

2019

Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps

Christopher N. Jacques
Western Illinois University

Robert W. Klaver
U.S. Geological Survey, bklover@iastate.edu

Tim C. Swearingen
Western Illinois University

Edward D. Davis
Western Illinois University

Follow this and additional works at: https://lib.dr.iastate.edu/nrem_pubs

Charles K. Anderson
 Part of the [Wildlife and Evolutionary Biology Commons](#), [Natural Resources and Conservation Commons](#), [Natural Resources Management and Policy Commons](#), [Spatial Science Commons](#), and the [Statistical Models Commons](#)
See next page for additional authors

The complete bibliographic information for this item can be found at https://lib.dr.iastate.edu/nrem_pubs/316. For information on how to cite this item, please visit <http://lib.dr.iastate.edu/howtocite.html>.

Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps

Abstract

Camera-trapping data analyzed with spatially explicit capture–recapture (SCR) models can provide a rigorous method for estimating density of small populations of elusive carnivore species. We sought to develop and evaluate the efficacy of SCR models for estimating density of a presumed low-density bobcat (*Lynx rufus*) population in fragmented landscapes of west-central Illinois, USA. We analyzed camera-trapping data from 49 camera stations in a 1,458-km² area deployed over a 77-day period from 1 February to 18 April 2017. Mean operational time of cameras was 52 days (range = 32–67 days). We captured 23 uniquely identifiable bobcats 113 times and recaptured these same individuals 90 times; 15 of 23 (65.2%) individuals were recaptured at ≥ 2 camera traps. Total number of bobcat capture events was 139, of which 26 (18.7%) were discarded from analyses because of poor image quality or capture of only a part of an animal in photographs. Of 113 capture events used in analyses, 106 (93.8%) and 7 (6.2%) were classified as positive and tentative identifications, respectively; agreement on tentative identifications of bobcats was high (71.4%) among 3 observers. We photographed bobcats at 36 of 49 (73.5%) camera stations, of which 34 stations were used in analyses. We estimated bobcat density at 1.40 individuals (range = 1.00–2.02)/100 km². Our modeled bobcat density estimates are considerably below previously reported densities (30.5 individuals/100 km²) within the state, and among the lowest yet recorded for the species. Nevertheless, use of remote cameras and SCR models was a viable technique for reliably estimating bobcat density across west-central Illinois. Our research establishes ecological benchmarks for understanding potential effects of colonization, habitat fragmentation, and exploitation on future assessments of bobcat density using standardized methodologies that can be compared directly over time. Further application of SCR models that quantify specific costs of animal movements (i.e., least-cost path models) while accounting for landscape connectivity has great utility and relevance for conservation and management of bobcat populations across fragmented Midwestern landscapes.

Keywords

bobcat, camera trap, density estimation, fragmentation, Illinois, *Lynx rufus*, spatial capture–recapture model, trap array

Disciplines

Ecology and Evolutionary Biology | Natural Resources and Conservation | Natural Resources Management and Policy | Spatial Science | Statistical Models

Comments

This article is published as Jacques, Christopher N., Robert W. Klaver, Tim C. Swearingen, Edward D. Davis, Charles R. Anderson, Jonathan A. Jenks, Christopher S. Deperno, and Robert D. Bluett. "Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps." *Wildlife Society Bulletin* (2019). doi: [10.1002/wsb.968](https://doi.org/10.1002/wsb.968).

Rights

Works produced by employees of the U.S. Government as part of their official duties are not copyrighted within the U.S. The content of this document is not copyrighted.

Authors

Christopher N. Jacques, Robert W. Klaver, Tim C. Swearingen, Edward D. Davis, Charles R. Anderson, Jonathan A. Jenks, Christopher S. Deperno, and Robert D. Bluett



Original Article

Estimating Density and Detection of Bobcats in Fragmented Midwestern Landscapes Using Spatial Capture–Recapture Data from Camera Traps

CHRISTOPHER N. JACQUES,¹ *Department of Biological Sciences, Western Illinois University, Macomb, IL 61455, USA*

ROBERT W. KLAVER, *Department of Natural Resource Ecology and Management, U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, IA 50011, USA*

TIM C. SWEARINGEN, *Department of Biological Sciences, Western Illinois University, Macomb, IL 61455, USA*

EDWARD D. DAVIS, *Department of Biological Sciences, Western Illinois University, Macomb, IL 61455, USA*

CHARLES R. ANDERSON, *Department of Natural Resources, Colorado Parks and Wildlife, 317 W Prospect Road, Fort Collins, CO 80526, USA*

JONATHAN A. JENKS, *Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA*

CHRISTOPHER S. DEPERNO, *Department of Forestry and Environmental Resources, Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Raleigh, NC 27695, USA*

ROBERT D. BLUETT, *Illinois Department of Natural Resources, 1 Natural Resources Way, Springfield, IL 62702, USA*

ABSTRACT Camera-trapping data analyzed with spatially explicit capture–recapture (SCR) models can provide a rigorous method for estimating density of small populations of elusive carnivore species. We sought to develop and evaluate the efficacy of SCR models for estimating density of a presumed low-density bobcat (*Lynx rufus*) population in fragmented landscapes of west-central Illinois, USA. We analyzed camera-trapping data from 49 camera stations in a 1,458-km² area deployed over a 77-day period from 1 February to 18 April 2017. Mean operational time of cameras was 52 days (range = 32–67 days). We captured 23 uniquely identifiable bobcats 113 times and recaptured these same individuals 90 times; 15 of 23 (65.2%) individuals were recaptured at ≥ 2 camera traps. Total number of bobcat capture events was 139, of which 26 (18.7%) were discarded from analyses because of poor image quality or capture of only a part of an animal in photographs. Of 113 capture events used in analyses, 106 (93.8%) and 7 (6.2%) were classified as positive and tentative identifications, respectively; agreement on tentative identifications of bobcats was high (71.4%) among 3 observers. We photographed bobcats at 36 of 49 (73.5%) camera stations, of which 34 stations were used in analyses. We estimated bobcat density at 1.40 individuals (range = 1.00–2.02)/100 km². Our modeled bobcat density estimates are considerably below previously reported densities (30.5 individuals/100 km²) within the state, and among the lowest yet recorded for the species. Nevertheless, use of remote cameras and SCR models was a viable technique for reliably estimating bobcat density across west-central Illinois. Our research establishes ecological benchmarks for understanding potential effects of colonization, habitat fragmentation, and exploitation on future assessments of bobcat density using standardized methodologies that can be compared directly over time. Further application of SCR models that quantify specific costs of animal movements (i.e., least-cost path models) while accounting for landscape connectivity has great utility and relevance for conservation and management of bobcat populations across fragmented Midwestern landscapes. © 2019 The Wildlife Society.

