



Research Article

Habitat Modeling Used to Predict Relative Abundance of Bobcats in Iowa

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ABSTRACT We combined observations of bobcats (*Lynx rufus*) from bowhunters with remotely-sensed data to build models that describe habitat and relative abundance of this species in the agricultural landscape of Iowa, USA. We calculated landscape composition and configuration from publicly available land cover, census, road, hydrologic, and elevation data. We used multiple regression models to examine county-level associations between several explanatory variables and relative abundance of bobcats reported by surveyed bowhunters in each county. The most influential explanatory variables in the models were metrics associated with the presence of grassland, including Conservation Reserve, along with configuration of this perennial habitat with forests, although human population density and abundance of eastern cottontails (*Sylvilagus floridanus*) also correlated with abundance of bobcats. Validation of predictions against 3 years of independent data provided confidence in the models, with 66% of predictions within 1 bobcat/1,000 hunter-hours and 95% within 5 bobcats/1,000 hunter-hours of observed values. Once we accounted for landscape differences, no residual spatial trend was evident, despite relatively recent bobcat recolonization of Iowa. Models suggested that future range expansion of the bobcat population may be possible in some northern Iowa counties where habitat composition is similar to counties in southern Iowa where bobcats are abundant. Results from the county-level model have been useful to the Iowa Department of Natural Resources in evaluating the expansion of this once rare species and for delineating harvest opportunities. © 2011 The Wildlife Society.

KEY WORDS bobcat, bowhunter survey, Geographic Information Systems (GIS), habitat model, Iowa, *Lynx rufus*, relative abundance.

In the last few decades, there has been great interest among conservation biologists and wildlife managers in the expansion of carnivores throughout North America (Breitenmoser et al. 2001). However, surveying sparse and secretive carnivores and anticipating changes in distribution and abundance over large regions is a difficult task. Wildlife ecologists want to understand the underlying ecological mechanisms influencing apparent changes in distribution, but often must begin with developing surveys and models that identify influential variables and provide reasonable methods to accurately assess trends. Much of the research on predicting large-scale distribution of wildlife has been to combine presence or abundance of the target species with habitat and environmental variables derived from Geographic Information Systems (GIS; Peterson 2001, Scott et al. 2002).

Bobcats (*Lynx rufus*) are the most broadly distributed felid in North America and populations are increasing (Roberts

and Crimmins 2010). Bobcats occur in a wide variety of habitats from southern Canada to Mexico and from the east coast to the west coast (Anderson and Lovallo 2003). Prior to European settlement, bobcats were distributed throughout the prairie-woodland mosaic of the midwestern United States, but by 1900 bobcats were largely extirpated from the corn belt region (Deems and Pursley 1983, Larivière and Walton 1997). This distribution gap has been attributed to the combination of unregulated trapping and hunting, and extensive conversion of the landscape to row crop agriculture (Bowles 1975, Woolf and Hubert 1998, Anderson and Lovallo 2003). Recently, a number of midwestern states, including Iowa, have documented a natural recolonization by bobcats in the corn belt region (Hamilton 1982, Woolf et al. 2002, Reding 2011).

The factors associated with this expansion might be as simple as conservative regulation of harvest (Roberts and Crimmins 2010) because bobcats can potentially be over-harvested (Fuller et al. 1985, Knick 1990, Anderson and Lovallo 2003). However, bobcats are completely protected from harvest in all or parts of most midwestern states (Rolley et al. 2001, Woolf et al. 2002, Reding 2011), suggesting that other factors have contributed to the observed changes in

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distribution despite the nearly complete landscape conversion from diverse prairie-woodland to predominately row crop agriculture. Bobcats are most often associated with woodland habitats (Anderson and Lovallo 2003), but also occupy more open landscapes comprised of bluffs and brushy habitat where there is adequate stalking cover (Hamilton 1982, Koehler and Hornocker 1991). They are generally not a species of open grasslands (Anderson and Lovallo 2003) although it is reasonable to hypothesize that changes in the agricultural landscape associated with the Conservation Reserve Program (CRP) might have improved habitat for bobcats (Tucker et al. 2008). Bobcats are adaptable and can be found in suburban habitat with dense cover even though they avoid humans (Riley et al. 2003, Roberts et al. 2010). Crooks (2002) characterized bobcats as moderately sensitive to habitat fragmentation. Although bobcats consume a variety of prey, the majority of their diet is lagomorphs in almost all regions (Larivière and Walton 1997, Anderson and Lovallo 2003). The distribution and abundance of lagomorphs has been related to bobcat ecology (Litvaitis et al. 1986, 2006; Knick 1990; Benson et al. 2006) as well as classically to population dynamics of other species of *Lynx* (Nellis et al. 1972, Aldama et al. 1991). Stalking cover and the avoidance of coyotes (*Canis latrans*; Litvaitis and Harrison 1989, Koehler and Hornocker 1991, Henke and Bryant 1999) has also been related to bobcat habitat selection behavior.

