



Research Article

Predicting Bobcat Abundance at a Landscape Scale and Evaluating Occupancy as a Density Index in Central Wisconsin

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ABSTRACT The abundance of low-density species like carnivores is logistically difficult to directly estimate at a meaningful scale. Predictive distribution models are often used as a surrogate for density estimation. But because density can continue to increase as occupancy asymptotes at 1, occupancy may have little value as an index, and home range expansion in marginal habitat may further confound the association. We sought to estimate bobcat population size at a landscape scale (14,286 km²) in central Wisconsin, which provided an opportunity to relate predicted occurrence to individual space use and population density. We sampled bobcats using motion-sensitive trail cameras at 9 arrays across central Wisconsin. We estimated bobcat site-specific occupancy, and regressed these estimates as linear or asymptotic functions of site-specific density to determine the strength and shape of their association. We subsequently modeled both parameters relative to habitat covariates and repeated the regression process. A linear functional relationship between density and occupancy was most supported when detection parameters were held constant ($w_i=0.97$, $R^2=0.72$) and when detection, occurrence, and density were modeled as a function of habitat covariates ($w_i=0.99$, $R^2=0.95$). This suggests that repeated presence-absence data alone may be an efficient and reliable method for inferring spatial patterns in bobcat density or identifying habitat types with greater density potential in the northern parts of its range. Bobcat occupancy and density were both positively associated with surrounding woody cover and wetland edge density. Our most supported spatially explicit capture-recapture model estimated bobcat abundance as 362 adult individuals (95% CI 272–490) across the study area.

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Carnivores are intrinsically difficult to manage or conserve because they exist at low density and are difficult to observe. Although noninvasive survey techniques have allowed capture-recapture estimates of carnivore abundance or density at small scales (e.g., Karanth and Nichols 1998, Mowat and Strobeck 2000, Ruell et al. 2009, Negroes et al. 2010, Stenglein et al. 2010), directly estimating abundance at more meaningful landscape scales requires large financial and logistical resources that are typically unavailable (Kendall et al. 2009). Hence, identifying methodologies to predict the abundance of cryptic, low-density species with reduced expense is an important research priority.

The bobcat (*Lynx rufus*) is widespread across North America but exists at low density at the edges of its distribution in the northern United States (Anderson and Lovallo 2003) where it appears to be repopulating historically

occupied regions, and managers are considering expanding harvest (Roberts and Crimmins 2010, Linde et al. 2012). Although estimates of population size would be the most useful information for revising harvest delineations, contemporary bobcat management has been guided by less intensive efforts to predict habitat suitability, distribution, or relative abundance (Woolf et al. 2002, Preuss and Gehring 2007, Long et al. 2011, Linde et al. 2012, Broman et al. 2014). An implicit assumption of these efforts and many other carnivore occurrence surveys (e.g., Karanth et al. 2011, Zielinski et al. 2013) has been that the probability of species presence is a useful index for density.

Although distribution or occupancy are intuitive and cost-effective surrogates for density, there are reasons to remain skeptical of using occupancy as a density index. Empirical tests across other taxa have found significant correlation but little predictive power between distribution and abundance (Nielsen et al. 2005, VanDerWal et al. 2009, Oliver et al. 2012, Torres et al. 2012). There are 2 fundamental concerns for using occupancy as an index. Most problematically, occupancy is mathematically bound at 1, and density is not

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mathematically bound. Therefore, density can continue to increase long after occupancy saturates, and occupancy-based metrics can be insensitive to larger changes in density (He and Gaston 2000, MacFarland and Van Deelen 2012, Tucker 2013, Ellis et al. 2014). Secondly, patterns in presence are also influenced by changes in individual space use that distribution models cannot estimate (Efford and Dawson 2012). Carnivore home range size is often larger in regions with poor habitat and low population density (Litvaitis et al. 1986, Herfindal et al. 2005, but see Van Horne 1983). An inverse relationship between home range size and density could render occupancy an unreliable or even misleading index of population size, because fewer individuals with larger home ranges might occupy or use as much total space as more individuals with smaller home ranges (Efford and Dawson 2012).

Alternatively, carnivore occupancy might be a suitable index for carnivore density given behavioral mechanisms governing individual distribution. Under theoretical expectations, carnivore home range distribution should reflect the balance between resource availability and intra-specific exclusion (Fretwell 1972). Both correlation and linearity between predicted occupancy and abundance is typically stronger for solitary organisms (Estrada and Arroyo 2012, MacFarland and Van Deelen 2012). Furthermore, many carnivore survey efforts rely on point detectors such as cameras or scent stations with very small direct sampling footprints. This has 2 consequences for the occupancy–density relationship. First, occupancy is mathematically defined as a site in which abundance is greater than 1 (Royle and Nichols 2003), and the 2 parameters converge as the upper limit of possible patch abundances approaches 1 (He and Gaston 2000). Given territoriality, any given point detector should be capable only of sampling a few individuals. Secondly, because the patch size is much smaller than an individual's home range, the species is not permanently available for detection over a finite survey duration and estimates of occupancy probability should be considered estimates of species use during the survey period (MacKenzie et al. 2006). Thus, even if the combined footprint of all individual home ranges saturates the study area, both observed and estimated occupancy may be less than 1.

In Wisconsin, bobcat harvest has been restricted to the northern third of the state since 1980. Increased public interest and anecdotal sightings prompted the Wisconsin Department of Natural Resources to consider allowing harvest in the central and southern parts of the state. The agency required an estimate of population size within a proposed harvest expansion zone before making a decision to revise harvest delineation. We accomplished our primary goal by modeling bobcat density as a function of land cover attributes across the study area using recently developed spatially explicit capture-recapture (SECR) models (e.g., Borchers and Efford 2008). We were also interested in assessing whether bobcat occupancy was a useful density index. Because SECR jointly estimates population density and individual movement, we were able to examine whether attributes influencing occupancy were related more to differences in density or in individual space use. We assessed

the functional relationship between occupancy and density. En route, we identified cover types and trail characteristics influential on bobcat presence and detection.

