



Research Article

# Density of American Black Bears in New Mexico

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**ABSTRACT** Considering advances in noninvasive genetic sampling and spatially explicit capture–recapture (SECR) models, the New Mexico Department of Game and Fish sought to update their density estimates for American black bear (*Ursus americanus*) populations in New Mexico, USA, to aide in setting sustainable harvest limits. We estimated black bear density in the Sangre de Cristo, Sandia, and Sacramento Mountains, New Mexico, 2012–2014. We collected hair samples from black bears using hair traps and bear rubs and used a sex marker and a suite of microsatellite loci to individually genotype hair samples. We then estimated density in a SECR framework using sex, elevation, land cover type, and time to model heterogeneity in detection probability and the spatial scale over which detection probability declines. We sampled the populations using 554 hair traps and 117 bear rubs and collected 4,083 hair samples. We identified 725 (367 male, 358 female) individuals. Our density estimates varied from 16.5 bears/100 km<sup>2</sup> (95% CI = 11.6–23.5) in the southern Sacramento Mountains to 25.7 bears/100 km<sup>2</sup> (95% CI = 13.2–50.1) in the Sandia Mountains. Overall, detection probability at the activity center ( $g_0$ ) was low across all study areas and ranged from 0.00001 to 0.02. The low values of  $g_0$  were primarily a result of half of all hair samples for which genotypes were attempted failing to produce a complete genotype. We speculate that the low success we had genotyping hair samples was due to exceedingly high levels of ultraviolet (UV) radiation that degraded the DNA in the hair. Despite sampling difficulties, we were able to produce density estimates with levels of precision comparable to those estimated for black bears elsewhere in the United States. © 2018 The Wildlife Society.

**KEY WORDS** American black bear, capture–recapture, density estimation, DNA degradation, New Mexico, *Ursus americanus*.

State agencies spend a large portion of their annual budget estimating abundance and population trends of game animals, in part, so they can set sustainable harvest levels. Survey methods for large ungulates are well-developed and can provide relatively robust estimates of abundance for common game species such as deer (*Odocoileus* spp.) and elk (*Cervus canadensis*; Bleich et al. 2001, Zabransky et al. 2016). In contrast, estimating the abundance or density of large carnivores such as American black bears (*Ursus americanus*; hereafter, black bears) is more difficult because their cryptic behavior and low population densities make common survey methods used for large ungulates (e.g., aerial counts)

ineffective because of low detection rates (Miller 1990, Obbard et al. 2010). Historically, many state agencies set harvest limits for carnivores based on harvest data, including sex ratio and age structure of the harvested animals, which can be used to infer harvest effects on a population (Garshelis 1990, Hristienko and McDonald 2007). Yet, hunter selectivity and sex-specific vulnerability may influence harvest composition (Miller 1990, Beston and Mace 2012).

In New Mexico, USA, as in other parts of the American Southwest, black bears inhabit forested mountain ranges separated by desert and grassland valleys resulting in fragmented populations with varying degrees of connectivity (Atwood et al. 2011). Prior to their designation as a game species in 1927, the statewide black bear population was reduced to 660 owing to unlimited hunting and government sponsored anti-predator programs (New Mexico Department of Game and Fish [NMGFD] 1926). With legislative

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protection in place, the statewide population increased to 3,000 animals by the mid-1960s (Lee 1967). For nearly 20 years, this population estimate, paired with hunter harvest data, was the basis for setting harvest limits by the NMDGF. However, uncertainty in trends in black bear abundance during the late 1980s resulted in NMDGF initiating a decade-long study of black bear ecology in the 1990s (Costello et al. 2001).

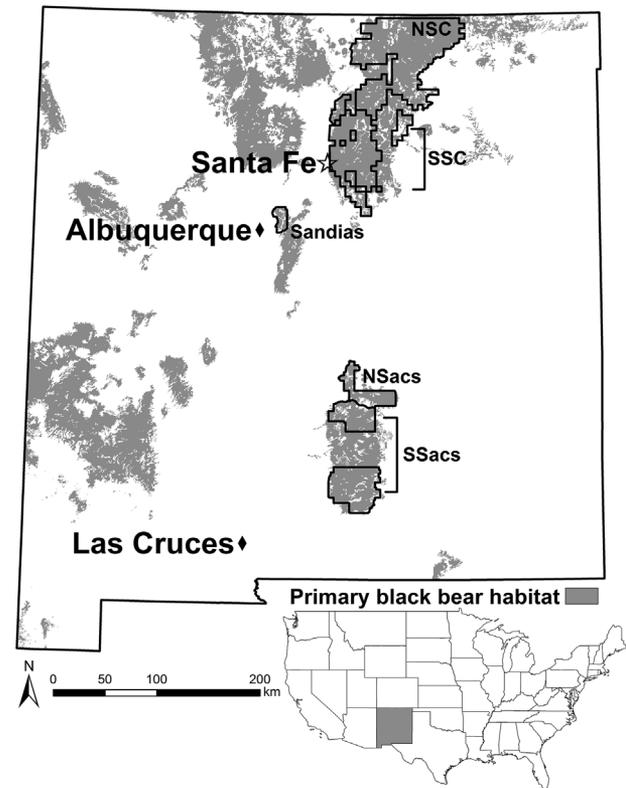
New Mexico's most recent density estimates for black bear were derived from Costello et al. (2001) by dividing the minimum population size that was calculated using population reconstruction, which counts the number of individuals known to be alive during the study based on known age, by the effective trapping area (Dice 1938, Wilson and Anderson 1985, Eberhardt and Knight 1996). Their minimum density estimates were 17.0 bears/100 km<sup>2</sup> for the more mesic Sangre de Cristo Mountains in northern New Mexico and 9.4 bears/100 km<sup>2</sup> for the more xeric Mogollon Mountains of west-central New Mexico with intermediate habitat conditions being assigned a density equal to the mean of these 2 density estimates (i.e., 13.2 bears/100 km<sup>2</sup>). Using a habitat suitability model, the NMDGF extrapolated these density estimates to similar land cover types throughout New Mexico. This extrapolation served as the basis for statewide estimates of abundance for black bears that were then incorporated into a population projection model to monitor abundance and its trend in each Bear Management Zone (BMZ).

Innovations in non-invasive genetic sampling techniques (NGS; Woods et al. 1999), coupled with robust statistical analyses such as spatially explicit capture–recapture (SECR; Efford 2004), have provided researchers with improved tools to estimate the abundance and density of carnivore populations from which harvest limits can be established. These tools have facilitated monitoring efforts and produced density estimates for black bear populations across much of their range (Stetz et al. 2014, Hooker et al. 2015, Sun et al. 2017).

Considering advances in NGS and SECR models, the NMDGF sought to update their density estimates for New Mexico black bear populations. Our objectives were to estimate the density of black bears in primary bear habitat within 7 of the 14 BMZs in New Mexico.