Given the various habitat factors that have been identified from region to region (Larivière and Walton 1997, Anderson and Lovallo 2003), development of region-specific habitat models has been a goal of bobcat conservation and management (Bluett et al. 2001). Many habitat models have been built based on data collected in landscapes that were primarily forested (e.g., Maine, Litvaitis et al. 1986; Wisconsin, Lovallo and Anderson 1996; Mississippi, Constible et al. 2006; Michigan, Preuss and Gehring 2007). On a statewide basis, the landscape of Illinois where Woolf et al. (2002) developed a bobcat habitat model is most similar to Iowa. Models have been developed from data summarized at various spatial resolutions, including 5-m grid cells (Roberts et al. 2010), home ranges (Nielsen and Woolf 2002, Constible et al. 2006, Preuss and Gehring 2007), townships (Litvaitis et al. 2006), and counties (Woolf et al. 2002). At the larger scales above that of individuals, often the response variable is presence-absence in a unit based on reports of sightings and road kills (Kautz et al. 2001, Woolf et al. 2002) although relative abundance is sometimes the modeled response. States use a variety of means to quantify distribution and trends (Roberts and Crimmins 2010) although relatively few use surveys of the general public or hunters (Hamilton et al. 1990) that are specifically designed to ensure statewide sample coverage (Roberts and Clark 2009).

Our goal was to associate habitat and landscape characteristics at the county level across Iowa with bobcat relative abundance quantified from surveys of hunters. We used a large data set that enabled us to develop multiple regression models to independently validate the models and explore model residuals for evidence of spatial correlation. Finally we

interpreted the associations between bobcat and landscape characteristics to draw inference about potential recolonization of bobcats throughout Iowa and similar landscapes in the Midwest.

STUDY AREA

Iowa encompasses 145,700 km² centrally located in the corn belt of the midwestern United States (Fig. 1). Major land uses are row crops (59%) consisting primarily of corn (*Zea mays*) and soybean (*Glycine max*), grassland and pastures (24%), forest (8%), and CRP perennial grassland (4%). The remaining 5% of the land area is classified as urban, road, water or wetland, or barren (Iowa Geological Survey and Iowa Department of Natural Resources 2004). Forested areas range from riparian corridors dominated by silver maple (*Acer saccharinum*), elm (*Ulmus* spp.), and cottonwood (*Populus* spp.) to upland woodlands dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.; Jungst et al. 1998). Topography is flat to moderately rolling, with slope ranging from 0% to 158% and a statewide average slope of 4.4%. Stream density ranges from a low of 0.39 km/km² in Emmet County in north central Iowa to 1.04 km/km² in Jackson County bordering the Mississippi River. Mean road density, including paved and unpaved roads, is 1.4 km/km². Average human population density ranges from 4.1/km² in Ringgold County in southwest Iowa to 247.0/km² in Polk County, where the city of Des Moines is located.

METHODS

Bobcat Relative Abundance

We compiled data on the distribution and relative abundance of bobcats from the Iowa Department of Natural Resources (IDNR) Bowhunter Observation Survey (BOS; Roberts and Clark 2009). This survey was mailed to 8,991 bowhunters during 2004–2009. Approximately 91 avid bowhunters in each of Iowa's 99 counties (Fig. 1) were randomly selected for participation in the survey. We defined avid bowhunters as individuals who obtained a bowhunting license for 3 consecutive years prior to the survey. Survey participants recorded data during the first portion of the archery deer season (1 Oct to early Dec), and provided the date of each hunting trip, the number of hours hunted, and the number of animals observed for a selection of wildlife species, including bobcats. We standardized the number of bobcats observed for hunter effort as bobcats/1,000 hunter-hours/county/year. This measurement represented the relative abundance of bobcats for county-level modeling. Using BOS data to model bobcat abundance ensures that the response is derived from a consistent, probabilistic sampling of observers in each county; thus, observer bias with respect to a specific county or region of the state is minimized by design.

Habitat and Landscape Variables

We summarized landscape composition and configuration for each county in Iowa to associate abundance of bobcats with habitat variables. We obtained land cover, elevation, road, stream, and human population density data from