STUDY AREA

Our study area was a 14,286-km² region in central Wisconsin defined by major road boundaries (Fig. 1). The region was primarily a mixture of forest (37%) and cropland (33%). Other cover types included wetlands (9%), hay and pasture (7%), and shrubland (1.5%; U.S. Geological Survey National Land Cover Database 2006). The area our trail camera arrays effectively sampled (1,883 km², or 13% of the study area) slightly over-represented forest (40%) and wetlands (11%), and under-represented cropland (25%). Heavily influenced by glaciation, the northern portion of the study area featured till soils dominated by mixed-forest uplands of pine (*Pinus* spp.), maple (*Acer* spp.), and oak (*Quercus* spp.), and mesic hardwood stands predominated by maple and ash (*Fraxinus* spp.). Predominant agricultural crops were corn and soybeans. The southern portion had sandier soils, and primary crops included cranberry, with forest types characterized by upland pine/oak mixes and lowland stands featuring spruce (*Picea* spp.) and tamarack (*Larix laricina*). Average high temperatures ranged from 27°C in July to –5°C in January, and average annual precipitation was 83 cm, with most falling between May and September (National Oceanic and Atmospheric Administration 2013).

METHODS

Data Collection

We systematically spaced 13 potential sites every 30 km across the study area, and were able to sample 9 of the 13 sites for 6 weeks each between 19 March 2012 and 8 February 2013. Minimum distance between cameras in different sites was 14 km. We attempted to place a 6 × 6-square sampling array composed of 36 4-km² grid cells at each site but allowed irregularity in array shape as dictated by access and private land permissions. Within each cell, we hung 1 PC800[®] or HC500[®] passive infrared remote camera (Reconyx, Inc., Holmen, WI). A subset of cells (8–15 at any given time within an array) included paired facing cameras to identify left and right flank pelage characteristics of bobcats. We selected double-set sites based on tree availability and presumed site potential, but we actively moved or added cameras in response to bobcat detections. Each array was active for approximately 6 weeks. We initially sorted all bobcat images into sequences (described as events) defined by at least 1-hour separation between subsequent bobcat images at a given camera. Three observers independently identified individuals using permanent unique pelage marks and patterns following the protocol of Larrucea et al. (2007). Misidentification of individuals can bias capture-recapture estimates (e.g., Creel et al. 2003), but misidentification models (e.g., Link et al. 2010) have not yet been developed for SECR. Consequently, we attempted to limit observer bias and misidentification by censoring detections without

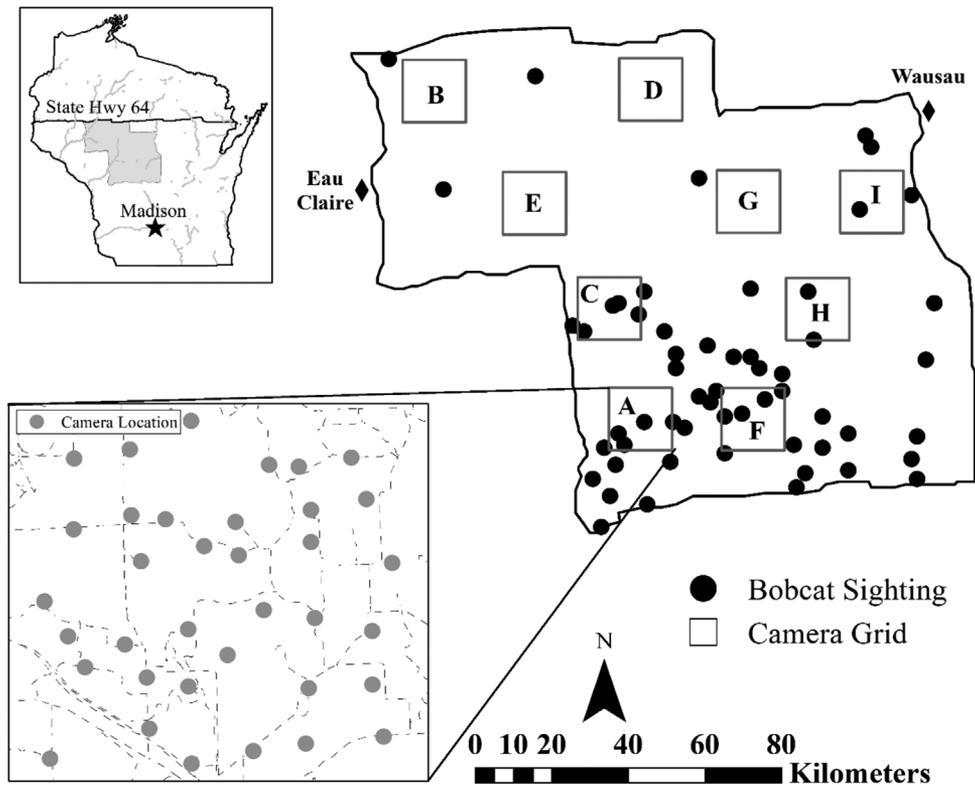


Figure 1. Location of remote camera sampling arrays and contributed sightings used to estimate bobcat occupancy and density in central Wisconsin in 2012. Major waterways designated in gray within top inset.

consensus agreement across all 3 observers (Kelly et al. 2008, Foster and Harmsen 2012).

We were further concerned that censoring unidentifiable detections could result in estimate bias if there was heterogeneity in individual identification probability (White and Shenk 2001). Although this was impossible to directly measure, we assumed that site and station-specific differences in probability of identification given bobcat detection could be used as a surrogate for individual heterogeneity because most individuals were likely to be detected only at a few stations and most stations detected only 1 or 2 different individuals. We used Pearson's chi-squared statistic to test for independence between identification and detection totals across arrays and across cameras within arrays.

The final capture history defined sampling occasions as 24-hour intervals during which an individual could be captured only once at an individual camera. Neither occupancy nor density detection histories included juvenile animals traveling alone or with adults, although we were likely unable to differentiate between young of the year and adults by early winter.