## STUDY AREA

The 7 BMZs were encompassed by 5 study areas located in the northern (NSC; 6,400 km<sup>2</sup>) and southern (SSC; 3,525 km<sup>2</sup>) Sangre de Cristo, Sandia (300 km<sup>2</sup>), and northern (NSacs; 925 km<sup>2</sup>) and southern (SSacs; 2,775 km<sup>2</sup>) Sacramento Mountains, New Mexico (Fig. 1). We sampled the Sandia Mountains in their entirety because of their smaller size. The 2 BMZs located in the NSC and the 2 in the SSacs are managed by NMDGF using the same estimate of density. Thus, we only report density for 5 study areas instead of 7 BMZs. Sampling within each study area was limited to primary bear habitat, which is defined as closed-canopy forest and woodland cover types (Fig. 1; Thompson et al. 1996, Costello et al. 2001). All 5 study areas



**Figure 1.** Primary American black bear habitat in New Mexico, USA highlighting the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains study areas.

were managed as multiple-use forests by federal and state agencies and private landowners encompassing portions of 4 National Forests, 6 wilderness areas, and 25 parcels of private land. The topography was diverse for each mountain range and maximum elevation was 4,011 m, 3,254 m, and 3,649 m for the Sangre de Cristo, Sandia, and Sacramento Mountains and minimum elevation was approximately 1,900 m, 1,700 m, and 1,500 m, respectively. The Southern Rocky Mountains floristic district characterized the Sangre de Cristo Mountains, whereas the Mogollon floristic district characterized the Sandia and Sacramento Mountains. Dominant vegetation types in the study areas included oak-mountain mahogany (*Quercus* spp.–*Cercocarpus* spp.) scrublands, piñon pine-juniper (*Pinus edulis*–*Juniperus* spp.) woodlands, ponderosa pine (*P. ponderosa*), white pine (*P. monticola*), Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), Engleman spruce-subalpine fir (*Picea engelmannii*–*Abies lasiocarpa*) mixed-forest, and bristlecone (*P. aristata*) and limber (*P. flexilis*) pine forests (Costello et al. 2001). Important mast-producing species included oak, piñon pine, juniper, red barberry (*Mahonia haematocarpa*), chokecherry (*Prunus virginiana*), gooseberry (*Ribes* spp.), alpine cancer-root (*Conopholis alpina*), cactus (*Opuntia* spp.), and sumac (*Rhus* spp.; Kaufmann et al. 1998, Costello et al. 2001). The average monthly temperature was highest in July across the Sangres (24–29°C), Sacramentos (22–29°C) and Sandias (33°C), and lowest in January across the Sangres

( $-15^{\circ}\text{C}$  to  $-8^{\circ}\text{C}$ ), Sacramentos ( $-7^{\circ}\text{C}$  to  $-5^{\circ}\text{C}$ ), and Sandias ( $-5^{\circ}\text{C}$ ; Western Regional Climate Center 2017). The average monthly precipitation was highest during the monsoon season (Jul–Oct) with rainfall peaking in August across the Sangres (7.10–8.15 cm), Sacramentos (7.62–12.70 cm), and Sandias (5.3 cm; Western Regional Climate Center 2017). Other common predators in the study areas included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and common ungulates included elk, mule-deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and exotic barbary sheep (*Ammotragus lervia*).

## METHODS

### Field Sampling and Genetic Analysis

We used hair traps (Woods et al. 1999) and bear rubs (Kendall et al. 2008) concurrently to sample each black bear population. We set hair traps and bear rubs across 4 sampling occasions in the NSC (22 Apr–5 Sep 2012) and SSC (29 Apr–9 Sep 2013) and across 6 sampling occasions in the Sandias, NSacs, and SSacs (5 May–6 Aug 2014). Because of logistical constraints, sampling occasions in the NSC and SSC lasted 4 weeks, whereas sampling occasions for the Sandias, NSacs, and SSacs were 2 weeks. We distributed a grid of 5-km  $\times$  5-km cells across the landscape with a randomly determined origin. Within each cell, we set a single hair trap. We located trap sites based on suspected travel routes, occurrence of seasonal forage (e.g., newly emergent green grass and ripe soft and hard mast), and presence of bear sign (Fig. 2; Figs. S1 and S2, available online in Supporting Information). A hair trap consisted of a single strand of barbed wire wrapped around  $\geq 3$  trees at a height of 45 cm, with a lure pile constructed from woody debris at the center (Woods et al. 1999). During each sampling occasion in the NSC and SSC, we randomly selected and applied 1 of 4 non-consumable lures (cow blood and fish emulsion mixture, anise oil, fatty acid scent tablet, or skunk tincture and lanolin mixture) to the lure pile to attract bears. A chi-square test of independence showed that the 4 lures were not collecting similar proportions of hair samples ( $\chi^2_3 = 616.29$ ,  $P \leq 0.001$ ); thus, we discontinued the use of anise oil and fatty acid scent tablets in the Sandia and Sacramento Mountains. A sample consisted of all hair caught in one barb. Bears will also roll around in the lure pile depositing hair. We used our best judgement to define hair samples in the lure pile that we believed originated from a single individual. We deposited each hair sample in a separate paper coin envelope and incinerated any remaining hair with a propane torch to prevent false recaptures. We moved hair traps (100 m to 2.5 km) each occasion to increase novelty and recapture rates (Boulanger and McLellan 2001, Boulanger et al. 2004).

Bears rub on a myriad of objects including trees and power poles (Burst and Pelton 1983, Kendall et al. 2008). We opportunistically identified and collected hair from bear rubs along trails used en route to hair traps. We identified bear rubs using evidence of rubbing behavior such as a smoothed

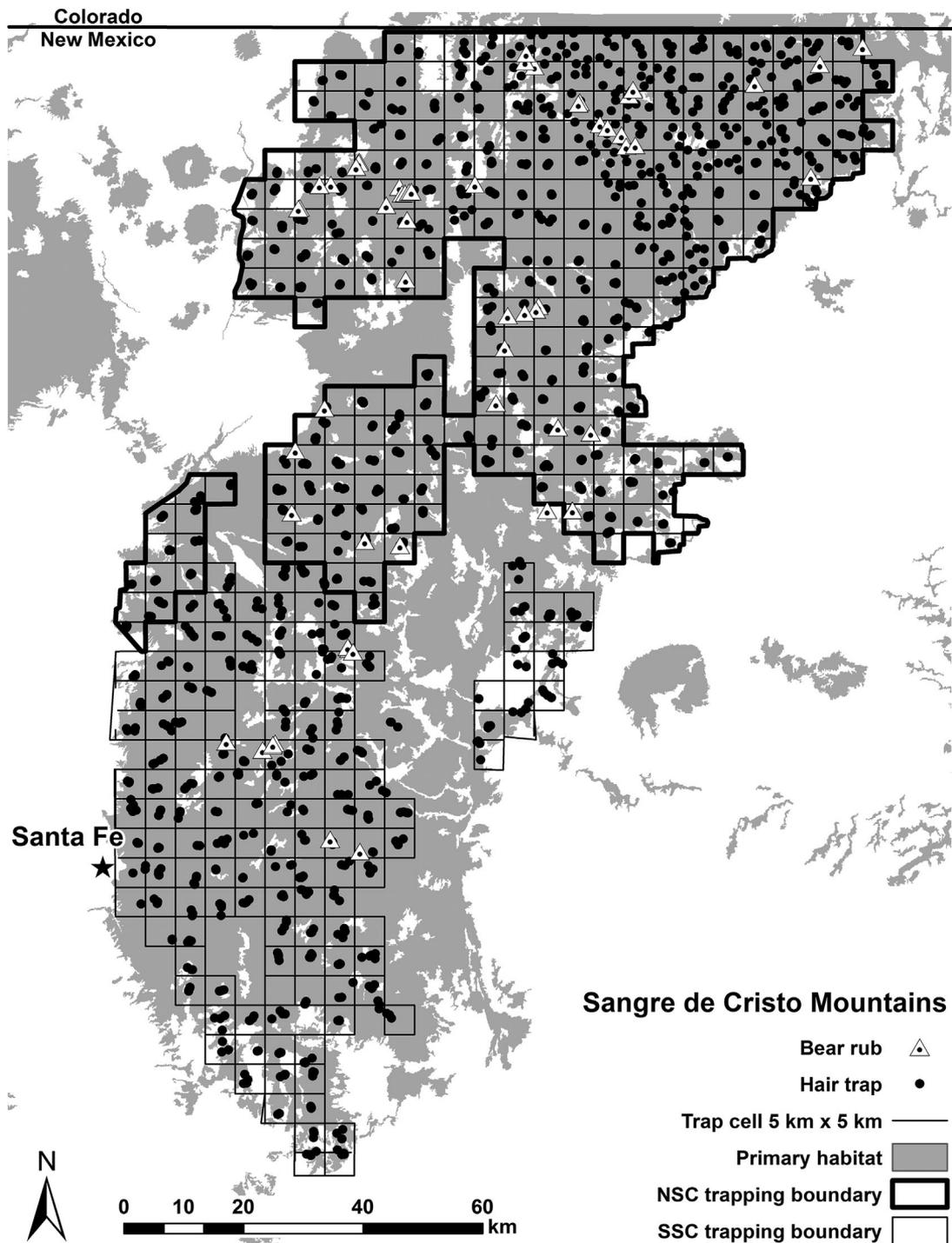
surface with snagged hair. We attached 3 to 4 short, vertical strands of barbed wire to the rub object covering the area of rubbing to collect discrete hair samples (Kendall et al. 2008, 2009; Stetz et al. 2014). We identified rubs at varying time intervals across sampling occasions, but once established we monitored them concurrently with nearby hair traps. We collected hair samples only from the barbed wire to ensure that the samples collected were from individuals that visited the rub during the sampling occasion. Hair collection protocols for bear rubs were identical to hair traps, and we stored all hair samples in an airtight container on silica desiccant at room temperature.

