1 mo (M. Jeffress, pers. obs.).

Most sites (82.7%) consisted of nine contiguous 400 m long by 5 m wide shoreline surveys. Each 400-m survey was considered an independent visit, thus allowing for spatial replication of surveys to determine the detection probability (MacKenzie *et al.*, 2006). Personnel

TABLE 1.—Data layers and sources used to measure variables associated with occupancy modeling of river otters based on sign survey data collected in eastern Kansas, USA, 2008–2009

Source	Description	Year of data	Resolution
Kansas Dept. of Transportation	State and county roads	2006	
Kansas Aquatic Gap Analysis Program	National Hydrography Dataset (NHD) streams with order classification	2003	1:24,000
U.S. Geological Survey	NHD waterbodies	2006	1:24,000
Kansas Applied Remote Sensing Program	Kansas Land Cover Patterns	2005	30-meter
Farm Services Agency	National Agriculture Imagery Program (NAIP) color aerial imagery by county	2006	1-meter
U.S. Environmental Protection Agency	NHD locations for Section 303(d) listed waters		
U.S. Geological Survey	Hydrologic Unit Code (HUC) 14 watersheds	1993	

conducting sign surveys were trained in sign identification for one day in the field before conducting surveys. Locations of all tracks (≥ 1 foot track) and scat/latrines (≥ 1 piece of scat), visually-estimated dominant substrate type (*i.e.*, mud, rock, litter, vegetative and snow), and the presence of active beaver sign, as indicated by fresh cuttings and tracks, were recorded for each survey.

DATA ANALYSIS

We created encounter histories for both sign types combined and used occupancy models that account for false absences (*e.g.*, Mackenzie *et al.*, 2006) to determine the local- and landscape-scale factors associated with river otter presence. The occupancy covariates were chosen based upon their potential influence on river otter use. We evaluated models at two spatial scales, a local scale and a landscape scale. The local-scale variables were measured within a 100-m buffer around the entire survey site (1200–3600 m) while HUC 14 watersheds (4000–16,000 ha) were used to assess the landscape-scale variables. Most variables were measured or derived using ESRI's ArcMap 9.3 from maps and databases acquired from the Data Access and Support Center (<http://www.kansasgis.org/>) of the Kansas Geological Survey and other similar Geographic Information System (GIS) data access sites or were collected at the survey site. A complete list of data files and sources is provided in Table 1 and both local- and landscape-scale variables are listed in Table 2. These variables were primarily related to land use, human disturbance, stream size and type and geographic position. We used *z*-transformations to standardize (*i.e.*, the mean was subtracted from each value and then divided by the standard deviation) all continuous covariates, except the land cover variables which were left as proportions, and coded all categorical covariates (0 or 1) prior to analysis.

We assumed: (1) that river otter sign was never falsely detected at a point when absent and (2) detection of sign at a point was independent of detecting sign at other points. Occupancy modeling also requires the assumption that the population is closed during the sampling period (MacKenzie *et al.*, 2002). We therefore assumed that otter movements over the survey season were random, which allowed us to relax this assumption (MacKenzie *et al.*, 2004; Longoria and Weckerly, 2007).

We developed a set of candidate models *a priori* based on our experience and the literature to model the factors associated with the probability of river otter occupancy (ψ)

TABLE 2.—Environmental variables evaluated for their effects on river otter occupancy, eastern Kansas, USA, 2008–2009. Values in the mean column for presence/absence (P/A) variables are the percentage of sites with the variable present (e.g., 44 sites (40.0%) were listed as 303(d) water quality impaired). SE = standard error

