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ORIGINAL PAPER

Estimating population size and density of a low-density population of black bears in Rocky Mountain National Park, Colorado

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Abstract Rocky Mountain National Park (RMNP) is home to a low-density black bear (*Ursus americanus*) population that exists at >2,400 m with a very limited growing season. A previous study (1984–1991) found bear densities among the lowest reported (1.37–1.52 bears/100 km^2). Because of concerns of viability of this small population, we assessed population size and density of black bears from 2003 to 2006 to determine the current status of RMNP's bear population. We used three approaches to estimate population size and density: (1) minimum number known, (2) occupancy modeling, and (3) catch per unit effort (CPUE). We used information from capture and remote-triggered cameras, as well as visitor information, to derive a minimum known population estimate of 20–24 individuals and a median density estimate of 1.35 bears/100 km^2. Bear occupancy was estimated at 0.46 (SE= 0.11), with occupancy positively influenced by lodgepole pine stands, non-vegetated areas, and patch density but negatively influenced by mixed conifer stands. We combined the occupancy estimate with mean home-range size and overlap for bears in RMNP to derive a density estimate of 1.44 bears/100 km^2. We also related CPUE to density estimates for eight low-density black bear populations to estimate density in RMNP; this estimate (1.03 bears/100 km^2) was comparable to the occupancy estimate and suggests that this approach may be useful for future population monitoring. The use of corroborative techniques for assessing population size of a low-density black bear population was effective and should be considered for similar low-density wildlife populations.

Keywords Black bear · Colorado · Density · Occupancy · Population estimation · *Ursus americanus*

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Introduction

Estimates of population size for black bears (*Ursus americanus*) are important for assessing trends and understanding dynamics of populations (Miller et al. 1997) but are difficult to obtain due to their low population densities, secretive nature, and use of relatively inaccessible habitat (McCutchen 1990; Costello et al. 2001; Pelton 2003; Romain-Bondi et al. 2004). Past data on size of the black bear population in Rocky Mountain National Park (RMNP), Colorado, suggested one of the lowest density populations recorded (1.37–1.52 bears/ 100 km^2; L. Zeigenfuss, United States Geological Survey, unpublished report). Monitoring such low-density populations is necessary to maintain viability, although extremely difficult (Romain-Bondi et al. 2004).

Many techniques have been used to estimate black bear densities, with mark–recapture techniques most frequently used (e.g., Lindzey and Meslow 1977; Miller et al. 1987; Clark and Smith 1994). However, results from mark–recapture are often biased because they do not meet ≥1 of the assumptions or do not clearly delineate the area used by the population (Miller et al. 1997; Pelton 2003). In particular, mark–recapture methods do not work well for low-density populations, as it is difficult to establish enough capture–recapture events to provide valid estimates (Seber 1982; Romain-Bondi et al. 2004).

Enumerating the minimum number of individuals may provide realistic estimates of population size (Beck 1991; McCutchen 1993). Enumerating bears can be accomplished from a variety of methods including capture (Beck 1991; Costello et al. 2001) and camera trapping (Beck 1997; Martorello et al. 2001). Physical descriptions of black bears are often provided by visitors to National Parks and can also provide evidence of unidentified black bears in low-density populations. Additionally, capture-related enumeration allows determination of the effort needed to capture individuals. Catch per unit effort (CPUE) has been used to relate grizzly bear (*Ursus arctos*) detection to density estimates (Romain-Bondi et al. 2004) and was effective at estimating density and population size for this extreme low-density population.

Alternatively, the proportion of an area occupied by black bears can be estimated through the use of presence–absence data. Various methods have been used to assess presence–absence of bears, including the use of camera traps (Beck 1997; Martorello et al. 2001). However, failure to detect individuals (i.e., when a bear is present at a site but is not photographed) at sampling locations will underestimate occupancy (MacKenzie et al. 2002; Gu and Swihart 2004). Recent approaches that incorporate imperfect detection into occupancy estimates can result in less-biased occupancy models (MacKenzie et al. 2002). Occupancy modeling also allows incorporation of habitat variables in the form of covariates into occupancy analyses, thereby further improving occupancy estimates. Once derived, occupancy values can be related to home-range size and overlap to estimate numbers of individuals in populations (Augeri et al. 2006).

Maintaining viable populations of all wildlife species is a fundamental management goal of National Parks and other biosphere reserves (National Park Service 1988). Black bears are a valuable resource in RMNP because of high recreational and aesthetic values, as well as their importance as a key component of the natural ecosystem. However, population size and trends are currently unknown, limiting development of effective management policies for black bears in RMNP. Because of the difficulty in estimating and monitoring large carnivores in very small populations, using multiple estimators is desirable to provide independent estimates of population size (Grogan and Lindzey 1999; Noyce et al. 2001), although at least one of these estimators should be statistically robust. We therefore assessed population size and density of black bears in RMNP from 2003 to 2006 using three approaches: minimum number known, occupancy modeling, and CPUE estimators. The use of multiple estimators should provide greater insight into the population size of black bears in RMNP while providing the framework for future long-term monitoring strategies.

