



Original Article

Applying Spatially Explicit Capture–Recapture Models to Estimate Black Bear Density in South Carolina

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ABSTRACT Population density is an important component of wildlife management decisions, but can be difficult to estimate directly for an itinerant, wide-ranging species such as the American black bear (*Ursus americanus*). In South Carolina, USA, where there has been growth in black bear populations and bear–human–conflict reports during the past several decades, managers need robust estimates of population size to inform management strategies. We used maximum-likelihood capture–recapture models, using hair snares to collect DNA samples, to estimate density and abundance for a harvested population of black bear in northwestern South Carolina during 2013 to 2014. Models were tested in a spatially explicit framework using the *secr* package in Program R. Black bear density was estimated at 0.133 bears/km² (SE = 0.034) in 2013 and 0.179 bears/km² (SE = 0.043) in 2014. Black bear abundance in our study area was estimated to be 586 bears (SE = 95) in 2013 and 680 bears (SE = 128) in 2014, which are 2–3-fold lower than previous estimates. We suggest that these estimates be considered a baseline for state biologists to employ in the population’s management and in developing future harvest-regulation strategies. Overall our study highlighted the potential for model choice to influence density estimates, and we concluded that spatially explicit models were appropriate for this study because geographic closure could not be assumed. © 2019 The Wildlife Society.

KEY WORDS abundance, black bear, density, hair snare, South Carolina, spatially explicit capture–recapture, *Ursus americanus*.

In recent decades, the American black bear (*Ursus americanus*) has begun to reoccupy portions of the North American landscape from which it had previously been eliminated through persecution and habitat destruction by European colonial settlers (Cowan 1972, Taber and Payne 2003, Garshelis and Hristienko 2006, Scheick and McCown 2014). Recent assessments indicate that the black bear now occupies 65–75% of its North American historical range, with 36 of 41 states in the United States with a resident black bear population report trends that are either stable or increasing (Hristienko et al. 2009, Noyce 2011, Scheick and McCown 2014).

As bear populations expand and face increasing anthropogenic pressures, there arises the need to implement

sustainable management practices that are scientifically informed and validated. Management plans for black bears vary with geography and distribution, depending on whether they are causing conflicts with humans, maintained for harvest, or conserved for viewing and demographic stability (Organ and Ellingwood 2000, Bowman et al. 2001, VDGIF 2012). Generally, most management strategies deal with harvest regulations, ranging from restrictions on bag limits and duration of hunting season, to full legal protection in some smaller refuges or parks (e.g., Nantahala National Forest, Great Smoky Mountains National Park). However, to develop adaptive management strategies that reconcile recovering or expanding bear populations with increasing human densities, it is important to establish robust estimates of population-level metrics.

The bear population in northwestern South Carolina, USA, has been subject to harvest since 1981, and 2 population estimates for restricted portions of bear range have been carried out. In 1993, researchers employing live-trapping

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mark–recapture estimated the density of the black bear population in the Pickens County (1 of 3 counties over which the resident population was assumed to range) Horsepasture Wildlife Management Area at 0.217–0.345 bears/km² (Willey 1995). In 2003, Settlage et al. (2008) estimated the bear density in a 3-state area that included northwestern South Carolina at 0.3 bears/km² based on capture–recapture based on DNA extracted from bear hair. State wildlife managers noted that the black bear population appeared to be stable or increasing, and reported informed estimates of 1,150 bears in 2007 and 1,800 bears in 2011 from bait-station indices and bear–human-conflict reports (Still 2007, Morton 2011). However, no formal study had been undertaken in the state to estimate the population density over their entire northwestern range. In 2015, a harvest reconstruction model was developed for black bears in northwestern South Carolina that showed a gradually increasing population during the previous 2 decades. Model limitations, however, mean that these estimates probably were not accurate for recent years (Azad et al. 2017a). At the same time, bear harvest numbers and bear–human conflicts continued to rise (Azad et al. 2017a). From 1970 to 1999, annual harvest was ≤ 20 individuals. Over the next decade, average annual harvest increased to 44.2 individuals (SE = 21.3), and from 2010 to 2015, average annual harvest was 79.8 individuals (SE = 30.7). Whereas there was some evidence that increased bear–human interactions could be attributed to cyclic food

abundance (Azad et al. 2017b), increasing urbanization, recreation, or hunting effort, it was not known if it also stemmed from an expanding population. It was thus important for state wildlife managers to establish a more robust and accurate population estimate to review hunting options or revise conflict management strategies.