Variable	Description	Mean (SE)	Range
<i>Local scale variables</i> (n = 110)			
CropS	Proportion of survey w/100 m buffer comprised of cropland	0.24 (0.02)	0–0.71
GrassS	Proportion of survey w/100 m buffer comprised of grassland	0.30 (0.02)	0–0.95
WoodS	Proportion of survey w/100 m buffer comprised of woodland	0.46 (0.02)	0.05–0.97
Sinuosity*	Survey segment sinuosity (length of survey line/ distance between end points; m/m)	1.72 (0.05)	1.01–5.17
Dist*	Stream distance of site to nearest of border line for either Missouri or Oklahoma (km)	93.80 (6.63)	1.07–257.01
303(d)	The waterbody is 303(d) impaired (P/A)	40.0%	
Third order**	The site was a 3 rd order stream (P/A)	32.7%	
Fourth order**	The site was a 4 th order stream (P/A)	30.0%	
Fifth order**	The site was a 5 th order stream (P/A)	12.7%	
Sixth-seventh order**	The site was a 6 th –7 th order stream (P/A)	8.2%	
Res	The site was a reservoir (P/A)	16.4%	
<i>Landscape scale variables</i> (n = 110)			
UrbanW	Proportion of watershed comprised of urban	0.02 (0.01)	0.00–0.46
CropW	Proportion of watershed comprised of cropland	0.26 (0.02)	0.01–0.88
GrassW	Proportion of watershed comprised of grassland	0.60 (0.02)	0.08–0.94
WoodW	Proportion of watershed comprised of woodland	0.13 (0.01)	0.03–0.51
Shore*	Sum of the waterbody perimeters/sum of waterbody areas for entire watershed (km/km ²)	0.06 (0.00)	0.00–0.09
Stream*	Sum of stream ($\geq 3^{\text{rd}}$ order) km within the watershed/watershed area (km/km ²)	0.26 (0.01)	0.08–0.70
Bodies*	Number of waterbodies within the watershed/ watershed area (count/km ²)	1.62 (0.68)	0.24–3.71
Road*	Sum of road km within the watershed/watershed area (km/km ²)	1.59 (0.05)	0.45–5.76

* Variables were standardized

** Based on Strahler order (Strahler, 1957)

and river otter sign detection probability (P; Table 3). Our most basic model included the probability of occupancy and detection probability held constant across all substrates, surveys and habitat types (ψ , P.). We then developed models with only local-scale variables, models with only landscape-scale variables, combination models with both local- and landscape-scale variables and a global model with all local- and landscape-scale variables. All models were additive, and all models included the intercept on both ψ and P. Since the probability of detecting sign could be affected by substrate type, models were run with substrate effect on P and with P held constant. Our model set consisted of a total of 41 candidate models.

TABLE 3.—Set of candidate models considered to explain river otter occupancy (ψ) and detection probability (P) at sites surveyed in eastern Kansas, USA, 2008 to 2009

Model name	Model structure*		No.
	ψ	P	Parameters*
<i>Local scale models</i>			
Waterbody	Sinuous Orders Res	Substrate	11
Pollution	303(d)	Substrate	7
Distance to borders	Dist	Substrate	7
Land cover	WoodS GrassS CropS	Substrate	9
<i>Landscape scale models</i>			
Water diversity	Shore Stream Bodies	Substrate	9
Disturbance	Road UrbanW	Substrate	8
Land cover	WoodW GrassW CropW	Substrate	9
<i>Hybrid models**</i>			
Local scale + landscape scale	See models above	See models above	≤ 20

* Intercept parameters for ψ and P were included in all models. Nineteen models were run for 2 scenarios of P (*i.e.*, substrate, P constant)

** Models consisted of every combination of a local-scale model (*e.g.*, waterbody, land cover) with a landscape-scale model (*e.g.*, water diversity, disturbance)

We performed a single-season, single-species, custom occupancy estimation analysis using Program PRESENCE Version 2.3 (Hines, 2006). We evaluated goodness-of-fit and overdispersion (\hat{c}) using the median \hat{c} value from a parametric bootstrap test ($n = 1000$) and adjusted for overdispersion prior to model selection (Burnham and Anderson, 2002; MacKenzie and Bailey, 2004). The estimated median \hat{c} value for our global occupancy model was 1.52, suggesting slight overdispersion of the data (Burnham and Anderson, 2002). Therefore, we ranked models using Akaike's Information Criterion corrected for small-sample size and overdispersion (QAICc; Burnham and Anderson, 2002), and used the QAICc differences and Akaike weights to evaluate model fit to the data. Models with $\Delta\text{QAICc} \leq 2.0$ were considered competitive models (Burnham and Anderson, 2002).

