October 2022

RH: Sultaire et al. Black bears in Nevada

Black bear density and habitat use variation at the Sierra Nevada-Great Basin Desert transition

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ABSTRACT

In the first two decades of the 21st century, American black bear (*Ursus americanus*) populations rebounded with documented range expansions into areas where the species was previously extirpated. While there are a number of factors that limit range expansion, habitat quality and availability are among the most important. Such factors may be particularly important in western Nevada at the transition zone of the Sierra Nevada and the Great Basin Desert. We deployed a multi-faceted data collection system including camera traps, noninvasive hair sampling and genotyping, and GPS tracking. The data were analyzed using spatial capture-recapture to estimate population density and dynamic occupancy models to estimate habitat use. We found that black bear habitat use and density were; *i*) substantially higher in the Sierra Nevada than the Great Basin Desert (β_{dens} = 1.99, SE = 0.17), and *ii*) had strong positive relationships with the presence of conifer land cover in the transition zone (β_{dens} = 0.72, SE = 0.18). The average black bear density was >4 times higher in the mixed-conifer forests of the Sierra Nevada (12.4 bears/100km^2) than in desert mountain ranges with piñon-juniper woodland (2.7 bears/100km^2). The low-elevation shrub and grassland portions of the study area had even lower estimated black bear density (0.6 bears/100 km^2) and probability of use (0.03, 95% CI = 0.00 – 0.09). Across these spatially-variable configurations in black bear density, we estimated the total population size to be 418 individuals (95% CI = 239-740). Declining density towards the range edge, coupled with a relatively stable range of black bears in Nevada observed over the last two decades, suggests that further species range expansion into the western Great Basin may be limited by habitat quality and availability.

KEYWORDS: integrated population model, noninvasive genotyping, spatial capture-recapture, occupancy model, range margin, *Ursus americanus*

After experiencing range-wide declines due to over exploitation and habitat loss (Laliberte and Ripple 2004), several species of large carnivores in North America have increased in population and expanded their ranges in the past half century (Gompper et al. 2015). These examples of species recoveries have resulted from both human translocation efforts (Fritts et al. 2008, Murphy et al. 2016) and natural range expansions (Malaney et al. 2018, LaRue et al. 2019). As carnivores have expanded their distributions, they have colonized novel habitats and landscapes that differ from locations where they persisted historically (Mladdenoff et al. 1999, Ditmer et al. 2015). Given these flexible colonization patterns, understanding the factors limiting carnivore populations in recolonized portions of their ranges can help determine whether continued population expansion is likely.

Population expansion is driven by individual dispersal events (Mladdenoff et al. 1999), with dispersal rates often positively associated with population density in mammals (Mathysen 2005). Thus, investigating population density trends across habitat gradients for recolonizing carnivores can indicate whether populations will continue to expand, or if lower population density at range margins may limit future expansion (Swenson et al. 1998, Sun et al. 2017). Spatial capture-recapture (SCR) models are useful in this context because they explicitly include animal movement during sampling (Borchers and Efford 2008, Royle et al. 2014), yielding spatially explicit estimates of population density from which estimates of abundance and the geographic extent of a population can be derived. Incorporating animal movement into capture-recapture models also facilitates integration with GPS and telemetry data (Royle et al. 2013) which can reduce uncertainty in estimates of the abundance and geographic extent of a population. As large carnivore range expansions were often followed by the initiation of hunting seasons to provide recreational opportunities and manage human-wildlife conflict (Mech 2010, Garshelis et al. 2020), abundance estimates provided by SCR models can guide efforts to sustainably harvest recolonizing carnivore populations (Murphy et al 2016).

Black bear (*Ursus americanus*) populations, after having been greatly reduced across much of their range by habitat loss and overhunting, are one species of large carnivore in North America that are now recovering (Murphy et al. 2016, Sun et al. 2017, Evans et al. 2017). In Nevada, black bears historically occurred across several mountain ranges in the state but were reduced to a remnant population in the Sierra Nevada along the California border (Hall 1946, Lackey 2004, Lackey et al. 2013). By the early 21st century, black bears had re-established across much of their historical range in western Nevada (Lackey et al. 2013). Species recovery was likely facilitated by combination of an expanding black bear population in adjacent California, where the population is presently estimated to be ~35,000 (Zielinski et al. 2005; California Department of Fish and Game-Draft Environmental Document 2011), and reforestation across mountain ranges in western Nevada (Lackey et al. 2013). As bears navigate the transition zone from the Sierra Nevada into the Great Basin Desert, they navigate a stark transition of habitat from conifer forest to piñon-juniper woodland (Malaney et al. 2018). These woodlands differ drastically in structure and productivity from the mixed-conifer forest (Gottfried et al. 1995) that black bears typically occur in throughout their western range.

Determining the factors limiting the expansion of this black bear population is critical for effective management. Although black bears are a charismatic species that provide several ecosystem services (Garshelis 1990; Stowell and Willging 1992; Miller et al. 1998, Moll et al. 2021), expanding black bear populations have also resulted in increased conflict with humans (Spencer et al. 2007; Don Carlos et al. 2009; Lackey 2010; Mazur 2010). In Nevada, the number of private citizen complaints and vehicle-black bear collisions increased by 10- and 17-fold, respectively, between 1990 and the early 2000s as black bears recolonized western Nevada (Beckmann and Berger 2003a), consistent with trends across North America (Gore et al. 2005, Siemer et al. 2007, Spencer et al. 2007). In response to this growing population, both geographically and numerically, Nevada’s first black bear hunting season was initiated in 2011 (Lackey et al. 2013). Quantifying density variation and overall abundance of black bears in their Nevada range will benefit management efforts aimed at maintaining the viability of this newly expanded population.

In this study, we deployed a multi-faceted data collection system to explore three research objectives relevant to assessing the status of Nevada’s black bear population. First, we used a broad-scale camera trap network to estimate black bear area of habitat use and temporal variation in habitat use across this transition zone. Second, we integrated black bear genotypes obtained through analysis of noninvasive hair samples with GPS movement data to estimate spatial variation in density in response to habitat availability and type (forest versus woodland). Finally, we used these spatially varying density estimates to produce an abundance estimate, with associated uncertainty levels, for the Nevada black bear population. We hypothesized that patterns of black bear density and habitat use are driven by both habitat availability and habitat quality at this ecotone. Under this hypothesis, we expected black bear density and habitat use to exhibit a strong positive relationship with the availability of conifer cover, either forest or woodland, in a region where this land cover is patchily distributed. However, because primary productivity is an important driver of black bear ecology in semi-arid regions (Gould et al. 2019), we predicted lower density and habitat use in the Great Basin Desert compared to the Sierra Nevada, due to lower habitat quality in less productive piñon-juniper woodlands.