We genotyped each hair sample using 8 polymorphic microsatellite loci (G1D, G10B, G10L, G10M, G10H, G10J, G10U, MU59; Paetkau et al. 1995, 1998; Taberlet et al. 1997). We also used the ZFX-ZFY marker to identify sex (Durnin et al. 2007). We selected specific markers for individual identification by ensuring that the mean expected heterozygosity for each marker was between 0.70 and 0.80 (Paetkau 2003, 2004). These markers were determined from an initial subsample from the NSC population in 2012. All hair samples were genotyped by Wildlife Genetics International in Nelson, British Columbia, Canada (WGI; Paetkau 2003, Kendall et al. 2009).

Technicians screened samples for suitability before analysis. First, they eliminated samples that contained insufficient genetic material for analysis (no root,  $< 1$  guard hair, or  $< 5$  underfur hairs) or appeared to be from heterospecifics. Next, they used the ZFX-ZFY marker as a prescreen to remove low-quality hair samples that were likely to fail during the multilocus genotyping phase. After the prescreen, technicians amplified the 9-candidate markers for each sample. They eliminated samples that amplified  $\geq 3$  alleles at 1 marker (indication of a mixed sample) or failed to amplify  $\geq 3$  loci. They reamplified the samples that failed at  $< 3$  loci, resulting in either a full 9-locus genotype or a discarded sample. They examined pairs of samples that were mismatched at 1 or 2 markers for evidence of amplification or human error. Technicians reamplified any mismatched pair under the assumption that genotyping error may have created the similarity between the 2 samples (Paetkau 2003). If 1 or 2 mismatched pairs remained between samples, we concluded the 2 samples were from separate individuals. We assigned an individual identification number to each sample with a unique multilocus genotype based upon the unique catalogue code from the first sample to identify the individual's genotype. Given each study area is not an isolated population, we calculated the expected and observed heterozygosity for each mountain range using program GENEPOP (Raymond and Rousset 1995, Rousset 2008; www.genepop.curtin.edu.au, accessed 15 Mar 2016).

### Density Estimation

We used SECR models (Efford 2004, Borchers and Efford 2008) implemented in the R software package secr (v. 2.9.5 and 2.10.4; Efford 2015, 2016) to estimate 3 parameters in separate analyses for each study area: density (D), detection probability of an individual at its activity center ( $g_0$ ), and the



**Figure 2.** Primary American black bear habitat identified by Costello et al. (2001) overlaid with hair traps and bear rubs set for the northern (NSC) and southern (SSC) Sangre de Cristo Mountains, New Mexico, USA, 2012–2013.

spatial scale over which detection probability declines as the distance between an individual's activity center to the detection device increases ( $\sigma$ ). We used a half-normal detection function for our observation model and a homogeneous Poisson distribution as our state model, which assumes latent activity centers are distributed evenly across the landscape (Efford et al. 2009). Spatially explicit capture–recapture also requires a habitat mask.

The habitat mask is the area of integration (i.e., area of interest that contains all possible latent activity center locations) and includes all animals with a non-zero probability of detection (Ivan et al. 2013). Individuals may reside beyond the habitat mask, but they have a negligible probability of detection (Borchers and Efford 2008, Royle et al. 2014). We generated the habitat mask by buffering the sampling detectors in the NSC, SSC, Sandias, NSacs, and SSacs by 18.75 km,

25.40 km, 13.23 km, 14.84 km, and 11.03 km, respectively, which we derived from the capture data using the suggest. buffer function (Efford 2016). Within our habitat mask, we limited our density estimates to primary habitat as identified by Costello et al. (2001) for black bears in New Mexico. Variability in sampling effort may negatively bias density estimates and reduce the ability to explain variation in detection probability, so we accounted for variable sampling effort by using the number of days each sampling detector was active (Efford et al. 2013).

Predictors of  $g_0$  and  $\sigma$  included time ( $t$ ; 4 or 6 sampling occasions depending on the study area), sex, elevation (elev), detector type (type; hair trap vs. bear rub), and 5 land cover categories (cover). We chose time and sex as covariates because detection probability and movement patterns may fluctuate over the sampling period and differ between males and females (Sawaya et al. 2012, Stetz et al. 2014). We selected elevation and land cover to represent the spatial heterogeneity of black bear food resources because this heterogeneity could influence  $g_0$  and  $\sigma$  depending on food availability and distribution (Rovang et al. 2015). We did not include land cover type and elevation in the same model because a box plot of elevation by land cover type revealed that these variables were not independent. We then conducted a 1-way analysis of variance that indicated within each study area elevation significantly differed among land cover types (NSC:  $F_4 = 618.02$ ,  $P \leq 0.001$ ; SSC:  $F_4 = 367.14$ ,  $P \leq 0.001$ ; Sandias:  $F_1 = 7.39$ ,  $P = 0.008$ ; NSacs:  $F_2 = 278.06$ ,  $P \leq 0.001$ ; SSacs:  $F_2 = 582.95$ ,  $P \leq 0.001$ ). Within each study area, *post hoc* pairwise comparisons of elevation across land cover types were also significant (Tukey-Kramer test,  $P \leq 0.01$  for all comparisons). We extracted elevation for each detector using the National Elevation Dataset 30-m resolution digital elevation model ([www.nationalmap.gov](http://www.nationalmap.gov), accessed 10 May 2015). We standardized elevation by subtracting the mean from each observation and dividing by 1 standard deviation (Gelman and Hill 2007).