RESULTS

A total of 110 sites were surveyed in 2008 and 2009, 35 of which resulted in river otter detections (Fig. 1). We sampled 18 reservoirs and 92 streams; 75% of the streams were third or fourth order. Beaver sign was recorded for all but six sites (95%), and therefore was not included in the occupancy modeling.

When examining a model where the probability of occupancy varied by our seven otter units, we observed regional differences throughout our study area. The probability of occupancy by otter landscape unit was highest in the Southeast unit ($\psi = 0.827$) and lowest in the Caney River ($\psi = 0.103$) and Kansas River units ($\psi = 0.114$). The Caney River unit had the highest proportion of grassland cover (0.844) and the lowest proportion of cropland cover (0.038). The Southeast Kansas unit had the highest proportion of woodland (0.173) while the Neosho River unit had the lowest (0.069). The proportion of urban area was highest in the Kansas River unit, but was still only 0.070.

Across all 14 watersheds in the study area, landscape-scale grassland covered the highest proportion of the HUC 14 watersheds (mean = 0.602) while woodland (mean = 0.125)

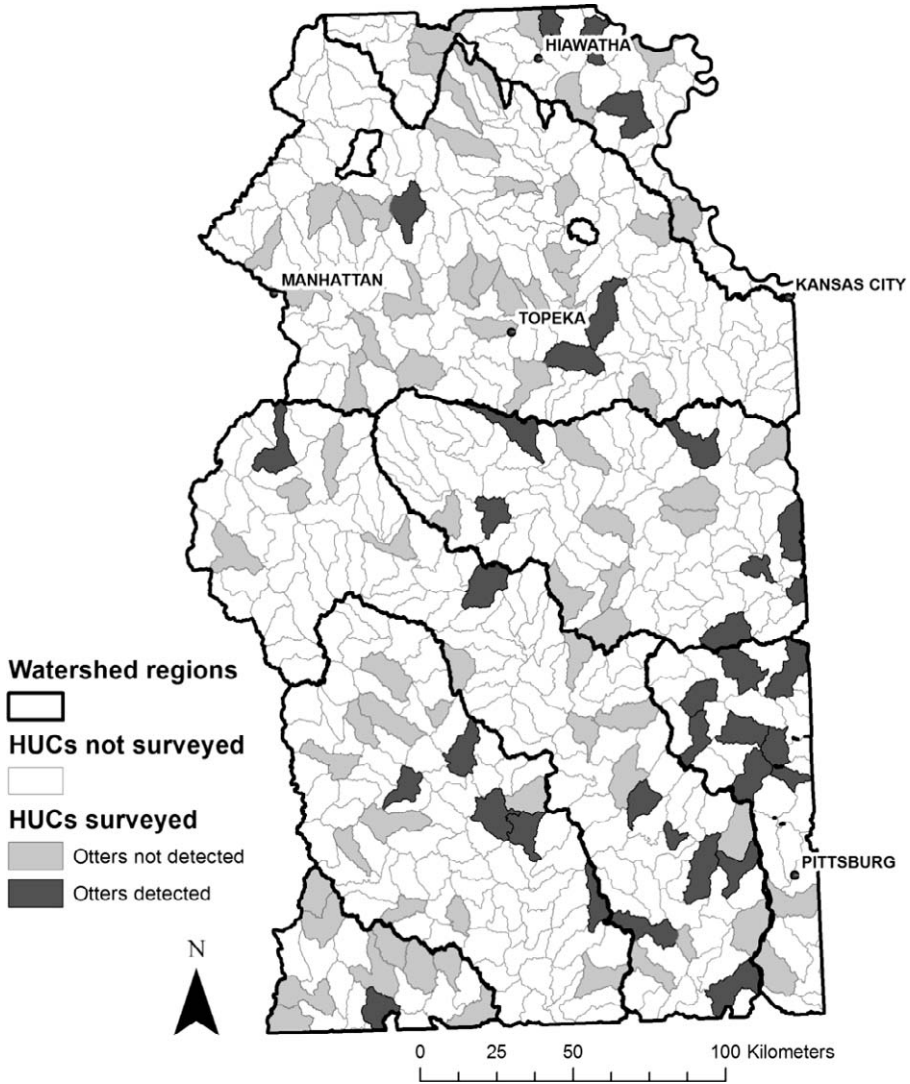


FIG. 1.—Watersheds (Hydrological Unit Code 14) surveyed and detection results for river otter sign in eastern Kansas, USA, 2008–2009. The seven watershed regions, or otter units, are distinguished with a thick black outline

followed by urban (mean = 0.020) were the least dominant land cover types. The cropland, grassland and woodland cover types at the local scale were relatively evenly distributed (Table 2). However, urban land cover was so sparse (only three sites were >0.01 urban) within 100 m of the stream (*i.e.*, at the local scale) that it was excluded from analysis. Urban land cover at the landscape scale was retained for further analysis because of the wide range of this variable (proportion of urban land cover varied from 0 to 0.46 of the watershed). Of

TABLE 4.—The highest-ranked models of river otter occupancy (ψ) and detection probability (P) based on sign surveys conducted in eastern Kansas, USA, 2008-2009. See Table 2 for model variables. Models with Akaike weights <0.05 are not shown. Information presented is the number of parameters (K), deviance ($-2 \times \log$ -likelihood), Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC_c; $\hat{c} = 1.52$), the difference between the model QAIC, and the best fit model QAIC_c (Δ QAIC_c) and the Akaike weight of the model (w_i)