STUDY AREA

We established our study area within the current black bear range in western Nevada, U.S. as defined by the Nevada Department of Wildlife (NDOW). Our study area was characterized by a stark transition in habitat types between the Sierra Nevada and the Great Basin Desert (Figure 1). Due to rain shadowing from the Sierra Nevada, vegetation communities along this ecotone transitioned from primarily mixed-conifer forest (*Pinus* and *Abies* spp.) and alpine vegetation in the Sierra Nevada to a mix of shrubland and grasslands at lower elevations in the Central Basin and Range ecoregion. Extensive areas of piñon-juniper woodland (*Pinus monophylla* and *Juniperus osterosperma*) occur at mid to higher elevations in the Great Basin ranges, constituting most of the black bear habitat outside the Sierra Nevada range. The entire region is characterized by rugged topography and elevations ranging from ~1,160 m at low lying terminal lakes in desert areas to 3,440 m at the summit of Mount Grant in the Wassuk Mountains. Climatic conditions covaried with elevation changes, mean annual temperature ranged from 3.4 °C to 13.0 °C and mean annual precipitation varied from 180 mm per year to >1400 mm per year across the elevational gradient (Prism Climate Group). At comparable elevations, areas within the Great Basin had lower precipitation than those with the Sierra Nevada Mountains. Reno, Nevada, a large metropolitan city with a human population ~250,000, lies in the north-central portion of the study area (Figure 1). Outside of urban and peri-urban areas, cattle (*Bos taurus*) grazing and hard rock mining were the primary human land use, with areas of irrigated agriculture in large valleys. With the exception of feral horses (*Equus ferus caballus*), black bears were the largest mammal species in the region. Other common carnivore species include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*) with mountain lions (*Puma concolor*) present at comparatively lower densities. Mule deer (*Odocoilleus hemionus*) occurred throughout the study area, with pronghorn (*Antilocapra americana*) primarily inhabiting lower elevation open habitats.

METHODS

Field methods

Within the study area, we selected 100 locations to deploy hair snare corrals and camera traps (Figure 1) at 49 km^2 resolution. To effectively estimate population density, SCR models rely on detecting animals at multiple sampling locations, with guidance on study design suggesting a minimum of two sampling sites per home range (Dillon and Kelly 2007). Given this evidence, and the fact that home ranges for black bears in Nevada vary from 52.9 and 519.6 km^2 (Beckmann 2002), we selected a resolution of 49 km^2 which is equivalent to between one and 10 traps per Nevada black bear home range. Hence, the 49 km^2 resolution was coarse enough to estimate the area of occurrence across the potential black bear range in Nevada while also being fine enough that we could expect to encounter individual bears at more than one sampling location within their home range. The 49 km^2 resolution was also comparable to previous published black bear SCR studies in the western U.S. (49 km^2 Stetz et al. 2018, 25 km^2 Gould et al 2018). Sampling sites were located at the center point of grid cells, unless that location was inaccessible (e.g., due to lack of roads) in which case we located sites at the nearest accessible location within a grid cell. Gaps in the sampling strategy represented areas that were federally designated Wilderness and private lands where permissions could not be granted. We established and monitored these 100 sites across a 28-month period from late May 2018 through October 2020.

Beginning in May 2018, we constructed a barbed wire hair snare corral and deployed a camera trap (Bushnell Trophy Cam HD, Model 119776C) at each of the 100 sites (Woods et al. 1999, Wilton et al. 2014, Figure 2). The hair snare corral consisted of two strands of barbed wire, one 8 cm above ground level and another 50 cm above ground level, strung between four trees or metal fence posts (Stetz et al. 2014). In the center of each corral, we deposited a mixture of raspberry extract (Mother Murphy's Laboratories, Inc., Greensboro, NC), fish oil, and anise extract (Minnesota Snareline Products, Pennock, MN; Pederson et al. 2012; Wilton et al. 2014). Next, we positioned a camera trap on a nearby tree or post with the viewshed of the camera oriented across the hair snare corral. To reduce the incidence of false triggers, which allowed cameras to operate longer without checks, we programmed the camera traps to take three pictures at each trigger and subsequently deactivate for 10 minutes (Lepard et al. 2019). Cameras were active year-round while hair snare corrals were maintained during 2–3-month season from late spring through summer each summer (June-August 2018-19; July-September 2020). During periods when hair-snares were active, we visited sites every 7-10 days to collect hair samples and apply lure. When collecting hair samples, each barb with hair was treated as a separate sample and we sterilized forceps in between sample collections. In response to a lack of bear detections at 67 sites in 2018-19 and delays related to the COVID-19 pandemic, in the third year of data collection we reduced the extent of our hair sampling to 58 sites (see Figure 2).

Genetic analyses

In the laboratory, we used one-centimeter lengths of each hair sample, including the follicle, for genomic DNA extraction using QIAamp Fast DNA Tissue Kit. We used one to five hair follicles from a given sample as the source of genomic DNA (Woods et al. 1999, Poole et al. 2001). The quality of genomic DNA and verification that it was of *Ursus americanus* origin were determined by bear-species specific mitochondrial DNA primers and polymerase chain reaction (PCR) amplification and melting curve analysis; we utilized a well-characterized mitochondrial primer pair (Hänni et al. 1994) based on bear mitochondrial analyses (Woods et al. 1999, Shields and Kocher 1991). Genotyping was carried out by fluorescently labeled multi-locus multiplexed PCR for 21 microsatellite loci. We utilized 18 of 23 microsatellite loci from previous studies of black bear genetics in Nevada (see Malaney et al. 2018) and eliminated 5 primer pairs that appeared to not be informative from that study. Three primer pairs were newly designed based on the repeat marker data obtained from the polar bear genomic data in University of California Santa Cruz Genome Browser. For sex identification, the primer set from Yamamoto et al. (2002) was modified for this study. The loci, fluorphores and primer sequences are shown in Table S1. The potential size range of each PCR product, the multiplexed groupings and the fluorophore for each set are shown in Figure S2, and an example of the PCR profile is shown in Figure S4. The variation of each microsatellite was verified with nuisance bear hair samples from Nevada provided by NDOW and muscle tissue from one Michigan black bear that was also used as an outlier for genomic analyses.

We combined fluorescently labeled amplicons with ABI GENESCAN^{TM} 500 LIZ allelic ladder (Applied Biosystems, Foster City, California) and ran the products on an ABI 3730 DNA Analyzer at the Michigan State University Research Technology Support Facility Genomics Core. We scored individual peaks with OSIRIS software (NIH), verified all genotypes manually, and conducted additional analyses on a subset of samples that amplified poorly in the first round of genotyping to increase success rates; the numbers of PCR reactions that yielded good, borderline, or poor amplifications are shown in Table S1 by collection year, and the total number of samples analyzed per year are shown. We adapted the genotyping data of 11 loci (UamB2, G10D, UarMU23, UarMU05, MIQL1, UamD102, UamB8, UarMU10, MIQL2, UA.P2H03, and MIQAmel.) that showed high data coverage for all samples (over 75%).