Estimating Array-Specific Occupancy and Density

To determine whether there was a relationship between site-specific density and occupancy, we first treated each array as an independent unit and regressed density and occupancy parameters. We used single season site-occupancy models (MacKenzie et al. 2006) that jointly estimate probability of detection (\hat{p}) and probability of occupancy ($\hat{\psi}$) to correct for

imperfect detection at each camera location (MacKenzie et al. 2006). We refer to ($\hat{\psi}$) as occupancy throughout following the terminology of Lele et al. (2013) but note that because bobcats were not permanently present within any patches (the camera's detection zone) over the survey duration, the parameter should be interpreted as the probability of any bobcat using the camera location during the survey period (MacKenzie et al. 2006). At stations with 2 cameras, we either randomly selected 1 camera's encounter history or chose the initial camera if a second was added later in response to prior detection. We divided each site's sampling duration into 7-day sessions. We constructed models in program PRESENCE v5.9 (Hines 2012).

We estimated density (\hat{D}) using maximum-likelihood spatial capture-recapture models in the R package secr (Borchers and Efford 2008, Efford 2012). These models incorporate the location of individual detections within the capture history, and assume that individual animals have a particular activity center during the survey period. Detection probability is then modeled as a function of the camera's proximity to an animal's activity center (Borchers and Efford 2008, Royle et al. 2009). We used half-normal detection functions in which the detection probability g_{ij} of individual i at station j during a sampling interval was estimated as

$$\hat{g}_{ij} = \hat{g}_0 \exp\left(\frac{-d_{ij}^2}{2\hat{\sigma}^2}\right) \quad (1)$$

where d_{ij} is the distance between the activity center i and detector j . Parameter g_0 represents an individual's detection probability at its activity center and σ represents the detection probability decay as a function of distance from its activity center (Efford 2004). Under an SECR framework, the distribution of activity centers is typically modeled using either a binomial or Poisson spatial point process over a discrete set of potential activity centers or grid-cells (Borchers and Efford 2008, Royle et al. 2009). Our models used the latter, where density is analogous to the intensity of the Poisson process: under the simplest model, the average number of activity centers per grid cell. Although a random spatial point process may not reflect model intra-sexual territoriality exhibited by bobcats, the species also practices considerable intersexual overlap, and the Poisson process appears robust to some deviation (Efford et al. 2009). We used the `secr` function `mask.check` both to evaluate fit of the spatial point process using different grid-cell sizes and to determine whether the spatial extent of the study area would include the activity centers of all individuals detected (Drewry et al. 2013). Because sample size at any given array was small, we initially held detection parameters for occupancy and density estimation (\hat{p} , \hat{g}_0 , and $\hat{\sigma}$) constant across all sites.

We evaluated the relationship between array-specific point estimates of $\hat{\psi}$ and \hat{D} , by comparing linear and asymptotic functional models. Because occupancy is the asymptotic parameter in occurrence-abundance models, we considered it as dependent upon either a linear or Michaelis-Menton function of density. We fit each model using least-squares and constrained the intercepts to pass through the natural origin, with the Michaelis-Menton curve also coerced to asymptote as occupancy approached 1. We compared model fit using Akaike's Information Criterion corrected for small sample size (AIC_c) and selected a functional relationship on the basis of AIC weight (w_i ; Burnham and Andersson 2002). However, we felt that density was generally the variable of greater management interest, and the variable more likely to be indirectly inferred on the basis of less-intensive data collection (Collier et al. 2013). Thus, we inverted the functional relationship post-hoc to estimate the proportion

of variance in density that was explained by occupancy using least-squares regression.

Predicting and Validating Occupancy

We further used single-season, site-occupancy models to identify important correlates with occupancy and to predict occurrence across the study area. As models considering multiple spatial scales often best predict animal presence (Meyer and Thuiller 2006), we considered 2 different window sizes (250-m and 1.5-km radius circular buffers around the camera) to calculate covariates explaining occupancy. The smaller buffer reflected within home range resource selection (Johnson 1980) and the larger roughly reflected the size of a bobcat 50% core area regionally (Nielsen and Woolf 2001, Preuss and Gehring 2007, Tucker et al. 2008) and represented resource selection between home ranges (Johnson 1980). The 1.5-km radius was also equivalent to inter-camera spacing within arrays and our initial estimate of $\hat{\sigma}$.

We considered 11 covariates to explain occupancy based on previous bobcat habitat studies (e.g., Lovallo and Anderson 1996, Woolf et al. 2002; Table 1). We calculated land cover proportions and fragmentation statistics for each window size using FRAGSTATS (McGarrigal et al. 2002) within the Patch Analyst extension v.5 (Rempel et al. 2012) for ArcMAP v10 (ESRI, Redlands, CA), using the 2006 National Land Cover Database (U.S. Geological Survey) as the base layer. We screened all covariates for multicollinearity using Spearman's rank correlation with an exclusion criterion of $P > 0.6$.

Most detection covariates were binary and related to trail characteristics where cameras were set (Table 2). General covariate categories included trail size, trail substrate, and whether the camera was placed along an anthropogenic linear feature or a natural corridor such as a dry drainage (Sollmann et al. 2011). We also classified sites as wetland (water-body directly adjacent) and open (no woody stems within the camera's field of view). The last categorical variable was biological season of camera deployment: breeding and gestation (31 Dec–31 May), nursing and weaning (31 May–31 Aug), or fall (31 Aug–31 Dec; Litvaitis et al. 1987).

Table 1. Candidate covariates, description, and FRAGSTATS window size used to model bobcat occurrence in central Wisconsin in 2012.