Model structure (ψ P)		K	Deviance	QAIC _c	Δ QAIC _c	w_i
ψ	P					
local land cover + water diversity	substrate	12	469.8	336.3	0.0	0.316
local land cover + water diversity	—	8	487.0	337.8	1.5	0.150
local land cover	substrate	9	484.2	338.3	2.0	0.116
distance to borders + water diversity	substrate	10	482.1	339.4	3.1	0.069

the sites surveyed, 40% do not meet the water quality standards of the state and have been listed as impaired under the U.S. Environmental Protection Agency Clean Water Act.

The overall probability of occupancy accounting for detection probability was 0.329 (SE 0.046). The overall probability of detection was 0.337 (SE 0.029) per 400-m survey. Models including the local-scale land cover variables and the landscape-scale water diversity variables ranked highest in explaining river otter occupancy (Table 4). The best model given our set of candidate models consisted of local-scale land cover and landscape-scale water diversity, including shoreline diversity, waterbody density and stream density effects on occupancy with a substrate effect on detection probability. Although the top three models (QAIC_c < 2.01) included local-scale land cover, none of the competing models contained land cover measured at the landscape scale.

The probability of river otter occupancy increased with increasing woodland and decreasing grassland and cropland at the local scale (Fig. 2). The probability of river otter occupancy decreased with increasing shoreline diversity, waterbody density and stream density (Fig. 3). Substrate type was also present in our top model for an effect on detection probability. Mud substrates (P = 0.600; SE 0.075) had the highest detection probability while litter (P = 0.267; SE 0.037) and snow (P = 0.180; SE 0.116) substrates had the lowest detection probabilities. Snow was the dominate substrate for very few sites (2.1%) and was typically hard pack or covered with ice and therefore river otter tracks often did not leave impressions (Jeffress *et al.*, 2011).