We identified individual bears by their unique combination of allele values at these loci using the R package allelematch, which helps account for genotyping uncertainty when matching genotypes (Galpern et al. 2012). To identify unique groups of multi-locus genotypes at a given dissimilarity criterion (i.e., number of allele mismatches), allelematch measures dissimilarity between samples using Hamming distance and subsequent dynamic hierarchical clustering (Galpern et al. 2012). We used profile plots to identify the optimal dissimilarity criterion based on the mismatch value that minimizes ambiguous matches, which included three loci from our data set. Under this dissimilarity criterion, samples could differ by up to two alleles and be classified as the same individual. At this value of dissimilarity, all P_{sib} values (Waits et al. 2001) were < 0.003, meaning less than 0.3% chance that two unique individuals would be classified as the same individual.

Statistical analyses

Habitat use estimation

We used a dynamic occupancy model to estimate black bear habitat use in Nevada via our camera trap data. Dynamic occupancy models use repeat surveys at sampling sites to estimate probability of detection for a species, and estimate occupancy in the initial year of sampling, and colonization and extinction at sites between sampling seasons (Mackenzie et al. 2003). Although the occupancy state of a site can change in between primary sampling periods (i.e., years) in dynamic occupancy models (i.e., colonization/extinction), an important assumption of occupancy models is that sites are closed to changes in occupancy within a season

(Mackenzie et al. 2017). Given that black bears are a wide-ranging species, this assumption was violated in our study, and in this context, occupancy was better interpreted as probability of black bear use of a site, rather than the probability that black bears occupy a site (Mackenzie and Royle 2005; Gould et al. 2019).

We fit a suite of candidate occupancy models to test our hypothesis regarding the importance of both habitat availability and quality to black bear habitat use in Nevada. For models, primary sampling periods spanned from early June through mid-October each year (2018-2020) and we specified 28 day sampling occasions, resulting in 5 secondary sampling periods each year at each site. Hence, estimated detection probability represented the probability of detecting a black bear over the one, 28-week period, given that black bears use the area in a year. We initially fit two competing detection models that tested the effects of two covariates on detection probability individually: 1) the date of secondary sampling period, and 2) the amount of conifer in a 1km buffer surrounding cameras. The model including date as a detection covariate tested whether seasonal shifts in black bear behavior altered detection at cameras. The model including the conifer detection covariate tested the prediction that sites with higher conifer cover in local neighborhood surrounding sites were more frequently used by black bears, increasing detection. We included the best supported detection covariate in subsequent models with habitat use (i.e., occupancy) covariates. Lure was applied for equal periods of time each year that spanned most secondary periods, and we did not include lure as a covariate on detection probability.

For covariates on habitat use, we considered two broad-scale covariates that captured variation in black bear habitat availability and differences in habitat quality, as our coarse resolution study was not conducive to estimating fine-scale effects of land cover on habitat use.

Because black bears were predominantly detected in forested areas, as opposed to lowland desert and shrubland, we included the effects of proportion conifer cover within a 5-km buffer surrounding sites (*sensu* Moll et al. 2021) on habitat use (i.e., occupancy). Conifer land cover in the Sierra Nevada portion of the study area largely consists of mixed-conifer forest whereas conifer in the Great Basin is almost entirely piñon-juniper woodland. To capture this variation, we included a binary covariate on habitat use indicating whether a site was located in the North American Desert Ecoregion (i.e., Great Basin, 89 sites) or the Northwestern Forested Mountains Ecoregion (i.e., Sierra Nevada, 11 sites). For this binary ecoregion covariate, the Great Basin Ecoregion was modeled as the intercept. The ecoregion covariate was derived from the U.S. EPA Level 2 North American ecoregion classification system (Omernik & Griffith 2014; EPA.gov/eco-research/Ecoregions). We fit three competing habitat use models, two models that tested each covariate in isolation (conifer and ecoregion) and a third model that assessed the combined effects of both covariates on habitat use. As we interpreted occupancy as site-level probability of use, the dynamic parameters extinction and colonization represent transitions in the probability of use between years, with extinction representing the probability a site was used in one year by black bears and not the next year, and colonization representing the probability a site was not used one year but was used by black bears the next year. Due to a limited number of sampling years, we did not include covariates on dynamic parameters (i.e., intercept only).

Dynamic occupancy models were fit in a Bayesian framework using R package *ubms* version 1.1.0 (Kellner et al. 2022). For each model, we used default priors for each parameter and ran three parallel chains for 10,000 iterations with a 5,000-iteration burn-in. We ranked models using the leave-one-out information criterion (LOOIC, Vehtari in al. 2017). We used the top ranked occupancy model to predict black bear habitat use across their Nevada range at a 25 km^2. We assessed the fit of our model to the data using a posterior predictive check based on the Mackenzie-Baily χ^2 test (Mackenzie and Bailey, 2003), with 500 draws from the posterior distribution.

Abundance estimation

We analyzed the capture histories of individual genotypes obtained from the hair samples using a spatial capture-recapture framework (SCR). Within this SCR framework, each bear's position on the landscape is represented by a center of activity (i.e., home range center). SCR models estimate individual detection probability at this activity center (p0) and use the spatial correlation of individual black bear recaptures across sampling sites to calculate the spatial scaling parameter, denoted as σ. The spatial scaling parameter measures of how quickly the detection of an individual animal declines as distance of a trap from its activity center increases (Royle et al. 2014). The two detection parameters are used to estimate the density of both observed and unobserved (i.e., not detected) animal activity center locations (Royle et al. 2014), and population size is estimated by summing density patterns across the entire study area.

Spatial capture-recapture (SCR) analyses require that individual animals are recaptured at multiple sampling locations (i.e., hair snag corrals), termed spatial recaptures, to effectively estimate population density (Borchers and Efford 2008, Sollmann et al. 2013). In practice, spatial recaptures can be difficult to obtain, particularly for studies across large geographic areas where spacing sampling sites close to one another is impractical. In situations where sufficient spatial recaptures are not obtained over the course of the study, movement information from GPS and telemetry data can be integrated with SCR data to help estimate σ (Royle et al. 2013). To strengthen the model, we integrated our genetic-SCR data with concurrent GPS tracking of black bears by NDOW. The GPS data included locations from 24 individuals including 11 males and

13 females (Table 1). We thinned the GPS data to one location per individual per week, equivalent to the frequency at which hair snag corrals were checked. We made this decision to better ensure independence of locations from the same individual (Royle et al. 2013), which resulted in 184 total GPS locations across the three years, 83 from males and 101 from females (Table 1). We did not include locations from black bears whose collars were deployed during hair sampling periods because of the potential for increased movement of recently collared bears to inflate estimates of population level movement. Capture and collaring of black bears followed the methods of Lackey et al. (2013) but briefly, bears were captured using culvert traps (Teton Welding, Choteau, MT) in conflict situations (n = 21), using Aldridge foot snares in wildland areas (n = 2), or tranquilized while unconfined (n =1). Culvert trap captures spanned the entire length of the Sierra Nevada (in Nevada) and included the Virginia Range (Figure 1). Foot snaring was conducted in the Northern Pine Nut Range (Figure 1). Bears were either released at the location of capture or within their home range (< 2.5 km from capture). Three bears were moved outside of their home ranges (9 km, 23 km, and 45 km), but for these bears, data from the same year as capture were not used in analysis. Dates of capture for bears varied from June 2016 (2 years prior to 2018 sampling) to July 2020 (~3 weeks before 2020 sampling). Capture techniques were conducted in accordance with NDOW protocols and American Society of Mammalogists guidelines (Sikes 2016).