KEY WORDS bobcat, camera trap, density estimation, fragmentation, Illinois, *Lynx rufus*, spatial capture–recapture model, trap array.

Managing or conserving solitary mammalian carnivores is intrinsically difficult because they exist at low population densities, occupy relatively large ranges, are difficult to

detect, and vulnerable to direct persecution by humans (Soule and Terborgh 1999, Crooks 2002, Ruell et al. 2009, Clare et al. 2015). Carnivores are of particular interest in assessing the efficacy of large-scale conservation planning, though obtaining financial and logistical resources to estimate abundance at meaningful landscape scales often is prohibitive (Crooks 2002, Kendall et al. 2009). Thus, identifying methodologies to rigorously quantify abundance

Received: 24 September 2018; Accepted: 6 January 2019
Published: 00 Month 2019

¹E-mail: cn-jacques@wiu.edu

of cryptic, low-density species, and at low economic cost is an important priority for population management and predicting long-term persistence of small populations subject to annual harvest (Roberts and Crimmins 2010, Clare et al. 2015).

Bobcats (*Lynx rufus*) are widespread across North America and population status across most of the current geographic range is stable or increasing (Roberts and Crimmins 2010, Linde et al. 2012). Nevertheless, population status of bobcats in other regions is unknown or of priority management concern (Soule and Terborgh 1999, Riley et al. 2003, Litvaitis et al. 2006). Viewed as an important furbearer of considerable conservation interest, bobcat density varies along a spatial continuum ranging from areas of high abundance in regions of the southern and western United States to pockets of low density in agriculturally dominated Midwestern states (Sunquist and Sunquist 2002, Thornton and Pekins 2015). In addition, a key conservation issue pertaining to bobcats across Midwestern landscapes is the effect of habitat fragmentation on space use and reliability of abundance estimation methods (Soisalo and Cavalcanti 2006, Ruell et al. 2009). Over the past century, fragmentation of North American forested ecosystems has been extensive and particularly evident across Midwestern landscapes (Radeloff et al. 2005). In Illinois, USA, forested landscapes have been reduced by 64% and currently characterized by young (<61-year-old) forests limited to the southern and western regions of the state (Crocker 2015). For these reasons, sound estimates of abundance are needed for monitoring the status of bobcat populations, detecting temporal changes in population trends, and promoting appropriate management decisions (Morin et al. 2018).

Despite widespread distribution of bobcats throughout North America, estimates of abundance are limited and often constrained by the inability to make direct comparisons with previous studies because of nonstandardized methodologies and associated variability in sources of sampling bias (Thornton and Pekins 2015, Morin et al. 2018). Nevertheless, early attempts to estimate density of bobcats have relied primarily on techniques that lack measures of accuracy and precision, including indices of relative abundance such as trap-nights per individual captured (Wood and Odum 1964, Jenkins et al. 1979), harvest (O'Brian and Boudreau 1998), snow-tracking (Golden 1995), mail questionnaires (Anderson 1987), and scent-station surveys (Linhart and Knowlton 1975, Johnson and Pelton 1981, Conner et al. 1983); previous studies have identified sex- and age-specific biases in each of these methods (Diefenbach et al. 1994). Furthermore, none of these methods considered the spatial context of the data. Thus, expansion of bobcat populations of historically low density and suboptimal habitat are ideally suited for demonstrating the potential utility of increasingly advanced abundance estimation techniques for population monitoring (Morin et al. 2018).

Closed population models have been used extensively to estimate density and abundance of animal populations from standardized trap arrays that provide information on encounter histories of study animals (Borchers et al. 2002).

However, model-derived estimates of population density are difficult to interpret because of uncertainty in what constitutes the effective area sampled by trap arrays (i.e., area from which captured and recaptured individuals are drawn; Royle et al. 2011). Previous studies have recognized the difficulty in defining the sampling area and included a wide range of *ad hoc* approaches, including drawing polygons around and buffering trapping arrays. Unfortunately, these approaches are arbitrary and inconsistent among studies, introduce uncertainty into density estimation, and fail to account for spatial heterogeneity in encounter histories among individuals (Royle et al. 2011).

A variety of increasingly sophisticated methods are available for estimating population density from capture–recapture studies (Pollock et al. 1990, Seber 1992, Pledger 2000, Williams et al. 2002, Efford 2004). Among these, spatial capture–recapture (SCR) models (Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2011) provide a rigorous analytical technique for inference that extends standard closed population models (Otis et al. 1978, Lukacs and Burnham 2005) by including a spatially explicit model that accounts for the distribution of individuals in space (Royle et al. 2011). An advantage of SCR models is they rely on spatial information readily available with camera data and use distance between traps and animal activity centers to model spatially explicit (i.e., camera trap) encounter probabilities (Royle et al. 2011). Spatial capture–recapture models have been used in population density estimation for a range of carnivores, including black bears (*Ursus americanus*; Gardner et al. 2010a, Wilton et al. 2014), tigers (*Panthera tigris*; Royle et al. 2009), small cats (Gardner et al. 2010b, Satter et al. 2019), wolverine (*Gulo gulo*; Royle et al. 2011), and mink (*Mustela vison*; Fuller et al. 2016). Density estimates for small cats are scarcely reported in the published literature; to our knowledge, the only previous applications of spatially explicit capture–recapture models to camera-trap data were by Thornton and Pekins (2015) and Satter et al. (2019), who reported average density estimates that ranged from 5.6 to 16.3 bobcats/100 km² and 7.2–22.7 ocelots (*Leopardus pardalis*)/100 km², respectively. Morin et al. (2018) extended the application of SCR models to genetic data, and reported density estimates of 5.9–20.3 bobcats/100 km² from 2 study sites across Virginia, USA. Nevertheless, additional bobcat density estimates are needed to generate more reliable population-level data to inform ecological questions related to long-term persistence, demography, and more defensible harvest regulations and conservation strategies across fragmented Midwestern landscapes. Thus, our objective was to evaluate the efficacy of spatially explicit capture–recapture models for estimating density of a presumed low-density bobcat population in fragmented landscapes of west-central Illinois.