DISCUSSION

Local-scale land cover was the best predictor of river otter occupancy in eastern Kansas. Our best model for the probability of river otter occupancy included effects of the local land cover and the water diversity characteristics measured within the watershed. We observed an increase in river otter occupancy with increased woodland cover and decreased grassland and cropland cover at the local scale. In addition, river otter occupancy decreased with increased shoreline diversity, waterbody density and stream density at the landscape scale and the significance of these variables may have been influenced by the presence of large reservoirs in the watershed. However, landscape-scale measures of land cover and human disturbance did not strongly affect river otter occupancy.

The positive relationship between woodland cover and occupancy supports our hypothesis that river otters prefer forested riparian areas even if sites averaged $>75\%$ grassland and cropland. Riparian land with woodland cover may provide more woody debris

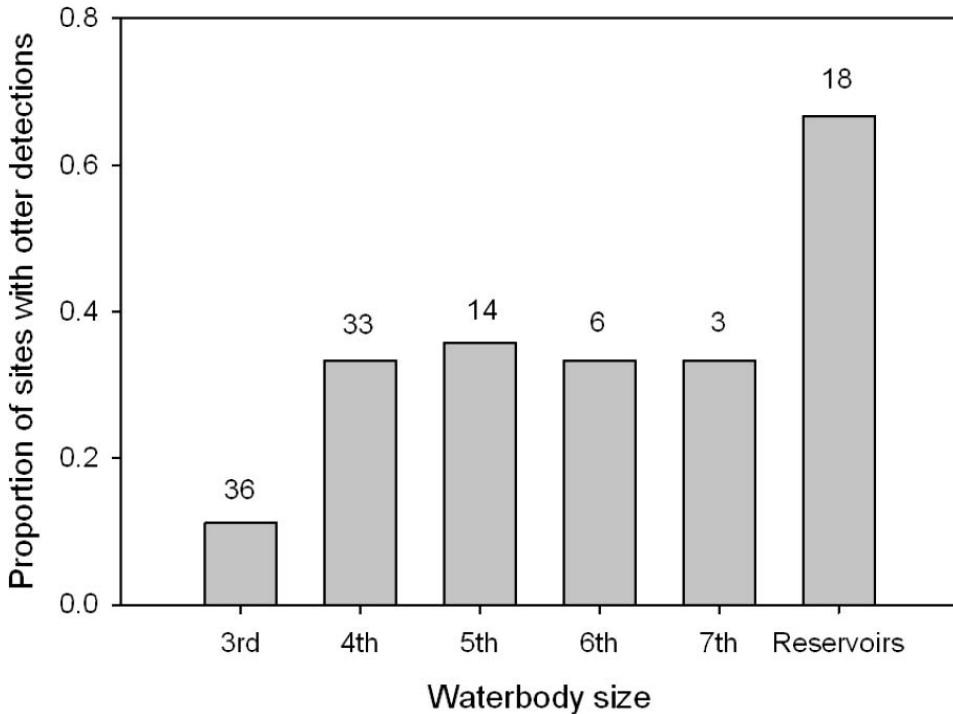


FIG. 2.—The proportion of sites surveyed with the river otter sign detection results by stream order and reservoir in eastern Kansas, USA, 2008–2009. Number of sites surveyed for each waterbody size provided above the bar

in the streams, which may increase fish abundance (Angermeier and Karr, 1984) and therefore prey availability for river otters. Additionally, obvious declines in habitat quality for fish have been observed when agriculture becomes the dominant land use at sites ($\geq 50\%$; Wang *et al.*, 1997). Although we expected grasslands to have higher occupancy than cropland, this finding might be explained by how grassland is defined. In our study, native, ungrazed grasslands could not be differentiated from grazed grasslands. We documented cattle activity at 39% of our sites, and grazed areas may differ from the semi-natural grasslands that were found to be positively associated with latrine activity of the Eurasian otter (White *et al.*, 2003). Furthermore, Bas *et al.* (1984) found that grazed land had fewer latrine sites for Eurasian otters, which supports our finding that grasslands were associated with low otter occupancy.