We analyzed the integrated genetic capture-recapture and GPS data in a multisession SCR model (Royle et al. 2014), with each year specified as a separate session. However, to reduce model complexity we estimated constant p0, σ, and density across the three years. Essentially, the SCR model estimated mean annual abundance of black bears across the three sampling years. As black bears were only detected at one third of sampling sites, to reduce zero inflation and increase computational efficiency, we only analyzed data from 58 sites that were regularly checked in all three study years in the integrated SCR + GPS models (Figure 2b). The sex of each collared and genetically-identified individual was known, allowing inclusion of sex as a covariate on detection probability. Sex effects on detection parameters are often supported in black bear SCR studies as male bears move farther than females, resulting in increased σ (Evans et al. 2017, Welfelt et al. 2019). For the model to converge, we removed one long distance recapture of a male bear of 85 km from the genotype data set. The longest movement of a telemetered individual during noninvasive hair sampling was 28 km. In addition to sex effects on detection parameters, we used the integrated SCR – resource selection function framework developed by Royle et al. (2013) to include proportion conifer at a 1-km resolution on black bear detection probability, consistent with detection covariates in our habitat use model. The detection level of a SCR model essentially relates to third order habitat selection of individuals (Royle et al. 2018) and including a conifer covariate accounted for bears selecting for conifer cover within their home range when estimating detection at sampling locations (Sollmann et al. 2016).

An important analytical decision for SCR models is specifying the geographic area over which animal density is estimated, known as the state space. As most of the bear habitat currently occupied in Nevada is near the border with California, specifying too large of a state space will include bears in California that do not include Nevada in their home range. Restricting the state space to only Nevada will not include bears whose center of activity is in California but include Nevada in their home range. With these considerations in mind, we selected the state space for our analysis via a 16.5-km buffer around the 58 sampling sites. The 16.5-km buffer corresponded to the minimum buffer required to contain all bear GPS locations during the hair sampling period (Figure 2b). Hence, a 16.5-km buffer size likely corresponds to the maximum effective sampling area of our study sites and is comparable to those used in published black bear spatial-capture recapture studies in western North America (15.5 km Loosen et al. 2019; 15 km, Stetz et al. 2019; 11-25 km depending on study area, Gould et al. 2018). Importantly, comparing estimates from this buffer size to a model fit with a 20-km buffer revealed low sensitivity of density estimates to larger buffer sizes (Table S2). Consistent with the covariates we included in the black bear occupancy, we modeled variation in black bear density as a function of a continuous covariate measuring proportion conifer cover (mixed-conifer and piñon-juniper combined) across the state space and a binary covariate indicating ecoregion (i.e., the Sierra Nevada or Great Basin). We estimated density and summarized proportion conifer at a 2.5 x 2.5 km (6.25 km^2) resolution across the state space. The 6.25 km^2 was computationally practical (~runtime 10 hours), while also a scale generally relevant to bear movement (i.e., intermediate between female and male σ; see Results). We summarized conifer cover at a finer resolution for the density covariate in the SCR model compared to the habitat use covariate in the occupancy model as the SCR model estimated the effect of conifer on activity center location, whereas the occupancy model estimated the effect of conifer on bear use of site, even if on the periphery of a home range. The integrated SCR-GPS model took the form:

$$p0 \sim \text{Conifer1km} + \text{Sex},\ \sigma \sim \text{Sex},\ \text{Density} \sim \text{Conifer2.5km} + \text{Ecoregion}$$

Using the SCR-GPS model, we constructed a map to visualize variation in black bear density (# of bears/100km^2) across the state space. We fit the integrated SCR + GPS model using a frequentist approach in R package *oSCR* version 0.42.0 (Sutherland et al. 2019).

RESULTS

We detected black bears 508 times on camera traps at 33 of the 100 sites (Table 1, Figure 2a), which resulted in 152 detections during 28-day secondary sampling periods that contributed to detection histories for the occupancy model. The proportion of conifer cover in a 5 km radius surrounding sites ranged from 0.0 to 0.95, with proportion piñon-juniper spanning the same range and a maximum proportion mixed-conifer of 0.64. The maximum proportion mixed-conifer surrounding sites in the Great Basin ecoregion was 0.02 and the maximum proportion piñon-juniper surrounding sites in the Sierra Nevada ecoregion was 0.06.

A positive effect of local-scale (1km) conifer cover on detection probability ($\beta = 0.54$, 95% CI = 0.23 – 0.85), was more supported than an effect of secondary period date on detection probability (Table 2, $\beta = 0.02$, 95% CI = -0.25 – 0.22). At the mean amount of conifer cover in the 1km buffer, black bear detection probability for 28-day secondary periods was 0.32. For habitat use (i.e., occupancy), a model containing the effects of both habitat availability (5km conifer cover) and habitat quality was most supported based on LOOIC (Table 2). The results of the goodness-of -fit test that compared simulated detection histories under parameters of top-ranked to actual detection histories indicated that the top-ranked model fit the data adequately (χ^2 = 314.15, Bayesian p-value = 0.14). Under the top-ranked model, black bear habitat use was higher in the Sierra Nevada than the Great Basin ($\beta = 4.14$, 95% CI = 1.82 – 7.38) and was positively correlated with the proportion of all conifer cover types combined in the landscape around sites ($\beta = 1.88$, 95% CI = 0.91 – 3.56). At 50% conifer cover, predicted site-level probability of use was 0.27 in the Great Basin (95% CI = 0.14 – 0.44) and 0.94 in the Sierra Nevada (95% CI = 0.71 – 1.00). At sites that lacked conifer in the surrounding landscape in the Great Basin, predicted probability use was 0.03 (95% CI = 0.00 – 0.09). The dynamic model estimated between year extinction probability (i.e., probability used one year and not the next) at

0.13 (95% CI = 0.02 – 0.27) and colonization probability at 0.11 (95% CI = 0.01, 0.20). The dynamic occupancy model predicted that black bears use habitat across 3,018 km^2 in Nevada (95% CI = 1,545 – 4,792 km^2, Figure 3a).