We conducted a 2-year capture–recapture survey of black bears in northwestern South Carolina. We selected the maximum-likelihood spatially explicit capture–recapture models developed to estimate density from capture histories without assuming geographic closure or effective area (Efford 2004). Our objectives were to 1) establish a baseline density estimate for the northwestern population to inform management decisions, 2) estimate sex ratios in the population and estimate its geographic distribution, and 3) assess assumptions and possible sources of bias in these models to make recommendations for the analysis of future capture–recapture surveys of black bear populations.

STUDY AREA

Our study area included about 2,200 km² in northwestern South Carolina across the counties of Oconee, Pickens, and Greenville (Fig. 1). The region was typically composed of forested habitat containing shortleaf pine (*Pinus echinata*), chestnut oak (*Quercus montana*), and scarlet oak (*Q. coccinea*) mixes on the southern Appalachian mountain slopes (Willey 1995, Butfiloski 1996; Fig. 2). The cooler northern

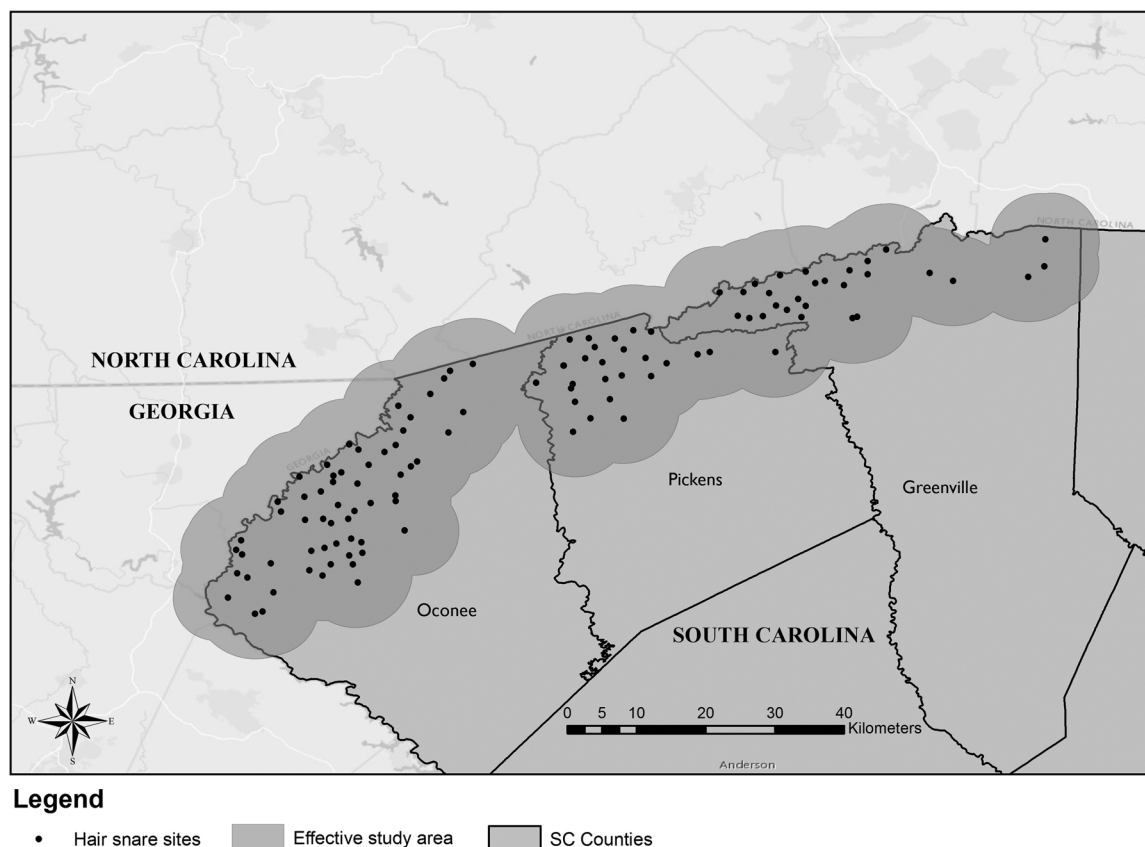


Figure 1. Location of hair snare sites, and sites buffered by Program R package *secr* suggested value of 8 km, in northwestern South Carolina, USA, 2013–2014. Site distribution within counties was as follows: 59 sites in Oconee, 28 sites in Pickens, and 28 sites in Greenville (115 total).

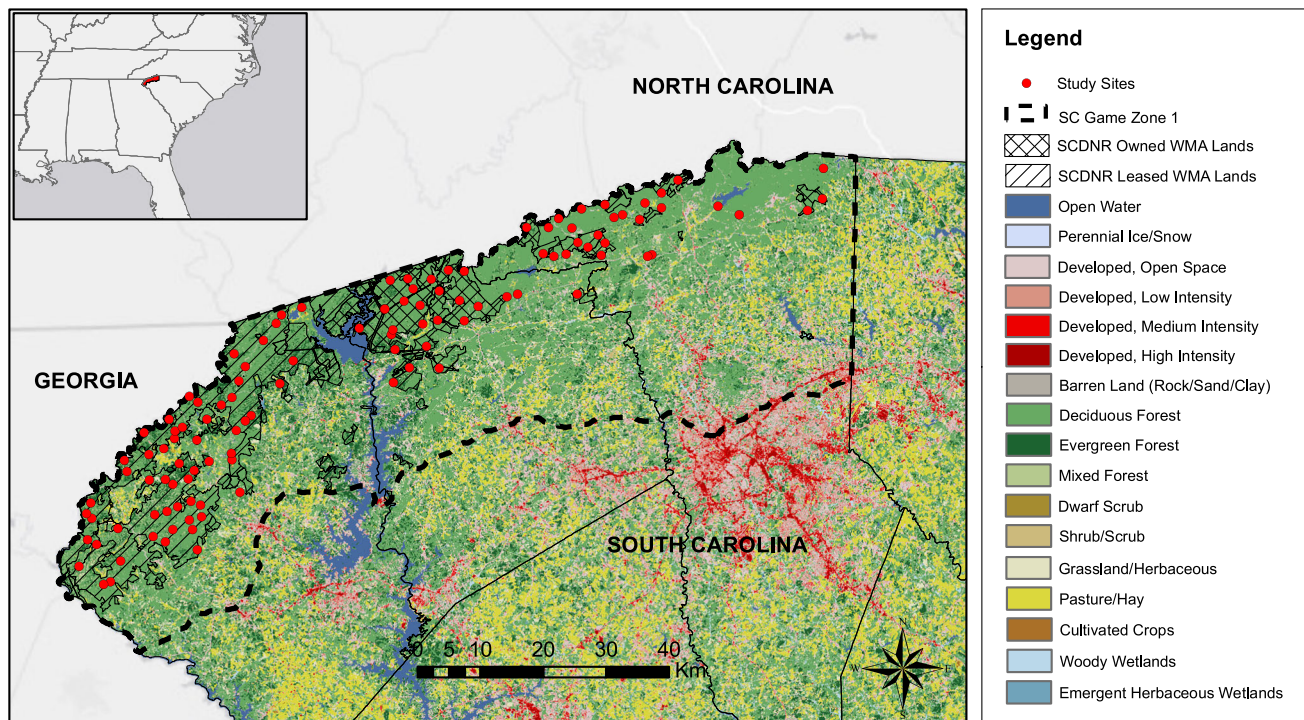


Figure 2. Land use map of northwestern South Carolina, USA, including state-defined boundaries of—South Carolina Game Zone 1 (SC Game Zone 1), and South Carolina Department of Natural Resources Owned/Leased Wildlife Management Areas (SCDNR Owned/Leased WMA) lands. Land use derived from National Land Cover Database 2011 LANDSAT-based spatial imagery (Homer et al. 2015).