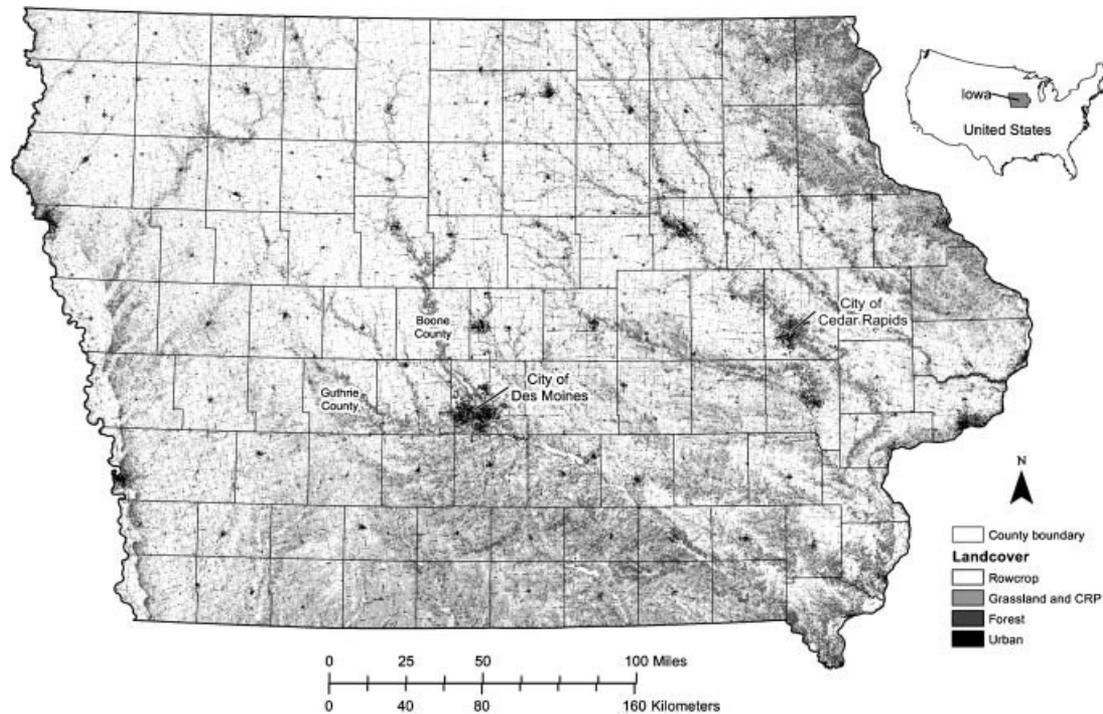


Figure 1. Landscape physiogamy and landcover used to model the relative abundance of bobcats in counties of Iowa, USA, 2004–2009. Rowcrop is primarily corn and soybean and grassland is perennial hay and pasture along with Conservation Reserve Program (CRP) land.

publicly available datasets. We also included variables describing positive and negative interspecific interactions, including principal prey (eastern cottontails [*Sylvilagus floridanus*]; Brockmeyer and Clark 2007) and principal antagonistic species (coyotes [*Canis latrans*]; Litvaitis and Harrison 1989, Henke and Bryant 1999). We averaged relative abundance of cottontails at the county scale from the IDNR August Roadside Survey (Bogenschutz et al. 2008) over years 2004–2008. We averaged relative abundance of coyotes at the county scale from the IDNR BOS. We obtained 2002 Iowa Land Cover data with 15-m resolution from the Iowa Geological Survey and the IDNR (2004). We delineated 8 major cover classes using ArcGIS 9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA): coniferous forest, deciduous forest, and bottomland forest were combined into Forest; planted grassland delineated CRP perennial grassland; ungrazed grassland, grazed grassland, and alfalfa/hay were combined into Grassland; corn, soybeans, and other rowcrop were combined into Rowcrop; water and wetland were classified into Water/Wetland; residential and commercial/industrial were combined into Urban; roads delineated Roads; barren was classified as Barren; and unclassified and cloud/shadow/no data were considered No Data. We obtained human population density data from the United States Census Bureau 2000 census data (United States Census Bureau 2001). We summarized road density for paved and unpaved roads using data from the Iowa Department of Transportation (Iowa Department of Transportation 2007). We summarized stream density from the National Hydrography Dataset, developed by the United States Geological Survey and the Environmental Protection Agency (IDNR: Geological

Survey Bureau 2000). We summarized slope from the United States Geological Survey National Elevation Dataset (United States Geological Survey 1999).

We used FRAGSTATS 3.3 (www.umass.edu/landeco/research/fragstats/fragstats.html, accessed 6 Jul 2009) to calculate landscape configuration variables at the county level. We computed metrics for each land cover class, representing the amount and spatial distribution of a single land cover type. We also calculated metrics at the landscape level, representing the structure of the landscape mosaic, regardless of habitat class (Constible et al. 2006). Past research suggested that Iowa bobcats selected forest habitat in their home range twice as often as predicted by random chance, grassland and CRP approximately equal to random chance, and row crop much less than random chance (Tucker et al. 2008). Consequently, we assigned edge between forest and row crop a high contrast (0.8), edges between forest and grassland and forest and CRP a moderate contrast (both 0.5), and edge between grassland and CRP a low contrast (0.1). We followed standard definitions and mathematical formulas of all FRAGSTATS metrics (Hargis et al. 1997, Tischendorf 2001, McGarigal et al. 2002). For landscape metrics requiring adjacency data, we used an 8-neighbor rule.

Model Development and Evaluation

We selected a group of habitat composition and configuration variables that reflected the combination of our a priori expectation of biological influence on bobcats and tractable statistical properties (Appendix). We included the proportion of the landscape composition in major cover types to examine the importance of CRP and Grassland in addition to Forest. Because we thought that bobcats may be sensitive

to fragmentation, especially in the Iowa landscape, we included 2 configuration variables related to patch characteristics (density and area), and 2 for core characteristics (core percentage of the landscape and disjunct core area) for each of the 5 major habitat classes. Bobcats could be sensitive to the availability of edges for stalking so we included a metric that quantified edges (contrast weighted edge density) and 2 metrics that quantified shape (landscape shape index, mean patch shape). In addition, we included 2 variables describing physiognomic factors (stream density and standard deviation of slope) that potentially identified course terrain that bobcats occupy in some regions. Finally, we included 2 metrics reflecting human factors (population density and road density) that have been identified as negative influences on bobcat habitat selection. For each variable, we calculated univariate summaries, and normalized or stabilized variance with natural log or square root transformations (Harrell 2001). In some cases, multiple variables were highly correlated with each other ($r > 0.80$). When this occurred, we retained a single variable that was more biologically meaningful, more easily understood, or easier to calculate. For example, we did not include percentage of the landscape in row crops because the metric was highly negatively correlated with percentage grassland ($r = -0.93$) and percentage forest ($r = -0.84$), but we did include a variable for row crop patch density to capture whether fields were small and numerous as opposed to large and continuous on the landscape.