From the hair snare surveys, we identified 121 individual bears detected 167 times across the three sampling years. We detected 36 individuals 48 times in 2018, 58 individuals 66 times in 2019, and 41 individuals 53 times in 2020 (Table 1). Compared to the black bear detections on cameras at 33 sites, we successfully obtained genotypes of individual bears from hair samples collected at 24 sites, including one site that did not photograph bears during the study. Estimates from the integrated SCR-GPS model supported the inclusion of sex as a covariate on detection parameters, with male bears having lower baseline detection probability (i.e., p0) and moving larger distances (i.e., larger σ) compared to female bears (Table 3). For third order habitat selection (i.e., within home range), the integrated-SCR-GPS model estimated an increase in baseline detection probability (p0) with increases in conifer cover (Table 3). For second order habitat selection (i.e., activity center location), estimated black bear densities were significantly higher in the Sierra Nevada ecoregion than the Great Basin ($\beta_{ecoregion}$ = 1.99, SE = 0.17, Figure 3b) and increased with proportion conifer independent of ecoregion ($\beta_{conifer}$ = 0.71, SE = 0.18; Figure 3b). These density relationships resulted in estimated black bear density averaging 4.5 times higher in the Sierra Nevada (12.4 bears /100km^2, 95% CI = 7.3–21.2) compared to average densities in desert mountain ranges with piñon-juniper (2.7 bears /100km^2, 95% CI = 1.6–4.8; Figure 3). Estimated bear density was lower still in landscapes that completely lacked conifer cover (0.6 bears /100km^2, 95% CI = 0.2–1.6). The integrated SCR-GPS model predicted a population of 418 black bears within the state space, with a 95% confidence interval of 239 to 740 bears.

DISCUSSION

Via a multi-faceted data collection system featuring camera traps, noninvasive hair collection and subsequent genotyping, and GPS tracking, we estimated black bear density and habitat use variation across a transition from the Sierra Nevada and Great Basin Desert in western Nevada. Estimates of black bear density varied across the study area, with higher densities in the mixed-conifer forests of the Sierra Nevada, lower densities in the drier mountain ranges to the east, and near zero bear density in low elevation grass and shrubland. Nine of 11 sites within the Sierra Nevada sampled at least one black bear individual, as assessed via genotyping, over the course of the study with the two remaining sites detecting bears on cameras. Outside of the Sierra Nevada, we identified hotspots of bear density in the northern Pine Nut and Sweetwater Mountains (Figure 3). However, several sites in the desert mountain ranges did not detect a single black bear over the course of the study, even at locations within piñon-juniper woodland, indicating that black bears are patchily distributed in their Nevada range outside the Sierra Nevada Mountains. These findings supported our hypothesis that habitat availability and habitat quality limit the Nevada black bear population, with lower density and habitat use in piñon-juniper woodland suggesting that this habitat is lower quality than mixed-conifer forest. Density can be misleading indicator of habitat quality if it does not correlate with reproductive success (van Horne, 1983). However, previous black bear studies that found piñon-juniper woodland is generally selected against by black bears (Johnson et al. 2015) and that bears move farther distances in this habitat (Gould et al. 2018), also support to our conclusion. Our results further emphasize that piñon-juniper woodland is suboptimal habitat for black bears compared to conifer forest.

Even within the Sierra Nevada ecoregion, average estimated density of 12.4 bears/100km^2 is lower than estimates reported in more productive areas of their range such as Washington, where black bear density averaged 19.2/100 km^2 east of the Cascades Mountains (Welfelt et al. 2019). Estimated black bear density from New Mexico, which has a similar semi-arid climate to western Nevada, averaged between 16.6 and 25.3 bears/100 km^2 across different mountain ranges (Gould et al. 2018). Our density estimates are also lower than past nonspatial density estimates from nearby California and in urban areas of this region of Nevada (17-20 bears/100km^2; Beckmann and Berger 2003a,b; Beckmann and Lackey 2018, Fusaro et al. 2017). Given an upper estimate of 21.1 bears/100km^2 in the Sierra Nevada, however, our analysis cannot rule out that bear densities in the eastern Sierra Nevada are comparable to elsewhere in the western U.S.

The variation in black bear density we identified contrasts with previous studies that applied SCR to estimate density patterns of expanding black bear populations in eastern North America (Sollmann et al. 2016, Sun et al. 2017). Black bear density did not have a positive relationship with forest cover where they were expanding from primarily forested into mainly agricultural landscapes in New York (Sun et al. 2017) and black bear density in a recently established Missouri population was similarly not associated with forest cover (Sollmann et al. 2016). Compared to these studies our results suggest that black bears are more constrained by the availability of forest cover in semi-arid western landscapes, although other factors correlated with forest cover (e.g., water availability) may also play a role. These differences in bear density patterns between regions are not surprising given that agricultural areas can provide both food resources and concealment for black bears (Garshelis et al. 2020) whereas desert shrub and grasslands provide neither.

The Lahontan Trough is an arid, sparsely vegetated portion of the Great Basin directly east of Nevada’s black bear range that influences dispersal of other large carnivores (e.g., mountain lions; Andreason et al. 2012). Lackey et al. (2013) identified mountain ranges east of the Lahontan Trough in Nevada as part of black bear historical range, however, the area of occurrence we identified in western Nevada is essentially the same as reported over the past two decades (Lackey et al. 2004). Dispersal rates, which drive population expansion, are often positively related to population density in mammals (Mathysen 2005), although evidence is mixed for black bears (Costello et al. 2008, Roy et al. 2012). Studied black bear populations in semi-arid regions most similar to Nevada exhibited strong positive density dependent dispersal (Costello et al. 2008), suggesting that the low density we observed in the periphery of Nevada black bear range could be a major impediment to continued range expansion. Although sporadic observations of black bears in eastern Nevada suggest colonization of these mountain ranges from the eastern edge of the Great Basin is possible, our density estimates suggest that continued range expansion of black bears in the western Great Basin is unlikely. A stable range of black bears in western Nevada is further suggested by the relatively low between-year colonization and extinction probabilities (~0.12) that offset each other. However, additional years of data are required to draw robust inference on the range dynamics of this species in Nevada, particularly as black bears are a long-lived species and range dynamics likely play out at larger time scales than the duration of this study.

Dispersal constraints aside, black bears are a highly mobile species, particularly males (Costello et al. 2010), with home ranges in wildland ecosystems typically >200 km^2, and individual males documented moving >280 km in a year (Liley and Walker 2015). Large home ranges make interpreting population size for a given area nuanced, particularly for transboundary populations where home ranges of many individuals overlap political boundaries (Bischof et al. 2016). This applies to the Nevada black bear population which is geographically and genetically connected to a much larger population in California (Malaney et al. 2018), estimated to be between 30,000 and 40,000 bears (California Department of Fish and Wildlife, unpublished data). Longer term GPS data from black bears collared in Nevada further support this conclusion, with 23 of 39 black bears GPS collared in NV from 2016-2020 spending at least some time in California (Figure S5). Given this context, it can be subjective to precisely distinguish a Nevada black bear versus a California black bear. This has implications for comparing our abundance estimate to previous estimates derived from nonspatial mark-recapture (Beckmann and Berger 2002a, Lackey et al. 2013). To account for transboundary movements our spatial analysis included areas of California, however, GPS data also indicate that bears collared in Nevada occasionally traverse into areas of California not included in our SCR state space (Figure S5). Hence, our abundance estimate does not include transient bears that do not have established home ranges in the study area but spend time in Nevada.