Categories	Covariates	Description	Buffer size
Competitor	Wolf	Categorical; camera within estimated wolf pack territory or not	
Proportion	Wooded cover	% Combined forest/shrub/wooded wetland	1.5 km
	Deciduous forest	% Deciduous forest	1.5 km
	Cropland	% Cropland	1.5 km
	Urban	% Urban	1.5 km
	Conifer	% Evergreen forest	250 m
	Shrub	% Shrub/scrub	250 m
Edge density	Wetland	Edge density (m/ha) of wooded and herbaceous wetland reclassified into 1 class	1.5 km
	Forest	Edge density (m/ha) of deciduous, evergreen, and mixed forest reclassified into 1 class	1.5 km 250 m
Mean distance to nearest neighbor	Wetland	Mean distance to nearest neighbor of reclassified wetland class	1.5 km

Table 2. The description of and acronyms for candidate covariates used to model bobcat probability of detection of bobcats at camera locations in central Wisconsin in 2012.

Covariate groups	Description	Covariate categories
Trail size ^a	The size of the trail or feature at camera location	Two car lanes, single car lane, single-track
Substrate ^a	The substrate of the trail or feature at camera location	Unpaved dirt or gravel, paved, mowed or cut grass, uncut grass
Feature ^a	The type of feature camera was hung along	A defined road or trail, naturally funneling riparian feature
Habitat ^a	The immediate habitat type surrounding the camera location	Wetland, Open
Season ^a	The phenological season in which a camera station was active	Nursing and weaning season, breeding and gestation
Competitor	The number of sympatric competitor detections recorded at the camera station	Coyote, wolf, fisher
Traffic	The number of human or vehicular photographs recorded at the camera station	Human photographs, vehicle photographs

^a Covariate group consisted of binary dummy variables, with an uncoded other category.

Because bobcats may avoid humans or other predators (Anderson and Lovallo 2003), we included a traffic covariate category, which considered both the total number of human foot and vehicular photographs (because assessing independence between those events was difficult), and a competitor covariate category, which was the total number of wolf (*Canis lupus*), coyote (*C. latrans*), and fisher (*Pekania pennanti*) detection events.

We first modeled p using our most parameterized ψ covariate model to compare candidate detection models (MacKenzie et al. 2006, Karanth et al. 2011). We compared 19 intra and inter-category detection models using AIC_c , defining the effective sampling size as the number of sampling locations (MacKenzie et al. 2006) and selecting the model with greatest w_i for prediction. We used the selected detection sub-model in conjunction with 36 a priori models for ψ to identify the strongest candidate for predicting use (Karanth et al. 2011). To determine if the model-set contained suitable candidates and met assumptions of detection independence, we ran 10,000 bootstrap goodness-of-fit tests on the most fully parameterized covariate model (MacKenzie and Bailey 2004). We projected this model across the study area by systematically placing points 750 m apart (the most supported pixel grain using secr's mask.check function) across the study area. We extracted covariates for each point using the means and buffers described above, and calculated probability of use logistically using the beta parameter estimates for $\hat{\psi}$.

We validated model predictions in 2 ways. First, we compared the observed binary state (bobcat detected or not) with our predicted probability of use at camera locations ($n=87$) surveyed in 2011 (J. D. J. Clare, University of Wisconsin—Stevens Point, unpublished data) and 1 array surveyed in 2012 using receiver operating characteristic (ROC) area under the curve. An ROC curve plots true positive fraction versus false positive fraction, and the area under the curve can be considered an index of discrimination where values of < 0.7 , $0.7-0.9$, and >0.9 are equivalent to a weak, useful, or excellent fits (Boyce et al. 2002).

The ROC is less reliable when positive outcomes are imperfectly detected, so we also tested predictive validity using presence-only bobcat sighting data compiled by the Wisconsin Department of Natural Resources from 2005–2013. We referenced all sightings ($n=58$) to square mile sections, and we averaged estimates of $\hat{\psi}$ drawn from overlapping pixels within our predictive occurrence map to derive a mean occupancy probability for the section. We followed the Boyce index methodology for validation using presence-only data (Hirzel et al. 2006). The Boyce index (Boyce et al. 2002) assumes that the ratio between area-adjusted frequency of observation and area-expected observation for independent data will monotonically rise in correspondence with predicted occurrence probability if the generating model is useful (Hirzel et al. 2006). We divided the study area into 10 predicted occupancy probability bins and used Spearman rank correlation to assess fit between each bin's predicted occupancy and observed sightings in those bins (Boyce et al. 2002); the strength of the non-parametric correlation is analogous to the ROC area under the curve (Hirzel et al. 2006)

Predicting Density and Determining Influences on Individual Space Use

To predict bobcat abundance within the study area and determine whether predicted occupancy reflected variance in density or individual space use, we fit candidate SECR models that related detection and density to covariates. Our candidate detection sub-models included models following the distance-based formulation described above, as well as detection functions that allowed g_0 and σ to vary following 2-part finite mixtures or in relation to habitat and trail covariates previously found to influence detection and occupancy, with the expectation that habitat suitability, trail characteristics, and phenological season would influence individual detection patterns (Sollmann et al. 2011, Royle et al. 2013a). These were implemented as camera-specific covariates such that the detection function parameters (see eqn 1) for an individual at camera j were respectively

estimated as $\text{logit}(\hat{g}_0) = \hat{\beta}_0 + \hat{\beta}_1 X_{1j} \dots \hat{\beta}_n X_{nj}$, and $\ln(\hat{\sigma}) = \hat{\beta}_0 + \hat{\beta}_1 X_{1j} \dots \hat{\beta}_n X_{nj}$. This formulation suggests that individuals will have different detection functions in relation to the attributes of specific camera locations (Efford 2012), and was a means of accommodating irregular individual space use that can improve estimates of density (Royle et al. 2013b). We modeled all detection covariates to influence both g_0 and σ parameters independently (Efford et al. 2009) and converted continuous detection covariates to rounded z-scores (nearest 0.5) to address computational limitations.

We modeled spatial variation in density as a spatial Poisson process with covariates drawn from our top occupancy model, such that the average intensity of the point process of a specific pixel z was estimated as $\ln(\hat{D}_z) = \hat{\beta}_0 + \hat{\beta}_1 X_{1z} \dots \hat{\beta}_n X_{nz}$. We fit all models across the entire spatial extent of the study area, and selected the candidate model with greatest w_i to estimate the study area's abundance. Because density is the principal variable within a Poisson spatial point process, expected abundance is derived as the summation of density predicted at each discrete point within the mask (Efford and Fewster 2013). We report estimates of realized abundance that exclude process variance associated with observed individuals (Efford and Fewster 2013), although the difference between realized and expected abundance confidence interval coverage was always negligible (<15).