We used multiple linear regression analysis (JMP 8.0, SAS Institute, Inc., Cary, NC) to examine the association between landscape composition, landscape configuration, and habitat variables. We developed and contrasted 90 models, including models that included those with only single variables that were highly correlated with the response variable, models with 2 variables, 3 variables, and so on. We ranked competing models that best approximated the data using Akaike's Information Criterion corrected for small sample size (ΔAIC_c) and by assessing weight of evidence for the i th model (w_i ; Burnham and Anderson 2002). We considered the issue of redundant or uninformative parameters by examining changes in deviance and root mean squared error (RMSE; Arnold 2010). We calculated the relative importance of each independent variable by summing the Akaike weights across all models where a particular variable occurred. For models with substantial statistical support (i.e., $\Delta AIC_c < 2$; Burnham and Anderson 2002) we also report the coefficient of determination (R^2) to indicate the relative explanatory power of the models.

We developed the models using only data from the even-numbered years, 2004, 2006, and 2008 and retained the odd-numbered years 2005, 2007, and 2009 for validation (Harrell 2001). We validated models by comparing predictions calculated from the model-averaged parameters (Burnham and Anderson 2002) that had been derived from the even-numbered years with the county-level means of the observed bobcat abundance from odd-numbered years.

Using all counties could inappropriately identify habitat variables related to BOS counts because of false absences if

bobcats have not colonized all counties of Iowa (Gosselink et al. 2011). To acknowledge this concern, we built a second set of models using the subset of 65 counties where bobcats have been reported in the BOS. By excluding counties where bobcats have never been observed in the survey, we reasoned that the resulting models would be conservative with respect to identifying landscape features selected by bobcats because they were based only on confirmed distribution. As before, we validated the resulting models by comparing predictions from the estimated best model against the data that we reserved from the odd years.

Animal species distribution data often display spatial autocorrelation because of internal contagious ecological processes (Scott et al. 2002). Naturally, spatial autocorrelation might also be detectable among the landscape metrics, although the degree of autocorrelation of the landscape variables and potential covariation with the response variable likely depends on scale (Fortin and Dale 2005). Unfortunately in other wildlife habitat modeling spatial autocorrelation is seldom considered but a complete spatial analysis was also beyond the scope of our work. Nonetheless, we recognized that standard statistical methods such as regression assume independence of observations, so we tested for spatial pattern in model residuals using Moran's I (Fortin and Dale 2005). We assessed Moran's I score statistic and standard deviate to indicate the significance of global spatial autocorrelation in model residuals (Dormann et al. 2007) because of the possibility of a gradient (e.g., south to north) related to colonization or spatial clustering associated with habitat regions within Iowa. Our approach assumed models related bobcat distribution to landscape features but there may have been additional unaccounted spatial pattern in the residuals. If so, the models we considered with first order (i.e., using the 8-neighbor rule) spatial autocorrelation should be highly ranked.

RESULTS

Bowhunter Observation Survey

Statewide participation in the Iowa BOS during 2004–2009 averaged 1,857 individuals (SD = 449), and ranged from 1,344 individuals in 2006 to 2,498 individuals in 2007. Corresponding participation rates averaged 21% (SD = 5%), and ranged from 15% in 2006 to 28% in 2007 of the 8,991 individuals receiving the survey each year. Across Iowa, participants reported observations of bobcats, coyotes, and other selected wildlife species during an annual average of 27,545 hunting trips (SD = 6,609) and provided an average of 94,020 hours (SD = 23,495) of observation time each year. At the county-level ($n = 99$), all hunters took an annual average of 278 trips (SD = 125) during 2004–2009, which ranged from 61 trips in Calhoun County to 574 trips in Pottawattamie County. From the perspective of detecting bobcats, the mean annual observation time per county during 2004–2009 was 950 hours (SD = 469), which ranged from 185 hours in Calhoun County to 2,228 hours in Clayton County. We standardized observation rates to the number of observations per

1,000 hours hunted and calculated 95% confidence limits for each estimate. Bowhunters did not report any observations of bobcats in 34 counties during the 6 years from 2004–2009. The mean coefficient of variation (CV) was 0.67 for 32 counties with 6-year mean bobcat observation rates > 2.0 observations/1,000 hours (i.e., counties with greater relative abundance), but more variable with a mean CV of 1.89 for 33 counties with positive observation rates <2.0 (lesser relative abundance). In contrast, coyotes were reported every year in every county with a mean observation rate of 24.58 coyotes/1,000 hours (CV = 0.41; Roberts and Clark 2009).