Lower stream density, fewer waterbodies and reduced shoreline diversity at the landscape scale were positively related to river otter presence. The negative influence of water diversity model variables on river otter occupancy also countered our predictions. However, we found that watersheds containing large reservoirs (≥ 3600 m shoreline) tended to have high river otter occurrences while having the lowest shoreline diversity, stream densities and waterbody densities. For example, six of the 10 watersheds that had the lowest stream densities contained large reservoirs, five of which were occupied by otters, and 13 of the 15 watersheds with the lowest shoreline diversities contained large reservoirs, 10 of which were occupied. Other researchers have proposed that the creation of impoundments has created

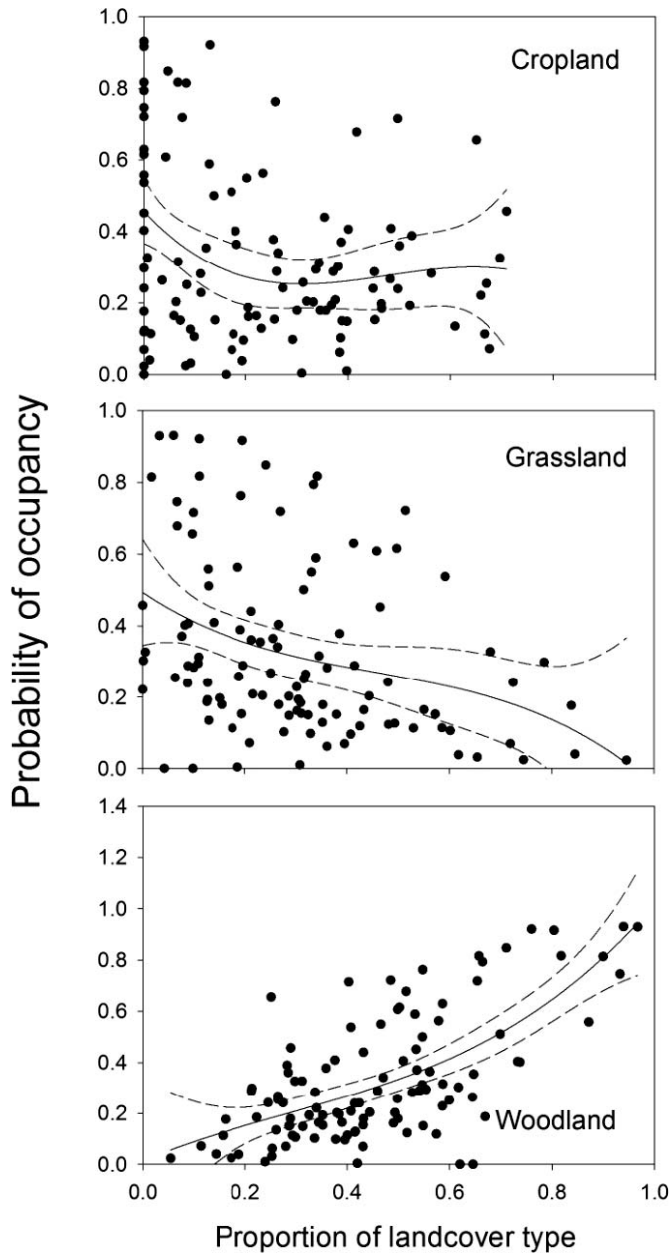


FIG. 3.—Relationships between the probability of river otter occupancy and the proportion of local-scale cropland, grassland and woodland cover types as derived from the best fit model, eastern Kansas, USA, 2008–2009. Confidence bands (95%) are presented as dashed lines

more surface area of permanent water and shorelines which river otters prefer (Shackelford and Whitaker, 1997; Melquist *et al.*, 2003). It is possible that sites with large reservoirs provide more suitable habitat, particularly in the winter when smaller ponds and streams are often frozen and inaccessible. Therefore, the relationship between river otter presence and the water diversity variables may be masked by the presence of reservoirs in the watershed.