We again used least-squares regression to compare models of the functional relationship between predicted density and occupancy. We multiplied our initial estimate of $\hat{\sigma}$ by 2.45, and used this product as the radius of a minimum concave buffer to approximate the 95% effective sampling area (ESA) of each array (Efford 2012, Sun et al. 2014). Within this 95% ESA, we averaged the predicted intensity of the spatial point process and used it as the regression variable that mean probability of occupancy ($\hat{\psi}$) was dependent upon, comparing the same linear and asymptotic functional models as before. Once again, we inverted the most supported functional relationship to estimate the precision of using occupancy to predict density.

RESULTS

We surveyed for 13,595 trap nights at 316 camera stations between March 2012 and February 2013 (Fig. 1). Average camera spacing within arrays was 1.5 km. We recorded 250 bobcat events (1.83 detections/100 trap-nights) at 101 stations, but 42 (17%) images were considered too poor to be individually assigned by any observer. Of the remaining 208 images, we assigned 187 (86% observer agreement) to 64 individual bobcats. We also removed 8 events in which an individual was captured at the same location in the same 24-hour interval, for a total of 179 captures of identifiable individuals. Number of individuals identified ranged from 1–11 at 1–5 stations (Fig. S1). We did not find any evidence that any array suffered systemic identification bias ($\chi^2_8 = 13.3$, $P = 0.89$) or that cameras within arrays showed independence between detection and identification totals (Table S1).

Table 3. Estimates of bobcat occupancy ($\hat{\psi}$) and density (\hat{D} ; individuals/100 km²) at 9 remote camera arrays in central Wisconsin in 2012 based upon site-specific state parameters with constant detection arranged in chronological order of sampling.

Site	$\hat{\psi}$	95% CI	\hat{D}	95% CI
A	0.35	0.19–0.55	3.24	1.53–6.93
B	0.11	0.03–0.29	1.89	0.72–5.13
C	0.62	0.40–0.80	5.04	2.79–9.09
D	0.20	0.09–0.39	2.79	1.26–6.21
E	0.73	0.48–0.89	5.13	2.79–9.27
F	0.70	0.46–0.87	4.68	2.52–8.82
G	0.07	0.02–0.25	0.45	0.09–3.42
H	0.28	0.14–0.48	3.06	1.35–6.93
I	0.50	0.31–0.70	3.69	1.80–7.38

Array-specific estimates of $\hat{\psi}$ ranged from 0.07–0.73, with corresponding point estimates of \hat{D} ranging from 0.45–5.13 adults per 100 km² (Table 3). We estimated $\hat{\sigma} = 1,480$ m (95% CI 1,316–1,665 m). A linear functional relationship between density and occupancy was vastly more supported ($w_i = 0.98$) than an asymptotic relationship ($\Delta\text{AIC}_c = 7.67$, $w_i = 0.02$). The inverted linear model exhibited strong correlation between predicted occupancy and density ($R^2 = 0.72$).

We found no evidence of overdispersion within our most saturated covariate model ($\hat{c} = 0.79$, $P = 0.85$) and made no variance-inflation adjustments. We found very strong AIC support for human traffic, bare trail substrates, immediate wetland habitat, and natural funnels as predictors of bobcat detection (Table 4). Four occupancy models encompassed 95% AIC_c support (Table 5); these models all included covariates at the large scale only (1.5-km radius buffer). The top model suggested that bobcat use was positively associated with surrounding woody cover and wetland edge density, whereas bobcat detection increased immediately adjacent to wetland, along natural funneling features, and on paths with bare substrates (Table 6). Increases in either foot traffic tended to reduce bobcat detectability. We estimated $\hat{p} = 0.216$ per weekly session (cumulatively $\hat{p} = 0.767$ over 6 weekly sampling intervals).

We used the top model to predict occupancy across the study area, given uncertainty regarding how to most appropriately model average beta parameter estimates missing from specific candidate models (Burnham and Anderson 2002, Nagawaka and Freckleton 2010). The location of independently contributed sightings was strongly correlated with area-adjusted predicted use ($P = 0.903$, $P < 0.001$). The ROC area under the curve using independent cameras was 0.726 (SE = 0.058), further indicating meaningful discrimination (Boyce et al. 2002).

We retained woody cover and wetland edge density as primary habitat-specific density and trap-specific detection covariates. Other trap-specific detection covariates included bare substrates and adjacency to wetlands. The most supported SECR model ($w_i > 0.99$) included woody cover and bare trail substrate as covariates for both detection parameters, and retained woody cover and wetland edge

Table 4. Parameterization (K), fit ($-2 \text{ Ln } \mathcal{L}$), second-order Akaike's Information Criterion score (AIC_c), differences in AIC_c (Δ_i), and Akaike weight (w_i) for highly supported probability of detection (p) models for bobcat at camera stations in central Wisconsin in 2012. We held probability of occupancy (ψ) constant for comparison.

Model	K	$-2 \text{ Ln } \mathcal{L}$	AIC_c	Δ_i	w_i
ψ (Full), $p(\text{Traffic}^a + \text{Habitat}^b + \text{Bare}^c + \text{NF}^d)$	17	869.02	905.36	0	0.60
ψ (Full), $p(\text{Traffic} + \text{Habitat} + \text{Bare} + \text{NF} + 2V^e)$	18	869.02	907.64	2.28	0.19
ψ (Full), $p(\text{Habitat} + \text{Bare} + \text{FootT} + 2V)$	17	871.77	908.11	2.75	0.15
ψ (Full), $p(\text{Substrate}^f + \text{Traffic} + \text{Wetland})$	17	874.48	910.82	5.46	0.04

^a Counts of total human photographs (FootT) and vehicles as separate covariates.