We extracted land cover using the Interagency Landfire Project (Rollins 2009; [www.landfire.gov](http://www.landfire.gov), accessed 10 May 2015) land cover classification at 30-m spatial resolution. We combined 6 land cover classifications into 5 categories: aspen-conifer, mixed conifer (combination of Douglas fir and white pine), piñon pine-juniper, ponderosa pine, and spruce-fir. Variation in the abundance and distribution of each land cover class across the study areas resulted in a different number of categories and, consequently, a different number of parameters modeled for each study area. Aspen-conifer and spruce-fir were included only in the NSC and SSC. Mixed-conifer was included in all study areas except the Sandia Mountains. Piñon pine-juniper and ponderosa pine were included in all study areas. We visually assessed and assigned the dominant land cover classification surrounding the location of each detector using ArcGIS 10.2.1 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA).

We modeled  $g_0$  and  $\sigma$  concurrently by fitting a model where both parameters varied by elevation, land cover, or

time. We also included models that varied by time for  $g_0$  and land cover for  $\sigma$  ( $g_0 \sim t$ ,  $\sigma \sim \text{cover}$ ), time for  $g_0$  and elevation for  $\sigma$  ( $g_0 \sim t$ ,  $\sigma \sim \text{elev}$ ), land cover for  $g_0$  and time for  $\sigma$  ( $g_0 \sim \text{cover}$ ,  $\sigma \sim t$ ), and elevation for  $g_0$  and time for  $\sigma$  ( $g_0 \sim \text{elev}$ ,  $\sigma \sim t$ ). We also constructed models for  $g_0$  and  $\sigma$  with time in an additive relationship with each covariate ( $g_0 \sim t + \text{covariate}$ ,  $\sigma \sim t + \text{covariate}$ ). We included additive effects because  $g_0$  and  $\sigma$  are likely to vary because the black bear mating season occurs during the late-spring and early summer, when male bears might be expected to move more than females; because hyperphagic foraging behavior occurs during early fall, when all bears move more to find food; and because the distribution of food varies across the period when bears are active (e.g., grasses green-up in the spring and mast ripens in the late summer and fall). We also ran each model with the addition of an animal by site learned response (bk) for  $g_0$  ( $g_0 \sim \text{covariate}(s) + \text{bk}$ ) because density estimates can be severely biased when a behavioral response occurs in the presence of missing data (e.g., hair samples that failed to amplify a complete genotype; Augustine et al. 2014). However, we believe we mitigated a behavioral response by moving hair traps and randomly applying lures between sampling occasions, and Murphy et al. (2016) reported negligible bias to SECR-based density estimates in such a scenario. Thus, our inclusion of the bk parameter was a precautionary measure.

We modeled density as a function of sex to investigate for an uneven sex ratio (Tredick and Vaughan 2009, Sun et al. 2017). We did so by selecting the top ranked model from each study area and comparing that model to another with the same detection submodel but with density as a function of sex. We did not use land cover type or elevation as predictors of density because black bears track the spatiotemporal variability of food resources resulting in a fluid use of the landscape (Costello and Sage 1994, Sun et al. 2017). Also, because the New Mexico black bear hunting season occurs from mid-August to November, the seasonal distribution of black bears may change from summer to fall. Consequently, fall harvest regulations based on the variation in density of black bears across land cover types during the summer would be inappropriate. This enabled us to estimate density in a way that would be most conducive to the current management system employed by the NMDGF, which was a single density estimate for each study area given the large extent and heterogeneous landscape encompassed by the BMZs.

We could not fit 4 models for the NSC because the computer we used for analysis was unable to allocate enough memory to initialize all models. The 4 models were when  $g_0$  and  $\sigma$  were modeled concurrently with elevation (i.e.,  $g_0 \sim \text{elev}$ ,  $\sigma \sim \text{elev}$ ), concurrently with time and elevation (i.e.,  $g_0 \sim t + \text{elev}$ ,  $\sigma \sim t + \text{elev}$ ), and with time and elevation for different parameters (i.e., either  $g_0 \sim t$ ,  $\sigma \sim \text{elev}$  or  $g_0 \sim \text{elev}$ ,  $\sigma \sim t$ ). We also excluded detector type in our model set for the NSacs because only 1 bear rub was set in the study area. We used Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>) to rank our model sets (Akaike 1973, Hurvich and Tsai 1989). When the top model received

<0.90 of the model weight we model averaged the estimates of the model parameters across all models to account for model selection uncertainty (Burnham and Anderson 2002). We assessed the strength of evidence (SOE) for variables in the top model by calculating the likelihood that the beta coefficient was not 0 (i.e., evidence ratios for the beta coefficients):

$$\frac{\mathbb{E}(\widehat{\beta\{i\}})}{\mathbb{E}(0)} = \exp\left(\left\{\frac{\widehat{\beta(i)}}{SE(\widehat{\beta(i)})}\right\}^2\right),$$

where  $\widehat{\beta(i)}$  is the beta coefficient for variable  $i$  and  $SE(\widehat{\beta(i)})$  is the standard error of the beta coefficient for variable  $i$  (Burnham 2015).

We obtained permits under the Convention on International Trade in Endangered Species (Export Permits 12US86417A/9, 13US19950B/9, and 14US43944B/9) to export samples to Canada for analysis. Our research was authorized by the NMDGF (Taking Protected Wildlife for Scientific and or Education Purposes Permit 3504) and approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol number 2011-027).

## RESULTS

### Field Sampling and Genetic Analysis

We set 557 hair traps that were open for 57,010 trap days and we collected 3,825 hair samples. In addition, we identified and sampled 112 bear rubs, which yielded 258 hair samples over 7,007 trap days (Fig. 2; Figs. S1 and S2; Table S1). Sampling effort varied across study areas and was dependent on the number of detectors set, the length of a sampling occasion (4 weeks vs. 2 weeks), and accessibility due to weather and wildfire. The number of hair samples collected during an occasion increased over the course of the summer and decreased toward the conclusion of sampling with peak collection during June and July.

The mean observed heterozygosity was 0.73, 0.73, and 0.68 for the Sangre de Cristo, Sandia, and Sacramento

Mountains, respectively. Of the 4,083 total hair samples collected, we eliminated 26.08% because of insufficient genetic material, 1.49% because of heterospecific contamination, and 0.17% because the samples contained DNA from >1 individual. We generated a full 9-locus genotype from 49.56% of the 2,950 remaining hair samples from which we identified 726 (368 males: 358 females) individuals (Table S1). The number of individuals that were mismatched at 1 or 2 markers was low with only 3 observed 1-mismatched pairs and 8 observed 2-mismatched pairs across all samples. Genotyping success varied across study areas (44–61%), but overall, success rates were lower than the 75% success rate observed in similar studies (D. Paetkau, Wildlife Genetics International, personal communication). When we shortened the length of the sampling occasion from 4 weeks (NSC and SSC) to 2 weeks (Sandias, NSacs, and SSacs), the percentage of successful genotypes increased by only 4%.