County Scale Model of Relative Abundance

We identified 4 competing models ($\Delta AIC_c < 2$) of BOS bobcat relative abundance, each of which included 7 variables in common (Table 1). A model with 10 parameters ranked highly based on ΔAIC_c but it was nearly indistinguishable from other competing models with respect to w_i and RMSE. Model ranking and variable importance weights (Table 2) indicated that the BOS abundance of bobcats was consistently positively associated with grassland patch density, grassland mean area, CRP disjunct core area density, and forest shape index, and negatively associated with human population density, grassland core percentage of the landscape, and grassland contrast-weighted edge density. Although the relative abundance of cottontails was included in 2 of the top models, it had a much lower Akaike parameter weight than landscape physiographic metrics (Table 2). Furthermore, models 3 and 4 that did not include cottontails had identical predictive power to models 1 and 2 that included cottontails.

Bobcat abundance was weakly correlated with coyote abundance ($r^2 = 0.21$, $P < 0.001$) but the association was positive, not negative as hypothesized. A model which differed from the top model (Table 1) by only the substitution of coyote abundance for cottontail abundance had a $\Delta AIC_c = 3.95$ ($K = 10$, $AIC_c = 220.43$, $RMSE = 0.73$).

We found no significant global spatial autocorrelation in the residuals of the top regression model (Moran's

$I = 0.083$, $P = 0.126$), indicating an error pattern that was neither clustered nor dispersed. A model with first order spatial autocorrelation added to the habitat variables in the top model was not competitive ($\Delta AIC_c = 110.4$, $K = 11$, $AIC_c = 326.89$, $RMSE = 1.24$).

Predicted values generated from the model with the weighted parameters of the variables accurately reflected the observed patterns of relative abundance (Fig. 2). Validation of the predictions against abundance from the reserved odd-numbered years illustrated that 66% of predictions were within 1 bobcat/1,000 hunter-hours of the observed value (i.e., within the 64th quantile of all observations) and 95% were within 5 bobcats/1,000 hunter-hours (within the 81st quantile). Modeling tended to over-predict in counties in the northern third of Iowa, whereas it tended to under-predict in counties on the border with Missouri. In nearly all counties where relative abundance of bobcats in the BOS was less than 1, no bobcats were observed in at least 4 of the 6 years of the survey (Fig. 2).

Conservatively constructed models, based on data that excluded counties where bobcats had never been observed to be present in the BOS, were very similar to models based on all counties in Iowa, including substantially the same variables. The best-fit conservative model ($AIC_c = 137.6$, $RMSE = 0.752$, $R^2 = 0.768$) included stream density, human population density, grassland patch density, grassland mean patch area, grassland core percentage of the landscape, grassland contrast-weighted density, and CRP disjunct core area density (Table 2). This model included 2 variables not included in the all-county model: forest core percentage of the landscape and forest disjunct core area density. Signs of the regression coefficients in these conservative models were the same as the models constructed using all-county data and confidence intervals of all of the coefficients in common overlapped. Predictions of relative abundance derived from the conservative model and applied statewide were similar to those derived from the model constructed using data from all counties. As expected, predictions from the conservative model were slightly less accurate than

Table 1. Characteristics of the 4 best approximating regression models that predict the relative abundance of bobcats based on observations from all counties in Iowa, USA, 2004–2009. Rankings are based on Akaike's information criterion corrected for small sample size (AIC_c), Akaike differences (Δ_i) and Akaike weights (w_i). K is the number of parameters. Root mean squared error (RMSE) and coefficient of determination (R^2) provide assessment of model performance.

Model ^a	K	AIC_c	Δ_i	w_i	RMSE	R^2
AllStreamDensAvg + \ln HumanPopDens + \ln Bunny + \ln graPD + \ln graAREAMN + \ln graCPLAND + graCWED + \ln crpDCAD + \ln crpCWED + forSHAPEMN	10	216.48	0	0.28	0.67	0.76
AllStreamDensAvg + \ln HumanPopDens + \ln Bunny + \ln graPD + \ln graAREAMN + \ln graCPLAND + graCWED + \ln crpDCAD + forSHAPEMN	9	216.69	0.21	0.25	0.67	0.75
AllStreamDensAvg + \ln HumanPopDens + \ln graPD + \ln graAREAMN + \ln graCPLAND + graCWED + PerGrassland + \ln crpDCAD + \ln crpCWED + forSHAPEMN	10	216.76	0.28	0.24	0.67	0.76
\ln HumanPopDens + \ln graPD + \ln graAREAMN + \ln graCPLAND + graCWEDPerGrassland + \ln crpDCAD + forSHAPEMN	8	216.83	0.35	0.23	0.68	0.75

^a AllStreamDensAvg: average stream density (km/km²); \ln [HumanPopDens]: human population density (persons/km²); \ln [Bunny]: average number of cottontails seen per 30-mile route; \ln [graPD]: grassland patch density (number/100 ha); \ln [graAREAMN]: grassland mean patch area (ha); \ln [graCPLAND]: grassland core percentage of the landscape; graCWED: grassland contrast-weighted edge density (meters/ha); PerGrassland: grassland percentage of the landscape; \ln [crpDCAD]: CRP disjunct core area density (number/100 ha); \ln [crpCWED]: grassland contrast-weighted edge density (meters/ha); forSHAPEMN: forest mean shape index.

Table 2. Model weighted parameter estimates of regression coefficients (β), 95% confidence intervals, and Akaike weights of models that predict the relative abundance of bobcats based on observations from all counties and those derived from models that exclude counties where bobcats were never seen in Iowa USA, 2004–2009.

