American black bear distribution and density in Missouri

Clay Michael Wilton

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American black bear distribution and density in Missouri

By

Clay Michael Wilton

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries, and Aquaculture
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

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2014
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Understanding species’ distribution, density, and sources of bias in population estimates is critical for reliable conservation strategies. I assessed American black bear distribution, density, and abundance in southern Missouri. Using anecdotal occurrence data, I demonstrated support for a northward trend in extent of occurrences over time and a positive correlation between bear distribution and human–bear incidents. I also used GPS telemetry and camera traps to investigate detection biases in DNA hair snare methods and tested efficacy of two sampling designs for estimating density using spatial capture-recapture models. Results demonstrated that detection probability decreased following a negative asymptotic relationship with decreasing bear proximity to snares and that hair deposition rates decreased over time. Precision of estimates for low density populations with non-uniform distribution increased when using multiple arrays with intensive snare spacing. Optimizing the tradeoff among snare spacing, coverage, and sample size is important for estimating parameters with high precision.
DEDICATION

To my father, for teaching me patience and persistence in everything I do, and my mother, for her unwavering support and love through every moment of my life.
ACKNOWLEDGEMENTS

I thank Jerry for giving me this great opportunity and taking the time to answer all my questions and teach me about wildlife ecology and research. I could not have done this project without the help of Joseph Barnett, Justan Blair, Mark Cancellare, Imogene Davis, Dan Dobesh, Dustin Geurts, Ryan Langendorf, Courtney Lockerby, Thad Moody, Spencer Lynch, Mat Salyer, and Kevyn Wiskirchen; thank you for all your constant hard work setting hair snares and collecting data through blazing heat, pouring rain, and swarms of ticks and chiggers. I thank Jeff Beringer for much needed support and advice during field work and development of this thesis. This work would have been impossible without the support of the many landowners throughout the Ozarks that graciously opened their doors and allowed us to work on their land. Many Missouri Department of Conservation staff also dedicated much of their time to set snares and help my field seasons run as smoothly as possible, including M. Curry, K. Hedgpeth, A. Humble, B. Jump, F. Loncarich, B. McKee, B. Mormann, J. Peter, L. Rieken, R. Roy, T. Russell, B. Schroeppe, and many others.

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I thank the Department of Wildlife, Fisheries, and Aquaculture and Forest and Wildlife Research Center at Mississippi State University, U.S. Fish and Wildlife Service Federal Aid in Wildlife Restoration, Missouri Department of Conservation, and Safari Club International Foundation for supporting this research.
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CHAPTER I
DISTRIBUTION OF AMERICAN BLACK BEAR OCCURRENCES AND HUMAN–BEAR INCIDENTS IN MISSOURI


Introduction

The range of American black bears (Ursus americanus) contracted throughout much of the early 20th century in the United States (Laliberte and Ripple 2004), mostly from habitat loss, forest fragmentation (Hellgren and Maehr 1992), and unregulated hunting (Hristienko and McDonald 2007). However, relaxation of these pressures, repatriation efforts, and black bear dispersal via contiguous forest and riparian corridors has facilitated their re-colonization over parts of their historical range in North America (Smith and Clark 1994, Pelton et al. 1998, Frary et al. 2011, Simek et al. 2012, Lackey et al. 2013). Likewise, bears in Missouri and surrounding Interior Highlands were thought to be extirpated by the early 1900s (Bennitt and Nagel 1937, Smith and Clark 1994, Schwartz and Schwartz 2001). Following the successful reintroduction of black bears in Arkansas during 1958–1968 (Smith and Clark 1994), populations have expanded throughout much of the Interior Highlands of Arkansas and Oklahoma (Smith et al. 1991, Bales et al. 2005, Gardner-Santana 2007, Faries et al. 2013). Proximity of bear
populations in Arkansas and increasing occurrences and nuisance reports in southern Missouri also suggested that black bears started expanding northward into the Ozark region of Missouri (Missouri Department of Conservation [MDC] 2008). Recent genetic evidence has demonstrated both the persistence of a remnant population and expansion of Arkansas’ bear population into Missouri following their reintroduction (Faries et al. 2013).

Large carnivores often exist at low densities (Lofroth and Krebs 2007, Sollmann et al. 2011, Sunarto et al. 2013) and monitoring their distribution over space and time presents many logistical and statistical challenges (Gese 2001, Bjornlie et al. 2013). The validity of anecdotal occurrence data (McKelvey et al. 2008) collected from numerous sources (e.g., sightings, photographs, tracks) to estimate distribution is often unreliable, and can be spatially and temporally biased (Kucera et al. 1995, Gese 2001, Hellgren et al. 2005, Lee et al. 2010). Inference from these sources is further confounded by nonrandom or non-independent observations, locational uncertainty, and habitat changes over long sampling periods (Agee et al. 1989, Stoms et al. 1993, Palma et al. 1999). Considerable attention has been given to improving the reliability of using anecdotal data for conservation decision-making (Aubry and Jagger 2006, McKelvey et al. 2008, Frey et al. 2013, van Strien et al. 2013). Nonetheless, more rigorous sampling methods spanning both the extensive spatial distribution of large carnivores and temporal scales necessary to elucidate trends in their distribution are often logistically impossible to implement for such wide-ranging and elusive species (Braunisch and Suchant 2010).

Black bear presence in southern Missouri has now been documented throughout much of the Ozark Highlands plateau and negative interactions with humans are of
increasing concern for wildlife managers. Many ecological and anthropogenic factors influence re-colonization by large carnivores (Mladenoff et al. 1999, Onorato and Hellgren 2001, LaRue and Nielsen 2008, Frary et al. 2011), and understanding patterns of re-colonization is important for developing conservation and management strategies (Swenson et al. 1998, Carroll et al. 2001, Bales et al. 2005). Our objectives were to use historical occurrence data and forest cover to characterize broad patterns of black bear re-colonization in Missouri, and summarize bear incident (Hopkins et al. 2010) reports to describe their distribution, frequency, and type of incident occurrence over time. We hypothesized that the distribution of occurrences would follow the distribution of forest cover, occurrence reports would follow a northward trend over time, and the distribution of bear incidents would follow a similar spatio-temporal pattern and be correlated with location of occurrences.

**Study area**

Missouri (35°57′–40°35′N, 89°8′–95°46′W) comprises 180,472 km² and includes 37% forest, 51% crop and pasture, 2% grassland, and 7% developed areas (Fry et al. 2011). Of the 66,390 km² of forest in Missouri, 80% occurs in the Ozark Highlands ecological region and is predominantly upland oak–hickory (*Quercus* spp., *Carya* spp.) and oak–pine (*Pinus* spp.; Raeker et al. 2010). Land ownership in the Ozark Highlands includes private homesteads and farms and public lands (e.g., Mark Twain National Forest, Ozark National Scenic Riverways). Elevations in Missouri range from 70 m to 540 m, with the greatest elevations found in the Ozark Highlands (Nigh and Schroeder 2002, United States Geological Survey 2009).
Methods

We used statewide public bear occurrence data obtained through MDC’s Report a Bear Sighting system (MDC 2013) from 1989 to 2010 to examine distribution and potential range expansion of bears throughout Missouri. This system collected bear occurrences by phone, email, and mail-in observation forms, until it was made available online in 2008 (MDC 2008). Public requests for bear occurrences by MDC were opportunistic and commonly solicited at MDC offices, in MDC’s magazine Missouri Conservationist, and in local newspapers. Type of occurrences from this data set included direct observations, sign (e.g., track or scat), vehicle collisions, illegal harvests, and bear incidents. Records included date, location, description of occurrence, and number of adult bears and dependent young observed. We created evidentiary standards (McKelvey et al. 2008) using 6 categories (i.e., bear mortality, nuisance complaint, observation, photograph, sign, and no data) based on descriptions provided for each occurrence record. To improve reliability of occurrences, we excluded all records with no data describing the occurrence and sign records based on insufficient evidence (e.g., unconfirmed scat). We also excluded occurrences that lacked geographic coordinates. Given the large size of black bears and lack of similar species in Missouri, we considered all other categories to be reliable sources of bear occurrence.

We used ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, California, USA) to map reported bear occurrences in relation to forest cover. We used Landsat-based, 30-m-resolution land-cover data from the 2001 National Land Cover Database (Homer et al. 2007) to describe distribution of forest cover (i.e., deciduous, evergreen, and mixed forests).
To examine whether occurrence data may reveal any northward trend in re-colonization over time, we regressed annual maximum latitude of occurrence on year of occurrence record ($\alpha = 0.05$). If there were $<10$ occurrences in a year, we omitted that year from analysis to minimize any effect of small sample size. We used simple linear regression using function `lm` in Program R (R Development Core Team 2013).

We summarized reported nuisance complaint records by incident type (anthropogenic food consumption, food consumption and property damage, property damage, and attack on domestic animal), and described sources of human-caused bear mortalities from 1989 to 2010. We used linear regression to test for a similar northward trend in reported bear incidents over time by regressing annual maximum latitude of incident on year of incident report. We also tested for correlation between number of incidents and number of observations by county ($\alpha = 0.05$) using Pearson’s product-moment correlation (function `cor.test`; R Development Core Team 2013).

**Results**

**Distribution of occurrences**

Total occurrences from the MDC Report a Bear Sighting system included 1,114 reports occurring in 79 of 114 counties, including 118 reports of dependent young in 34 counties, from 1989 to 2010. Overall, most (61%) reports were direct observations; 8% were sign; 5% were bear incidents; 5% were photographs of bears; 2% were bear mortalities, and 19% lacked adequate data to categorize. We excluded 211 records lacking adequate descriptions, 17 records based on inconclusive evidence from sign, and 10 records lacking observation date. This resulted in 876 reliable occurrences, including 103 of dependent young (Figure 1.1). The distribution of all reports was bimodal across
years, with the first peak in 1993 \((n = 158)\) and the second in 2009 \((n = 142)\). The distribution remained bimodal following exclusion of unreliable records, with peak occurrences in 2009 \((n = 134)\) and 2010 \((n = 110;\) Fig. 1.1). Occurrences excluded due to poor reliability were greatest in 1992 \((n = 29)\) and 1993 \((n = 50)\), and averaged 11 each year \((SD = 13)\). For regression analysis of total occurrences, we excluded an additional 14 records without spatial data and 24 records from years with <10 occurrences. This resulted in the loss of 5 years \((1989, 1996, 2000, 2001, 2006)\) from the data set, with 838 occurrences \((75\%\) of total) considered reliable for analyses.