STUDY AREA

Our study was conducted in a 1,458-km² area throughout portions of Hancock and Schuyler counties across west-central Illinois (Fig. 1). The region was rural and sparsely populated (3.9 persons/km²; United States Census Bureau 2010). The majority (53.2%) of land across the study site

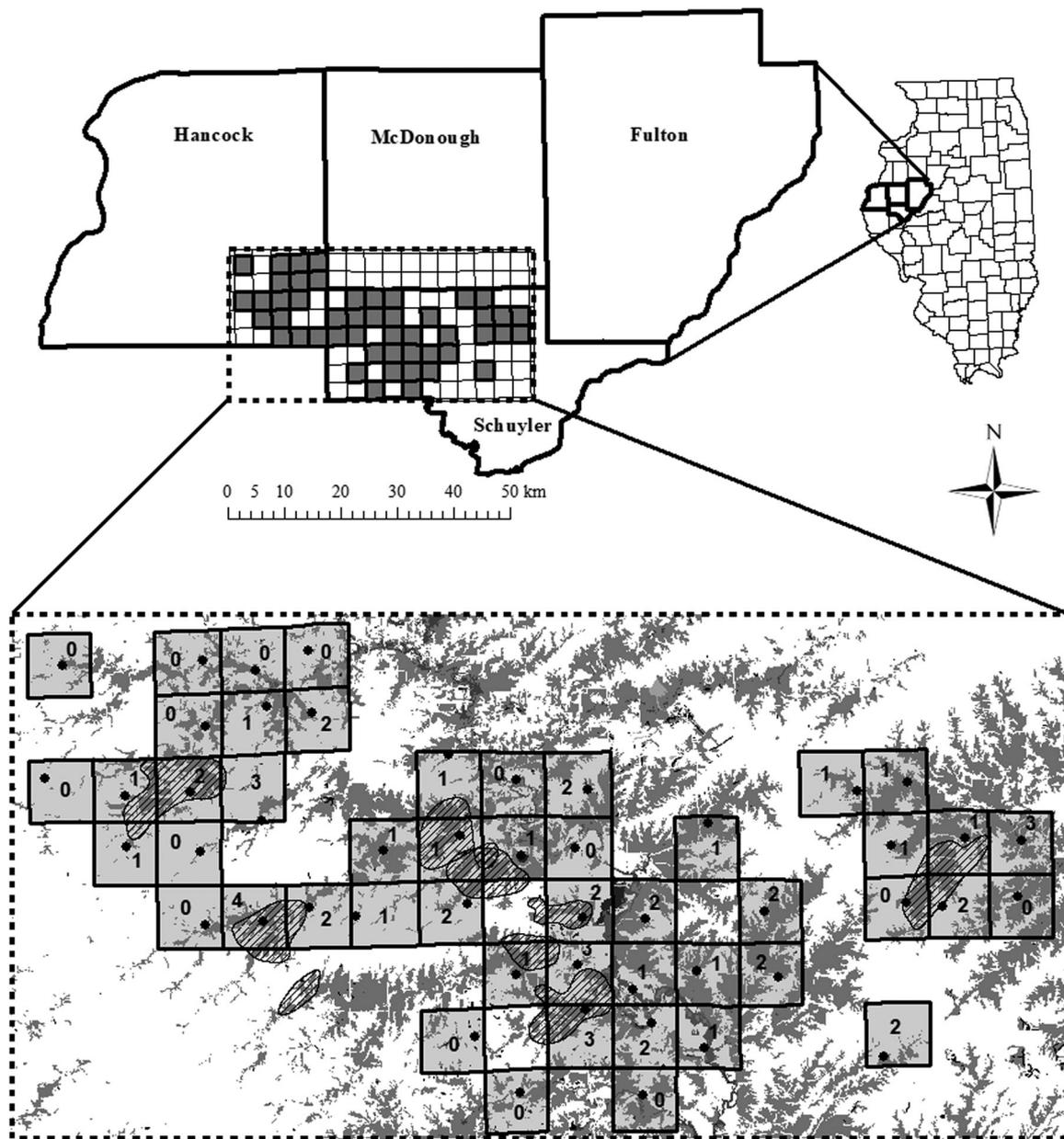


Figure 1. Bobcat camera-survey grids (10.7 km² blocks; thin black lines) were located in a 1,458-km² study site (camera-trapping array; thick dashed line situated across portions of Hancock and Schuyler counties) of west-central Illinois, USA, winter 2017. Thick black lines delineate county boundaries and the gray shaded regions within the trapping array denote the spatial distribution (locations) of camera survey grids. Bobcat camera-station locations were selected by overlaying 10.7-km² camera-survey grids (light gray shaded areas with boundaries delineated by thick black lines) over the 2011 National Landcover Database imagery (dark gray shaded areas in background) in Hancock and Schuyler counties. Camera station locations (black circles) were placed as close to centroid locations as possible, though varied depending on availability of suitable bobcat habitat (i.e., forested cover). Numbers within camera survey grids represent the number of uniquely identified bobcats at each camera station location and cross-hatched polygons depict locations of 50% home ranges of female bobcats throughout the study area.

was characterized by row-crop (i.e., corn [*Zea mays*] and soybeans [*Glycine max*]) agriculture, whereas remaining acreage constituted forest (27.3%), development (5.2%), wetland (1.1%), and pasture-hay (12.6%; Homer et al. 2015). Elevation across the region ranged from 130 m to 244 m above sea level (Walker 2001, Preloger 2002, Tegeler 2003). Dominant overstory woody vegetation consisted of white oak (*Quercus alba*), post oak (*Q. stellata*), black oak (*Q. velutina*), and mockernut hickory (*Carya tomentosa*; Luman et al. 1996).

METHODS

Camera-trapping

We conducted camera surveys using passive infrared-triggered remote cameras (i.e., Browning Recon Force, Model BTC-7FHD; Prometheus Group, LLC Birmingham, AL, USA). To meet basic assumptions of closed populations, we limited our SCR analysis to data collected during the 2017 breeding season (1 Feb 2017–18 Apr 2017), during which time we also avoided logistical constraints (e.g., land

access issues, vegetation growth, damage to cameras by farming equipment, increased risk of theft) during summer sampling intervals and maximized the likelihood of detecting bobcats during seasonal changes in habitat use (Rolley and Warde 1985, Kamler and Gipson 2000). Prior to camera deployment, we divided our study site evenly into 10.7-km² camera survey units (i.e., approximate area of 50% home-range size for radiocollared female bobcats in west-central IL [E. D. Davis, unpublished data]). Estimated home-range sizes for bobcats across our study area were relatively large compared with previous estimates across Midwestern landscapes (Lovallo and Anderson 1996, Nielsen and Woolf 2001, Tucker et al. 2008).