^b Binary distinctions for immediate wetland habitat (Wetland) and immediate herbaceous habitat as separate covariates.

^c Binary distinction for a path with a bare substrate.

^d Binary distinction for a natural funnel (e.g., riparian corridor).

^e Binary distinction for a path with 2 vehicular lanes versus narrower.

^f Includes binary distinctions for bare, maintained grass, or unmaintained grass trail substrates.

Table 5. The formulation, parameterization (K), fit ($-2 \text{ Ln } \mathcal{L}$), second-order Akaike's Information Criterion score (AIC_c), differences in AIC_c (Δ_i), and Akaike weight (w_i) of highly supported models of bobcat occupancy (ψ) central Wisconsin in 2012. We compared models by holding the best fitting detection probability (p) model constant.

Model	K	$-2 \text{ Ln } \mathcal{L}$	AIC_c	Δ_i	w_i
ψ (Wooded cover ^a + Wetland edge ^b + Wetland distance ^c), $p(\text{Best})$	11	872.87	895.86	0	0.38
ψ (Wooded cover + Wetland edge), $p(\text{Best})$	10	875.4	896.22	0.36	0.32
ψ (Wooded cover + Wetland edge + Forest edge ^d + Wetland distance), $p(\text{Best})$	12	872.76	897.93	2.07	0.14
ψ (Wooded cover + Wetland edge + Forest edge), $p(\text{Best})$	11	875.31	898.30	2.44	0.11
ψ (Wooded cover + Wetland distance), $p(\text{Best})$	10	881.84	902.66	6.80	0.01

^a Proportion of all woody cover types within 1.5-km radius circular buffer.

^b Edge density of wetland cover types within 1.5-km radius circular buffer.

^c Mean distance between nearest-neighbor wetland patches in 1.5-km radius circular buffer.

^d Edge density of forest cover types within 1.5-km radius circular buffer.

density as density covariates. A 2-part finite mixture within the detection parameters was the second most supported model; other trap-covariate detection models formed the remainder of models within $\Delta_i < 30$. Null and seasonal detection models had the least support (Table S2).

The most supported model suggested woody cover and wetland edge density were associated with increased density

(Table 7), and exhibited far better fit than site-specific homogenous density models ($\Delta \text{AIC}_c > 300$; Table S2). Trap covariates had varied effect on detection function parameters. Both woody cover and wetland edge density trap covariates increased bobcat movement relative to activity center and decreased detection magnitude, though woody cover had a much stronger effect size. Local trail covariates increased \hat{g}_0 but had minor and mixed relationship to $\hat{\sigma}$ (Table 7).

Abundance point estimates ranged from 339 to 430 (Table S4) and the most supported model estimated adult bobcat abundance within the study area to be 362 (95% CI = 272–490), an average density of 2.53 adults per 100 km² (95% CI = 1.90–3.42). Predicted density across the sampled arrays ranged from 1.52–5.61 individuals per 100 km², and predicted abundance over defined 100 km² subsections of the study area ranged from 0.6–6.7 adults (Fig. 2). A linear functional relationship between covariate-based predictions of density and occupancy was also far more supported ($w_i > 0.99$, Fig. 3) than an asymptotic function. The inverted linear relationship again exhibited very strong fit ($R^2 = 0.95$).

DISCUSSION

Our study provides one of the few published predictive estimates of carnivore abundance over a large geographic area incorporating uncertainty inherent in capture-recapture analysis. Spatially explicit capture-recapture appears to be

Table 6. Coefficient estimates ($\hat{\beta}$) and 95% confidence intervals for occupancy (ψ) and probability of detection (p) parameters used to predict bobcat occurrence in central Wisconsin in 2012 based on remote camera detections.

Parameter	Covariate ^a	$\hat{\beta}$	95% CI	
			Lower	Upper
ψ	Intercept	-3.68	-5.09	-2.27
	Wooded cover (%)	4.25	2.54	5.96
	Wetland edge (m/ha)	2.47	0.79	4.16
	Wetland distance (m)	-0.20	-0.47	0.07
p	Intercept	-1.54	-1.85	-1.22
	Foot traffic	-0.87	-1.63	-0.11
	Vehicle traffic	-0.11	-0.27	0.05
	Wetland	1.20	0.51	1.89
	Open	0.58	-0.42	1.58
	Bare	0.99	0.50	1.48
	Natural funnel	2.08	0.53	3.63

^a All occupancy covariates are measured within a 1.5-km radius circular buffer of the detection. Probability of detection covariates are binary based on location characteristics

Table 7. Coefficient estimates ($\hat{\beta}$) and standard errors (SE) for predicted bobcat occurrence (Ψ), detection probability (p), density (D), individual encounter rate (g_0), and individual movement (σ) in central Wisconsin in 2012 based on remote camera detections. Values with an asterisk (*) indicate 95% confidence intervals do not overlap 0.

Covariate ^a	Ψ		p		D		\hat{g}_0		σ	
	$\hat{\beta}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE
Wooded cover (%)	4.25*	0.87			1.78*	0.72	-0.86*	0.16	0.48*	0.14
Wetland edge (m/ha)	2.71*	0.88			1.61*	0.54	-0.31 ^b	0.15 ^b	0.15 ^b	0.06 ^b
Wetland distance (m)	-0.20	0.14								
Bare			0.99*	0.25			0.82*	0.31	0.17	0.13
Wetland			1.20*	0.35			1.94 ^{a,b}	0.38 ^b	-0.77 ^{a,b}	0.17 ^b

^a All covariates are measured within a 1.5-km radius circular buffer of the detection except for bare and wetland, which are binary based on location characteristics.