There are additional factors to consider when interpreting our estimates. As sampling was limited to the summer months, our density estimates do not capture potential seasonal variation in bear movement between Nevada and California, such as increased movement in fall during hyperphagia (Noyce and Garshelis 2011). Furthermore, resource subsidies often increase black bear density in areas of moderate human population density (Evans et al. 2017, Fusaro et al. 2017), including in Nevada (Beckman and Berger, 2003b). Although a few sampling sites were located at the urban-wildland interface, generally it was not feasible to locate sites in areas of higher human density, and our density maps do not reflect the effect of human density. However, our abundance estimate includes all age classes because cubs were not distinguishable from adults in genetic hair samples (Welfelt et al. 2020) and camera-traps detected sows with cubs entering hair-snare corrals. Previous population and density estimates from this region, while nonspatial, were based on intensive capture-mark-recapture methods over a larger spatial and longer temporal scale (10-20 years) with much larger sample sizes and produced estimates with tighter confidence intervals (see Beckmann and Berger 2003a, b, Lackey et al. 2013, and Beckmann and Lackey 2018). Additionally, the previous more intensive methods allowed for population estimates for different segments of the population (e.g., subadults vs adults), and allowed demographic estimates (e.g., survival) across different age classes of bears that were not possible with the current study (see Lackey et al. 2013). Finally, GPS collar data from those intensive capture efforts informed the SCR models presented here. Moving forward the SCR approach we describe here, if applied over larger temporal scales, represents a less intensive and less intrusive way of estimating bear populations in this region over time, which may not be feasible through studies that rely on the physical capture of animals across many decades.

Our study, which incorporated multiple survey techniques, provides additional insight into the potential for additional data integration for future monitoring of the Nevada black bear population. Noninvasive hair sampling and genotyping, and camera traps both provide advantages and disadvantages for sustained population monitoring of lower density species such as black bears across their Nevada range. Abundance and density are difficult to estimate from camera-trap data (Gilbert et al. 2020, Ruprecht et al. 2021, but see Evans and Rittenhouse 2018). Sampling across black bear range in Nevada necessitated coarse resolution sampling with hair snare corrals, which need to be checked frequently in desert regions where high ultra-violet radiation degrades DNA (Gould et al. 2018). Consequently, we obtained few spatial recaptures, requiring integration with GPS data to produce population estimates. Further data integration between noninvasive techniques employed here could leverage higher detection on cameras with individual identification provided by noninvasive hair sampling and genotyping to increase precision (Tourani et al. 2020, Ruprecht et al. 2021). However, such a design would need to avoid violations of independence between data sets induced by colocation (Clare et al. 2018). Genotyping from hair sampling requires estimating of the levels of genetic variation in the study population to effectively determine the minimum number of genetic markers to use (Waits et al. 2001, Paetkau 2003). Depending on the genetic variability of the population this can greatly increase the labor and cost of a study, in the case of low genetic variability more loci will need to be utilized and individual identities may still not be possible. In this study, we created two multiplexed panels comprised of 22 primer pairs and the data from 11 primer pairs were selected for the analysis. The 11 selected primer pairs have higher sensitivity than the others and supports creating a more cost-efficient multiplex panel by utilizing these selected sets; these 11 pairs were useful even with samples of poor DNA quality.

These monitoring considerations are important for assessing the impact of long-term landscape changes to this population. Reforestation following historical logging facilitated the expansion of black bears into the western Great Basin and our results emphasize that maintaining conifer forest and woodland is critical to ensuring the long-term persistence of the Nevada black bear population. However, this may be challenging given the recent prevalence of large-scale wildfires in the region that may convert conifer forest and woodland to grass and shrubland (Coop et al. 2020). Although black bear habitat quality can increase after burns (Crabb et al. 2022), post-fire conifer regeneration is closely linked to precipitation in the region (Paudel et al. 2022). Although dry conditions prevail in the high desert portion of Nevada’s black bear range, pronounced ongoing drought may inhibit black bear habitat recovery following wildfire in the western Great Basin. Furthermore, piñon-juniper removal to benefit sagebrush obligate species is widespread in the Great Basin (Olson et al. 2021), leading to potential tradeoffs between black bear conservation in Nevada and conservation of sagebrush species imperiled though out their range (Gallo et al. 2016, Zeller et al. 2021). Our study design and estimates presented here provide important population baseline information and a useful framework to assess the impact of these ongoing landscape changes on black bear distribution and abundance in Nevada.

MANAGEMENT IMPLICATIONS

Black bears in western Nevada are an extension of the Sierra Nevada subpopulation in California and management of this population should reflect this connectivity. A large portion of Nevada's black bear population likely have home ranges that span both jurisdictions. Although our spatial estimate of abundance is difficult to compare with previous nonspatial estimates, the 95% confidence interval of our abundance estimate suggests that the population has been stable to growing over the past decade. However, the relatively constant habitat use across years observed during this study, a static range of bears in the state over past two decades, and low density in piñon-juniper woodland suggests that further geographic expansion of this population into the Great Basin, if it continues, will be slow. Continued monitoring of this relatively low-density black bear population will benefit from additional integration of different survey methods to obtain precise population estimates.

ACKNOWLEDGEMENTS

We would like to thank the following investigators from the Institute for Quantitative Health Science and Engineering at Michigan State University: M. Schott, M. Kuhnert, E. Ural, Dr. S.J. Chung, and Dr. B. Unluturk for assistance in selecting hairs and extracting DNA from black bear hair samples, and L. Ford for her assistance in validating the primer sets. We thank several field technicians including W. Ortiz, D. Heit, J. Eaton, S. Miller, M. Verch, C. Blommel, L. Margadant, and N. Everett for their hard work collecting samples. We thank D. Linden for assistance fitting the SCR-RSF model. Comments from two anonymous reviewers greatly improved this manuscript.

ETHICS STATEMENT

Camera-trapping and noninvasive hair sampling was assessed exempt by the Michigan State University Institutional Animal Care and Use Committee on 1 May 2018. Capture and handling of black bears by the Nevada Department of Wildlife followed guidelines by the American Society of Mammalogists for the use of wild animals in research.

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Table 1 Summaries of black bear (*Ursus americanus*) camera detections, hair snare detections, and GPS locations by sex in western Nevada, U.S. (2018-2021).

	Bear Photos	**Hair-snare Individuals**		**Hair-snare Redetections**		**GPS Collared Individuals**		**GPS Points**	
	-	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
2018	122	10	26	4	7	7	7	29	38
2019	212	31	27	4	4	1	4	12	43
2020	87	16	25	4	8	5	3	42	20
Total	421	54*	67*	12	19	11*	13*	83	101

*Some individuals common across years (2 years at most for GPS)

Table 2 Model selection results for the black bear dynamic occupancy model based on the leave-one-out information criterion (LOOIC, Vehtari et al. 2017). In addition to LOOIC we present the expected log predictive density (ELPD), and the difference in LOOIC from the top model (ΔLOOIC). Lower LOOIC, ELPD, and ΔLOOIC are indicative of a better fitting model. Colonization and extinction parameters were present in the dynamic model, but we did not include covariates on these parameters due to the short duration of the study. Data included in model collected with camera traps at 100 sites in northwest Nevada, U.S., June-October, 2018-2020.