Most bear occurrences \((95\%)\) were located in the Ozark Highlands and concentrated in the forested southern and eastern regions, with occurrences of dependent young following a similar spatial distribution (Figure 1.2). We detected a significant positive effect of year of occurrence on annual maximum latitude of occurrence \(\left(\beta_1 = 0.083, SE = 0.027, R^2 = 0.408, P = 0.008;\right.\) Figure 1.3). Although the earliest reported occurrence north of the Ozark Highlands was in 1991, most \((76\%)\) occurred after 2000. In addition, occurrences north of the Ozark Highlands continued to increase during 2000–2010, with 75\% reported from 2006 to 2010. Only one occurrence of dependent young was reported north of the Ozark Highlands in 2001, although no details of the observation were recorded.

**Human-bear incidents**

Reported bear incidents from the Report a Bear Sighting system \((n = 58; 2\) records without observation date) averaged 2.5 reports/year \((SD = 3.2)\) from 1989 to 2010, with a maximum of 11 reports in 1995. Of these reports, 60\% involved bears eating anthropogenic food, 26\% involved anthropogenic food and property damage, 10\%
involved property damage, and 4% involved a bear purportedly attacking or killing a domestic animal. We did not find support for a relationship between maximum annual latitude and year of reported incident ($\beta_1 = 0.013$, SE = 0.032, $R^2 = 0.014$, $P = 0.685$). Number of incidents by county was positively associated with number of bear occurrences per county ($r_{77} = 0.76$, $P < 0.001$).

Twenty human-caused black bear mortalities were reported during 1989–2010 (1 record without observation date, 5 records without location). Mortalities were greatest in 2008 and 2009, with 4 mortalities each year. Mortalities resulted from vehicle collisions ($n = 12$), illegal harvest ($n = 3$), bear incidents ($n = 2$), and undetermined causes ($n = 3$). Three records of mortalities from vehicle collisions were not verified. Sex of bears killed was recorded for 5 records comprising 4 males and 1 female. The female mortality was an illegal harvest and the male mortalities were from 2 vehicle collisions, 1 illegal harvest, and 1 undetermined. All bear mortalities with spatial data were located within the Ozark Highlands.

**Discussion**

Black bears often depend on forest cover for parts of their life history (Herrero 1972, Rudis and Tansey 1995), and as expected, the spatial distribution of both total and dependent young occurrences closely reflected the distribution of forest cover. The Ozark Highlands contain the largest contiguous tracts of forest in Missouri and represent the most suitable black bear habitat in the state (Smith 2013), whereas areas north of this region are primarily agricultural and contain few forests that are highly fragmented (Raeker et al. 2010). Though the current distribution of reports in Missouri reflects the importance of forest cover, it is also important to recognize that the proximity of these
forests to source populations in Arkansas has likely also contributed to the underlying distribution of occurrences throughout the state. The current distribution of dependent young reports in Missouri further supports the importance of this relationship and suggests reproducing bears primarily occur in the Ozark Highlands.

Though we did not observe any northward trend in the distribution of reported bear incidents over time, our results did suggest an overall northward increase in reported occurrences. We recognize that these data are insufficient to confirm any northward expansion of Missouri’s black bear population. However, the observed trends generally support known northward dispersal from source populations in Arkansas (Faries et al. 2013), and suggest that this has contributed to bears colonizing or moving through areas of Missouri without known bear occurrences. Although the latitudinal extent of occurrences has apparently increased over time, it is important to note that most bear occurrences and mortalities remained concentrated in the more forested southern and eastern areas of the Ozark Highlands in close proximity to source populations.

The bimodal pattern in annual number of reported black bear occurrences likely reflects MDC requests for public information on black bear occurrences (Hellgren et al. 2005, Danielsen et al. 2009), rather than actual changes in black bear abundance. Reports increased dramatically from 1991 to 1993 following a MDC publicized request for occurrences in 1990 and 1991 (MDC 1993) and during 2008–2010 (J. Beringer, unpublished data). Evolving public attitudes and agency management strategies can also influence trends both within and among bear occurrences and incident reports (Garshelis and Hristienko 2006). Though not quantifiable, we also suggest that in years without MDC requests for occurrences, citizen reporting rates may have declined with decreasing

Although variation in MDC and citizen effort may account for much of the observed trends, variability in anthropogenic and natural food abundance can also influence annual variation in bear occurrences and nuisance reports. Availability of anthropogenic food can result in increased attraction by black bears to human settlements (Hristienko and McDonald 2007, Merkle et al. 2013). It is important to recognize that the likelihood of reporting occurrences or nuisance behavior is closely associated with proximity of bears to human settlements. Therefore, the positive correlation between bear occurrences and incidents is expected, but further illustrates the attractiveness of anthropogenic food to bears (Lyons 2005). Disturbance of garbage and anthropogenic food sources was the most common human–bear incident reported in Missouri, and the most common incident reported to other state and provincial wildlife agencies (Spencer et al. 2007).

Sources of human-caused bear mortalities were similar to other regions without a bear hunting season, with vehicle collisions and illegal harvests being greatest (Pelton et al. 1998, Williamson 2002, Simek et al. 2012). The 2 bears killed because of nuisance activity were both associated with apiary damage, with 1 being shot by the property owner.

Increasing interest in managing Missouri’s bear population has led to greater efforts by MDC to standardize and improve reporting of bear occurrences. Our exclusion of unreliable occurrences did not influence the overall spatial or temporal distribution of occurrences and we suggest that verified public reports of black bears in Missouri are
suitable as broad-scale data on bear observations. Moreover, broad-scale patterns of the distribution of occurrences relative to source populations in Arkansas and general land-cover associations (i.e., forests) corroborate our understanding of black bear ecology. Nonetheless, anecdotal reports of wildlife occurrences should be evaluated under species- and status-specific evidentiary standards (McKelvey et al. 2008), and inferences based on anecdotal data must be sensitive to potential spatial and temporal inconsistencies. For low-density, wide-ranging species such as black bear in Missouri, anecdotal occurrence records are often the only statewide data available and provide a low-cost approach to understanding basic distribution and habitat association patterns (Palma et al. 1999, Woolf et al. 2002, Hartin et al. 2007, Lackey et al. 2013). Therefore, we suggest this database revealed basic, but important, information on statewide bear occurrences and human–bear incident patterns, which will be useful for establishing future research and management plans in Missouri.

Black bears appear distributed throughout most of Missouri’s forested areas. Although land conversion and habitat fragmentation may ultimately limit recovery and range expansion (Larivière 2001), distribution of occurrences indicates that black bears have potential to occupy large portions of Missouri. As black bears in Missouri continue to re-colonize historical range, understanding large-scale spatial and temporal changes in their distribution, abundance, and interactions with humans will help managers better assess research and management objectives.
Figure 1.1  Number of reliable American black bear occurrence reports with (light gray) and without (dark gray) dependent young, Missouri, USA, 1989–2010.
Figure 1.2  Distribution of all American black bear occurrences (a) and occurrences of dependent young (b) during 1989–2010 in Missouri (USA), including locations of unreliable bear occurrences.
Figure 1.3  Linear regression of annual maximum latitude of American black bear occurrence on year of occurrence report ($R^2 = 0.408$, $P = 0.008$) during 1989–2010 in Missouri (USA).
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CHAPTER II
SPATIO-TEMPORAL CAPTURE-RECAPTURE BIASES IN BLACK BEAR
DETECTION PROBABILITY

Introduction

Understanding the ecological and biological sources of bias persistent in population estimates is critical for development of efficient experimental designs and reliable conservation strategies (Noyce et al. 2001, Boulanger et al. 2004a, Boulanger et al. 2004b). Noninvasive genetic capture-recapture using remotely collected hair samples from barbed wire snares is a nearly ubiquitous method among bear (Ursus spp.) genetic and demographic studies (Belant et al. 2005, Garshelis 2006). However, bias caused by variation in detection probability may limit the efficacy of hair snares to estimate population parameters (Garshelis and Noyce 2006, Belant et al. 2011). Though many population estimators account for heterogeneity in detection (Otis et al. 1978, Huggins 1991, Royle et al. 2014), improving sampling designs to reduce bias in the data itself relies on knowledge of the specific behavioral differences within populations that give rise to unequal detection (Boulanger et al. 2004a).

The American black bear (Ursus americanus) is a wide-ranging species, often persisting at low densities (Noyce and Garshelis 2011, Baldwin and Bender 2012), with large intra- and inter-population variation in home range size (Koehler and Pierce 2003, Carter et al. 2010). Black bear resource selection within a home range is influenced by
distribution of resources, and can introduce further variation in space use (Johnson et al. 1980, Lyons et al. 2003). Moreover, differences in sex-specific space use and behavior are common among bear populations and are often reflected in unequal detection probabilities (Boulanger et al. 2004b, Belant et al. 2011). Temporal variation in hair trapping success (e.g., seasonal molting) and encounter rate (e.g., habituation, breeding behavior) can also influence detectability (Noyce et al. 2001, Wegan et al. 2012). These characteristics often preclude adequate sampling at a spatial scale large enough for population level inference (Boulanger et al. 2004a, Settlage et al. 2008). Therefore, understanding the relationship between variable space use at the home range scale and detection probability at different hair snares within a home range is important for improving guidelines for snare spacing and the spatial extent of sampling designs.

Our objective was to examine how various measures of space use and differences between sexes affect detection probability and number of hair samples collected during a DNA capture-recapture study of a recolonizing black bear population in south-central Missouri (Wilton et al. in prep). We predicted that detection probability would decrease following a negative asymptotic relationship as bear proximity to snares decreased, and would increase when snares were located in areas of higher probability of home range use. We also predicted that number of hair samples collected would be positively related to frequency of bear encounters at snares, but inversely related to the temporal progression of sampling.
Methods

Study area

We collected data from a colonizing black bear population in the Ozark Highlands region of south-central Missouri, USA (Wilton et al. 2014, Wilton et al. in prep). Dominant landcover types include forest (37%), crop and pasture (51%), grassland (2%), and developed areas (7%; Fry et al. 2011). About 80% of Missouri’s 66,390 km² of forest is located in the Ozark Highlands ecological region and is primarily upland oak-hickory (Quercus spp., Carya spp.) and oak-pine (Pinus spp.; Raeker et al. 2010). Landownership in the Ozark Highlands includes private homesteads and farms and public lands (e.g., Mark Twain National Forest, Ozark National Scenic Riverways). Elevation in Missouri ranges from 70 to 540 m with highest elevations in the Ozark Highlands (Nigh and Schroeder 2002).