slopes consisted of yellow poplar (*Liriodendron tulipifera*), white pine (*P. strobus*), eastern hemlock (*Tsuga canadensis*), and mixed mesophytic hardwood overstories (Willey 1995, Butfiloski 1996). Slopes and coves often had dense understories of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*), and intermediate stands were generally oak–pine mixtures (Myers et al. 1986). The study area was generally characterized by a mean annual temperature of 16.1° C (max = 22.1° C, min = 10.1° C) and total annual precipitation of 169.1 cm in 2013; and a mean annual temperature of 15.7° C (max = 21.6° C, min = 9.9° C) and total annual precipitation of 119.1 cm in 2014 (NOAA–National Climatic Data Center 2015).

METHODS

Data Collection

South Carolina Department of Natural Resources (SCDNR) personnel sampled black bear hair within grid cells using barbed-wire hair snares during 2013 and 2014 as described by Woods et al. (1999). We assumed that black bear habitat included the entire grid area. To establish sampling sites, we first defined a sampling grid across a total area of 2,200 km², with cells 5.8 km² in size. We based size of cells in the sampling grid on a previously estimated black bear density of 0.3 bears/km² or 1 individual/5.8 km² (Settlage et al. 2008), so as to establish a nontrivial chance of sampling ≥1 bear/snare. The study had limited funding for (only 115) hair snare sites, so it was necessary to subsample these grid squares. We sub-selected grid squares for sites as those either located within the

core occupied area by black bear (designated by SCDNR as South Carolina Game Zone 1), or located on forested lands owned or leased by SCDNR, South Carolina Department of Parks, Recreation & Tourism, United States Forest Service, The Nature Conservancy, Natural Land Trust, and the D&M Hunt Club. We established one hair snare somewhere within each grid cell with goal of relatively uniform spacing between adjacent sites, but also to facilitate access (Fig. 1). Our goal was to facilitate visitation of multiple sites by individuals, as well as sample known bear habitat to capture a good representation of sex ratios in the population. Average site spacing over the study area was 2.71 km; with a minimum spacing of 0.70 km and a maximum spacing of 6.61 km. There were 115 sites in total, and we used the same hair-snare site locations in both 2013 and 2014.

A hair snare or corral consisted of 2 strands of barbed wire stretched between 3–5 trees spaced ≥2.0 m apart. We strung wires at 35- and 70-cm above-ground. We hung sardines, pastry baits, and a scent lure in the center of the corral 1.5–2.0 m above-ground. Beginning late May, we checked sites weekly for 8 weeks in 2013 and 7 weeks in 2014. We gathered samples using tweezers sterilized between individual collections, and used a propane torch to burn off remnant hair from the barbed wire before rebaiting.

We sent hair samples to Wildlife Genetics International (WGI), Nelson, British Columbia, Canada, for genotyping. Financial constraints meant we had to subsample which hair samples were used for genetic analysis. Following recommendations by Tredick et al. (2007), we developed a protocol to maximize capture and recapture probabilities, focus

on high-quality samples, and spatially and temporally balance our sampling across the entire study area. In 2013, we subsampled as follows: 1 sample was chosen from a single week–site combination with ≤ 3 samples, 2 samples from a single week–site with 4–6 samples, and 3 samples from a single week–site with ≥ 7 samples. In 2014, we developed a more conservative subsampling criterion to increase the proportion of samples analyzed; 1 sample was randomly chosen from a single week–site with ≤ 2 samples, 2 samples from a single week–site with 3–5 samples, and 3 samples from a single week–site with ≥ 6 samples.

We extracted DNA from hair samples using QIAGEN DNeasy Blood and Tissue kits (Qiagen, Valencia, CA, USA), following standard protocols (Paetkau 2003, Roon et al. 2005). We carried out individual analysis using 7 microsatellite markers (G1A, G1D, G10L, G10C, G10M, G10P, MU23) and 1 sex marker (ZFX/ZFY) selected from Settlage et al. (2008). The samples underwent 3 phases of analysis. First, we performed an initial pass of identification, whereby we separated samples having high confidence scores. Second, a cleanup phase took place whereby we repeatedly reanalyzed data points that were incomplete or difficult to read and discarded samples that still had low confidence scores in any marker. We classified genotype scores using a combination of objective (peak height) and subjective (appearance) criteria; we identified low confidence by a 2-digit rather than a 3-digit score (D. Paetkau, WGI, personal communication). Third, we conducted an error-checking phase in which we extended mismatching markers in a pair of genotypes to 11 microsatellite loci to confirm that it was the same bear and not a genotyping error (D. Paetkau, personal communication).