^b Indicates estimate not contained within top model.

a powerful tool for modeling variation in population size over broad spatial extents. Although other regional estimates of bobcat population size were derived using different analyses and methodologies, bobcats in central Wisconsin appear to

have lower overall density than in northern Wisconsin (4.3/100 km² over the harvested region; R. Rolley, Wisconsin Department of Natural Resources, personal communication). The range of densities that we predicted overlap with previous small-scale estimates in northern Wisconsin, Michigan, and Minnesota (Berg 1979, Lovallo and Anderson 1996, Stricker et al. 2012) but fall far below estimates from southern latitudes (Nielsen and Woolf 2001, Larrucea et al. 2007, Ruell et al. 2009).

As previously found within the region, both forest cover and wetlands appear to be requisite for bobcat occupancy (Woolf et al. 2002, Pruess and Gehring 2007, Tucker et al. 2008). Wetlands may be particularly valuable; the cover type was associated with both increased bobcat density and increased individual use. We expect these associations relate to foraging value. Wetland cover in Wisconsin may harbor greater small-mammal density than other cover-types (Lovallo and Anderson 1996), and wetland-upland edges offer greater diversity of potential small-mammal prey species (Stephens and Anderson 2014). Although woody cover was important at large scales, bobcat detection was equivalent or lesser within local forest cover than sites with wetland or open habitats, suggesting fine-scale selection for habitat heterogeneity and coarser scale selection for woody cover (Chamberlain et al. 2003, Tucker et al. 2008). Use of grassy habitats at small scales may reflect the habitat selection of cottontail rabbit (*Sylvilagus floridanus*; Althoff et al. 1997), a common and important prey item for bobcats (Litvaitis et al. 2006, Brockmeyer and Clark 2007), and edges between forest and herbaceous vegetation also exhibit more small-mammal diversity (Stephens and Anderson 2014).

Occupancy as a Density Index

Our 2 primary concerns regarding occupancy as a density index were 1) individuals in marginal habitat would use more space than individuals in higher density areas, resulting in no net increase in the total population footprint, and 2) that occupancy would saturate and density would continue to increase, providing no ability to discern occupancy differences between regions of high density. Our analysis found little evidence supporting either concern within our sample, and we are guardedly optimistic that spatial patterns in

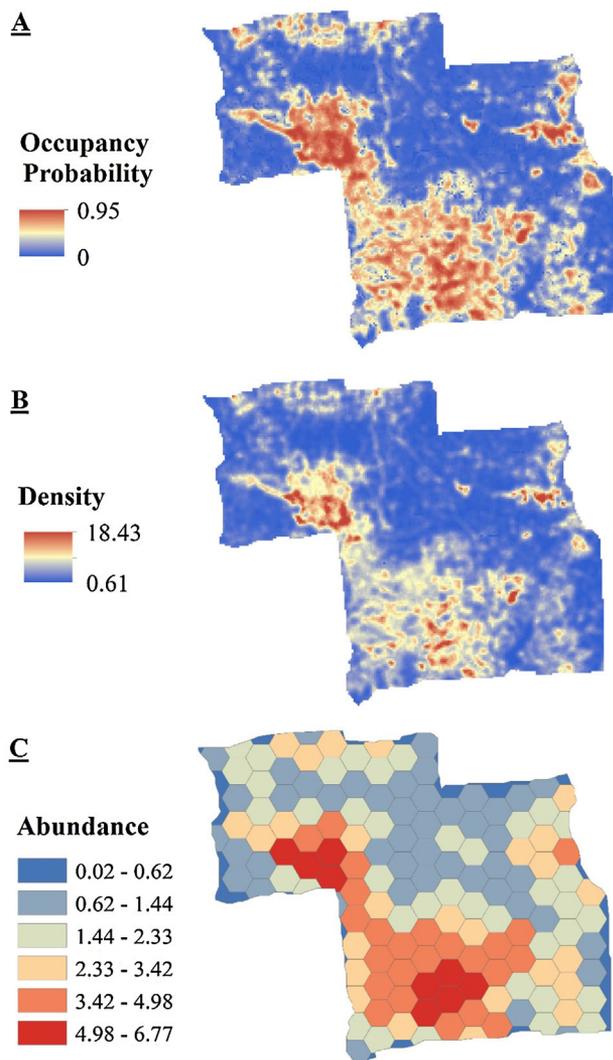


Figure 2. Predicted bobcat occupancy in central Wisconsin in 2012 derived from trail camera detections (A), predicted intensity of the bobcat density spatial point process (per 100 km²) using spatial capture-recapture (B), and predicted bobcat abundance over discrete 100-km² hexagons (C).