Data collection

We collected black bear hair samples using barbed-wire hair snares (Woods et al. 1999) with scent lures as described by Wilton et al. (in prep). In 2011, we used an array with 100 km² cells covering 13,508 km². We distributed 378 snares proportionate to the number of historical bear sightings per array cell following methods similar to Dreher et al. (2007) while attempting to maintain a minimum distance of 3 km between snares. In 2012, we established 403 hair snares in 5, 9 x 9 sampling arrays with 1 snare per 2.6 km² cell (210 km²/array; \( \bar{x} = 81 \) snares/array, SD = 1). Wilton et al. (in prep) and Puckett et al. (2014) provide a detailed description of field and DNA genotyping methods, respectively.
In June–August each year, we re-lured snares every 10 days at the beginning of each of 6 consecutive sampling sessions, and collected hair samples at the end of each session. We genotyped samples using 15 microsatellites, allowing 2 mismatches between samples, and determined sex for unique individuals by amplification of the Amelogenin gene followed by BsII digestion (see Carmichael et al. 2005).

We mounted 100 motion-sensitive infrared triggered cameras (Cuddeback Attack IR and 4300 NoFlash, Green Bay, Wisconsin, USA) each year at hair snares. We placed one camera per snare with each camera mounted 1–2 m above ground on a tree 5–10 m from a snare to capture the entire snare and immediate surroundings. All cameras recorded one still image and one 30-second video with date and time per activation with a 1-minute delay between events.

We live-captured bears using Aldrich foot snares and culvert traps (Johnson and Pelton 1980, Reagan et al. 2002) during 2010–2012. We immobilized bears with 7 mg/kg tiletamine-zolazepam (Telazol®; A. H. Robins Company, Richmond, Virginia, USA; Kreeger and Arnemo 2007) administered using a CO2-powered rifle or syringe pole (White et al. 1996). We recorded sex and collected hair and tissue (biopsy from ear tagging) samples for microsatellite genotyping. We fitted male and female bears with a Global Positioning System (GPS) telemetry collar (Northstar NSG-LD2, RASSL Globalstar, King George, Virginia, USA) programmed to collect one location every 10 minutes during our hair snare sampling period. All capture and handling complied with the American Society of Mammalogists guidelines (Sikes et al. 2011) and the Institutional Animal Care and Use Committee protocol (approval 10-037) at Mississippi State University.
**Encounter rate and probability of use**

Because of variation in percentage of successful locations among bears, we randomly subsampled one location per day during each year’s sampling period (60 days) to estimate 95% fixed kernel utilization distributions (UD; Millspaugh et al. 2006, Keating and Cherry 2009) for bears with ≥30 locations using program R (R Development Core Team 2013). We used the plug-in bandwidth estimator and fixed cell size at 100 x 100 m for all bears to calculate the relative probability of use per cell (UD score). To compare values among bears, we scaled each bear’s UD scores between 0 and 1, where 1 represents the greatest relative probability of use. We used a geographic information system (GIS; ArcMap 10.0; Environmental Systems Research Institute, Redlands, California, USA) to assign each snare the scaled UD score of the cell corresponding to its location within a UD. Genotypes from hair samples collected at snares were then matched with genotypes of GPS-collared bears to create an individual-specific database of collared bears detected and not detected within their 95% UD during each session.

Using a GIS we calculated the closest distance bears approached each snare located within their 95% UD during each session using all possible locations per bear, excluding individuals with <30 locations or when the minimum location interval exceeded 24 hours. We included detections for bears detected at multiple snares/session. We used the Breusch-Pagan (BP) test (Breusch and Pagan 1979) for heteroscedasticity (function bptest; Zeileis and Hothorn 2002) in program R to test for an effect of sample size against closest distance to hair snares and truncated the data at the distance that included 100% of detections.
We used a binomial generalized linear mixed model (GLMM; function glmer) in package lme4 (version 1.0-5; Bates et al. 2013) in program R to estimate the probability of detection at a snare. We specified individual detection as a binary response variable and UD score, nearest distance to snare (dist), and sex as fixed effects. We centered (mean = 0) and scaled (standard deviation = 1) UD scores and distances to snare to allow equal weight among predictor variables. We included a quadratic (dist^2) and cubic (dist^3) effect for distance to snare to test different relationships between detection probability and distance to snare (Boulanger et al. 2004b). Because all predictor variables could independently influence detection, we ran all possible model combinations as main effects. We included year-specific individual bear identification as a random intercept to account for variation among bears and sampling years. Following Boulanger et al. (2004b), we considered the y-intercept at 0 distance to represent the probability of detecting a collared bear when the snare was encountered, assuming that bias was equal for closest distances between bears detected and not detected at snares.

We estimated an approximate overdispersion parameter by comparing the ratio of the sum of squared Pearson residuals to the residual degrees of freedom, but found no evidence of overdispersion (\(\hat{\phi} = 0.78; P = 1.0\)). Therefore, we used sample size corrected Akaike information criterion (AIC\(_c\)) to rank model support and considered models competing if within 2 AIC\(_c\) units from the most supported model (Burnham and Anderson 2002). Significance of fixed effects was evaluated at \(\alpha = 0.05\), and we model averaged competing models using Akaike weights \((w_i)\) to estimate coefficients and 95% confidence intervals. We used model averaging to mitigate effects of uninformative parameters and disregarded their influence if intervals included zero (Arnold 2010).
**Intensity of use**

We reviewed camera images and retained independent images of bears for analyses. We considered visits as independent if the interval between pictures at the same site was ≥ 30 min or if bears could be individually identified (Kinnaird et al. 2003, Bowkett et al. 2008). We tested for a relationship between the total number of bear hair samples collected and number of independent bear visits from images at snares during each sampling session. We specified the number of hair samples as the response variable, and number of bear visits and sampling session as fixed effects. We centered and scaled number of visits and session. We initially included year as a random effect, but an estimate of zero variance indicated that the variability between sampling years was not greater than expected by random variation in the response variable (Bolker et al. 2009). Therefore, we fit a Poisson generalized linear model (GLM; function glm) in package lme4. We ran all possible fixed effect combinations (n = 5), including interaction effects between session and number of visits. We tested for overdispersion under the null hypothesis of equidispersion, and rejected the null if the dispersion parameter was greater than 1 (function dispersiontest; Kleiber and Zeileis 2008). Model selection followed the same criteria as for the encounter rate analysis.

**Results**

**Encounter rate and probability of use**

We estimated 95% UDs for 22 bears (12 F, 10 M), comprising 24 UDs during both sampling years. These contained 332 unique snares (43% of total snares). Female UDs (\( \bar{x} = 81.7 \text{ km}^2 \), SD = 85.6, \( n = 12 \)) contained on average 13.0 (SD = 16.6) snares and male UDs (\( \bar{x} = 590.3 \text{ km}^2 \), SD = 686.2, \( n = 12 \)) contained on average 36.3 (SD = 25
snares. Fourteen (64%; 6 F, 8 M) individuals were detected 44 times, including 23 female detections at 13 snares and 21 male detections at 20 snares (32 total unique snares).

Based on residuals of the BP test and to ensure homoscedasticity of data, we calculated distances to nearest snares each session for individual bears with at least 180 locations during the respective session. Truncating the dataset at the closest distance containing 100% of detections (1293 m) retained 674 GPS collar locations (19% of total) for analysis. The reduced data set resulted in 19 unique bears (12 F, 7 M) during both sampling years, including one male with data during both years (i.e., 20 total UDs). Ten individuals (6 F, 4 M) were detected 31 times, with 21 female detections at 13 snares and 10 male detections at nine snares. Mean closest distance for detected individuals was 256.3 m (SD = 307.0 m) and for undetected individuals was 613.7 m (SD = 345.5 m). Mean UD scores were similar between snares that captured (\( \bar{x} = 0.41, \) SD = 0.29) and did not capture (\( \bar{x} = 0.43, \) SD = 0.29) collared bears.

Nearest distance, including both polynomial forms, and sex were the most supported predictors of detection at a snare (Table 2.1). Although the addition of a sex parameter to models with distance remained within 2 \( \Delta AIC_c \), the marginal change in log likelihood suggested no improvement in explanatory power. Additionally, support for a cubic effect on distance was nearly identical to a quadratic effect, and confidence intervals for both overlapped zero (Table 2.2). Though not competing under our selection criteria, a model with distance and UD score predictors approached inclusion with \( \Delta AIC_c = 2.01 \), but did not influence probability of detection (\( \beta = 0.04, P = 0.87 \)).
Predicted values of the logistic curve fitted from raw distances indicated detection probability at encounter (i.e., distance = 0 m) was 0.15 (95% CI = 0.07–0.28), and was reduced to <0.05 (0.03–0.09) at closest distances >325 m (Figure 2.1). However, model averaging of competing models suggested detection probability at encounter was 0.27 (95% CI = 0.12–0.49). On average, females were recorded within 325 m of a snare 9.2 times (95% CI = 7.6–10.7, n = 12) and males 12.0 times (9.5–14.5, n = 6).

**Intensity of use**

We collected 319 total hair samples associated with 240 independent bear visits (33 in 2011 and 207 in 2012). Total hair samples collected averaged 53.2 (SD = 20.0) per session, and declined from 68 in session 1 to 29 in session 6. Number of independent visits averaged 40.0 (SD = 8.3) per session, and declined from 50 in session 1 to 35 in session 6. Average hair samples per snare each visit was 1.6 (SD = 2.1), and declined from 1.8 during session 1 to 0.9 during session 6.

As our data were moderately overdispersed (ĉ = 2.74, P < 0.001), we used quasi AICc (QAICc) for model selection. Session and number of visits were included in the best supported model and no models were competing (Table 2.3). The number of hair samples collected increased with number of bear visits to snares whereas the number of hair samples declined across sessions (Table 2.4; Figure 2.2).

**Discussion**

The model averaged estimate of the y-intercept suggested that detection probability when encountering a snare was 0.27, assuming nearest GPS location to snares is an adequate predictor of encounter. Black bear detection probabilities at hair snares can
be highly variable, ranging from 0.02 (Dreher et al. 2007) to 0.68 (Belant et al. 2005), with probabilities \( \leq 0.30 \) common among low density bear populations (Baldwin and Bender 2012, Drewry et al. 2012, Wilton et al. in prep). This suggests that we missed an estimated 73% of bears that encountered snares, compared to 37% observed by Boulanger et al. (2004b). However, detection probability represents only bears previously live-captured, which can reduce detection probability at hair snares (Boulanger et al. 2004a, Kendall et al. 2009). Thus, our estimate may be biased low compared to the population. Other behavioral differences among individuals also likely affect detection probability, but cannot be described by encounter rate alone (Boulanger et al. 2004b).