### Density Estimation

We detected the majority (61–85%) of individuals in each study area only once with a similar number of repeat detections for males and females (Table 1). The number of unique individuals detected during each occasion for the NSC, NSacs, and SSacs increased over the course of sampling, peaking mid-summer, and subsequently decreasing toward the end of summer; this pattern was similar to the number of hair samples collected per sampling occasion. The number of unique individuals detected increased each occasion for the Sandias and SSC. Mean maximum recapture distance for males in a single year of sampling ranged from 4.23 km to 12.46 km with a maximum distance of 52 km by 1 individual in the NSC. Mean maximum recapture distance for females in a single year of sampling ranged from 0.38 km to 4.59 km with a maximum distance of 47 km by 1 individual, also in the NSC (Table 1). Three individuals were detected in 2 study areas in successive years. We detected 2 males in the NSC in 2012 and then again in the SSC in 2013; we detected 1 female in the SSC in 2013 and 90 km away in the Sandia Mountains in 2014.

**Table 1.** A summary of the capture history data for American black bears identified by hair samples collected across the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014.

	Males								Females							
	<i>N</i> <sup>a</sup>	Det <sup>b</sup>	Avg <sup>c</sup>	SD <sup>d</sup>	Max <sup>e</sup>	R <sup>f</sup>	MMR (km) <sup>g</sup>	MaxD (km) <sup>h</sup>	<i>N</i> <sup>a</sup>	Det <sup>b</sup>	Avg <sup>c</sup>	SD <sup>d</sup>	Max <sup>e</sup>	R <sup>f</sup>	MMR (km) <sup>g</sup>	MaxD (km) <sup>h</sup>
NSC	190	239	1.26	0.43	3	33	7.57	52.03	189	216	1.14	0.35	3	23	3.98	47.41
SSC	67	80	1.19	0.38	3	8	12.46	29.33	64	77	1.20	0.39	2	12	2.53	20.33
Sandias	9	15	1.67	0.46	2	3	8.27	9.84	9	14	1.56	0.73	3	4	0.38	0.69
NSacs	49	74	1.51	0.74	5	14	9.22	36.18	39	58	1.49	0.72	3	12	2.47	7.05
SSacs	53	69	1.30	0.41	3	10	4.23	8.02	57	73	1.28	0.54	3	11	4.59	14.88
Total	368	477	1.39	0.48	5	68	8.35	27.08	358	438	1.33	0.55	3	62	2.79	18.07

<sup>a</sup> Number of animals detected.

<sup>b</sup> Number of detections across all sampling occasions.

<sup>c</sup> Average number of detections per individual detected across all sampling occasions.

<sup>d</sup> Standard deviation for the average number of detections.

<sup>e</sup> Maximum number of detections of a single individual across all sampling occasions.

<sup>f</sup> Number of recaptured individuals across all sampling occasions.

<sup>g</sup> Mean maximum recapture distance.

<sup>h</sup> Maximum distance moved by an individual.

**Table 2.** The top *a priori* spatially explicit capture–recapture models that accounted for the total model weight ( $w_i$ ) for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014, derived using Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ ). Models were ranked by the difference in  $AIC_c$  score ( $\Delta AIC_c$ ) between the top-ranked model and competing models were evaluated using changes in model deviance.

Study area	$g_0^a$	$\sigma^a$	$K^b$	$AIC_c$	$\Delta AIC_c$	$w_i$	Deviance <sup>c</sup>
NSC	t + cover	t + cover	17	3,149.15	0.00	1.00	3,113.5
SSC	t + elev	t + elev	11	1,169.98	0.00	0.87	1,145.8
	t + cover	t + cover	17	1,173.85	3.87	0.13	1,134.4
Sandias	sex	sex	5	209.23	0.00	0.96	194.23
	constant	constant	3	216.23	6.99	0.03	208.51
	elev	elev	5	219.20	9.97	0.01	204.20
NSacs	t + cover	t + cover	17	868.31	0.00	0.96	825.57
	cover	t + cover	10	874.86	6.55	0.04	852.01
SSacs	cover	cover	7	1,168.68	0.00	0.50	1,153.58
	t + cover	t + cover	17	1,169.62	0.94	0.31	1,128.97
	t + elev	t + elev	15	1,170.58	1.90	0.19	1,135.47

<sup>a</sup> Detection probability at the activity center ( $g_0$ ) and the spatial scale over which  $g_0$  declines ( $\sigma$ ) a function of elevation (elev), sex, time variation (t), or land cover type (cover); + = additive effect; constant = no variation. Density was held constant for all models listed.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Model deviance =  $-2(\log\text{-likelihood})$ .

None of the top models included an animal by site learned response; however, the parameter structure of the top model with the addition of bk was the second ranked model in each study area except for the SSacs, where the behavioral model was third (Tables S2–S6). Although models that included bk reduced the deviance and appeared competitive in the model set, the deviances were nearly identical to the top model, so the extra parameter failed to substantially improve model fit. As a result, the support for bk models was likely a result of an identical model structure to the well-supported top models (Arnold 2010). Therefore, we removed all models that included bk from our model sets, and we report only on the reduced model sets hereafter.

There was little model selection uncertainty in each study area except in the SSacs with the top model garnering 50% of the total model weight (Table 2; Tables S7–S11). Detection probability ( $g_0$ ) was highest for the Sandias ( $g_0 = 0.029$  and  $0.0017$  for females and males, respectively), but overall,  $g_0$  was low across all study areas (Table 3). The land cover type or elevation at which the detector was deployed were helpful covariates in explaining heterogeneity in both  $g_0$  and  $\sigma$  for all

study areas except for the Sandias, which included sex as the only important explanatory variable (Table 2; Tables S7–S11). Models allowing  $g_0$  to vary over time were supported because  $g_0$  was low in early summer, increased as the summer progressed, and then decreased in late summer except in the SSC where  $g_0$  increased in each occasion. Detection probability increased as elevation increased in the SSC with  $\sigma$  exhibiting an inverse relationship. The SOE that the effect of elevation was not 0 was high for both  $g_0$  and  $\sigma$  (Table A1). In the Sandias, males showed a lower detection probability ( $g_0$ ) and higher movement rate ( $\sigma$ ) than female black bears, and the SOE that the effect of sex on both parameters was not 0 was high (Table A1). The influence of land cover on  $g_0$  and  $\sigma$  across the NSC, NSacs, and SSacs was variable. The most consistent relationship was that  $g_0$  was lower and  $\sigma$  was higher within the piñon pine–juniper land cover type with aspen–conifer (NSC) and mixed conifer (NSacs and SSacs) land cover types as reference categories, respectively (Table A1). The SOE that the effect of land cover type was not 0 was high for all parameter–study area combinations except for  $\sigma$  in the NSacs. The effect of the

**Table 3.** Estimated abundance ( $\hat{N}$ ) and density ( $\hat{D}$ ; bears/100 km<sup>2</sup>), coefficient of variation of the density estimate ( $CV[\hat{D}]$ ), detection probability at the activity center ( $g_0$ ), spatial scale over which detection probability declines ( $\sigma$ ; km), and their 95% confidence intervals for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014. We model averaged  $\hat{N}$  and  $\hat{D}$  for the SSC and SSacs using models with model weights  $> 0.00$  and for the NSacs using the top-ranked model with density held constant and varying by sex.