Model parameters ^a	All counties			Excluding zero counties	
	β	CI	Akaike weight	β	CI
Intercept	-26.32	-36.70 to -15.94		-22.85	-33.19 to -12.51
AllStreamDensAvg	-1.07	-2.79 to 0.65	0.77	-3.50	-6.20 to -0.08
lnHumanPopDens	-0.47	-0.69 to -0.25	1.00	-0.44	-0.82 to -0.06
lnBunny	0.12	-0.18 to 0.42	0.53		
lngraPD	7.88	4.38–11.38	1.00	12.03	6.81–17.25
lngraAREAMN	6.29	2.81–9.77	1.00	11.25	6.71–15.79
lngraCPLAND	-2.36	-3.24 to -1.48	1.00	-4.93	-6.83 to -3.03
graCWED	-0.13	-0.19 to -0.07	1.00	-0.14	-0.24 to -0.04
PerGrassland	0.04	-0.04 to 0.12	0.47		
lnrcpDCAD	1.76	1.02–2.50	1.00	2.49	1.35–3.63
lnrcpCWED	-0.25	-0.39 to 0.89	0.52		
forSHAPEMN	8.21	2.25–14.17	1.00		
lnforDCAD				1.45	0.35–2.55
lnforCPLAND				-0.58	-1.1 to -0.06

^a AllStreamDensAvg: average stream density (km/km²); ln[HumanPopDens]: human population density (persons/km²); ln[Bunny]: average number of cottontails seen per 30-mile route; ln[graPD]: grassland patch density (number/100 ha); ln[graAREAMN]: grassland mean patch area (ha); ln[graCPLAND]: grassland core percentage of the landscape; graCWED: grassland contrast-weighted edge density (meters/ha); PerGrassland: grassland percentage of the landscape; ln[rcpDCAD]: CRP disjunct core area density (number/100 ha); ln[rcpCWED]: grassland contrast-weighted edge density (meters/ha); forSHAPEMN: forest mean shape index; ln[forDCAD]: forest disjunct core area density (number/100 ha); ln[forCPLAND]: forest core percentage of the landscape.

predictions from the model based on all counties when compared to the validation data, with 58% of predictions within 1 bobcat/1,000 hunter-hours and 91% within 5 bobcats/1,000 hunter-hours of validation data.

DISCUSSION

Nearly all studies of bobcat habitat relationships have concluded that bobcat presence and abundance is influenced by the distribution and characteristics of forested habitat

(Woolf et al. 2002, Preuss and Gehring 2007), especially at the local scale (Lovallo et al. 2001, Constible et al. 2006, Tucker et al. 2008). However, our analyses and modeling highlight that the quantity and configuration of other habitats, especially perennial grassland cover in association with woodlands, predicted relative abundance of Iowa bobcats at the county scale. This result might be viewed as contrasting with the results of Woolf et al. (2002), whose data from a similar landscape in the corn belt led them to conclude that

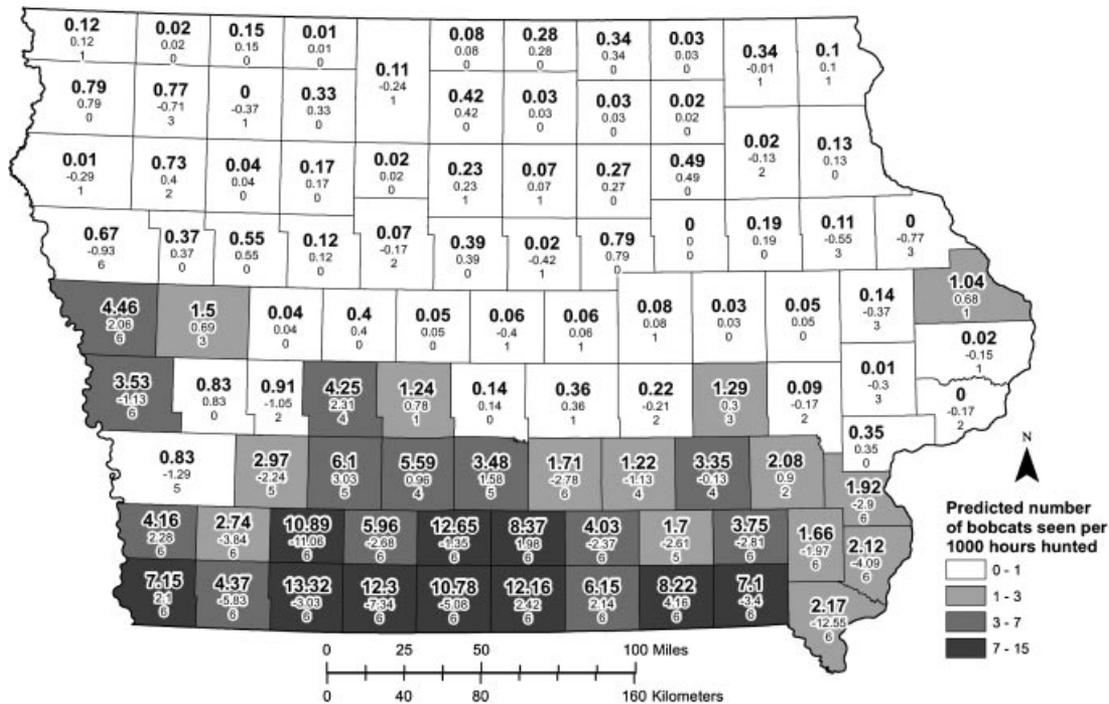


Figure 2. Predicted relative abundance (bobcats observed/1,000 hunter-hours, first bold value) based on the model averaged parameters, difference between the predicted values and independent data from odd years (second value), and the number of years that bobcats were observed in the bowhunter observation survey (last value), 2004–2009 in Iowa, USA.