Anecdotal evidence indicated that some individuals appeared to show an aversion to snares, such as a male that approached within 325 m of 19 different snares 24 times, but was only detected once. Low detection probabilities are influenced by trap configuration and decrease precision of density estimates (Tobler et al. 2013). Heterogeneous detection probabilities among individuals are common in bear population studies and are difficult to account for in sampling design or statistical methods (Ebert et al. 2010). Therefore, our low detection probability at trap encounter may also reflect differences in behavior among bears.

Whereas Boulanger et al. (2004b) used a 4 hr location interval and suggested grizzly bear (\textit{Ursus arctos}) detection probability was \(< 0.05\) at distances >1.69 km from a snare, our 10 min interval predicted the same response when bears were >325 m from a snare. Although we cannot discern the actual distance a bear becomes attracted to a scent lure, increasing the GPS location frequency provided a more detailed description of a bear’s proximity to snares and therefore improved our ability to detect the relationship
between detection probability and observed nearest distances (Moorcroft 2012). We note that differences among species, habitat characteristics, and sampling designs can also greatly affect the observed relationship (Herrero 1972, Powell and Mitchell 1998, Sollmann et al. 2012). However, our results support Boulanger et al. (2004b) in that bears are more likely to be attracted to lured snares when closer to the snare, and that detection probability may therefore benefit from spacing traps closer together. To avoid biased density estimates, trap spacing must also be balanced with extent of array coverage, and be sensitive to individual variability in home range size (Tobler and Powell 2013).

Differential space use within the home range was less supported than nearest distance as a predictor of detection probability. One possible explanation is that if bears lose interest in snares without a food reward, even snares located in high probability use areas may only elicit ≤1 detection (Boulanger et al. 2006, Sawaya et al. 2012). Similarly, snares located in low use areas may also elicit ≤1 detection due to habituation to scent lures and lack of incentive to return to the snare. Indeed, 73% of snares with detections only detected an individual once and no individuals were detected >3 times at a snare. It is plausible that lack of food reward and limited detection distance of lures may reduce the likelihood of a bear deviating from its normal pattern of space use to investigate a snare (Gardner et al. 2010, Obbard et al. 2010, Howe et al. 2013). This is supported by the narrow range of distances associated with detection probabilities >0.05 in this study and Boulanger et al. (2004b). Black bear resource selection also may be occurring at a scale finer than could be detected given our UD cell size and measurement error from GPS collars (Belant and Follmann 2002). Therefore, although not predicted, our sampling methods may not have demonstrated the true relationship between probability of space
use and detection. We suggest probability of detection may be more influenced by probability of home range use when other methods are used that are less likely to induce a behavioral response to detection (e.g., un-baited cameras along natural travel routes).

Sex-specific detection probabilities also were not supported in model averaged estimates. Differences in detection between sexes may lead to underestimation of density (Boulanger et al. 2004, Tobler et al. 2013), although studies have found variable support for its inclusion in bear capture-recapture models (Kendall et al. 2009, Gardner et al. 2010, Sollmann et al. 2012, Wilton et al. in prep). Though females showed a 50% greater detection probability at encounter than males, this difference is likely an artifact of our data. Sex-specific detections were nearly equal in the full data set, but correcting for heteroscedasticity resulted in the loss of 3 male bears and 11 distinct detections, but no females were excluded and only 2 female detections were lost. Nonetheless, male detection probabilities can be lower due to closure violation among sampling arrays (Boulanger and McLellan 2001) or less attraction to baited snares from reduced male foraging during the breeding season (June–July; Garshelis and Pelton 1980, Noyce and Garshelis 1998). Including covariates for sex in capture-recapture models may reduce bias, but the additional covariate combined with low sample sizes typical of large mammal surveys often limits precision of density estimates (Tobler and Powell 2013).

Predicted curves from our regression analysis of remote camera data suggest a negative relationship between number of hair samples per known visit and the temporal progression of sampling. Wegan et al. (2012) tested various metrics of snare efficiency over time using DNA genotypes and found that a declining number of hair samples collected per trap visit corresponded to the progression from molting to post-molting
periods. Our study also encompassed these periods and we further support the idea that sampling during the spring-summer molting period increases hair deposition rates. We also improved on estimating the number of known encounters by including information on occasions where bears encountered snares, but did not have their hair detected. Although these results corroborate a molting effect, behavioral changes to entering a snare may also affect the likelihood of barbed-wire snagging hair. For example, we reviewed videos of bears approaching but not entering snares or exhibiting behaviors (e.g., stepping on wire) to avoid wire contact when entering snares. By placing remote cameras at a subset of snares, we were able to observe the efficiency of snares over time when encounter is known.

Our results expand our understanding of causes of heterogeneity among detection probabilities in capture-recapture population studies by explicitly considering variability in home range space use and incorporating information on individuals observed, but not detected at snares. In general, results support findings by Boulanger et al. (2004b) and Wegan et al. (2012), and we maintain that obtaining adequate data to estimate detection probabilities relies on optimizing spatial sampling design, which depends on an understanding of a species’ spatial ecology and behavior (Sollmann et al. 2012). Though advances in density estimators (e.g., spatial capture-recapture) may account for much of the bias caused by heterogeneity in detection (e.g., Royle et al. 2014), directly accounting for sources of bias through improved sampling designs may also increase precision of estimates (Tobler and Powell 2013). To improve detection probability estimates, we recommend that black bear hair snare studies should correspond to seasonal periods of molting, and trap dispersion (i.e., spacing and extent) must be sensitive to potentially
wide variation among home range sizes and movement. Although our study was specific to black bears, our approach should be applicable to capture-recapture studies of other species exhibiting variation in detection probabilities over time or among individuals or demographic classes.
Table 2.1  Results for competing models used to describe black bear detection probability at hair snares, Missouri, USA (2011–2012).

<table>
<thead>
<tr>
<th>Model</th>
<th>$K^b$</th>
<th>Log L$^c$</th>
<th>AIC$_c$$^d$</th>
<th>$\Delta$AIC$_c$$^e$</th>
<th>$w_i^f$</th>
</tr>
</thead>
<tbody>
<tr>
<td>dist + dist$^2$</td>
<td>4</td>
<td>-100.48</td>
<td>209.01</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>dist + dist$^3$</td>
<td>4</td>
<td>-100.50</td>
<td>209.06</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>dist + dist$^2$ + sex</td>
<td>5</td>
<td>-100.15</td>
<td>210.40</td>
<td>1.38</td>
<td>0.09</td>
</tr>
<tr>
<td>dist + dist$^3$ + sex</td>
<td>5</td>
<td>-100.17</td>
<td>210.43</td>
<td>1.41</td>
<td>0.09</td>
</tr>
<tr>
<td>dist + dist$^2$ + dist$^3$</td>
<td>5</td>
<td>-100.45</td>
<td>210.99</td>
<td>1.98</td>
<td>0.07</td>
</tr>
<tr>
<td>intercept only</td>
<td>2</td>
<td>-115.08</td>
<td>234.17</td>
<td>1.38</td>
<td>0.09</td>
</tr>
</tbody>
</table>

$^a$Models ranked from most to least supported by AIC$_c$. Predictor variables used to describe detection probability include closest distance to hair snares (dist), including two polynomial forms (dist$^2$, dist$^3$), and sex of bear.

$^b$Number of parameters, including an intercept and error term in the model.

$^c$Log likelihood of the model.

$^d$Sample size corrected Akaike information criterion.

$^e$The difference between each model and the model with lowest AIC$_c$ score.

$^f$The Akaike weight of each model, representing model support from a total of 1.00.

Table 2.2  Model averaged parameter estimates from competing models ($\Delta$AIC$_c$ ≤ 2), including the intercept, closest distance to hair snares (dist, dist$^2$, dist$^3$), and sex for male relative to female black bears detected during a hair snare capture-recapture study in Missouri, USA (2011–2012).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\beta$</th>
<th>SE</th>
<th>$P$-value</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>-3.83</td>
<td>0.45</td>
<td>&lt; 2e-16</td>
<td>-4.71</td>
<td>-2.96</td>
</tr>
<tr>
<td>dist</td>
<td>-2.93</td>
<td>0.98</td>
<td>0.003</td>
<td>-4.84</td>
<td>-1.02</td>
</tr>
<tr>
<td>dist$^2$</td>
<td>2.48</td>
<td>2.42</td>
<td>0.306</td>
<td>-2.27</td>
<td>7.23</td>
</tr>
<tr>
<td>dist$^3$</td>
<td>1.61</td>
<td>1.68</td>
<td>0.337</td>
<td>-1.68</td>
<td>4.91</td>
</tr>
<tr>
<td>sex.M</td>
<td>-0.54</td>
<td>0.66</td>
<td>0.410</td>
<td>-1.84</td>
<td>0.75</td>
</tr>
</tbody>
</table>

$^*$Scaled (mean = 0, SD = 1) logistic regression coefficients and 95% confidence intervals for the intercept and predictor variables included in competing models. Parameters are ranked in order of decreasing support ($\alpha = 0.05$).
Table 2.3  Results from all models used to describe the number of black bear hair samples collected as a function of number of black bear visits to hair snares (visits) and time of year (session), Missouri, USA (2011–2012).

<table>
<thead>
<tr>
<th>Modela</th>
<th>Kb</th>
<th>Log Lc</th>
<th>QAICc d</th>
<th>ΔQAICc e</th>
<th>wi f</th>
</tr>
</thead>
<tbody>
<tr>
<td>session + visits</td>
<td>3</td>
<td>-329.49</td>
<td>243.10</td>
<td>0.00</td>
<td>0.59</td>
</tr>
<tr>
<td>session + visits + session : visits</td>
<td>4</td>
<td>-329.43</td>
<td>245.20</td>
<td>2.11</td>
<td>0.21</td>
</tr>
<tr>
<td>visits</td>
<td>2</td>
<td>-336.27</td>
<td>245.80</td>
<td>2.71</td>
<td>0.15</td>
</tr>
<tr>
<td>session</td>
<td>2</td>
<td>-339.83</td>
<td>248.40</td>
<td>5.25</td>
<td>0.04</td>
</tr>
<tr>
<td>intercept only</td>
<td>1</td>
<td>-348.40</td>
<td>252.40</td>
<td>9.27</td>
<td>0.01</td>
</tr>
</tbody>
</table>

aModels ranked from most to least supported by QAICc. Predictor variables used to describe detection probability include time (session) of collected hair sample and number of independent bear visits to snares.
bNumber of parameters in the model, including an intercept and error term.
cLog likelihood of the model.
dSample size corrected quasi Akaike information criterion.
eThe difference between each model and the model with lowest QAICc score.
fThe Akaike weight of each model, representing model support from a total of 1.00.