Statistical Analysis

We used individuals identified in the genetic analysis to create capture histories to estimate density using spatially explicit capture–recapture methods. The spatially explicit analysis method combines a distance-dependent detection probability function with the spatially referenced locations of trap sites. The model establishes a spatial point process of activity centers, the intensity of which is a direct estimator of density (Efford 2004). Advantages associated with spatially explicit models are well-documented and include inherent accommodation of spatial heterogeneity in capture probabilities, and accommodation of nonuniform sampling designs in space (Efford 2004, Efford et al. 2009, Gerber et al. 2012, Efford and Fewster 2013, Efford and Mowat 2014), provided intertrap spacing is not too small relative to animal movement such that spatial recaptures are feasible (Sollmann et al. 2012, Sun et al. 2014). We modeled data assuming individuals had stationary activity centers (i.e., no permanent immigration or emigration) using the following model arguments: 1) we modeled capture events as binary (detector type = ‘proximity’); 2) we modeled number of activity centers as a Poisson distribution assuming uniform distribution of individuals across the study area, because bears are not gregarious and exhibit mutual avoidance within overlapping ranges (Obbard et al. 2010); and 3) we

modeled detection as a half-normal function assuming that detection was a continuous (not step) function from the activity centers to a point of zero capture probability (Borchers and Efford 2008, Goode et al. 2014). Detection parameters for models were probability of individual detection at the activity center (g_0), and rate of decrease in capture probability with distance from activity center (σ). We used the maximum-likelihood package *secr* in Program R (ver. 2.10.3, <http://cran.r-project.org/package=secr>). We fit a null model with no covariates and 8 models with varying effects on the detection parameters g_0 and σ . Effects included year (*session*), global trap response (b), and site-specific trap response (b_k); where trap response behavior depicted whether an individual was likely to revisit or avoid a snare after having being captured once. We tested models separately for each sex, and used 2-point mixture distributions to model individual heterogeneity (b_2) within sex. We estimated density (D) by *secr* within each model as the sole parameter of a homogenous Poisson process. We tested top-ranked models again pooling both sexes, with sex defined as the 2-point mixture, to determine the sex ratio.

White et al. (1982) separated the assumptions of population closure into demographic closure (i.e., no permanent births, deaths, immigration or emigration over the study period) and geographic closure (individuals do not move on and off the study area over the study period). We assumed a capture season of 7 or 8 weeks outside of hunting season would not violate demographic closure for bears (Mowat and Strobeck 2000). We used a buffer from the *suggest.buffer* () function in *secr*, rounded to the nearest km (8 km). We also considered a range of initializing buffers (2,000 m–11,000 m), corresponding to a range of preliminary home-range estimates; but found that precision of density estimate improved at the *secr* buffer recommendation. Our total state space including the buffer was 3,047 km². We assumed that the area enclosed by the buffer polygon was comprised of equally probable black bear habitat (that is, we did not exclude any nonbear habitat). We ranked our models using Akaike’s Information Criterion corrected for small samples (AIC_c) and model-averaged parameter estimates using AIC_c weights of competing models, where competing models were defined as $\Delta AIC_c \leq 10$ (Burnham and Anderson 2003). We estimated values of g_0 and σ separately for each sex.

RESULTS

Genetic Analysis

Year 1 (2013).—Subsampling and technical protocols resulted in 298 of 650 samples being genotyped. Microsatellite analysis of the 298 samples revealed 143 individual bears (76 M:67 F, M:F ratio of 1.134:1). The genotyping success rate for individual identification was 89%. We detected the 143 individuals at 83.5% (96 of 115 sites) of the hair snare sites in 2013. Recapture probability for both males and females was 0.37 (SE = 0.09).