We generated centroid locations for each camera survey unit (hereafter, survey units) and systematically selected 50 survey units. In particular, we navigated to survey unit centroids and selected fine-scale camera station (2 cameras situated on opposite sides of known trails [vehicle, game, human]) locations based on topographic or vegetation features typical of suitable habitat or travel routes (Thornton and Pekins 2015, Alexander and Gese 2018). In cases when centroid locations were not located in potential habitat (i.e., forested cover; Kolowski and Woolf 2002, Nielsen and Woolf 2002, Tucker et al. 2008, Linde et al. 2012) or along travel routes, we adjusted them by placing cameras in or along the edge of the nearest forested habitat. In instances where survey units consisting primarily of row crop agriculture were selected, we systematically selected the nearest survey units that contained sufficient forest cover to maximize the likelihood that bobcats had a nonzero probability of being captured and spatially recaptured. However, restricted land access necessitated the placement of several camera stations in survey units with limited forested cover (Fig. 1).

We placed each camera at a height of 0.3 m above ground (i.e., measured to center of lens) and fastened them to wooden surveyor stakes (61 cm × 7.62 cm) or suitable woody vegetation. We positioned each camera approximately 2.3 m perpendicular to the line of travel and ensured that they faced one another. In addition, we offset each camera by approximately 4.6 m to minimize the likelihood of overexposure or blackout events associated with cameras placed directly across from one another along trails (Karanth 1995, Negrões et al. 2012, Rovero et al. 2013). This configuration increased the chance of obtaining bilateral images of an animal as it passed through a camera station (Kelly et al. 2008, Foster and Harmsen 2012, Rovero et al. 2013, Thornton and Pekins 2015, Alexander and Gese 2018). We attached visual attractants (i.e., compact disks) to vegetation out of the field of view of camera stations (Nielsen and McCollough 2009). We assumed that gross bobcat movements (and thus estimates of space use [i.e., movement] parameters [σ] in SCR analyses) were not appreciably affected by use of visual attractants at camera station locations. We spaced camera stations such that the mean home-range size of a female bobcat (40.4 km²; E. D. Davis, unpublished data) would encompass 4 camera stations (Otis et al. 1978, Rovero et al. 2013, Alexander and Gese 2018),

and thus, increase the likelihood that all animals within our study site had some positive probability of capture.

To avoid potential effects of dependence among multiple photographs of bobcats during a single night on density estimation, we considered a capture event as a photograph of an animal at ≥ 1 camera at a station within a 1-hr time period (Kelly et al. 2008); bobcat photographs separated by < 1 hr were not considered unique capture events unless ≥ 2 different individuals were positively identifiable. We sorted individual bobcats into positive identifications (e.g., based on presence of radiocollars, ear tags, or unique pelage marks or spot patterns), tentative identifications, and unidentifiable animals based on poor image quality (Kelly et al. 2008). For tentative identifications, we conducted further analyses using 2 additional observers to confirm the identity of individuals determined by the primary observer. We were confident that image quality and identifying features for positively identified individuals did not warrant confirmation by multiple observers; thus, analyses of these photographs was limited to the primary observer (Tim C. Swearingen). We attempted to further limit observer bias and misidentification in subsequent capture–recapture estimates, by censoring detection events of all tentative identification photographs without consensus agreement by ≥ 2 observers (Creel et al. 2003, Kelly et al. 2008, Foster and Harmsen 2012, Clare et al. 2015). In addition, we discarded tentative capture events only if all associated photographs were classified by all 3 observers as unidentifiable because of poor image quality (Kelly et al. 2008). When applicable, we used capture photos of previously captured and radiocollared bobcats ($n = 13$) to aid in uniquely identifying individuals photogenerated at camera stations. When available, we associated sex information with each bobcat in the capture history, and recorded it as unknown for individuals whose sex could not be determined (Satter et al. 2019). Unfortunately, we obtained too few confirmed photographs ($n = 1$) of female bobcats, which precluded modeling intersexual variation in space use in capture–recapture detection function parameters (Sandell 1989, Sollman et al. 2011).

Data Analyses

We developed SCR models for estimating bobcat density across our study site following Royle et al. (2011). Unlike classical closed-population capture–recapture models, SCR models formally relate encounters of individuals to where individuals spend time over trapping intervals (Royle et al. 2011). Thus, individuals that center activities across a defined area over a given period of time should be expected to encounter a trap as a function of the distance between that animal's activity center to the trap (Royle et al. 2011). Functionally, SCR models are essentially standard, closed population models augmented by a spatial random effect that describes the juxtaposition of individuals within the trap array (Royle et al. 2011). We conducted Bayesian analyses using Markov-Chain Monte Carlo (MCMC) methods over the region where camera station locations were distributed (i.e., state-space of the point process; Royle et al. 2011).

We followed Royle et al. (2011) to define the continuous state space by overlaying the trap array on a rectangular region extending a maximum of 20 km beyond camera traps in each cardinal direction. We scaled the state-space by defining it near the origin and fit models for a range of choices of the rectangular state-space (Royle et al. 2014). The buffer of the state-space should be sufficiently large to ensure that encountering individuals with activity centers beyond the state-space boundary are minimal (Royle et al. 2014). To evaluate this, we fit models for various choices of a rectangular state-space based on buffers from 5 km to 20 km (Royle et al. 2014). We modified the `wolvSCR0` function provided in the `scrbook` package in Program R (R Core Team 2015) and fit models in JAGS using data augmentation with $M=100$ – 150 individuals, a state-space buffer of 1 standardized unit, 3 MCMC chains each of 12,000 total iterations, and discarded the first 2,000 as burn-ins (Royle et al. 2014). We related individuals in specific traps to their home-range center (a latent variable) using a bivariate normal distribution of their activities (Royle et al. 2014). We assessed convergence of MCMC chains to their stationary distributions by visually inspecting time series plots for each monitored parameter and compared R-hat statistics to 1.0 (Gelman and Rubin 1992, Royle et al. 2014).

RESULTS

Spatially Explicit Capture–Recapture Model and Density Estimates

We deployed 50 camera stations (i.e., 2 cameras/station) in a 1,458-km² area over a 77-day period from 1 February to 18 April 2017, of which 49 were used in analyses because of theft of cameras at one station (Fig. 1). Mean operational time of cameras was 52 days (range = 32–67 days). Total number of bobcat capture events was 139, of which 26 (18.7%) were discarded from analyses because of poor image quality or capture of only a part of an animal in photographs. Of 113 capture events used in analyses, 106 (93.8%) contained high-quality photographs that enabled positive identifications of bobcats; number of photographs obtained per capture event ranged from 1 to 12. Remaining capture events (6.2%) were classified as tentative identifications, of which agreement on identifications of bobcats was high (71.4%) among 3 observers. We photographed bobcats at 36 of 49 (73.5%) camera stations, though 2 stations were removed from analyses because of the inability to positively identify individuals. We captured 23 uniquely identifiable bobcats 113 times and recaptured these same individuals 90 times; 15 of 23 (65.2%) individuals were recaptured at ≥ 2 camera traps (Table 1). Individual encounter frequencies ranged from 4 individuals captured 1 time in a single trap to 1 individual captured 17 times in 5 different traps (Table 1).