Table 2.4  Parameter estimates and 95% confidence intervals for the top supported model (session + visits) describing the number of black bear hair samples collected at snares in Missouri, USA (2011–2012).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>β</th>
<th>SE</th>
<th>P-value</th>
<th>2.50%</th>
<th>97.50%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.75</td>
<td>0.1</td>
<td>2.63 x 10⁻¹²</td>
<td>0.55</td>
<td>0.94</td>
</tr>
<tr>
<td>visits</td>
<td>0.2</td>
<td>0.07</td>
<td>0.003</td>
<td>0.06</td>
<td>0.32</td>
</tr>
<tr>
<td>session</td>
<td>-0.21</td>
<td>0.1</td>
<td>0.031</td>
<td>-0.4</td>
<td>-0.02</td>
</tr>
</tbody>
</table>

*Scaled (mean = 0, SD = 1) logistic regression coefficients and 95% confidence intervals for the intercept and predictor variables included in competing models. Parameters are ranked in order of decreasing support (α = 0.05).
Figure 2.1  Predicted values and 95% confidence interval (dotted lines) of black bear detection probability as a function of nearest observed GPS collar location to hair snares in Missouri, USA (2011–2012).

Probabilities were derived from the model using only distance and the random intercept for predictors.
Figure 2.2  Predicted values from the top supported model (session + visits) showing the session-specific relationship between number of black bear hair samples collected at snares and number of independent bear visits in Missouri, USA (2011–2012).
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CHAPTER III

TRAP ARRAY CONFIGURATION INFLUENCES ESTIMATES AND PRECISION OF BLACK BEAR DENSITY AND ABUNDANCE

Introduction

Knowledge of population size and spatial distribution is important for protection of threatened or endangered species (Eggert et al. 2003, Kendall et al. 2009, Gray and Prum 2012), and management of harvested animal populations (Williams et al. 2002, Garshelis and Hristienko 2006). Estimates of species’ abundance or density are useful as a baseline for developing protected areas (Gross et al. 2008, Stokes et al. 2010), prioritizing conservation actions (Master 1991, Neel et al. 2012), and allocating harvest quotas (Peacock et al. 2011). However, large mammals often persist at low densities over large areas, are not uniformly distributed, and have large home ranges (Damuth 1981, Frary et al. 2011, Sunarto et al. 2013). These characteristics may undermine abundance estimation and hinder subsequent conservation efforts (Ebert et al. 2010, Sollmann et al. 2011).

Capture-recapture methods are often used to estimate density and abundance of rare or elusive carnivores (Kendall et al. 2009, O’Brien and Kinnaird 2011, Sollmann et al. 2011). Remote collection of DNA samples (e.g., hair, feces) enables researchers to sample wide geographic areas (Mowat and Strobeck 2000, Dreher et al. 2007), and has become almost universal for bear (Ursus spp.) capture-recapture studies (Belant et al. 2011).

The spatial nature of sampling designs (e.g., trap distribution) and wildlife populations (e.g., home range distribution) are important components of estimating animal abundance (Apps et al. 2004, Wegge et al. 2004, Royle and Young 2008). Non-spatial capture-recapture models often require study designs to cover several times the area of an individual home range (Bondrup-Nielsen 1983), while maintaining trap spacing narrow enough to ensure no individuals have zero capture probability (Dillon and Kelly 2007, Tobler and Powell 2013). However, for species with large home ranges and individual movements, logistical constraints may require a tradeoff between extensive coverage of a study area with wide trap spacing or intensive coverage of a portion of the study area with close spacing (Boulanger et al. 2004, Sun et al. 2014).

Spatial capture-recapture (SCR) models explicitly include animal movement and trap distribution, and therefore reduces constraints placed on sampling wide ranging species over large areas (Borchers and Efford 2008, Royle and Gardner 2011). Moreover, SCR defines a spatial point process model to estimate the home range (i.e., activity) centers of individuals detected, eliminating the need for ad hoc estimates of the effective sampling area (Royle et al. 2014). Therefore, SCR models address a primary source of heterogeneity inherent in most carnivore populations by addressing unequal exposure to traps and edge effects (Gardner et al. 2009, Efford and Fewster 2013). Simulations of parameter estimates from black bear trapping configurations were unbiased when
movement was at least half the distance between traps and when trap coverage was similar to the extent of movement (Sollmann et al. 2012, Sun et al. 2014). Although SCR models are robust to unequal trap exposure and appear flexible to various spatial trapping designs (Efford and Fewster 2013), few studies have empirically tested the efficacy of SCR models using different large-scale trap array configurations.

The large home ranges of bears and constraints to large-scale sampling often preclude adequate coverage of individual space use (Gardner et al. 2010). We tested a spatially extensive and intensive trapping scenario to compare how trap coverage and spacing affects precision of SCR parameter estimates using black bear (*Ursus americanus*) DNA encounter history data from hair snare arrays. To generalize the findings of our spatial sampling configurations and evaluate their accuracy, we also conducted simulations to measure bias under realistic densities and detection probabilities for large carnivores. We also consider effects of snare design on detections and provide insights towards implementing large scale capture-recapture sampling designs for SCR models for low density, wide ranging species.

**Methods**

**Study area**

We collected data from a recolonizing black bear population in south-central Missouri, USA (Figure 3.1). Missouri (35°57′–40°35′N, 89°8′–95°46′W) is 180,472 km² and contains 37% forest, 51% crop and pasture, 2% grassland, and 7% developed areas (Fry et al. 2011). About 80% of forest in Missouri occurs in the Ozark Highlands ecological region and is primarily upland oak-hickory (*Quercus* spp., *Carya* spp.) and oak-pine (*Pinus* spp.; Raeker et al. 2010). Landownership in the Ozark Highlands
includes private homesteads, farms, and public lands (e.g., Mark Twain National Forest, Ozark National Scenic Riverways). Elevation in Missouri ranges from 70 to 540 m with greatest elevations in the Ozark Highlands (Nigh and Schroeder 2002, United States Geological Survey 2009).

**Data collection**

We collected black bear hair samples using barbed-wire hair snares (Woods et al. 1999). Snares were constructed using 4-barbed, 15.5 gauge wire to create an enclosure around 3 or more trees. For the extensive design, we constructed snares using a single strand of barbed-wire set 50 cm above ground. For the intensive design, we constructed snares using 2 strands of barbed-wire with strands 20 and 50 cm above ground. We applied raspberry oil (intensive design only; Mother Murphy’s Laboratories, Inc., Greensboro, NC), anise oil (Minnesota Snareline Products, Pennock, MN), and Ultimate Bear Lure (Wildlife Research Center, Ramsey, MN) on perimeter trees forming the enclosure, about 2 m above ground. We placed decaying logs in the center of the enclosure and saturated them with 0.5 L of fish oil as an attractant (Belant et al. 2005). Hair snare stations were re-lured every 10 days at the beginning of each consecutive sampling session. We collected hair samples at the end of each session and considered all hair found on a barb or single tree one sample. We placed hair in separate coin envelopes, and air dried samples before processing.

**Extensive sampling design**

We derived the sampling boundary from a 70% fixed kernel isopleth applied to historical bear sightings (1989–2010) reported to the Missouri Department of
Conservation by citizens throughout the state (Wilton et al. 2014). This area comprised 13,508 km² in south-central Missouri. We used the 70% isopleth because this was the maximum logistically feasible extent of sampling and contained the core area of interest by state biologists. We used an array with 10 x 10 km cells to generate a distribution of bear sightings per array cell, excluding cells with zero bear sightings. We allocated 378 snares proportionate to the number of sightings per cell (Figure 3.1) following methods similar to Dreher et al. (2007). Cells containing 1–3 bear sightings received 1 snare, cells containing 4–5 sightings received 4 snares, cells with 6–7 sightings received 5 snares, and cells with >8 sightings received 6 snares. Cells with suitable habitat (i.e., forest) containing zero sightings adjacent to cells with similar habitat containing bear sightings were allocated snares similar to adjacent cells. We selected hair snare locations based on habitat characteristics and availability of forested private and public land. We used ArcMap 9.3.1 (Environmental Systems Research Institute, Redlands, California, USA) to select approximate locations for hair snares using forest cover data (30 m resolution, Missouri Spatial Data Information Service 2005) as initial criteria to maximize bear detection; excluding open water, agricultural, and developed areas.

We selected final snare locations within about 300 m of initial locations and out of sight from human trails or dwellings. Additionally, we used previous bear sightings, recent bear activity, and habitat and topographic features to select hair snare locations to maximize black bear capture (Dreher et al. 2007). We attempted to maintain a minimum distance of 3 km between snare sites, and conducted oversampling of snare locations in the event existing land use or ownership precluded snare placement. We monitored snares over six, 10-day sessions during June–August 2011.
**Intensive sampling design**

We established 403 hair snares in five, 9 x 9 sampling arrays (A–E) with 2.6 km² cells (210 km²/array) in south-central Missouri ($\bar{x} = 81$ snares/array, SD = 1; Figure 3.1). We selected array locations to maximize coverage of the largest available forested regions known or expected to contain bears based on information from our extensive sampling effort and prior radio-collaring efforts (Boulanger et al. 2004). Four arrays (A–D) were contained within the previous extensive survey area and array E was about 15 km east of the extensive survey boundary (Figure 3.1). We allocated one hair snare to each cell and monitored all snares over six, 10-day sessions during June–August 2012. Snares were set in forests on both private and public lands. We selected preliminary and final snare sites following the same criteria as the extensive sampling protocol.

**DNA extraction and microsatellite genotyping**

We cut follicles from the shafts of hair to minimize the amount of melanin, a known PCR inhibitor (Gagneux et al. 1997). Number of follicles per sample ranged from one to twelve depending on amount of hair removed from each barb. We placed follicles in 1.5mL Eppendorf tubes before adding 250µL InstaGene matrix (BioRad, Hercules, CA). Samples incubated overnight at 56°C, then at 100°C for 15min (Eggert et al. 2005). Following centrifugation at 13krpm for 3 min, we transferred supernatant to a clean 1.5mL tube before use in downstream reactions.