Study area <sup>a</sup>	$\hat{N}$ (95% CI)	$\hat{D}$ (95% CI)	$CV(\hat{D})$	$\hat{g}_0$ (95% CI)	$\hat{\sigma}$ (95% CI)
NSC	1,249.5 (1,019–1,532.1)	21.9 (17.8–26.8)	0.10	0.00060 (0.00023–0.0015)	3.31 (2.09–5.25)
SSC	646.8 (444.3–941.6)	19.7 (13.8–28.3)	0.19	0.000018 (0.0000061–0.000052)	18.12 (12.38–26.53)
Sandias	43.3 (22.2–84.2)	25.7 (13.2–50.1)	0.35	0.029 <sup>b</sup> (0.015–0.078)	0.76 <sup>b</sup> (0.49–1.15)
				0.0016 <sup>c</sup> (0.00048–0.0055)	4.99 <sup>c</sup> (2.47–10.10)
NSacs	77.5 <sup>b</sup> (56.2–107.1)	10.0 <sup>b</sup> (7.2–13.9)	0.17	0.0027 (0.00058–0.012)	5.42 (2.03–14.44)
	85.8 <sup>c</sup> (62.8–117.3)	11.0 <sup>c</sup> (7.8–15.5)	0.18		
SSacs	412.3 (293.2–579.8)	16.5 (11.6–23.5)	0.18	0.0032 (0.0011–0.0093)	2.67 (1.69–4.21)

<sup>a</sup> Primary bear habitat: NSC = 5,716 km<sup>2</sup>; SSC = 2,944 km<sup>2</sup>; Sandias = 168 km<sup>2</sup>; NSacs = 776 km<sup>2</sup>; SSacs = 2,488 km<sup>2</sup>.

<sup>b</sup> Parameter estimate for female black bears.

<sup>c</sup> Parameter estimate for male black bears.

ponderosa pine cover type on both  $g_0$  and  $\sigma$  was negligible relative to aspen-conifer and mixed conifer (Table A1). In the NSC, spruce-fir and mixed conifer showed a negative relationship with  $g_0$  and a positive relationship with  $\sigma$  relative to aspen-conifer (Table A1).

There was marginal support that density varied by sex in the NSacs ( $\Delta AIC_c = 0.87$ ;  $w_i = 0.61$  for the top model) and no support in all other study areas ( $w_i \geq 0.75$  for the top models holding density constant; Table S12). Mean density estimates varied within and between mountain ranges (range = 16.6–25.3 bears/100 km<sup>2</sup>; Table 3) as did estimates of abundance given the different sizes of the study areas (range = 43.3–1,249.5 bears; Table 3).

## DISCUSSION

By employing NGS with SECR models, we provided density estimates that will aid in setting harvest limits and serve as a benchmark for comparison with future research for multiple black bear populations in New Mexico. Our density estimates were similar to (SSacs) or higher (NSC, SSC, Sandias, and NSacs) than the previous estimates used by NMDGF to manage these populations (Costello et al. 2001). The differences in our estimates of density from those of Costello et al. (2001) are most likely due to differences in analytical techniques (the previous method did not account for imperfect detection) and we speculate due to potential changes in black bear population dynamics over the past decade. It should be noted, however, that the 95% confidence intervals surrounding our estimates typically encompassed those of Costello et al. (2001).

There is strong evidence that piñon pine-juniper land cover is associated with lower detection rates and increased movement rates, whereas an increase in elevation has the opposite association (Table A1). Like other ursid NGS studies, estimates of detection probability and movement rate varied over time and by sex in our study (Kendall et al. 2009, Sawaya et al. 2012, Stetz et al. 2014). For example, detection probabilities were lower and movement rates were higher during early and late summer, and males, in general, had higher movement rates than females. Detection probabilities also differed between the sexes in the Sandias (Table 3).

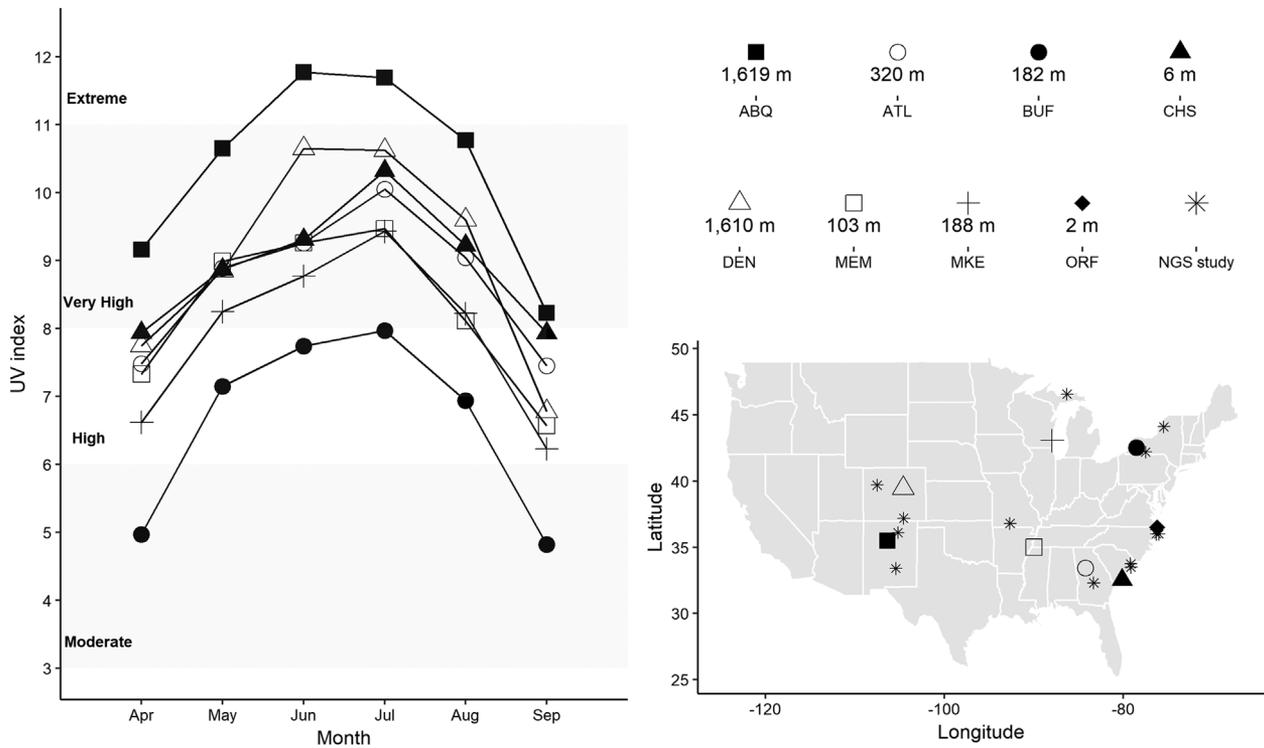
The importance of a temporal effect on  $g_0$  and  $\sigma$  in the NSC, SSC, NSacs, and SSacs is likely a result of seasonal mating and foraging behaviors (Alt et al. 1980, Garshelis and Pelton 1981, Costello et al. 2003). During the breeding season, males increase movement rates as they traverse their home range searching for receptive females (Young and Ruff 1982, Costello 2008, Lewis and Rachlow 2011). In fall, bear home range size and distance between sequentially recorded movements increases as bears travel outside their core area to exploit the spatially and temporally variable oak mast (Ostfeld et al. 1996, Costello 2008), which is an important food source that was previously shown to be correlated with black bear reproductive output in New Mexico (Costello et al. 2003). These behavioral differences during mating season and hyperphagia would increase movement rates and enlarge home range size, thereby reducing  $g_0$  while

increasing  $\sigma$  because of the compensatory relationship between the 2 parameters (Efford and Mowat 2014).