For the 5-km continuous state-space model, our analysis revealed a slight effect on the posterior distribution of density because the state-space was not sufficiently large (Table 2). However, posterior summary density statistics for the 10-km, 15-km, and 20-km continuous state-space

Table 1. Individual capture frequencies for bobcats captured in camera traps in west-central Illinois, USA, 1 February to 18 April 2017. Rows index unique trap frequencies and columns depict total number of captures (e.g., 4 individuals captured 1 time in 1 trap vs. 1 individual captured 17 times in 5 different traps). Bobcat density estimates were generated using 23 uniquely identifiable individuals, of which 15 were recaptured at ≥ 2 camera traps.

No. traps	No. captures									
	1	2	3	4	5	6	7	9	12	17
1	4	3	0	1	0	0	0	0	0	0
2	0	0	3	0	2	1	2	0	0	0
3	0	0	0	1	0	0	0	0	0	0
4	0	0	0	0	0	1	2	0	0	0
5	0	0	0	0	0	0	0	0	0	1
6	0	0	0	0	0	0	0	1	1	0

models were identical (Table 2). Density estimates were 1.52 and 1.40 bobcats/100 km² (posterior medians), though these ranged from 1.00 to 2.02 individuals/100 km² (Table 2). Our estimate of R-hat was 1.00 for all chains, indicating good model convergence within and between chains.

DISCUSSION

Spatially Explicit Capture–Recapture Model and Density Estimates

Our study represents one of the first efforts to incorporate uncertainty in capture–recapture analyses to improve predictive estimates of bobcat abundance across fragmented Midwestern landscapes. In addition, camera-trapping combined with SCR analysis provided a rigorous analytical framework for generating comparable range-wide density estimates for bobcats (Thornton and Pekins 2015). In the context of previous research, modeled bobcat density across west-central Illinois (1.00–2.02 individuals/100 km²) was far below the mean and median of reported densities (16.2 and 10.0 individuals/100 km², respectively) from a range of studies summarized in Thornton and Pekins (2015), and among the lowest yet recorded for the species. However, most previously reported densities for bobcats were estimated using classical

Table 2. Posterior summaries of spatial capture–recapture model parameters for bobcat camera-trapping data from west-central Illinois, USA (1 Feb–18 Apr 2017) using state-space buffers from 5 km to 20 km. Analyses were based on 3 chains, 12,000 iterations, 2,000 burn-in, for 30,000 total posterior samples. σ is a movement parameter related to α_1 by $\alpha_1 = 1(2\sigma^2)$, as the radius of the bivariate normal model of space usage. N = population size for the prescribed state-space, D is the density per 100 km², and 95 CRI = 95% credible intervals.

Buffer	σ		N		D	
	Median	95 CRI	Median	95 CRI	Median	95 CRI
5	4.44	3.87, 5.18	30.00	25.00, 38.00	1.52	1.27, 1.93
10	4.39	3.84, 5.13	42.00	32.00, 57.00	1.40	1.07, 1.90
15	4.39	3.82, 5.14	59.00	42.00, 82.00	1.40	1.00, 1.94
20	4.38	3.83, 5.10	79.00	55.00, 114.00	1.40	1.00, 2.02

capture–recapture methods, making direct comparisons to SCR-derived estimates complicated (Satter et al. 2019). In cases for other carnivores, classical capture–recapture methods have reported positively biased density estimates (Soisalo and Cavalcanti 2006, Dillon and Kelly 2007, Gerber et al. 2012), which were likely associated with inadequately estimated movement parameters attributable to small grid sizes and small sample sizes (Satter et al. 2019); such may also be the case with previously reported bobcat densities. Outside of Midwestern landscapes, classical capture–recapture methods have estimated the greatest bobcat densities across the Southern Great Plains at 48.0 bobcats/100 km² (Heilbrun et al. 2006), and 39.0 bobcats/100 km² in northern California, USA (Larrucea et al. 2007). However, 3 recent studies used SCR methods to estimate bobcat density across central Texas, western Virginia, and central Wisconsin, USA, and resulted in bobcat densities ranging from 0.45 to 20.3/100 km², which encompassed our reported density estimates (Clare et al. 2015, Thornton and Pekins 2015, Morin et al. 2018). Whether the low range of density estimates we report is associated with variation in analytical approaches or reflective of true population differences remains uncertain, though it warrants the use of standardized survey methods and analyses in future studies. Previous bobcat density estimates derived using classical capture–recapture methods could be re-evaluated with SCR models to quantify to what extent they are positively biased given the limitations of such approaches (Satter et al. 2019). Nevertheless, our ability to estimate density of a medium-sized felid with relatively high precision across fragmented Midwestern landscapes is encouraging, and should increase the confidence and flexibility of using camera-trapping concurrent with SCR modeling for routine monitoring of carnivores across a range of habitat types and animal densities. In addition, camera-trapping combined with SCR modeling could provide a reliable (i.e., standardized) analytical framework for comparing range-wide density data for bobcats from multiple studies, and inform hypotheses regarding range-wide ecological drivers of density (Thornton and Pekins 2015).

We emphasize that our reported density estimates could be used to inform future evaluations of bobcat density derived from consistent survey methodologies, and analyzed in a meta-analytic framework that incorporates regional environmental drivers of bobcat density across fragmented Midwestern landscapes (Thornton and Pekins 2015). Assessing causative factors for reported low bobcat densities across west-central Illinois are ongoing, though previous studies have documented that habitats characterized by intense cultivation negatively affect movement and distribution of bobcats (Riley et al. 2003, Ordenana et al. 2010, Reding et al. 2013). Additionally, habitat selection studies across the Midwest also indicate that selection for forest cover and avoidance of modified habitats are requisites for site occupancy by bobcats (Woolf et al. 2002, Preuss and Gehring 2007, Tucker et al. 2008, Lesmeister et al. 2015). Thus, our reported density estimates support the notion that bobcat abundance across our study site may reflect negative associations within highly altered habitats. Presumably, our reported densities also reflect the recent expansion (i.e., recolonization) of bobcats from distant source populations

into previously occupied Midwestern landscapes (Woolf and Hubert 1998, Tucker et al. 2008).