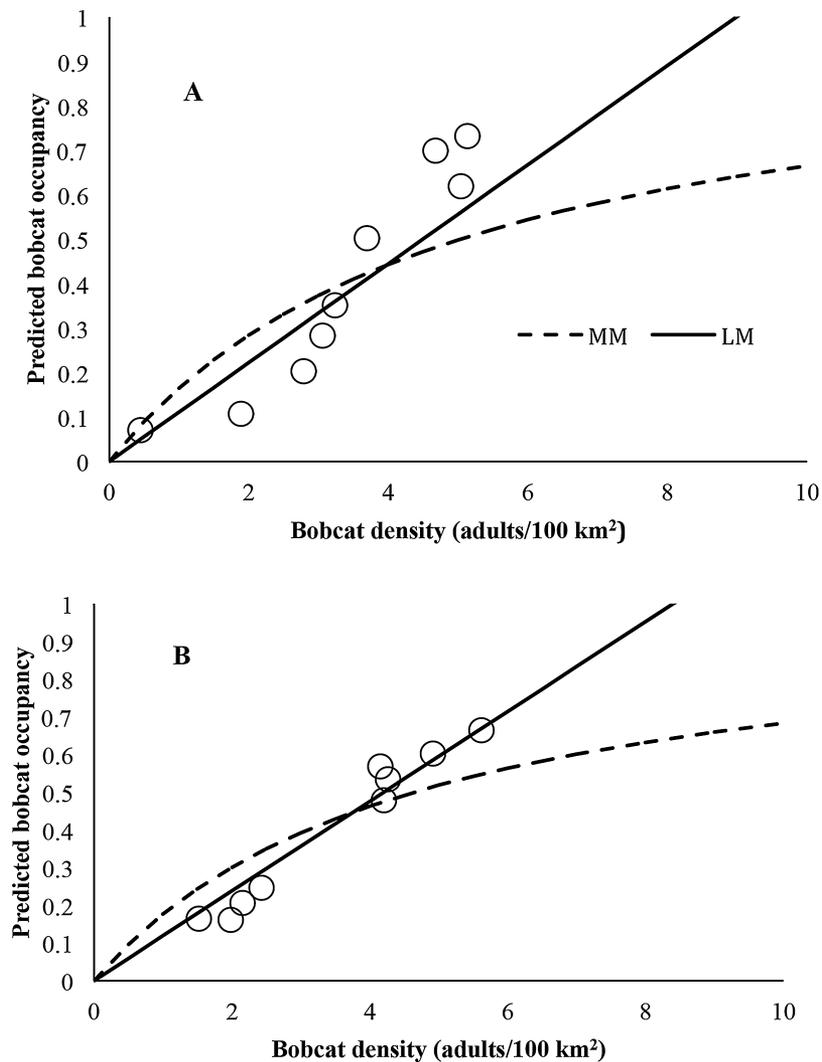


Figure 3. Predicted bobcat occupancy and density (adults/100 km²) in central Wisconsin predicted using array- (panel A) or habitat- (panel B) specific covariates based upon remote camera surveys in 2012. Regression predictions from linear (LM), or Michaelis-Menten (MM) functions are respectively displayed as solid and dashed.

occupancy are useful indices for spatial patterns in density for bobcats under certain circumstances.

Contrary to our expectation, we did not observe individual bobcats using more space within more marginal habitats. Parameter estimates (\hat{D} , $\hat{\sigma}$, and \hat{g}_0) indicated that broad-scale coverage of wetlands and woody cover both increased the probability that a bobcat would establish a home range, increased the distance at which an individual was detected from its activity center, and decreased repeat usage of camera locations. Radiotelemetry data strongly suggests bobcat home range expansion in marginal habitat (Anderson 1988, Nielsen and Woolf 2001, Tucker et al. 2008). Thus, these parameter estimates likely reflect changes in individual space usage over short-term periods with the spatial configuration of individual use reflecting bobcat avoidance of directly traversing agricultural areas and resulting in distinct clusters of use along suitable corridors within an inhospitable matrix (Tucker et al. 2008, Reding et al. 2013). In contrast, large contiguous tracts of woody cover and wetlands appeared to

be used relatively equitably by individuals. This spatial pattern of detection is consistent with within home range resource selection (Royle et al. 2013b).

Likewise, across the range of densities we encountered, we found no evidence that increases in occupancy probability was decelerating in asymptotic fashion. Instead, the functional relationship appeared more linear, with reasonably strong correlation. Occupancy and density also shared similar associations with predictors. This suggests that probability of occupancy can be a useful relative index for density and supports the viability of using low-intensity presence-absence surveys as a surrogate for or in conjunction with capture-recapture models (e.g., Chandler and Clark 2014) for research purposes. It also provides support for previous use of using predictive distribution models to guide bobcat management decisions. We are guardedly optimistic that common monitoring efforts based on presence-absence information may be useful tools for assessing trends in density but recommend further investigation of this topic

(sensu Tempel and Gutiérrez 2013) given that our sample lacked temporal replication or experimental manipulation required to rigorously test how occupancy estimates respond to changes in density. Regardless of the state parameter of interest, we recommend camera surveys for bobcat focus fine-scale placement along well-worn dirt roads, natural funneling features with limited human activity, and adjacent to wetlands to increase detection rates.

Despite our findings, there may be many situations in which probability of occupancy might not be a useful surrogate for density. Both occupancy and density were relatively low across the region we sampled. In the southern United States, where bobcats exist at higher density and exhibit greater spatial overlap than in our study area (Nielsen and Woolf 2001), occupancy estimates might exist near or at 1 and lack enough variance to effectively predict density. As the spatial extent of sampling effort within a unit increases, the more likely the unit is to be observed or estimated as occupied, resulting in increased curvilinearity or reduced correlation strength in the occupancy-density relationship (Efford and Dawson 2012, Latham et al. 2014). Thus, occupancy surveys based on track or sign where the sampling extent or intensity within a unit can be arbitrarily picked should carefully consider survey unit size if seeking to make inference about abundance (Webb and Merrill 2012). Using baits to increase detection rates might be an additional source of bias by altering individual space-use patterns (but see Popescu et al. 2014). We encourage further empirical consideration of the occupancy-density relationship for the bobcat using different sampling methods and within regions of higher density.

Finally, predicting abundance over large spatial expanses has inherent risks. Differences in individual bobcat selection over large areas can bias population estimates (Boyce and MacDonald 1999, Boyce 2006). Because independent data generally fit predicted occupancy patterns, it seems unlikely that habitat selection drastically differed in regions of the study area that were un-sampled. Carnivore population size is often linked to prey density and levels of human exploitation more than vegetation cover types (Carbone and Gittleman 2002). The bobcat population within our study area was not subject to direct human harvest, and harvest of its primary prey items is either regulated or inconsequential such that local extirpation was unlikely. Consequently, the land cover metrics we used for prediction may have been more suitable phenomenological variables than would be true for many populations of bobcats or other carnivores.

MANAGEMENT IMPLICATIONS

Spatially explicit capture-recapture models allowed us to predict overall bobcat density (2.53/100 km²) and population size (362 adults) across central Wisconsin. These estimates suggest that bobcat density within the study area was comparable to neighboring states and northern Wisconsin where harvest is allowed, and have been used to justify managerial changes. Modeling density and presence as a function of covariates allowed identification of woody and

wetland landscapes that may be important habitat for bobcats. Our results suggest that low-intensity occupancy surveys have promise as an index for evaluating relative density and identifying habitat types with high density potential, but we recommend empirical validation of the occupancy-density relationship in other regions where densities and selection patterns of bobcats may differ or when other survey methods are used.

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SUPPORTING INFORMATION

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