The influence of land cover and elevation on  $g_0$  and  $\sigma$  is also likely a function of black bears responding to spatiotemporal changes in food abundance (Costello and Sage 1994, Mazur et al. 2013, McCall et al. 2013). During spring, or the pre-mast season, grasses, forbs, and ants dominate bear diets (den emergence to mid-Jul; Costello et al. 2001). Diets then shift toward soft mast species such as berries in the late summer and early fall (56% of scat volume, mid-Jul to mid-Sep), with fall (mid-Sep through Oct, den immergence) diets dominated by acorns (87% of scat volume) and supplemented with juniper berries (Costello et al. 2001, Guntley 2016). Mid-elevation land cover types (i.e., mixed conifer) are more likely to contain a higher abundance of grasses and forbs because of earlier snowmelt compared to higher elevations and higher levels of precipitation compared to lower elevations (Zlotin and Parmenter 2008). As snow melts, the availability of grasses and forbs increases with soft mast ripening with the arrival of summer rains. Once hard mast species begin to ripen in late August (Zlotin and Parmenter 2008), black bears shift their attention toward land cover types containing those species (Costello and Sage 1994, Onorato et al. 2003). Thus, the availability of grasses and soft mast at mid- to high- elevations and the scarcity of food in the low elevation piñon pine-juniper cover type during summer (Zlotin and Parmenter 2008) may explain the negative relationship with  $g_0$  and the positive relationship with  $\sigma$  for piñon pine-juniper and low elevations for all study areas except the Sandias (Table A1). Black bears are also predators of elk calves in portions of New Mexico and they may move toward calving grounds in spring, which are commonly found at higher elevations (Quintana 2016).

Half of our samples that met our quality threshold failed to produce a reliable genotype, which reduced the number of unique individuals identified and the number of recaptures. The lack of data also likely contributed to the low detection probabilities and affected our ability to estimate  $\sigma$  precisely (Efford et al. 2004, Sollmann et al. 2012, Sun et al. 2014). However, simulation has shown that SECR models provide relatively robust estimates of density under data dilution scenarios (Mollet et al. 2015). The relatively more precise NSC density estimate, despite a low  $g_0$ , may be a result of a greater number of unique individuals and recaptures, which provided sufficient data for the model to predict unobserved movement distances (Table 1; Sollmann et al. 2012, Sun et al. 2014). Whereas  $g_0$  was the highest for the Sandias, the density estimate was the least precise. This relatively low level of precision was most likely caused by the few individuals detected ( $n = 18$ ) and a low number of spatial recaptures, which may have contributed to poor estimates of  $\sigma$  and an inability to predict unobserved movement distances (Sollmann et al. 2012). The low sample size and few recaptures is further evident in the simple structure of the top models and the high coefficient of variation for the estimate of density (Tables 2 and 3).

We suspect that for all study areas, intense ultraviolet (UV) radiation coupled with extended sampling intervals were the



**Figure 3.** Mean monthly ultraviolet radiation (UV) index generated by the National Oceanic and Atmospheric Administration showing estimated noontime intensity of UV radiation coupled with the World Health Organization human health hazard UV index classification for Albuquerque, New Mexico (ABQ); Atlanta, Georgia (ATL); Buffalo, New York (BUF); Charleston, South Carolina (CHS); Denver, Colorado (DEN); Memphis, Tennessee (MEM); Milwaukee, Wisconsin (MKE); and Norfolk, Virginia (ORF), USA, 2012 (left) along with a map showing the aforementioned cities and the non-invasive genetic sampling studies conducted on American black bears in the United States that used a spatially explicit capture–recapture framework (bottom right) and their elevations (top right).

**Table 4.** Mean density estimates ( $\hat{D}$ ) for American black bears (bears/100 km<sup>2</sup>), 95% confidence intervals, and the proportion of hair samples successfully genotyped for noninvasive genetic sampling studies conducted in the United States that used a spatially explicit capture–recapture framework.

Study area	State	$\hat{D}$	95% CI	Genotyping success	Reference
Ozark Highlands	MO	1.70	1.10–2.40	0.70	Wilton et al. 2014 <sup>a</sup>
Carver Bay	SC	4.60	2.40–6.70	0.90 <sup>b</sup>	Drewry et al. 2013
Picture Rocks National Lakeshore	MI	10.56	8.59–12.79	0.91	Sollmann et al. 2012 <sup>c,d</sup>
Glacier National Park	MT	12.00	10.00–14.40	0.72	Stetz et al. 2014 <sup>d,e</sup>
Southern Black Bear Range	NY	11.20 <sup>f</sup>	1.50–77.80 <sup>g</sup>	0.89	Sun et al. 2017 <sup>a</sup>
Southern Sacramento Mountains	NM	16.55	11.64–23.53	0.44	This study
Southern Sangre de Cristo Mountains	NM	19.74	13.77–28.30	0.48	This study
Fort Drum Military Installation	NY	20.00	15.00–26.00	0.89	Gardner et al. 2010 <sup>c</sup>
Northern Sacramento Mountains	NM	20.17	15.35–26.52	0.61	This study
Durango	CO	21.00–38.00	16.00–55.00	0.75 <sup>b</sup>	Apker et al. 2016
Spanish Peaks	CO	21.00–44.00	16.00–57.00	0.73 <sup>b</sup>	Apker et al. 2016
Northern Sangre de Cristo Mountains	NM	21.86	17.83–26.80	0.49	This study
Central Georgia Population	GA	23.20–24.00	15.95–30.45	0.87 <sup>b</sup>	Hooker et al. 2015 <sup>d</sup>
Sandia Mountains	NM	25.75	13.22–50.14	0.53	This study
Kentucky–Virginia Border	KY, VA	26.00	18.00–37.00	0.45 <sup>b</sup>	Murphy et al. 2016
Greenhorn Mountain	CO	26.00–33.00	19.00–43.00	0.74 <sup>b</sup>	Apker et al. 2016
Piedra	CO	32.00–60.00	25.00–82.00	0.72 <sup>b</sup>	Apker et al. 2016
Lewis Ocean Bay	SC	33.90	22.90–44.80	0.88 <sup>b</sup>	Drewry et al. 2013
Alligator River National Wildlife Refuge	NC	37.00–46.00	30.70–66.00	0.82 <sup>b</sup>	Tredick and Vaughan 2009
Great Dismal Swamp National Wildlife Refuge	NC, VA	46.00	34.60–57.30	0.84	Tredick and Vaughan 2009
Pocosin Lakes National Wildlife Refuge	NC	58.00–77.00	49.10–88.50	0.85 <sup>b</sup>	Tredick and Vaughan 2009

<sup>a</sup> Genetic analysis not conducted by Wildlife Genetics International.

<sup>b</sup> Value averaged over multiple sampling years.

<sup>c</sup> Bayesian-based analysis.

<sup>d</sup> Analyzed hair samples were a subset of the total hair samples collected.

<sup>e</sup> Black bear population sympatric with grizzly bears (*Ursus arctos*).

<sup>f</sup> Baseline density estimate averaged across all top models.