Year 2 (2014).—Subsampling and technical protocols resulted in 396/838 samples analyzed. Microsatellite analysis of

the 396 samples revealed 149 individual bears (59 M:90 F, M:F ratio of 0.666:1) detected in 2014. Fifty-one of 149 (23 M and 28 F) were recaptures from 2013, and 98 (36 M and 62 F) were previously undetected individuals. The genotyping success rate in 2014 was lower than in 2013, with successful individual identification achieved for 77% of all samples genotyped in 2014. Recapture probability for both males and females was 0.58 (SE = 0.01). We detected these 149 individuals at 80.9% (93 of 115 sites) of the hair snare sites in 2014. Two individuals in the data set were captured in >1 counties. The first was in Pickens in 2013 and Oconee in 2014 (approximate distance between sites = 23.9 km); the second in Greenville in 2013 and both Pickens and Greenville in 2014 (1 capture in Pickens in Week 3, captures in Greenville in each week from 1–6; approximate distance between sites = 49.5 km). We excluded the latter individual as an outlier from spatial models.

Spatially Explicit Analysis

Males.—Our top model ($D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim b_2$) included year, and site-specific trap response for g_0 , and heterogeneity in g_0 and σ expressed as 2 heterogeneous mixtures (Tables 1, 2). Our model-averaged density was 0.067 male bears/km² (SE = 0.012) in 2013 and 0.045 male bears/km² (SE = 0.008) in 2014. Based on our buffer of 8,000 m around the outermost hair-trap locations, our sampling area was 3,047 km². The estimated number of male bears in our sampling area was 212.4 (SE = 36.9, 95% CI = 151.4–297.8) in 2013 and 134.5 (SE = 23.5, 95% CI = 95.8–188.8) in 2014.

Our model-averaged estimate for g_0 (detection probability) was 0.052 (SE = 0.012) in 2013 and 0.070 (SE = 0.019) in 2014. Our model-averaged estimate for σ (scale parameter for detection probability) was 4.09 km (SE = 0.75) in 2013, and 4.16 km (SE = 0.80) in 2014.

Females.—Our top model ($D \sim 1$, $g_0 \sim b_2 + b_k$, $\sigma \sim b_2$) included site-specific trap response as a covariate for g_0 and heterogeneity in g_0 and σ expressed as 2 heterogeneous

mixtures (Tables 1, 2). Our model-averaged density was 0.126 female bears/km² (SE = 0.032) in 2013 and 0.175 female bears/km² (SE = 0.042) in 2014. The estimated number of female bears in our sampling area was 373.8 (SE = 88.0, 95% CI = 237.1–589.2) in 2013 and 545.4 (SE = 125.8, 95% CI = 349.3–851.8) in 2014.

Our model-averaged estimate for g_0 (detection probability) was 0.043 (SE = 0.014) in 2013 and 0.046 (SE = 0.016) in 2014. Our model-averaged estimate for σ (scale parameter for detection probability) was 2.89 km (SE = 0.92) in 2013 and 2014 (SE = 0.94).

Both sexes.—Totals when combining sexes were 0.193 bears/km² (95% CI = 0.125–0.261) or 586.2 (95% CI = 388.4–887.0) total bears in 2013 and 0.220 bears/km² (95% CI = 0.134–0.306) or 679.9 (95% CI = 445.1–1040.6) total bears in 2014. The sex ratio estimated from pooling data was M:F = 0.563:1 in 2013, and M:F = 0.333:1 in 2014.

DISCUSSION

Our study provides novel insights into black bear densities in northwestern South Carolina, and highlights the potential for analytical methods to influence density estimates. Our estimates of black bear density from *secr* models were lower, but still within the 95% CI of previous density estimates from a larger scale 2004 study in this region (0.336, 95% CI = 0.177–0.637) based on a spatially explicit reanalysis of those data (Settlage et al. 2008; J. D. Clark, unpublished data). We do not believe this necessarily indicates that bear populations have declined since 2004; recent population reconstruction studies reported a generally increasing trend over the past 2 decades (Azad 2017a). However, the preliminary lack of evidence of genetic movement across state borders as well as reports of greater black bear densities in North Carolina, USA, indicate that black bear density in South Carolina is likely lower than surrounding states (Olffenbuttel 2013).