patchy forested landscapes correlated with bobcat presence. In our analyses, models with percentage forest were not highly competitive when predicting the BOS counts, although a metric of forest shape was included among the top models. Certainly, part of the distinction in models is due to the fact that the landscape of southern Illinois is more continuously forested than southern Iowa. Focusing on the inclusion of the biotic variable, cottontail abundance, suggests an interpretation that is consistent with our analyses, the results of Woolf et al. (2002), and the ecology of bobcats and their prey. We propose that the inclusion of grasslands (including pastures, hay, idle, and CRP) in our competing models not only distinguishes counties in Iowa with both grasslands and forests, but also indicates that bobcats were less abundant in landscapes with hard edge transitions (Ims 1995) where there is no grassland between row crops and forests. Soft edge habitat is highly suitable for cottontails (Mankin and Warner 1999, Chapman and Litvaitis 2003) as well as hunting habitat for bobcats (Litvaitis et al. 1986). We argue that the models reflect the influence of grasslands in this landscape context not grasslands in isolation. Our statewide modeling is entirely consistent with the finer scale analyses of Tucker et al. (2008) who found that bobcats focused home range cores around forested patches but preferentially used patches that were surrounded by grassland, including CRP. In neighboring Illinois, the predictive modeling of Woolf et al. (2002) showed that bobcats are most abundant in the southern counties where they report that there was a nearly equal proportion of 29% forest, 22% grassland, and 36% agriculture. And results from both of these states in the heart of the corn belt reinforce the conclusion that bobcats avoid areas dominated by row crop agriculture, even if isolated forest patches are present (Nielsen and Woolf 2002, Tucker et al. 2008).

Relative abundance of cottontails was predictive of bobcat relative abundance although as we suggested above, we interpret this as coincidental distribution linked to the same habitat features, rather than a causal predator-prey interaction. Cottontail abundance has declined in much of the corn belt over the last 50 years as perennial grasslands have been converted to row crops (Mankin and Warner 1999). Cottontail abundance in Iowa fluctuates erratically, although the statewide trend has been downward (Bogenschutz et al. 2008). Cottontails persist in intensively-farmed areas across the state but they are substantially restricted to small areas of suitable habitat. The counties with the greatest abundance of cottontails are in the southern part of the state where mixed agriculture and perennial habitat is most prevalent on the landscape (Bogenschutz et al. 2008). Our modeling did not support hypothesized negative associations between bobcat and coyote abundance. Instead, models that included coyotes also suggested that the distribution of both carnivores is positively influenced by the appropriate perennial habitat features on the landscape.

The inclusion of human population density in the competing models distinguishes low counts in highly populated counties of Iowa. Iowa has a relatively uniform human density with few large population centers (Fig. 1); 45% of

census blocks have <4 people/km². But the importance weight of this variable, and the fact that cities like Des Moines and Cedar Rapids are located along potential habitat corridors, suggests that these densely populated areas could represent dispersal barriers to bobcats. Reding (2011) demonstrated this effect with least cost path modeling of bobcat dispersal routes in the Iowa landscape.

Three results argue that the patterns we modeled are not simply due to time lags associated with colonization patterns of bobcats into Iowa from the south or west. First, we specifically checked for, and did not find, spatial autocorrelation in prediction errors that would have been expected if there was a gradient of relative abundance from south to north. Secondly, the models we built by excluding counties where bobcats have never been reported in the BOS identified essentially the same variables as the models built from observations in all counties. Thirdly, models consistently predicted that bobcats should be, and were observed to be, more abundant in counties where grassland was present than in counties where it was not, regardless of whether the county was in the southern or central region of Iowa. For example, predicted abundance was high in Guthrie County, where land cover is dominated by the Raccoon River watershed (Fig. 1), but predicted abundance was quite low in Boone County where the Des Moines River corridor is a dominant feature. The difference is due to forests along the upper part of the Des Moines River, which have high edge contrast with no transitional grassland to the surrounding row crop agriculture, whereas the Raccoon watershed is an interspersed grassland-forest landscape (Fig. 1). Furthermore, Linde (2010) constructed logistic regression models of presence at much finer watershed resolution (HUC-12 units, approximately 86 km²; United States Geological Survey et al. 2009) and drew essentially the same conclusion. Linde's models showed that the presence of grassland habitat along with patches of forest largely distinguishes watersheds in southern Iowa, where bobcats are present, from those in northern Iowa, where they are largely absent.