Additionally, our method of modeling stream order as a categorical variable may have reduced its ranking by penalizing the model for a high number of parameters. A model that included waterbody size as an effect on the probability of occupancy indicated that third order streams had a low probability of occupancy ($\psi = 0.115$; SE 0.054) compared to the higher order streams ($\psi = 0.340$ – 0.372 ; SE 0.085– 0.160) and reservoirs ($\psi = 0.683$; SE 0.115; Fig. 4). Furthermore, after combining stream orders *a posteriori* to reduce the model to three variables (third order, fourth-seventh order and reservoirs), waterbody type became a competing model (AIC weight = 0.339). Our results suggest larger streams and reservoirs had higher river otter occupancy, similar to the results of White *et al.* (2003). Although river otters may use a wide variety of deepwater and wetland habitats (Newman and Griffin, 1994), watersheds containing larger streams and reservoirs may be better suited for river otters in Kansas.

Contrary to Robitaille and Laurence (2002), higher human presence and road density did not influence river otter occupancy in Kansas. Lack of influence for some variables could be a result of their low variability among sites. For example, most watersheds were rural with a low proportion of urban land cover (0.016). Road density, which may affect wildlife distributions (Mech *et al.*, 1988; Robitaille and Laurence, 2002), was not related to river otter occupancy. However, road densities in Kansas were low (85 m/km^2) compared to densities in Oklahoma (118 m/km^2), Missouri (123 m/km^2) and Arkansas (189 m/km^2), all of which have established river otter populations (LaRue and Nielsen, 2008). Additionally road density does not necessarily represent human presence and disturbance. For instance, studies of wolves in North America have shown that wolves will select areas of higher road density if human presence is low (Boyd-Heger, 1997; Whittington *et al.*, 2005). Furthermore, European countries had similar road densities to our study area, although the human population densities in Europe (109 people/km^2 ; Robitaille and Laurence, 2002) are much higher than Kansas (13 people/km^2 ; U.S. Census Bureau, 2000) and likely equate to higher road use and other indicators of human presence compared to the many rural county roads in eastern Kansas. Finally, Robitaille and Laurence (2002) found that Eurasian otters were consistently absent when human densities reached $>183 \text{ people/km}^2$ because otters appeared to have a threshold for human density. States in the Great Plains typically have much lower population densities and human disturbance appears to have little effect on river otter occupancy in this region.

Our study is the first to describe river otter habitat associations after accounting for imperfect detection. Pagano and Arnold (2009) documented that surveys based on the assumption of perfect detection underestimated waterfowl abundance by 10–29%, and Mazerolle *et al.* (2005) found that not accounting for detection probability led to underestimation and overestimation of the influence of habitat variables on pond occupancy by frogs. Measuring detection probability reduces bias and provides stronger inference about studies of habitat associations. Our study was the first to examine the detectability of river otter sign, and we found substrate type to be a factor affecting the detection probability. Therefore, we hope future studies will account for substrate in their habitat analysis. Further details about the detectability of otter sign during surveys from this study can be found in Jeffress *et al.* (2011).