We observed considerable variation in estimates of density among different models fitted to the same data set,

Table 1. Top models of the spatially explicit maximum-likelihood capture–recapture analysis using package *secr* in Program R for black bears in South Carolina, USA, 2013–2014.

Model ^a	AIC _c ^b	ΔAIC _c	AIC weight ^c	No. of parameters	Log likelihood
Males, top models					
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim b_2$	2,318.17		0.50	9	–1,149.36
$D \sim \text{session}$, $g_0 \sim b_2 + b_k$, $\sigma \sim h_2$	2,320.06	1.88	0.19	8	–1,151.45
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim \text{session} + b_2$	2,320.49	2.32	0.16	10	–1,149.35
$D \sim \text{session}$, $g_0 \sim b_2 + b_k$, $\sigma \sim \text{session} + b_2$	2,320.57	2.40	0.15	9	–1,150.56
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim 1$	2,341.59	23.41	0.00	8	–1,162.22
Females, top models					
$D \sim \text{session}$, $g_0 \sim b_2 + b_k$, $\sigma \sim b_2$	2,015.43		0.53	8	–999.23
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim h_2$	2,017.24	1.80	0.22	9	–999.01
$D \sim \text{session}$, $g_0 \sim b_2 + b_k$, $\sigma \sim \text{session} + b_2$	2,017.64	2.21	0.18	9	–999.21
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim \text{session} + b_2$	2,019.34	3.91	0.08	10	–998.92
$D \sim \text{session}$, $g_0 \sim \text{session} + b_2 + b_k$, $\sigma \sim 1$	2,032.42	16.99	0.00	8	–1,007.73

^a D is estimate of density, g_0 is the probability of detection at activity center, σ is rate of decrease in detection with distance from activity center, *session* is an estimator that accounts for heterogeneity between both years of sampling, b_2 is an estimator that accounts for 2-mixture heterogeneity within a year, and b_k is a predictor variable that accounts for site-specific bias.

^b AIC_c is Akaike's Information Criterion adjusted for small samples.

^c AIC weight is relative AIC_c support for models.

Table 2. Estimates of density D , and detection parameters g_0 (probability of detection at activity center) and σ (rate of decrease in detection with distance from activity center, km) with their standard errors (SE) for top models of the spatially explicit maximum-likelihood capture–recapture analysis using package *secr* in Program R for black bears in South Carolina, USA, 2013–2014. Top models were determined using AIC_c (Akaike’s Information Criterion adjusted for small samples; see Table 1).

Model ^a	D		g_0		σ	
	2013	2014	2013	2014	2013	2014
Males, top models						
$D \sim \text{session}, g_0 \sim \text{session} + b_2 + b_k, \sigma \sim b_2$	0.070 (0.012)	0.044 (0.008)	0.049 (0.011)	0.076 (0.021)	4.12 (0.74)	4.12 (0.74)
$D \sim \text{session}, g_0 \sim b_2 + b_k, \sigma \sim b_2$	0.062 (0.010)	0.051 (0.009)	0.060 (0.013)	0.060 (0.013)	4.18 (0.77)	4.18 (0.77)
$D \sim \text{session}, g_0 \sim \text{session} + b_2 + b_k, \sigma \sim \text{session} + b_2$	0.070 (0.012)	0.044 (0.008)	0.048 (0.012)	0.078 (0.026)	4.19 (0.77)	4.10 (0.89)
$D \sim \text{session}, g_0 \sim b_2 + b_k, \sigma \sim \text{session} + b_2$	0.067 (0.011)	0.046 (0.009)	0.060 (0.013)	0.060 (0.013)	3.99 (0.76)	4.56 (0.96)
Females, top models						
$D \sim \text{session}, g_0 \sim b_2 + b_k, \sigma \sim b_2$	0.122 (0.029)	0.178 (0.042)	0.044 (0.014)	0.044 (0.014)	2.90 (0.92)	2.90 (0.92)
$D \sim \text{session}, g_0 \sim \text{session} + b_2 + b_k, \sigma \sim b_2$	0.133 (0.037)	0.168 (0.041)	0.039 (0.014)	0.048 (0.018)	2.86 (0.92)	2.86 (0.92)
$D \sim \text{session}, g_0 \sim b_2 + b_k, \sigma \sim \text{session} + b_2$	0.125 (0.033)	0.176 (0.044)	0.044 (0.014)	0.044 (0.014)	2.88 (0.93)	2.95 (0.99)
$D \sim \text{session}, g_0 \sim \text{session} + b_2 + b_k, \sigma \sim \text{session} + b_2$	0.133 (0.039)	0.169 (0.040)	0.036 (0.013)	0.050 (0.028)	2.92 (0.91)	2.70 (1.04)