Despite a high rate of success positively identifying photographs from most (76%) bobcat capture events, nearly 20% of our capture events were unusable in analyses primarily because of poor image quality. The relatively high rate of discarded photos is surprising, especially because we followed recommendations of Kelly et al. (2008) by placing cameras relatively short distances (<4 m) apart along known travel corridors to increase the likelihood of obtaining high-quality photos. We acknowledge that discarding inconclusive (i.e., nonusable) images may contribute to negatively biased estimates, though our analyses indicated that SCR models are a viable approach for estimating bobcat abundance across Midwestern landscapes. We emphasize that the range of bobcat densities we reported are conservative estimates, and warrant further investigation aimed at further improving survey designs used in conjunction with SCR analyses. Fortunately, researchers have developed increasingly sophisticated camera survey designs and model advancements to improve precision of estimates, reduce sampling effort, and standardize camera survey methods (Kelly et al. 2008, Morin et al. 2018). These include techniques for improving the identity of individuals from photos (e.g., modifying density, placement and orientation of cameras, minimizing observer bias, use of white flash cameras; Larrucea et al. 2007, Kelly et al. 2008, Mendoza et al. 2011), more rigorous analyses of data from single-side and hybrid camera station designs (McClintock et al. 2013, Augustine et al. 2018), and accounting for a proportion of individuals that cannot be positively identified (Rich et al. 2014). Collectively, these advancements should aid in developing more rigorous camera survey designs and increase confidence and utility of camera-trapping for density estimation of small felids that may be more difficult to detect and positively identify than other larger and more recognizable species (e.g., jaguars [*Panthera onca*], leopards [*Panthera pardus*], and tigers) that are commonly used in camera-trap research (Thornton and Pekins 2015). The flexibility afforded by camera-trap data to conduct multiple analyses (e.g., occupancy, density estimation, activity, habitat selection; George and Crooks 2006, Heilbrun et al. 2006, Ordenana et al. 2010, Royle et al. 2014, Clare et al. 2015) and greater efficiency of cameras for surveying mammals over other techniques (e.g., hair snares, live trapping; Downey et al. 2007, Tucker et al. 2008) justifies their continued use in carnivore population monitoring. In particular, camera-trap data coupled with SCR analyses may provide substantial information about population demographics for bobcats and other small carnivores that have been poorly surveyed to date (Thornton and Pekins 2015, Satter et al. 2019).

Our primary concerns regarding the application of SCR models to estimate bobcat density across fragmented landscapes were 1) ensuring that camera survey units were small enough to contain no holes that could completely encompass an animal's home range, thus resulting in a 0 capture probability; 2) meeting assumptions of demographic closure during the camera-trapping period; and 3) meeting assumptions of isotropic (circular shaped) home-range centers that were distributed randomly in Poisson fashion

across space (Royle et al. 2011, 2013). We recognize that size of camera survey grids are of considerable importance to ensure that all individuals have a nonzero probability of being captured (Otis et al. 1978), but we followed the recommendation of previous researchers by using regional estimates of bobcat home-range size into our study design to guide our camera-trap spacing and configuration of our camera-trapping array (Wallace et al. 2003, Dillon and Kelly 2007). In addition, our survey grids comprised one-fourth of the mean 95% home-range size of female bobcats ($n = 15$) across our study site (as recommended by Otis et al. 1978) and were largely situated in forested habitats to ensure a nonzero probability of detection during camera-trapping. However, achieving consistent coverage of camera-trapping arrays will remain challenging in field situations because of spatial heterogeneity in individual capture probabilities attributed to logistical constraints (i.e., landowner access), local environmental conditions, and spatial configuration of animal home ranges near the borders of trap arrays across large study areas (Otis et al. 1978, Royle et al. 2014). Despite the lack of uniformity in the placement of cameras across our trapping array, our results revealed that obtaining sufficiently large numbers of spatially dispersed capture and recapture events of bobcats across fragmented landscapes was achievable. Further, our trapping period occurred over a relatively short (i.e., 77 days) duration and core-use-area estimates (based on weekly locations) for the majority of our current sample of radiocollared bobcats ($n = 13$; of which 9 [69.2%] were detected by cameras) were encompassed within our camera-trapping array, further indicating minimal closure assumption violations.

To the extent that nonclosure was present and associated with variability in home range use by transients, such heterogeneity could be modeled as an individual-specific encounter probability that accounts for intraspecific variation in home range size (Royle et al. 2011). Most applications of SCR have assumed that animals distribute their activity based on Euclidean distance between activity centers and camera traps and, thus, ignore effects of landscape structure on animal movement, though recent applications of SCR models based on ecological distance have facilitated direct estimates of animal density, space use, and landscape connectivity (Royle et al. 2013, Sutherland et al. 2015, Fuller et al. 2016). Bobcat home ranges across our study site were largely isotropic, but it is possible that space use and movements were constrained by dendritic geometries (e.g., riparian networks, roads) across fragmented landscapes of west-central Illinois, and contributed to low reported density estimates. Nevertheless, we are guardedly optimistic that SCR in combination with camera-trapping provided a technique for obtaining density data for bobcats, which are largely understudied in Midwestern landscapes. Additionally, further extensions of SCR models that account for intrasexual variation in home range size, movements between activity centers, home range shifts due to a range of biological phenomena, and landscape structure and connectivity may account for heterogeneity in individual

capture probabilities and improve density estimates of bobcats across Midwestern landscapes (Royle et al. 2011, 2013; Satter et al. 2019).

MANAGEMENT IMPLICATIONS

Use of SCR models to predict bobcat density (1.00–2.02/100 km²) was a viable population estimation technique across fragmented Midwestern landscapes. Our estimate suggests that bobcat density within our study area was lower than abundance estimates reported in neighboring states where harvest is permitted, and subsequently used to justify science-based management decisions. Continued expansion of bobcat abundance across Illinois over the past 25 years prompted the reinitiation of regulated harvest concurrent within our study area; thus, our density estimate is timely and may aid in statewide management and conservation of bobcats. Our research has established ecological benchmarks for understanding potential effects of colonization, habitat fragmentation, and exploitation on future assessments of bobcat density using standardized methodologies that can be compared directly over time. For instance, future use of SCR models concurrent with radiotelemetry will provide wildlife managers with direct estimates of density (e.g., to set harvest quotas or bag limits) and finite rates of population increase to better assess whether management goals of reducing, maintaining, or increasing abundance are being met. In addition, modeling density as a function of covariates may aid in identifying habitat types with high potential for occupancy across fragmented Midwestern landscapes, though validation of the density–camera-trap relationship in other regions that reflect heterogeneity in bobcat densities, habitat composition, photocapture and recapture probabilities, or where alternative survey methods are used is warranted. Further application of SCR models that quantify specific costs of animal movements (i.e., least-cost path models) while accounting for landscape connectivity has great utility and relevance for conservation and management of bobcat populations across fragmented Midwestern landscapes.