<sup>g</sup> 85% confidence interval.

main factors explaining the poor genotyping success we observed (Stetz et al. 2015). Ultraviolet radiation causes DNA degradation by forming dimers between adjacent pyrimidine bases, instead of those bases binding with their cross-strand partners, which prevents the DNA polymerase from progressing past the dimer and results in an incomplete genotype (Jagger 1985). Factors influencing UV levels include cloud cover, elevation, latitude, shade, length of exposure, season, ozone depletion, and atmospheric turbidity (Piazena 1996, Stetz et al. 2015). For example, UV radiation increases with decreasing cloud cover, increases with elevation (9–11% per 1,000 m), and increases with decreasing latitude (Blumthaler et al. 1997). The UV radiation levels across much of New Mexico are higher than across most of the United States and are higher than other regions where NGS methods have been used to estimate bear abundance and density (Fig. 3; National Oceanic and Atmospheric Administration [NOAA] 2012). Further, we would expect UV radiation levels to be 1–26% higher in our study areas compared to those for Albuquerque, New Mexico, where the NOAA (2012) UV measurement was taken, because our study areas were at equal or higher elevations. Reducing the sampling interval should have increased genotyping success; however, when we reduced our sampling interval from 4 to 2 weeks (which is a common period used by similar NGS studies in the western United States), we observed only marginal improvement in genotyping success (4%).

In the SSC, we also lost hair samples because of 2 forest fires, the Tres Lagunas (4,135 ha) and the Jaroso (4,511 ha). These fires affected 450 km<sup>2</sup> (12.7%) of the trapping grid and prevented us from accessing and checking hair traps located near the fire, primarily during the second and third sampling occasions (3–13% of total hair traps; Fig. S3). Moreover, many of the fire-affected traps were in an area where we expected higher bear abundance. Anecdotally, these hair traps consistently yielded more hair samples post-fire than hair traps located in some areas that were unaffected by the fires. The limited access also prevented us from identifying more bear rubs across the SSC, restricting our use of multiple sampling methods and hindering our ability to minimize the impacts of capture heterogeneity present with any one survey method (Boulanger et al. 2008).

Despite UV radiation and sampling difficulties, our density estimates had levels of precision comparable to those obtained in other black bear studies conducted across the United States that used NGS and a SECR estimator (Table 4). The level of precision we achieved may have been a consequence of the large extent of our study areas, which may have allowed us to detect a large proportion of the population within each mountain range even though we failed to amplify approximately half of our samples. Our density estimates fell within the middle range of NGS and SECR-based black bear density studies (Table 4). Black bear density was highest on the east coast in pocosin, which is characterized by high food production and cover, low human disturbance, and agricultural food resources mixed throughout (Tredick and Vaughan 2009, Drewry et al. 2013). Eastern populations inhabiting pine plantations were at densities comparable to

New Mexico populations likely because pine plantations had limited food, insufficient cover, and fewer agricultural food resources as compared to pocosin (Tredick and Vaughan 2009, Drewry et al. 2013, Hooker et al. 2015). Locally, our estimates are similar to or lower than those in southern Colorado, USA, and similar to or higher than those in northern Colorado (Table 4); however, estimates for southern Colorado fluctuated substantially within each study area and over multiple years. Populations with densities lower than ours were expanding their range (Sun et al. 2017), recolonizing (Wilton et al. 2014), residing in habitat with low food resources (Drewry et al. 2013), or were sympatric with grizzly bears (*Ursus arctos*; Stetz et al. 2014).

We provided updated density estimates for an important game species in New Mexico. Our estimates add to a growing number of studies that have used NGS coupled with SECR models to estimate the density of black bear populations across the United States. Our data suggest that the detection probability of black bears is likely influenced by the abundance and distribution of food resources on the landscape, which in turn, may be influenced by land cover type and elevation. Furthermore, UV radiation levels in New Mexico appear to be higher than elsewhere in the contiguous United States and are also most likely responsible for our low rate of genotyping success, a rate comparable to those in the high Arctic of North America (Dumond et al. 2015).

## MANAGEMENT IMPLICATIONS

Our estimates of density will assist the New Mexico Department of Game and Fish in setting sustainable harvest limits for multiple populations of black bears in New Mexico. We suggest that researchers using hair samples to monitor wildlife populations incorporate a pilot study to evaluate the effects of UV degradation, among other factors, on genotyping success. To help reduce UV exposure, researchers could set detectors in more shaded areas (e.g., north facing slopes), set fewer detectors so that they can be checked more frequently, or increase the number of personnel used to check detectors. We believe more personnel is preferable to fewer detectors because it allows for a larger study area, a denser trapping array, or alternative trapping configurations to be sampled. A larger study area will help mitigate the effects that seasonal movement patterns can have on parameter estimates, particularly in areas with highly variable food resources, and provide density estimates at the spatial scale at which many agencies make management decisions.

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## **SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher's website.

## APPENDIX A. Relationship and effect of covariates on spatially explicit capture–recapture model parameters.

**Table A1.** The beta coefficient (Beta), standard error (SE), and lower (LCL) and upper (UCL) 95% confidence intervals for covariate variables from the top ranked spatially explicit capture–recapture model for American black bears in the northern (NSC) and southern (SSC) Sangre de Cristo, Sandia, and northern (NSacs) and southern (SSacs) Sacramento Mountains, New Mexico, USA, 2012–2014. Included is the strength of evidence (SOE) of the likelihood that the beta coefficient is not 0 where larger values indicate a greater SOE that the effect of the variable is not 0. The reference categories for land cover type were aspen-conifer (NSC) and mixed-conifer (NSacs and SSacs), and the reference category for sex (Sandias) was female. Model parameters include detection probability at the activity center ( $g_0$ ) and the spatial scale over which  $g_0$  declines ( $\sigma$ ).

Variable	Parameter	Study area	Beta	SE	LCL	UCL	SOE
Elevation	$g_0$	SSC	1.57	0.25	1.08	2.07	273,870,708.14
Elevation	$\sigma$	SSC	-0.62	0.12	-0.84	-0.39	1,570,914.27
Sex	$g_0$	Sandias	-2.92	0.80	-4.49	-1.36	824.02
Sex	$\sigma$	Sandias	1.89	0.42	1.07	2.71	26,688.19
Piñon pine-juniper	$g_0$	NSC	-3.07	0.48	-4.02	-2.12	564,259,121.57
Piñon pine-juniper	$g_0$	NSacs	-2.55	0.71	-3.93	-1.16	669.32
Piñon pine-juniper	$g_0$	SSacs	-2.38	0.52	-3.40	-1.36	33,281.84
Piñon pine-juniper	$\sigma$	NSC	1.33	0.24	0.87	1.79	8,592,700.16
Piñon pine-juniper	$\sigma$	NSacs	-0.04	0.38	-0.80	0.71	1.01
Piñon pine-juniper	$\sigma$	SSacs	0.72	0.25	0.23	1.21	63.55
Ponderosa	$g_0$	NSC	-0.59	0.49	-1.56	0.37	2.06
Ponderosa	$g_0$	NSacs	0.15	0.33	-0.50	0.79	1.11
Ponderosa	$g_0$	SSacs	0.39	0.52	-0.63	1.41	1.32
Ponderosa	$\sigma$	NSC	0.05	0.23	-0.40	0.50	1.03
Ponderosa	$\sigma$	NSacs	-0.24	0.19	-0.62	0.14	2.19
Ponderosa	$\sigma$	SSacs	-0.39	0.24	-0.86	0.09	3.54
Mixed-conifer	$g_0$	NSC	-1.84	0.44	-2.71	-0.97	5,363.23
Mixed-conifer	$\sigma$	NSC	0.94	0.21	0.52	1.35	16,038.76
Spruce-fir	$g_0$	NSC	-2.09	0.53	-3.13	-1.04	2,140.41
Spruce-fir	$\sigma$	NSC	1.21	0.26	0.70	1.71	56,102.60