We genotyped samples at 15 microsatellite loci (G1A, G10B, G10C, G1D, G10J, G10L, G10M, G10O, G10P, G10U, UarMU05, UarMU10, UarMU23, UarMU59, and P2H03; Paetkau et al. (1998), Sanderlin et al. (2009), and Taberlet et al. (1997)) following the protocol of Puckett et al. (2014). We randomly selected 25 samples
genotyped at all loci to calculate the probability of identity between siblings (PID\textsubscript{sb}) in Gimlet (Valière 2002). We set \( \alpha \) to 0.001 resulting in \( \text{PID}_{\text{sb}} = 7.18 \times 10^{-4} \); this level of PID\textsubscript{sb} required samples to be genotyped at eight loci for inclusion in the study. When determining recaptures we allowed two mismatches between samples. We determined the sex of unique individuals by amplification of the Amelogenin gene and BsII digestion as detailed in Carmichael et al. (2005).

**Population analysis**

We used DNA-based encounter history data from hair snares and SCR models to estimate black bear density in southern Missouri. We analyzed data using package secr (version 2.7.0; Efford 2013) in program R (R Development Core Team 2013). We fit each model using a binominal observation model with the half-normal detection function, where the parameter \( g_0 \) is the probability of detection at the activity center of an individual and \( \sigma \) is the spatial scale parameter of the detection function (Efford et al. 2009). The spatial scale parameter describes the rate of decrease in capture probability as a function of increasing distance from a trap and an individual’s activity center (Royle et al. 2014). We compared 12 *a priori* models for each array configuration (Table 3.1). We fit a null model with no covariates and 11 models with varying effects on the detection parameters (\( g_0, \sigma \)). We created models based on expected sources of variation in black bear detection probability within our study area. Models with effects on \( g_0 \) included one model with time as a factor (t), and three models with behavioral responses following initial detection (global learned response (b), snare-specific learned response (bk), and a snare-specific Markovian response (Bk)). We also fit seven models using sex as a
categorical individual covariate to specify sex-specific effects on $g_0$ and $\sigma$ and in combination with the behavioral response models.

We defined the state space (i.e., area of integration) as the area encompassing snares and all individuals potentially exposed to capture (Borchers and Efford 2008). This area defines the extent of the distribution of home range centers in the population (Royle et al. 2014). We used 3 times the estimated $\sigma$ to calculate the state space radius around snares (Royle et al. 2014) and tested if this was large enough using the mask.check function in package secr. The state space radius was 45 km for the extensive design and 30 km for the intensive design, resulting in 41,121 km$^2$ and 16,812 km$^2$ areas, respectively. To estimate population size, we used the expected population size ($E(N)$) derived from the top supported model (Efford and Fewster 2013). For the extensive design, we estimated population size using a 30 km radius (29,898 km$^2$), as this represented our area of interest. We compared precision of parameter estimates using coefficients of variation (CV).

We selected the top supported model for each configuration using Akaike’s Information Criterion corrected for small samples (AICc) and considered models competing if within 2 AICc units from the top supported model (Burnham and Anderson 2002). Since we only added a lower strand of barbed wire to hair snares in the intensive configuration, we also ran all models excluding detections captured on the lower strand to improve comparison between configurations and test its effect on sample size and distribution of detections.
Simulations

We used our field sampling designs to simulate spatial capture-recapture datasets to evaluate accuracy of density estimates under each sampling configuration. We chose density and detection parameter values to represent both the observed values in our study and values commonly observed in other black bear studies (Carter et al. 2010, Frary et al. 2011, Baldwin and Bender 2012, Drewry et al. 2012). For density, we used values of 1 and 2.5 individuals per 100 km², and capture probability (g₀) values of 0.1 and 0.2. We also tested the scale parameter (σ) at 5, 10, and 15 km to investigate the effect of varying σ on density between sampling designs. We used a state space radius of 30 km when σ was 5 and 10 km and a radius of 45 km when σ was 15 km, with default point spacing of 64 x 64 points. Number of sampling intervals was set at six sessions. We then ran 100 replicates for each combination of density and detection parameter values (n = 12) under both configurations. For each scenario, we fit SCR models using the half-normal detection function in program DENSITY v5.0 (Efford 2012). To compare accuracy of density estimates to the true values from each sampling configuration we assessed average percent relative bias (%RB) and proportional coverage of confidence intervals (%COV).

Results

Extensive sampling design

We collected 98 black bear hair samples suitable for DNA extraction over six sessions from 30 unique snares (8% of the total number of snares). Number of black bear hair samples declined over time ( \( \bar{x} = 16.3 \) samples in session one to 8 samples in
Mean distance of each snare to nearest neighbor within arrays was 3.6 km (SD = 0.04 km). Mean distance between consecutive detection locations was 9.6 km.

Microsatellite marker analysis of hair samples revealed 25 unique individuals (11 F, 14 M) detected at 7% of all snares monitored. Total detections per session ranged from 6 to 9 (SD = 1.1), with 42 total detections, including within-session recaptures (Table 3.2). Individuals were detected on average 1.7 times (range = 1–5, SD = 1.0). Females were detected on average 1.9 times (range = 1–5, SD = 1.3) and males 1.5 times (range = 1–3, SD = 0.7). Fourteen individuals were not recaptured, including 55% of females and 57% of males. We detected individuals at an average of 1 snare (SD = 0.5, max = 2). Snares with ≥1 detection per session remained about constant (range = 6–8) across sampling sessions.

The snare-specific learned response model (bk) was most supported and 2 times more supported than the single competing model (g0[bk], σ[sex]; Table 3.1). However, we used parameter estimates from the top model as results between competing models were similar. Capture probability (g0) under the top model increased following initial detection at the same trap (Table 3.3). The estimated scale parameter of the detection function (σ) was 14.8 km (95% CI = 10.2–21.6 km). Density was 0.3 bears per 100 km² (95% CI = 0.2–0.6). Expected population size (E(N)) was 91 individuals (SE = 31, 95% CI = 47–175) in our 29,898 km² area of interest. Coefficients of variation (CV) ranged from 19% to 43% for all parameters. Activity centers estimated from the model were located primarily in the north-central and eastern portions of the trap array (Figure 3.2).
Intensive sampling design

We collected 540 black bear hair samples suitable for DNA extraction over six sessions from 113 unique snares (28% of total). Number of black bear hair samples collected in each array per session was variable (mean range = 2–42, grand mean = 18) and the total number of black bear hair samples collected declined over time ($\bar{x} = 90.0$; 111 samples in session one to 56 in session six). Mean distance of each snare to nearest neighbor within arrays was 1.0 km (SD = 0.04 km). Mean distance between consecutive detection locations was 2.5 km.

Microsatellite marker analysis of hair samples from snares revealed 90 unique individuals (59 F, 31 M; 4–48 individuals/array) detected at 23% of all snares monitored (Table 3.2). Total detections per session ranged from 25 to 43 (SD = 7.5), with 224 total detections, including within-session recaptures. Individuals were detected on average 2.5 times (range = 1–10, SD = 2.5). Females were detected on average 2.6 times (range = 1–10, SD = 2.7) and males 2.3 times (range = 1–10, SD = 2.2). Fifty-five individuals were not recaptured, including 63% of females and 61% of males. Two individuals were detected in two arrays, a male with an inter-trap distance of 57 km and a female with an inter-trap distance of 31 km. We detected individuals at an average of 2.0 snares (SD = 1.6, max = 8), and number of snares having ≥1 detection varied from 4 to 36 among arrays (Table 3.2).

The snare-specific learned response model (bk) was most supported and 3 times more supported than the next best model (g₀[bk], σ[sex]; Table 3.1). Capture probability under the top model increased following initial detection at the same trap, and σ was 8.5 km (95% CI = 7.0–10.4 km; Table 3.3). Density of the pooled arrays was 1.7 bears per
100 km$^2$ (95% CI = 1.1–2.4). Expected population size ($E(N)$) was 279 individuals (SE = 54, 95% CI = 193–406) in the 16,812 km$^2$ state space. Coefficients of variation ranged from 10% to 19% for all parameters. Estimated activity centers were primarily clustered within and around arrays B and D (Figure 3.2).

Of the 224 total detections, 35 (16%) resulted from hair samples collected from the bottom strand and represented 30 individuals (23 females, 7 males). Exclusion of these detections resulted in the loss of 14 unique bears (10 females, 4 males) from the dataset. The learned trap response model (bk) with sex-specific $\sigma$ was most supported and 13 times more supported than the same model without sex-specific $\sigma$. Capture probability was similar to estimates from the full dataset (Table 3.3). The estimated sex-specific $\sigma$ decreased and for females was 5.0 km (95% CI = 4.0–6.3 km) and for males was 3.6 km (95% CI = 2.8–4.6 km). Density increased to 3.5 bears per 100 km$^2$ (95% CI = 2.5–5.0) and expected population size was 586 bears (95% CI = 413–834).

**Simulations**

For our low density simulations (1.0 bear per100 km$^2$) with $\sigma < 15$ km, both array configurations had relative bias less than $\pm 2.0\%$ and 95% confidence interval coverage $\geq 92\%$ (Table 3.4). Similarly, at 2.5 bears per 100 km$^2$ both configurations produced almost unbiased density estimates at both $g_0$ levels and when $\sigma < 15$ km. At $\sigma = 15$ km, relative bias for the extensive design remained similar to other scenarios, but showed a positive increase for the intensive design. Both configurations performed well when simulation scenarios reflected field results of each configuration.
Discussion

We found that multiple arrays spaced across a landscape using intensive snare coverage yielded more captures and recaptures of more individuals than extensive coverage spaced over an area approximately 13 times larger. Consequently, estimated density using the intensive configuration was 5.5 times greater than that under the extensive configuration. By pooling detections among our arrays with closer snare spacing and using SCR models to explicitly account for variable exposure to traps, we were able to increase precision while retaining the ability to estimate average density over a landscape (Efford et al. 2005, Ngoprasert et al. 2012, Howe et al. 2013). However, placement of intensive arrays was informed largely by the distribution of detections from the extensive sampling effort. Therefore, although results support the intensive design, prior knowledge of bear distribution was critical to increasing detections in the intensive configuration. When population distribution and space use are poorly understood, adjusting sampling design over multiple surveys may be required (Boulanger et al. 2004).