ACKNOWLEDGMENTS

Funding was provided by Federal Aid in Wildlife Restoration administered by the Illinois Department of Natural Resources, Study No. W187R1, Furbearers Unlimited, Illinois Humane, Illinois Bobcat Foundation, and Western Illinois University (WIU). We thank researchers at South Dakota Department of Game, Fish and Parks; South Dakota State University; and North Carolina State University for providing access to field equipment. We thank numerous WIU students and other volunteers for assistance during animal captures and processing of trail camera photographs. We are indebted to all the private landowners who allowed access to their property throughout our study. We thank M. Alldredge, J. Ivan, D. Morin, 2 anonymous reviewers, and the Associate Editor for their insightful reviews and editorial suggestions on earlier drafts of our manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government.

LITERATURE CITED

- Alexander, P. D., and E. M. Gese. 2018. Identifying individual cougars (*Puma concolor*) in remote camera images—implications for population estimates. *Wildlife Research* 45:274–281.
- Anderson, E. M. 1987. A critical review and annotated bibliography of literature on the bobcat. Colorado Division of Wildlife, Terrestrial Wildlife Research Special Report No. 62, Fort Collins, USA.
- Augustine, B. C., J. A. Royle, M. J. Kelly, C. B. Satter, R. S. Alonso, E. E. Boydston, and K. R. Crooks. 2018. Spatial capture–recapture with partial identity: an application to camera traps. *Annals of Applied Statistics* 12:67–95.
- Borchers, D. L., S. T. Buckland, and W. Zucchini. 2002. Estimating animal abundance: closed populations. Springer-Verlag, London, England, United Kingdom.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385.
- Clare, J. D. J., E. M. Anderson, and D. M. MacFarland. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. *Journal of Wildlife Management* 79:469–480.
- Conner, M. C., R. F. Labisky, and D. R. Progulsk. 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes and opossums. *Wildlife Society Bulletin* 11:145–152.
- Creel, S., G. Spong, J. L. Sands, R. Rotella, J. Zeigle, L. Joe, K. M. Murphy, and D. Smith. 2003. Population size estimation in Yellowstone wolves with error-prone microsatellite loci. *Molecular Ecology* 12:2003–2009.
- Crocker, S. J. 2015. Forests of Illinois, 2014. Resource Update FS-39, U.S. Department of Agriculture, Forest Service, Northern Research Station, St. Paul, Minnesota, USA.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16:488–502.
- Diefenbach, D. R., M. J. Conroy, R. J. Warren, W. E. James, L. A. Baker, and T. Hon. 1994. A test of the scent-station survey technique for bobcats. *Journal of Wildlife Management* 58:10–17.
- Dillon, A., and M. Kelly. 2007. Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* 41:469–477.
- Downey, P. J., E. C. Hellgren, A. Caso, S. Carvajal, and K. Frangioso. 2007. Hair snares for noninvasive sampling of felids in North America: do gray foxes affect success? *Journal of Wildlife Management* 71:2090–2094.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Foster, R. J., and B. J. Harmsen. 2012. A critique of density estimation from camera-trap data. *Journal of Wildlife Management* 76:224–236.
- Fuller, A. K., C. S. Sutherland, J. A. Royle, and M. P. Hare. 2016. Estimating population density and connectivity of American mink using spatial capture–recapture. *Ecological Applications* 26:1125–1135.
- Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010a. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* 91:3376–3383.
- Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt, and P. D. Curtis. 2010b. Estimating black bear density using DNA data from hair snares. *Journal of Wildlife Management* 74:318–325.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. *Biological Conservation* 133:107–117.
- Gerber, B. D., S. M. Karpanty, and M. J. Kelly. 2012. Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology* 54:43–54.
- Golden, H. N. 1995. Wildlife research and management: furbearer track county index testing and development. Alaska Department of Fish and Game, Project Number AK W-024-1/Study 7.17, Anchorage, USA.
- Heilbrun, R. D., N. J. Silvy, M. J. Peterson, and M. E. Tewes. 2006. Estimating bobcat abundance using automatically triggered cameras. *Wildlife Society Bulletin* 34:69–73.
- Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Jenkins, J. H., E. E. Provost, T. T. Fendley, J. R. Monroe, I. L. Brisbin Jr., and M. S. Lenarz. 1979. Techniques and problems with a consecutive twenty-five year furbearer trapline census. *Proceedings, National Wildlife Federation, Science and Technology Series* 6:92–96.
- Johnson, K. G., and M. R. Pelton. 1981. A survey of procedures to determine relative abundance of furbearers in the southeastern United States. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies*. 35:261–272.
- Kamler, J. F., and P. S. Gipson. 2000. Home range, habitat selection and survival of bobcats, *Lynx rufus*, in a prairie ecosystem of Kansas. *Canadian Field-Naturalist* 114:388–394.
- Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. *Biology Conservation* 71:333–338.
- Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera trapping across 3 study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* 89:408–418.
- Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. *Journal of Wildlife Management* 73:3–17.
- Kolowski, J. M., and A. Woolf. 2002. Microhabitat use by bobcats in southern Illinois. *Journal of Wildlife Management* 66:822–832.
- Larrucea, E. S., G. Serra, M. M. Jaeger, and R. H. Barrett. 2007. Censusing bobcats using remote cameras. *Western North American Naturalist* 67:538–548.
- Lesmeister, D. B., C. K. Nielsen, E. M. Schaub, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs* 191.
- Linde, S. A., S. D. Roberts, T. E. Gosselink, and W. R. Clark. 2012. Habitat modeling used to predict relative abundance of bobcats in Iowa. *Journal of Wildlife Management* 76:534–543.
- Linhart, S. B., and F. F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. *Wildlife Society Bulletin* 3:119–124.
- Litvaitis, J. A., J. P. Tash, and C. L. Stevens. 2006. The rise and fall of bobcat populations in New Hampshire: relevance of historical harvests to understanding current patterns of abundance and distribution. *Conservation Biology* 128:517–528.
- Lovallo, M. J., and E. M. Anderson. 1996. Bobcat (*Lynx rufus*) home range size and habitat use in northwest Wisconsin. *American Midland Naturalist* 135:241–252.
- Lukacs, P. M., and K. P. Burnham. 2005. Review of capture–recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* 14:3909–3919.
- Luman, D., M. Joselyn, and L. Suloway. 1996. Critical trends assessment land cover database of Illinois. Illinois Natural History Survey, Champaign, USA.
- McClintock, B. T., P. B. Conn, R. S. Alonso, and K. R. Crooks. 2013. Integrated modeling of bilateral photo-identification data in mark–recapture analyses. *Ecology* 94:1464–1471.
- Mendoza, E., P. R. Martineau, E. Brenner, and R. Dirzo. 2011. A novel method to improve individual animal identification based on camera-trapping data. *Journal of Wildlife Management* 75:973–979.
- Morin, D. J., L. P. Waits, D. C. McNitt, and M. J. Kelly. 2018. Efficient single-survey estimation of carnivore density using fecal DNA and spatial capture–recapture: a bobcat case study. *Population Ecology* 3: 197–209.
- Negrões, N., R. Sollmann, C. Fonseca, A. T. Jácomo, E. Revilla, and L. Silveira. 2012. One or two cameras per station? Monitoring jaguars and other mammals in the Amazon. *Ecological Research* 27: 639–648.
- Nielsen, C. K., and M. A. McCollough. 2009. Considerations of the use of remote cameras to detect Canada lynx in northern Maine. *Northeastern Naturalist* 16:153–157.
- Nielsen, C. K., and A. Woolf. 2001. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. *American Midland Naturalist* 146:43–52.
- Nielsen, C. K., and A. Woolf. 2002. Habitat–relative abundance relationship for bobcats in southern Illinois. *Wildlife Society Bulletin* 30:222–230.