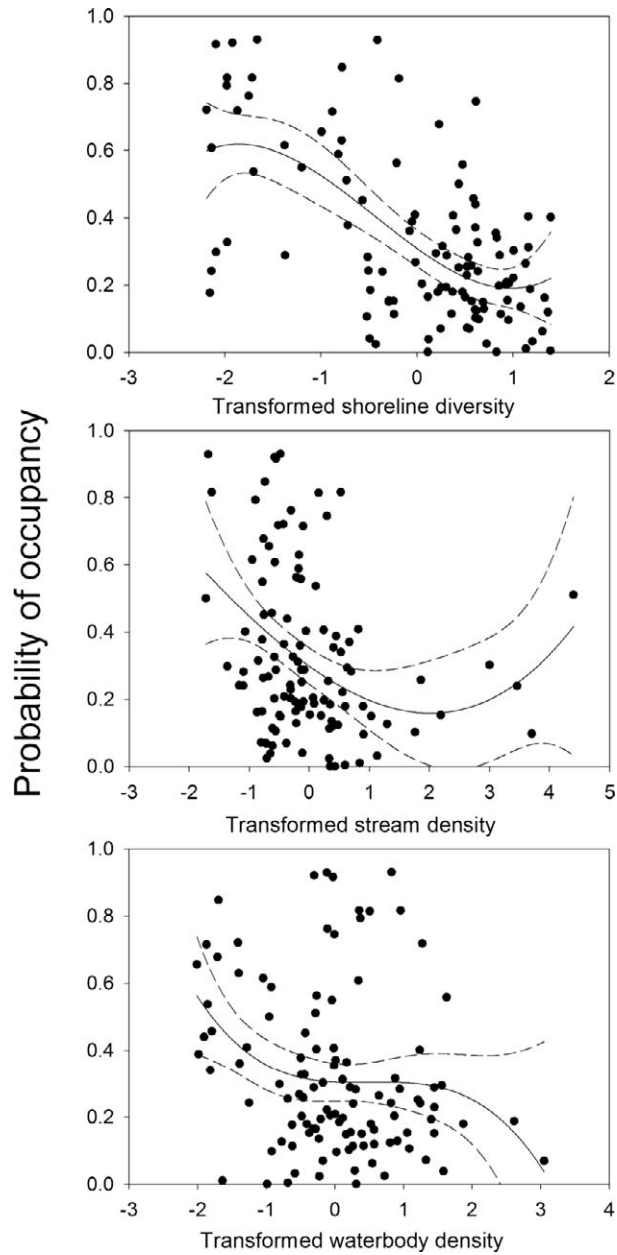


FIG. 4.—Relationship between probability of river otter occupancy and the Z-transformed shoreline diversity (km/km^2), stream density (km/km^2) and waterbody density (count/km^2) as derived from the best fit model, eastern Kansas, USA, 2008–2009. Confidence bands (95%) are presented as dashed lines

Although beaver activity was not included in the modeling, we found evidence of fresh beaver activity at every site where river otters were detected, anecdotally supporting previous findings that river otter activity is highest where beavers are also present (Melquist and Hornocker, 1983; Dubuc *et al.*, 1990; Waller, 1992; Newman and Griffin, 1994; Boege-Tobin, 2005; Rosell *et al.*, 2005). River otters appeared to be distributed throughout eastern Kansas. However, the highest occupancy was in southeastern Kansas, which coincides with a high number of fur harvester sighting reports in that area (Shardlow *et al.*, 2009) and increased woodland cover. High occupancy may be attributed to the high proportion of woodland cover in the unit. Furthermore, occupancy by otter unit was lowest in the Caney River, Kansas River and Missouri River units, which had the highest proportions of grassland cover (Caney River), urban use (Kansas River) and cropland cover (Missouri River). Our results show that grassland at the local scale negatively influences river otter occupancy and this may also be the cause at this larger scale. Also, studies have found that the high urban and agricultural land use in watersheds reduces the biotic integrity of the aquatic system, which could consequently have negative impacts on otters (Wang *et al.*, 1997, 2001). However, our analysis indicated that pollution (*i.e.*, sites that were listed as impaired by the US EPA) was not a strong predictor of river otter occupancy. These correlations suggest there may be an effect of land cover at an even larger scale and future studies should consider examining these and other variables in the future.

Wildlife ecology and management is recognizing the need to account for scale in wildlife-habitat associations, but scale has not been thoroughly analyzed in previous river otter studies. River otters tend to be generalist species (Habib *et al.*, 2003), and it is possible they are able to make use of locally-distributed resources in a variety of landscapes (Pearson, 1993). Future work should further examine the impacts of land use practices on river otter habitat, and our results suggest that habitat restoration and management may be most beneficial at the local scale. Studies should also look for trends at a regional scale. Furthermore, research of wildlife-habitat relationships should use occupancy modeling techniques that account for imperfect detection for less biased estimates and inferences.

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