With intensive sampling, CV of parameter estimates decreased on average by 53% compared to extensive sampling. Pollock et al. (1990) recommended a CV <20% for reasonable precision of estimates, which we achieved for all parameters with our intensive configuration. Boulanger et al. (2004) also demonstrated increased capture probability and precision under intensive sampling of a grizzly bear (*Ursus arctos*) population. However, over 50% of individuals in our study were not recaptured under both sampling designs and capture probability remained below recommended levels (i.e., >0.2; Boulanger et al. 2004). The lack of food reward at snares, summer migration to find food, mating opportunities, or dispersal (Noyce and Garshelis 2011, Sawaya et al. 2012),
may partially explain low recaptures observed during our summer (June–August) surveys. We suggest greater precision under the intensive design was largely due to detecting a greater proportion of individuals and increased detections at multiple snares (Boulanger et al. 2004, Sun et al. 2014). Though we cannot discern potential demographic changes between years, it is important to consider potential year effects on parameter estimates. For example, seasonal food abundance can affect movements and responses to baited sites (Noyce and Garshelis 2001, Noyce and Garshelis 2011). However, model selection results suggest bears responded to lured snares similarly between years. Therefore, we suggest our comparisons are appropriate given the constraints of implementing such large scale capture-recapture studies.

Although our two sampling designs are not comparable experimentally, results demonstrate the interplay among spatial sampling design, population distribution, and precision of detection parameters (Efford et al. 2005, Sollmann et al. 2012). The extensive configuration covered a wide geographic area, but snare distribution either covered large areas of unoccupied habitat or snare spacing was too wide given individual movements (Sun et al. 2014). Low precision of parameter estimates with extensive sampling may illustrate the reality of simulations by Tobler and Powell (2013), where precision decreased as trap spacing increased with larger array size. The logistical constraints of implementing such a large survey and risk of obtaining insufficient detections makes this approach unattractive for low density populations, especially those unevenly distributed over the landscape. This sampling design has proved effective in populations with higher bear density and larger home range size when population estimation was combined with independent data from hunter harvests (Dreher et al. 55)
In less studied and non-harvested populations, such as in Missouri, auxiliary information is often unavailable or too cursory to accurately inform study design or analyses.

Detections over the extensive and intensive arrays were not uniformly distributed, with most detections concentrated in two distinct areas during both years (Figure 3.2). If the low detection areas of the extensive design resulted from insufficient sampling alone, we would expect detections to increase in these areas when using intensive sampling (Otis et al. 1978), assuming minimal demographic changes between years. Although overall detections were greater using the intensive design, two of the four arrays that overlapped the extensive design area still received low detections. Though ancillary, this spatial pattern of detections during both years suggests a low, heterogeneous density as opposed to insufficient sampling design. Moreover, one would expect a positive relationship between spatial coverage and total animals detected (Karanth et al. 2011). With extensive sampling, we detected 25 bears over a nominal array area of about 13,500 km² and with intensive sampling we detected 90 bears over about 1,000 km². That our results disagree with Karanth et al. (2011) further supports a population where most individuals occurred in clustered regions with few bears interspersed between these areas. Heterogeneous densities and non-uniform space use are common among large carnivore populations in a varied landscape (Drewry et al. 2013, Howe et al. 2013), particularly among recently recolonizing populations (Bales et al. 2005, Frary et al. 2011, Puckett et al. 2014).

Changes to the intensive design, including the addition of a lower strand of barbed wire, increased the number of unique individuals and overall detections. Rerunning our
models excluding lower strand detections greatly affected the number and spatial
distribution of detections, and hence density and detection parameters. One of the male
detection losses represented the largest detected distance (57 km) between snares. This
and the loss of other inter-trap detections decreased sigma by 50%, increased density by
110%, and increased confidence intervals for density. Moreover, excluding these
detections also improved model support for a sex-specific spatial scale parameter. Sex-
specific space use can bias detection in carnivore population surveys (Sollmann et al.
2011), and our results illustrate the potential sensitivity of SCR parameter estimates to the
interaction between spatial sampling design and sex-specific movements among snares.
Some studies have attempted to quantify the effectiveness of using a second, lower strand
of barbed wire to increase capture probability or identify family groups (Boulanger et al.
2004, Dreher et al. 2007). Whereas Boulanger et al. (2006) found that a lower strand did
not greatly affect estimates for a grizzly bear population, we contend that for low density
populations a second strand may sufficiently increase data on encountered individuals
and movements.

Simulations of our extensive and intensive configurations showed low bias and
adequate confidence interval coverage for all scenarios. Although bias was low, the
positive bias for the intensive design when $\sigma = 15$ km suggests increasing distance
between snares to extend spatial coverage may increase the likelihood of detecting large
movements (Sollmann et al. 2012). Increasing spacing in the intensive design likely
wouldn’t affect precision of $\sigma$ as our effective trap spacing (i.e., spacing/$\sigma$; Sun et al.
2014) was much narrower than the $<2\sigma$ suggested by Sun et al. (2014). Whereas both
designs had low bias in simulations, few detections and inter-trap recaptures precluded
precise density estimation for the extensive design field study, though precision of σ remained adequate (i.e., CV < 20%). These results show that although SCR models are robust to variable spatial sampling designs (Sollmann et al. 2012, Sun et al. 2014), in low density populations, or populations with non-uniform space use, optimizing the tradeoff between snare spacing, coverage, and sample size is critical for estimating σ and density with high precision and accuracy.

Management decisions for large mammals are typically made over large spatial scales (Dreher et al. 2007, Lofroth and Krebs 2007, Russell et al. 2012), and inferences informing these decisions should cover a similar area (Turner et al. 1995). However, logistical constraints and carnivore ecology often preclude large scale inference (Settlage et al. 2008, Kéry et al. 2011). For example, although SCR may be robust to our extensive sampling design, low detections still hindered precise density estimation over such a large region (Pollock et al. 1990, Sollmann et al. 2012). Moreover, increasing trap intensity over a smaller region poses limits to the extent of density extrapolation to a larger area (Settlage et al. 2008). Thus, our extrapolation of density to a population estimate of 279 (95% CI = 193–406) black bears in a 16,812 km² area must be treated with caution (Boulanger et al. 2004, Settlage et al. 2008). This estimate also cannot be compared to that from extensive sampling as they were derived from different areas. However, given knowledge of bear presence and movements within this region (J. Beringer, unpublished data), the location of our intensive arrays likely sampled a representative range of bear densities and focused on areas with known populations (Efford et al. 2005).
Conclusion

Our study highlights important considerations in sampling design for attaining precise estimates using SCR models for wide-ranging mammals. Although SCR models are flexible to various spatial designs (Efford and Fewster 2013), they remain sensitive to the number of detections and inter-trap recaptures across the range of individual movements (Sollmann et al. 2012). Complete spatial coverage with sufficient trap spacing is challenging when animals with large home ranges exist at low densities and are not uniformly distributed (Soisalo and Cavalcanti 2006, Sollmann et al. 2012, Howe et al. 2013). Given these conditions, multiple arrays with intensive trap spacing similar in extent to individual movements should increase precision of detection parameters. We demonstrated support for sampling recommendations from simulated SCR analyses of black bear data sets (Sollmann et al. 2012, Sun et al. 2014) and illustrated realistic challenges of tailoring large scale spatial trap designs to a species’ behavior and spatial ecology. Although our study was specific to black bears, we suggest our findings are applicable to other wide ranging and low density species. The flexibility of SCR models to various sampling designs and techniques provide increased opportunities to accurately survey rare and elusive animals of high management or conservation priority.
Table 3.1  Model selection results for fitted models to estimate black bear density in Missouri, USA, for extensive and intensive sampling designs.

<table>
<thead>
<tr>
<th>Design</th>
<th>Model(^a)</th>
<th>(K(^b)</th>
<th>Log (L(^c)</th>
<th>AICc(^d)</th>
<th>(\Delta AICc(^e)</th>
<th>(w_I(^f)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extensive</td>
<td>(g_0(bk), \sigma(.))</td>
<td>4</td>
<td>-254.5</td>
<td>519.0</td>
<td>0.0</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>(g_0(bk), \sigma(sex))</td>
<td>5</td>
<td>-253.6</td>
<td>520.3</td>
<td>1.4</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>(g_0(Bk), \sigma(.))</td>
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<td>-255.9</td>
<td>521.8</td>
<td>2.8</td>
<td>0.1</td>
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<tr>
<td></td>
<td>(g_0(Bk), \sigma(sex))</td>
<td>5</td>
<td>-254.9</td>
<td>523.0</td>
<td>4.0</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>(g_0(sex), \sigma(sex))</td>
<td>5</td>
<td>-266.6</td>
<td>546.4</td>
<td>27.4</td>
<td>0.0</td>
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<tr>
<td></td>
<td>(g_0(.), \sigma(.))</td>
<td>3</td>
<td>-274.0</td>
<td>555.1</td>
<td>36.1</td>
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</tr>
<tr>
<td></td>
<td>(g_0(.), \sigma(sex))</td>
<td>4</td>
<td>-272.7</td>
<td>555.4</td>
<td>36.4</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>(g_0(b), \sigma(.))</td>
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<td>-271.8</td>
<td>556.7</td>
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<tr>
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<td>-273.7</td>
<td>557.3</td>
<td>38.3</td>
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<tr>
<td></td>
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<td>572.1</td>
<td>53.1</td>
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<tr>
<td></td>
<td>(g_0(t), \sigma(sex))</td>
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<td>-272.3</td>
<td>574.6</td>
<td>55.6</td>
<td>0.0</td>
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<tr>
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<td>(g_0(bk), \sigma(.))</td>
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<td>-1175.8</td>
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<td>(g_0(bk), \sigma(sex))</td>
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<td>2610.6</td>
<td>250.6</td>
<td>0.0</td>
</tr>
<tr>
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<td>2612.5</td>
<td>252.5</td>
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<tr>
<td></td>
<td>(g_0(t), \sigma(sex))</td>
<td>9</td>
<td>-1296.7</td>
<td>2613.6</td>
<td>253.6</td>
<td>0.0</td>
</tr>
</tbody>
</table>

\(^a\) Models were fit using the half-normal detection function and ranked from most to least supported by AICc. Effects on baseline capture probability \((g_0)\) and spatial scale parameter \((\sigma)\) included time as a factor \((t)\), global learned response \((b)\), snare-specific learned response \((bk)\), snare-specific Markovian response \((Bk)\), and sex. Parameters with “.” indicate no effect.

\(^b\) Number of parameters.

\(^c\) Log likelihood of the model.

\(^d\) Sample size corrected Akaike information criterion.

\(^e\) The difference between each model and the model with lowest AICc score.

\(^f\) The Akaike weight of each model, representing model support from a total of 1.00.
Table 3.2  Summary of sampling statistics for extensive and intensive (arrays A–E) black bear sampling configurations in south-central Missouri, USA.