Model	ELPD	LOOIC	ΔLOOIC
ψ ~ Eco* + Conifer5km, p ~ Conifer1km	-290.88	581.75	0.00
ψ ~ Eco, p ~ Conifer1km	-300.67	601.34	19.59
ψ ~ Conifer5km, p ~ Conifer1km	-302.14	604.29	22.54
ψ ~ Intercept, p ~ Conifer1km	-316.67	633.37	51.62
ψ ~ Intercept, p ~ Date	-321.31	642.63	60.88

*Ecoregion

Table 3 Parameter estimates and lower and upper 95% confidence intervals for black bear (*Ursus americanus*) detection function parameters in western Nevada, U.S. (2018-2020) from the integrated SCR (hair samples) + GPS model. The detection estimates reported for each sex are the intercepts, and because covariates were scaled and centered, represent detection at the mean value of proportion conifer. The $p_{Conifer}$ covariate estimated higher detection probability with increasing conifer cover and is reported on the logit scale. We report all other values on the real scale, with σ estimates in kilometers.

Parameter	**Estimate**	**Lower 95%**	**Upper 95%**
$p0_{female}$	0.08	0.05	0.12
$p0_{male}$	0.01	0.005	0.04
$p_{conifer}$	0.49	0.30	0.68
σ_{female}	1.81	1.63	2.01
σ_{male}	5.99	5.28	6.79

Figures

Figure 1. Study area in western Nevada, U.S., depicting the 100 study sites (black points) within each 49 km^2 grid cells (gray boxes), the current black bear (*Ursus americanus*) range as reported by the Nevada Department of Wildlife (black line), and relevant geographic features (2018-2020). The inset map depicts the position of Nevada's black bear population in the context of the overall Sierra Nevada population.

Figure 2. Locations of sampling sites and the sites at which black bears (*Ursus americanus*) were detected on cameras indicated in blue (n = 33) and sites where black bear individuals were identified from bear hair outlined in white (n = 24) in western Nevada, U.S. (panel a). The size of the blue dots is proportional to the number of bear camera detections at each location. Note one location in the southern Wassuk mountains where bear hair was collected but not photographed. The state space generated by buffering 58 cameras (white points) by 16.5 km (polygon), along with GPS locations of black bears collared in Nevada across the sampling period (2018-2020; panel b). The green shaded portion of the state space represents the Sierra Nevada ecoregion and the brown shading depicts the Great Basin Desert ecoregion. The different color dots represent individual black bears with triangles depicting females and circles representing males.

Figure 3 Predicted black bear (*Ursus americanus*) occupancy at a 5 x 5 km resolution across the species range in western Nevada, U.S. as defined by the Nevada Department of Wildlife (panel a). The black lines depict the major mountain ranges for spatial reference. The predicted density of black bears at a 2.5 x 2.5 km resolution from the integrated SCR-RSF model, predicted at the resolution in which density was estimated (6.25 km^2, panel b).

Figure 1

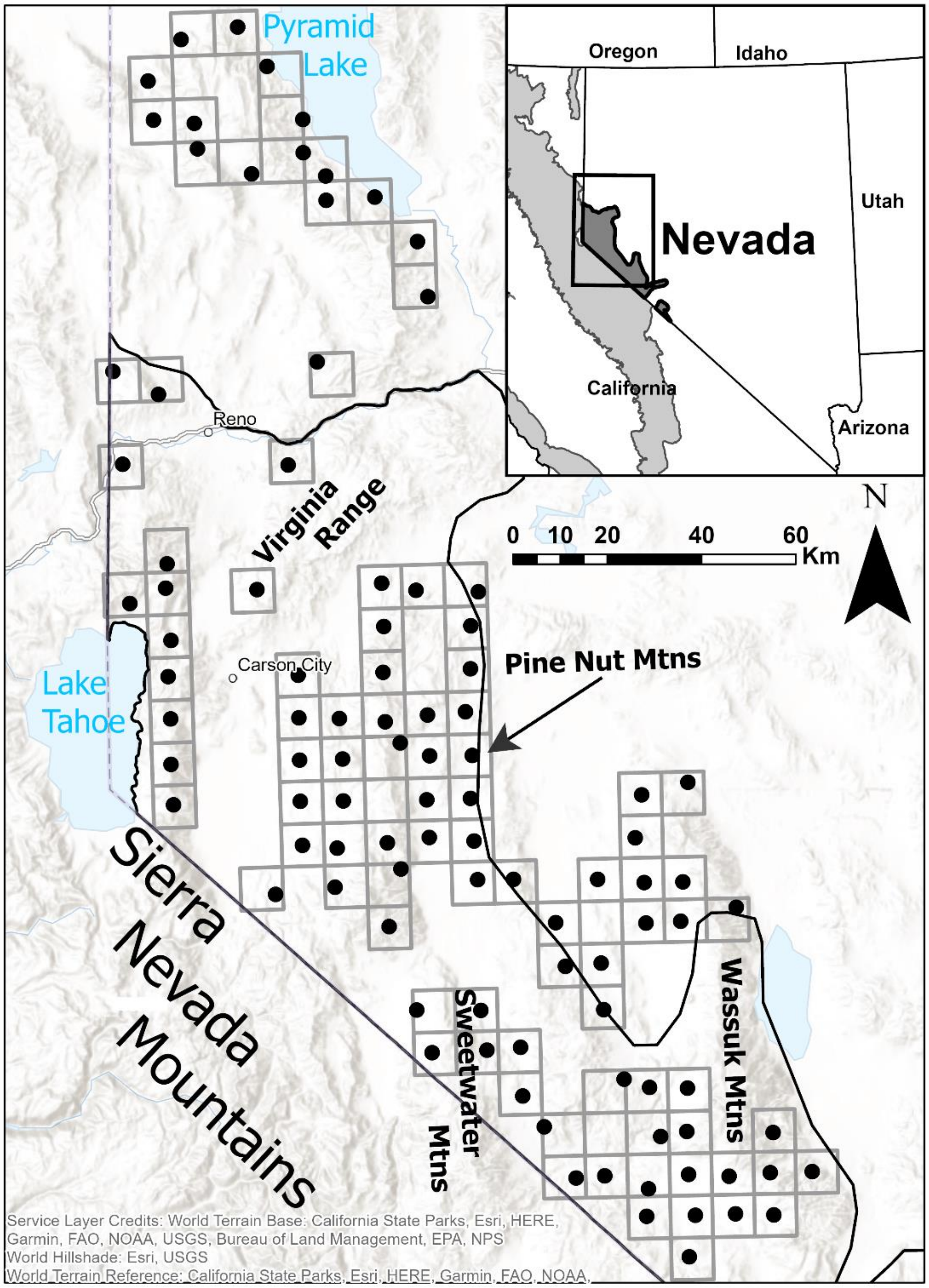

Pyramid Lake
Oregon
Idaho
Utah
Nevada
California
Arizona
Reno
Virginia Range
0 10 20 40 60 Km
N
Carson City
Pine Nut Mtns
Lake Tahoe
Sierra Nevada Mountains
Sweetwater Mtns
Wassuk Mtns
Service Layer Credits: World Terrain Base: California State Parks, Esri, HERE, Garmin, FAO, NOAA, USGS, Bureau of Land Management, EPA, NPS
World Hillshade: Esri, USGS
World Terrain Reference: California State Parks, Esri, HERE, Garmin, FAO, NOAA,