- O'Brian, M., and M. Boudreau. 1998. Species abundance as recorded by fur harvests. *Northern States Trapping Newsletter* 34:10–11.
- Ordenana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Studyla, C. D. Haas, S. Harris, S. A. Hathawa, G. M. Turshak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy* 91:1322–1331.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 73.
- Pledger, S. A. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* 56:434–442.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- Preloger, D. 2002. Soil survey of McDonough County, Illinois. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA.
- Preuss, T. S., and T. M. Gehring. 2007. Landscape analysis of bobcat habitat in the northern lower peninsula of Michigan. *Journal of Wildlife Management* 71:2699–2706.
- Radeloff, V. C., R. B. Hammer, and S. I. Stewart. 2005. Rural and suburban sprawl in the U.S. Midwest from 1940 to 2000 and its relation to forest fragmentation. *Conservation Biology* 19:793–805.
- Reding, D. M., S. A. Cushman, T. E. Gosselink, and W. R. Clark. 2013. Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (*Lynx rufus*). *Landscape Ecology* 28:471–486.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 10 Aug 2017.
- Rich, L. N., M. J. Kelly, R. Sollmann, A. J. Noss, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, Y. E. De Blanco, and M. S. Di Bitetti. 2014. Comparing capture–recapture, mark–resight, and spatial mark–resight models for estimating puma densities via camera traps. *Journal of Mammalogy* 95:382–391.
- Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology* 17:566–576.
- Roberts, N. M., and S. M. Crimmins. 2010. Bobcat population status and management in North America: evidence of large-scale population increase. *Journal of Fish and Wildlife Management* 1:169–174.
- Rolley, R. E., and W. D. Warde. 1985. Bobcat habitat use in southeastern Oklahoma. *Journal of Wildlife Management* 49:913–920.
- Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* 24:148–156.
- Royle, J. A., R. B. Chandler, K. Gazenksi, and T. Graves. 2013. Spatial capture–recapture models for jointly estimating population density and landscape connectivity. *Ecology* 94:287–294.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture–recapture. Elsevier, Waltham, Massachusetts, USA.
- Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density estimation in a wolverine population using spatial capture–recapture models. *Journal of Wildlife Management* 75:604–611.
- Royle, J. A., J. D. Nichols, K. U. Karanth, and A. M. Gopalaswamy. 2009. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* 46:118–127.
- Royle, J. A., and K. Young. 2008. A hierarchical model for spatial capture–recapture data. *Ecology* 89:2281–2289.
- Ruell, E. E., S. P. D. Riley, M. R. Douglas, J. P. Pollinger, and K. C. Crooks. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture–recapture techniques. *Journal of Wildlife Management* 90:129–135.
- Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 in J. L. Gittleman, editor. *Carnivore behavior, ecology and evolution*. Cornell University Press, Ithaca, New York, USA.
- Satter, C. B., B. C. Augustine, B. J. Harmsen, R. J. Foster, E. E. Sanchez, C. Wultsch, M. L. Davis, and M. J. Kelly. 2019. Long-term monitoring of ocelot densities in Belize. *Journal of Wildlife Management* 83:283–294.
- Seber, G. A. F. 1992. A review of estimating animal abundance II. *International Statistical Review* 60:129–166.
- Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129:487–496.
- Sollman, R., B. Gardner, and J. L. Belant. 2011. How does spatial study design influence density estimates from spatial capture–recapture models? *PLoS ONE* 7:e34575.
- Soule, M. E., and J. Terborgh. 1999. *Continental conservation: scientific foundations for regional reserve networks*. Island Press, Washington, D.C., USA.
- Sunquist, M. E., and F. Sunquist. 2002. *Wild cats of the world*. University of Chicago Press, Chicago, Illinois, USA.
- Sutherland, C., A. K. Fuller, and J. Royle. 2015. Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. *Methods in Ecology and Evolution* 6:169–177.
- Tegeler, R. A. 2003. Soil survey of Schuyler County, Illinois. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA.
- Thornton, D. H., and C. Pekins. 2015. Spatially explicit capture–recapture analysis of bobcat (*Lynx rufus*) density: implications for mesocarnivore monitoring. *Wildlife Research* 42:394–404.
- Tucker, S. A., W. R. Clark, and T. E. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. *Journal of Wildlife Management* 72:1114–1124.
- United States Census Bureau. 2010. 2010 Census TIGER/Line Shapefiles and the 2010 Census Summary File 1. U.S. Census Bureau, Washington, D.C., USA. <<https://www.census.gov/geo/maps-data/data/tiger-data.html>>. Accessed 10 Oct 2017.
- Walker, M. B. 2001. Soil survey of Hancock County, Illinois, U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA.
- Wallace, R. B., H. Gomez, G. Ayala, and F. Espinoza. 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. *Journal of Neotropical Mammalogy* 10:133–139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.
- Wilton, C. M., E. E. Puckett, J. Beringer, B. Gardner, L. S. Eggert, and J. L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. *PLoS ONE* 9(10), e111257.
- Wood, J. E., and E. P. Odum. 1964. A nine-year history of furbearer populations on the AEC Savannah River Plant Area. *Journal of Mammalogy* 45:540–551.
- Wolf, A., and G. F. Hubert Jr. 1998. Status and management of bobcats in the United States over three decades: 1970s–1990s. *Wildlife Society Bulletin* 26:287–293.
- Wolf, A., C. K. Nielsen, T. Weber, and T. J. Gibbs-Kieninger. 2002. Statewide modeling of bobcat, *Lynx rufus*, habitat in Illinois, USA. *Biological Conservation* 104:191–198.

Associate Editor: Applegate.