^a *Session* is an estimator that accounts for heterogeneity between both years of sampling, b_2 is an estimator that accounts for 2-mixture heterogeneity within a year, and b_k is an estimator that accounts for site-specific bias.

particularly when individual heterogeneity was incorporated in the model. This demonstrates the potential for *secr* to produce biased estimates when an inappropriate (in this case, overparameterized) model is fit. A number of studies suggest that density estimates are conservative for models that do not incorporate heterogeneity (Ebert et al. 2010, Proctor et al. 2010, Howe et al. 2013). Although our top models included 2-mixture heterogeneity within a sex, it is possible that our estimates had low precision due to our not having modeled other sources of heterogeneity. We also observed that precision was improved in models that pooled data from both years, with standard errors for all parameters generally lower than in models of either year. We suggest that future surveys be designed for >2 years to incorporate greater precision in density estimates. We also suggest incorporating in future models additional sources of information to better estimate σ , such as range estimates from radiocollared bears.

Sex ratios were biased toward females in both years, as compared with sex ratios simply reported from the DNA analysis of hair samples. However, *secr* estimates sex ratios from a stationary distribution of activity centers, whereas sex distribution in the sample is influenced by differential movement and capture probability by sexes; therefore, we suggest that sex ratios returned by spatial models are more likely a better representation of the sex ratios in the population (Sollmann et al. 2011).

A potential source of bias leading to underestimation of density is the assumption that bears can move with equal ease across the entire landscape (Rayan et al. 2012, Rinehart et al. 2014). However, most study areas will include unavailable habitat stemming from topographic barriers and anthropogenic features (Rayan et al. 2012). At the time of this study, the authors in collaboration with state wildlife biologists determined that non-black bear habitat could not easily be delineated. Black bear sightings in the study area have occurred over a range of landscapes including forests, towns, and (both in and near) large water bodies (T. Wactor, personal communication). In future

investigations for South Carolina, we recommend delineating areas that could be defined as historically unoccupied or not bear habitat. Once defined, these habitat features or geographical boundaries could be used in the habitat mask feature of *secr*. Detection parameters could be modeled with these covariates to exclude nonhabitat areas, improve density estimates, and reduce probable underestimation in future surveys (Efford and Fewster 2013, Hooker et al. 2015).

Overall, we recommend that estimates from this study be used as a baseline for state biologists to refine a management plan for the population. Density is an important parameter in population ecology studies, and often a crucial component of conservation or wildlife management actions. For a harvested species such as the black bear, inflated estimates of abundance or skewed sex ratios can lead to management plans that put the population at risk (Gardner et al. 2010, Obbard et al. 2010, Sollmann et al. 2011, Gerber et al. 2012, Noss et al. 2012). For instance, a female-skewed sex ratio in harvest can indicate overharvest (Garshelis 1990); however, this disparity could also be attributed to older animals automatically having reduced male bias due to greater male vulnerability in younger age classes. Inferring population structure from age and sex data in harvest alone has the potential to be misleading, and management plans may be better served when multiple data streams can be used to interpret population dynamics. Our study includes a conservative predicted abundance for the population, placed in context against “best guesses” by managers and studies previously carried out (Still 2007, Settlage et al. 2008, Morton 2011, Azad 2017a). Spatially explicit capture–recapture models, which assume no permanent immigration or emigration (Efford 2004), are generally more suitable when there is uncertainty about study design effectiveness either due to itinerant nature or underestimated home ranges of the species, and can be a valuable tool in estimating the extent of recovery of a wide-ranging species such as the American black bear.

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