<table>
<thead>
<tr>
<th>Design</th>
<th>Array</th>
<th>Snares&lt;sup&gt;a&lt;/sup&gt;</th>
<th>u&lt;sup&gt;b&lt;/sup&gt;</th>
<th>n&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Detections&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Snares Visited&lt;sup&gt;e&lt;/sup&gt;</th>
<th>No. Hair Samples&lt;sup&gt;f&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extensive</td>
<td>378</td>
<td>4.2 (2.4, 25)</td>
<td>6.5 (1.4, 39)</td>
<td>7.0 (1.1, 42)</td>
<td>6.8 (0.8, 26)</td>
<td>16.3 (7.2, 98)</td>
<td></td>
</tr>
<tr>
<td>Intensive</td>
<td>A</td>
<td>81</td>
<td>0.7 (0.8, 4)</td>
<td>0.8 (0.8, 5)</td>
<td>1.0 (0.9, 6)</td>
<td>1.0 (0.9, 4)</td>
<td>2.3 (2.4, 14)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>79</td>
<td>8.0 (6.7, 48)</td>
<td>14.7 (5.1, 88)</td>
<td>18.5 (7.0, 111)</td>
<td>12.8 (3.6, 36)</td>
<td>40.2 (18.5, 241)</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>81</td>
<td>1.2 (0.8, 7)</td>
<td>1.8 (0.8, 11)</td>
<td>2.8 (1.2, 17)</td>
<td>2.7 (1.2, 10)</td>
<td>7.8 (6.7, 47)</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>81</td>
<td>3.7 (2.9, 22)</td>
<td>8.0 (2.3, 48)</td>
<td>11.8 (2.7, 71)</td>
<td>9.2 (1.8, 29)</td>
<td>33.3 (12.0, 200)</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>81</td>
<td>1.8 (1.8, 11)</td>
<td>2.7 (2.0, 16)</td>
<td>3.2 (2.2, 19)</td>
<td>2.5 (1.9, 12)</td>
<td>6.3 (4.2, 38)</td>
</tr>
<tr>
<td>Intensive Total</td>
<td>403</td>
<td>3.1 (2.6, 92)</td>
<td>5.6 (2.2, 168)</td>
<td>7.5 (2.8, 224)</td>
<td>5.6 (1.9, 91)</td>
<td>18.0 (8.8, 540)</td>
<td></td>
</tr>
</tbody>
</table>

Order of values are mean (standard deviation, total) over six sessions.
<sup>a</sup>Number of lured snares in each sampling session.
<sup>b</sup>Number of individuals detected for the first time on each session. Note the sum was 92 total individuals for the intensive design due to two individuals being detected in two arrays (i.e., total individuals was actually 90).
<sup>c</sup>Number of individuals detected on each session.
<sup>d</sup>Number of detections, including within-session recaptures.
<sup>e</sup>Number of snares having at least one detection per session.
<sup>f</sup>Number of bear hair samples collected per session.
Table 3.3  Real parameter estimates and their precision (CV) for the top supported models to estimate American black bear density for extensive and intensive array configurations in Missouri, USA.

<table>
<thead>
<tr>
<th>Design</th>
<th>Area</th>
<th>Density$^a$</th>
<th>$g_0^b$</th>
<th>$\sigma^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$\hat{D}$</td>
<td>SE</td>
<td>95% CI</td>
</tr>
<tr>
<td>Extensive</td>
<td>29,898</td>
<td>0.3</td>
<td>0.1</td>
<td>0.2–0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intensive$^e$</td>
<td>16,812</td>
<td>1.7</td>
<td>0.3</td>
<td>1.1–2.4</td>
</tr>
<tr>
<td>Intensive$^f$</td>
<td>16,812</td>
<td>3.5</td>
<td>0.6</td>
<td>2.5–5.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$Bears per 100 km$^2$

$^b$Capture probability at the activity center of an individual for initial capture ($bk_0$) and for previously captured individual ($bk_1$).

$^c$Spatial scale parameter of the detection function derived from mean distances between recaptures at different snares (km).

$^d$State space (km$^2$) defining the extent of the distribution of home range centers in the population.

$^e$Estimates for the full dataset from the intensive sampling design.

$^f$Estimates derived from samples collected on the top barbed wire strand from the intensive sampling design.
Table 3.4  Percent relative bias (%RB) and percent coverage of 95% confidence intervals (%COV) of mean density estimates for simulations of spatial capture recapture models under extensive and intensive trap configurations.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Extensive</th>
<th></th>
<th>Intensive</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>D g0 σ</td>
<td>D SE %RB %COV</td>
<td>D SE %RB %COV</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.0 0.1 5</td>
<td>1.01 0.09 1.21 92</td>
<td>1.00 0.16 -0.01 93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>0.99 0.07 -0.72 96</td>
<td>0.99 0.09 -0.84 94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>1.00 0.13 0.07 93</td>
<td>1.01 0.07 0.66 97</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.2 5</td>
<td>1.00 0.08 -0.08 97</td>
<td>1.00 0.14 -0.28 94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>1.00 0.07 -0.18 97</td>
<td>1.02 0.09 1.94 96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>1.00 0.13 -0.26 96</td>
<td>1.03 0.07 3.43 93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5 0.1 5</td>
<td>2.47 0.01 -1.01 95</td>
<td>2.50 0.03 -0.01 90</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>2.49 0.01 -0.45 95</td>
<td>2.51 0.02 0.28 91</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>2.49 0.09 -0.22 98</td>
<td>2.53 0.11 1.36 96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.2 5</td>
<td>2.51 0.13 0.58 92</td>
<td>2.49 0.02 -0.52 97</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>2.50 0.01 -0.01 92</td>
<td>2.53 0.01 1.22 92</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>2.51 0.12 0.59 96</td>
<td>2.57 0.11 2.62 91</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Mean density estimates (\( \hat{D} \)) are based on averages over 100 replicates for each scenario of density (D; 1.0, 2.5 bears per100 km²), capture probability (g₀; 0.1, 0.2), and spatial scale parameter (σ; 5, 10, 15 km).
Figure 3.1  Location of the extensive and intensive configurations to estimate black bear density in south-central Missouri, USA.

State space boundary for extensive (solid line) and intensive (dotted line) configurations represents the area used to estimate population size. For the extensive design, snares (black circles) were allocated proportionate to density of historical bear sightings. For the intensive design, five arrays were distributed in areas of expected bear occurrence and one snares was placed in each cell; specific locations omitted for clarity. The five arrays were designated alphabetically (A–E) from west to east.
Figure 3.2  Location of hair snares and estimated activity (i.e., home range) centers of identified bears with the extensive and intensive configurations in south-central Missouri, USA.
References


CHAPTER IV
CONCLUSION

Understanding population density, abundance, and spatial distribution is important for species’ conservation (Garshelis and Hristienko 2006, Gray and Prum 2012, Neel et al. 2012). However, monitoring large carnivore distribution and density over space and time presents many logistical and statistical challenges (Gese 2001, Bjornlie et al. 2013). Large carnivores often are secretive, exist at low densities over large geographic areas, are not uniformly distributed, and exhibit wide intra- and inter-population variation in space use and behavior (Lofroth and Krebs 2007, Sollmann et al. 2011, Sunarto et al. 2013). Therefore, implementing effective field studies to survey spatio-temporal patterns of distribution or estimate population parameters has remained a persistent challenge (Boulanger and McLellan 2001, Tobler and Powell 2013).

Following their near extirpation in the early 1900s, American black bears now occur throughout much of Missouri’s Ozark Highlands region (Puckett et al. 2014). The recolonization of this area by bears provided a unique opportunity to better understand the ecological and anthropogenic factors that influence spatial patterns of recolonization. Using statewide anecdotal occurrence data, I demonstrated support for the hypothesis that recolonization followed a northward trend in latitudinal extent from source populations to the south in Arkansas. I also used this data to illustrate the potential importance of anthropogenic food sources to the distribution of reported bear occurrences;
anthropogenic food sources were the most common cause of bear incidents and were positively correlated with distribution of occurrences. Although the spatial and temporal inconsistencies of occurrence data often preclude accurate large scale inferences on species’ distribution (McKelvey et al. 2008), I showed that the conservative treatment of such data can reveal basic, yet important information on large scale patterns of distribution. Occurrence records are often the only statewide data available for low density, wide-ranging species and provide a low-cost approach to understanding basic spatio-temporal patterns of distribution and human-bear incidents.

Estimating density or abundance of widely distributed species is also confronted by numerous challenges, and much research has been performed on the development of effective sampling designs for estimating population parameters over large geographic areas (Long et al. 2008). However, variation in detection probability among individuals may limit the efficacy of capture-recapture sampling designs or collection methods (Ebert et al. 2010). I demonstrated that bears are more likely to be detected at hair snares when in close proximity to snares, and suggested that detection may benefit from spacing snares closer together. I also showed a negative relationship between number of hair samples per known visit and the temporal progression of sampling. To improve detection probability estimates, I recommended that black bear hair snare studies should coincide with seasonal periods of molting, and that spacing between snares and spatial extent of sampling configurations must be sensitive to potentially wide variation among home range sizes and movement. My results expand our understanding of the underlying causes among heterogeneous detection probabilities in capture-recapture population studies by
explicitly considering variability in home range space use and incorporating information on individuals observed, but not detected at snares.

The complex interaction among spatial sampling design, individual space use and behavior, and detection probability places further challenges on obtaining precise and accurate estimates of density or abundance (Boulanger et al. 2004, Sollmann et al. 2012). Spatial capture-recapture (SCR) models have advanced our ability to estimate population density for wide ranging animals by explicitly incorporating individual movement (Royle et al. 2014), yet the performance of these models under various spatial sampling designs has received little attention (Sollmann et al. 2012, Sun et al. 2014). I found that a spatially extensive trap configuration resulted in less precise density and detection parameter estimates compared to those estimated from a spatially intensive configuration. Although estimates were more precise under intensive sampling, density estimates were sensitive to the number of detections and spatial distribution of recaptures across the range of individual movements. With limited resources, allocating available traps to multiple arrays with intensive trap spacing increased the amount of information needed to inform parameters with high precision.

Results demonstrated that in low density populations with non-uniform space use, optimizing the tradeoff among snare spacing, coverage, and sample size is of critical importance to estimating parameters with high precision. Moreover, understanding the various ecological sources of bias that give rise to unequal detection probabilities is important for advancing development of experimental designs. Although the flexibility of SCR models may greatly improve accuracy and precision, the ecological characteristics
of the species and population of interest will ultimately determine the effectiveness of any spatial design (Boulanger et al. 2004, Sollmann et al. 2012, Royle et al. 2014).
References