Figure 2

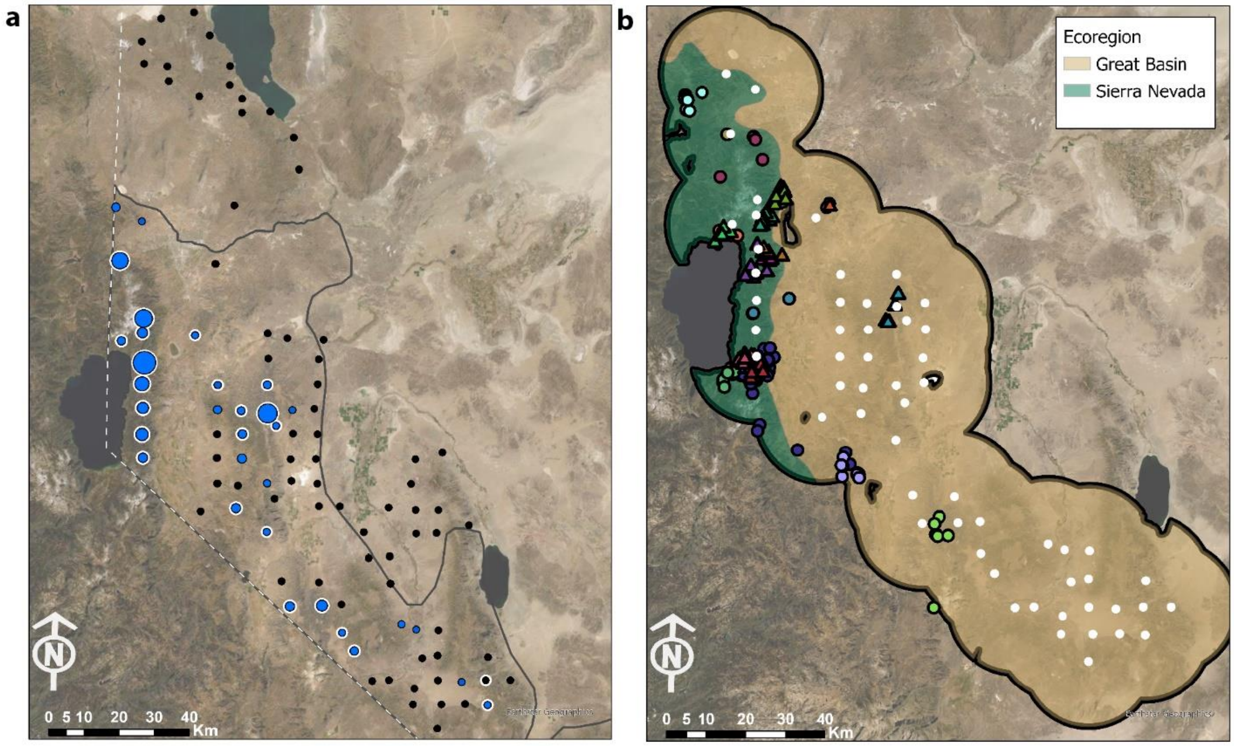
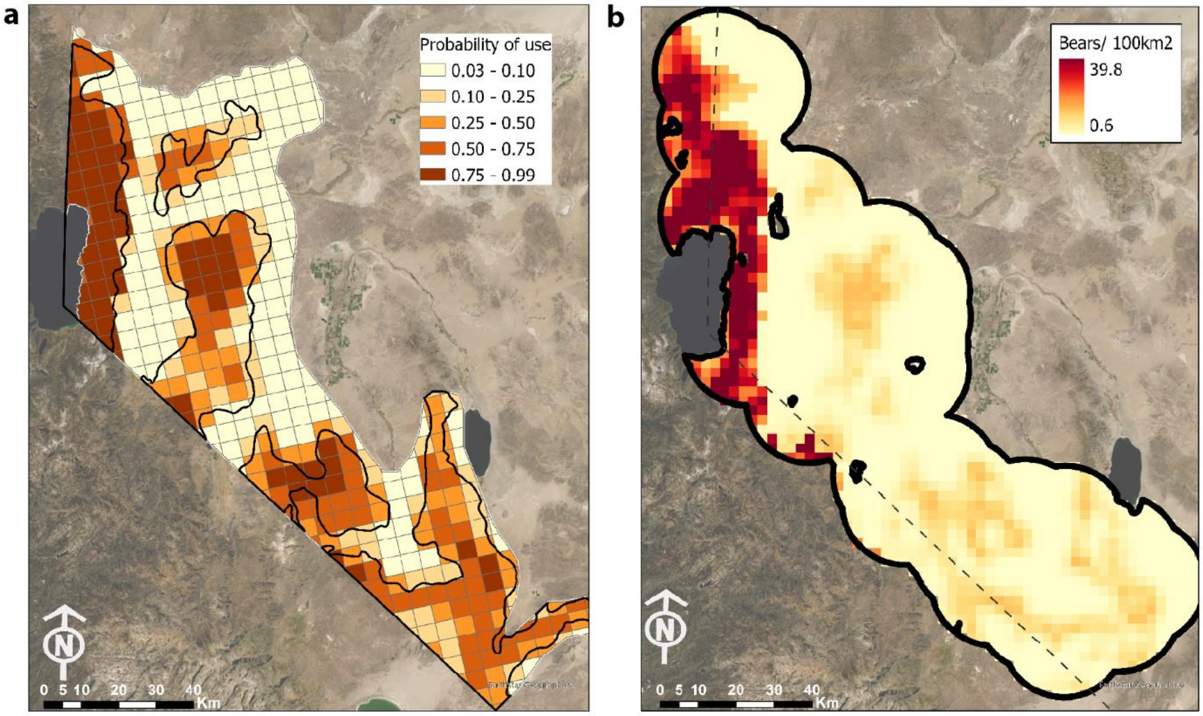

a
b
Ecoregion
Great Basin
Sierra Nevada
N
0 5 10 20 30 40
Km
N
0 5 10 20 30 40
Km

Figure 3


a
Probability of use
0.03 - 0.10
0.10 - 0.25
0.25 - 0.50
0.50 - 0.75
0.75 - 0.99
N
0 5 10 20 30 40
Km
b
Bears/ 100km2
39.8
0.6
N
0 5 10 20 30 40
Km