We acknowledge that failing to detect bobcats at very low levels of abundance has the potential to influence our conclusions and the application of our models (MacKenzie et al. 2006). We have combined 6 years of BOS observations from the county sampling units, diminishing the probability that bobcats that were present in a sample unit went undetected. We sampled BOS hunters in each county at the same intensity each year, and although response rates varied among years and counties, there is no evidence that reports consistently varied with regard to a particular county. In fact, we argue that with an average of about 950 hunter-hours per county per year concentrated in perennial habitats it would be more likely that bobcats would be detected in the limited habitat of northern Iowa compared to the more complex habitats of the southern part of the state.

With regard to statewide distribution, bobcats may already occupy most of the areas of favorable habitat predicted by the models and it is possible that they will not substantially expand distribution into the regions of Iowa with a very high percentage of row crops (Gosselink et al. 2011). Tucker

et al. (2008) estimated that density in the good habitat in southern Iowa has reached similar levels to that in comparable habitat in the adjacent states of Missouri and Minnesota. Alternatively, bobcats may prove to be more adaptable and able to use more marginal habitat than is currently predicted by this research. The models identify some counties in the northern half of Iowa where bobcats are apparently not abundant but where the habitat matches the landscape conditions in southern Iowa. This result therefore stimulates the need to further elucidate the interactions between landscape characteristics, dispersal behavior, and bobcat population dynamics in the corn belt.

MANAGEMENT IMPLICATIONS

Research on distribution, abundance, and habitat relationships were listed among the top 5 research needs for bobcats in a 1996 survey of state agencies (Bluett et al. 2001) because they fall under the jurisdiction of the Convention on International Trade in Endangered Species (United States Fish and Wildlife Service 2010). The IDNR has not only used the results in evaluating the expansion of this once threatened species and changing its protection status, but also for delineating harvest opportunities (IDNR 2010). Because the landscape databases we used are all publicly available, other states in the Midwest with similar wildlife surveys could also use this approach. We demonstrate that maintaining a diverse landscape of grassland and forested perennial habitat in the corn belt could not only enable the continued recolonization of bobcats in the region, but likely will also benefit other wide-ranging wildlife species.

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Appendix. Variables used to develop linear regression models.

Variable	Variable describes	Variable name
Number of bobcats seen per 1,000 hr hunted, averaged over 2004, 2006, 2008	Response variable: relative abundance of bobcats	$\sqrt{[040608]}$
Number of bobcats seen per 1,000 hr hunted, averaged over 2005, 2007, 2009	Test response variable: relative abundance of bobcats	$\sqrt{[050709]}$
Percent forest	Landscape composition	$\ln[\text{PerForest}]$
Percent grassland	Landscape composition	PerGrassland
Percent CRP	Landscape composition	$\ln[\text{PerCRP}]$
Slope standard deviation	Landscape physiognomy	$\ln[\text{SlopeStDev}]$
Stream density	Landscape physiognomy	AllStreamDensAvg
Unpaved road density	Human factors	UnpavedDensAvg
Human population density	Human factors	$\ln[\text{HumanPopDens}]$
Relative abundance of cottontail rabbits	Prey availability	$\ln[\text{Bunny}]$
Relative abundance of coyotes	Abundance of antagonistic species	coy5yrAvg
Forest patch density	Landscape configuration: fragmentation	$\sqrt{[\text{forPD}]}$
Grassland patch density	Landscape configuration: fragmentation	$\ln[\text{graPD}]$
CRP patch density	Landscape configuration: fragmentation	$\ln[\text{crpPD}]$
Rowcrop patch density	Landscape configuration: fragmentation	$\ln[\text{rcpPD}]$
Forest landscape shape index	Landscape configuration: shape	$\sqrt{[\text{forLSI}]}$
Grassland landscape shape index	Landscape configuration: shape	graLSI
CRP landscape shape index	Landscape configuration: shape	crpLSI
Forest mean patch area	Landscape configuration: fragmentation	$\ln[\text{forAREAMN}]$
Grassland mean patch area	Landscape configuration: fragmentation	$\ln[\text{graAREAMN}]$
CRP mean patch area	Landscape configuration: fragmentation	$\ln[\text{crpAREAMN}]$
Forest mean shape	Landscape configuration: shape	forSHAPEMN
Grassland mean shape	Landscape configuration: shape	graSHAPEMN
CRP mean shape	Landscape configuration: shape	crpSHAPEMN
Forest core percentage of landscape	Landscape configuration: core area	$\ln[\text{forCPLAND}]$
Grassland core percentage of landscape	Landscape configuration: core area	$\ln[\text{graCPLAND}]$
CRP core percentage of landscape	Landscape configuration: core area	$\ln[\text{crpCPLAND}]$
Forest disjunct core area density	Landscape configuration: core area	$\ln[\text{forDCAD}]$
Grassland disjunct core area density	Landscape configuration: core area	$\ln[\text{graDCAD}]$
CRP disjunct core area density	Landscape configuration: core area	$\ln[\text{crpDCAD}]$
Forest contrast weighted edge density	Landscape configuration: adjacency	$\sqrt{[\text{forCWED}]}$
Grassland contrast weighted edge density	Landscape configuration: adjacency	graCWED
CRP contrast weighted edge density	Landscape configuration: adjacency	$\ln[\text{crpCWED}]$
Spatial lag variable	First-order spatial autocorrelation	$\text{lag}\sqrt{[\text{BobK135}]}$