Study area

Rocky Mountain National Park is a 1,080-km^2 biosphere reserve located in the Rocky Mountain Front Range of north central Colorado. Topography in RMNP was shaped by glaciation and consists of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevations range from 2,400 to 4,345 m. The continental divide bisects RMNP, creating different climatic patterns to the east and west. The eastern part is drier, with precipitation averaging 35.1 cm in the town of Estes Park. Western RMNP is more mesic, with precipitation averaging 50.8 cm in the town of Grand Lake. Seventy-five percent of precipitation falls from April to September. In Estes Park, mean daily high temperatures range from 7.2°C in February to 27.8°C in July, while in Grand Lake, mean daily high temperatures range from 0.0°C in December and January to 23.9°C in July.

Vegetation in RMNP consists of >700 plant species. Lower slopes and valleys are comprised of forests of lodgepole (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*), blue spruce (*Picea pungens*), Douglas-fir (*Psuedotsuga menziesii*), juniper (*Juniperus* spp.), and aspen (*Populus tremuloides*) interspersed with bunchgrass and sedge-dominated herbaceous meadows. At higher elevations, subalpine forests of Engelmann spruce (*Pinus engelmannii*) and subalpine fir (*Abies bifolia*) predominate. Elevations above timberline are dominated by tundra and bare rock.

Methods

Capture efforts

We used modified Aldrich foot snares to capture black bears, with a culvert trap and wire box trap also used opportunistically in areas of heavier human use (e.g., campgrounds). Capture efforts were focused on sites with reported or observed bear activity and at sites predicted to be used by black bears (L. Zeigenfuss, unpublished report). We baited snares and traps with sardines and a sweet attractant (usually honey or molasses) and checked snares daily. Primary capture efforts occurred from late June–early October, 2003 and early June–mid-August, 2004–2006, with additional efforts occurring opportunistically from mid-August–late October, 2004–2006, based on reports of bear activity. We anesthetized bears with a 5:1 mixture of ketamine hydrochloride (approximately 7.4 mg/kg body mass) and xylazine hydrochloride (approximately

1.3 mg/kg body mass). Once sedated, we sexed, weighed, fitted bears with a VHF radio collar (Advanced Telemetry Systems, Isanti, MN, USA) containing a mortality sensor and ear-tagged individuals for visual identification.

Camera operation

We used ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to design a saturation trapping grid for camera sites throughout the study area. We placed cameras in grids with camera locations spaced approximately 5 km apart, which equated to the diameter of the approximate minimum female black bear home-range size in RMNP (L. Zeigenfuss, unpublished report), to ensure that no potential home range of a black bear was excluded from the camera-trapping grid (Karanth and Nichols 1998). When a pre-selected site was inappropriate (i.e., located on tundra, rocky cliff, etc.), we selected the closest appropriate site to place the camera. The same camera sites were used across years to remove confounding spatial variation (MacKenzie et al. 2006).

We used 25 passive infrared-triggered cameras (DeerCam®, Non Typical, Inc., Park Falls, WI, USA) loaded with 24 exposure 400 ASA film and programmed cameras to record date and time on photographs. We set time delays on cameras at 2–5-min intervals to maximize repeat photographs while reducing the chance that a single roll of film would be used before it could be replaced. We attached baits consisting of burlap sacks containing sardines and a sweet attractant (usually honey or molasses) to a tree approximately 2 m above the ground and 3–5 m from the camera. We checked film, bait, and batteries weekly and removed the cameras after 2 weeks for a total of 14 days of operation per site. Occasionally, we left cameras operational for longer durations due to logistical constraints, but cameras were operational for a minimum of 14 days in all but two cases (10 days for one location in 2004; 13 days for one location in 2005). Camera-trapping dates were from 10 August–25 October, 2004; 12 August–27 October, 2005; and 8 August–20 October, 2006.

Population and density estimation

We determined a minimum number known estimate (Elowe 1987) based on captured black bears (excluding cubs; cubs were similarly excluded from all other population estimates) and unique individuals identified from camera traps. Although non-captured individuals were unmarked, we were confident that we could individually identify most bears based on highly variable color patterns and size (Bowman et al. 1996), particularly given the low number of individuals in the population. Nonetheless, we could not conclusively differentiate some bears in photographs. To be conservative, we considered the indistinguishable bears as previously identified individuals. In addition, we used physical descriptions of bears from RMNP staff and visitor reports to determine presence of additional unidentified bears and included these with marked and uniquely photographed individuals to provide a minimum estimate of population size. We constructed a 3,203-m buffer (radius of mean female 95% minimum convex polygon (MCP) home-range size for RMNP; Baldwin 2008) around the boundary of RMNP in ArcView 3.3 to serve as the area of effect and added this to the total area of RMNP for density estimation. We divided estimated population size by the total area (1,627 km^2) to derive a density estimate.

We also used occupancy modeling to estimate population size and density. This approach incorporates imperfect detection of bears at camera sites resulting in an unbiased occupancy model (MacKenzie et al. 2006) and also incorporates habitat variables in the form of covariates to strengthen occupancy estimates (MacKenzie et al. 2002). For habitat attributes, we used land cover types (Table 1) developed from GIS coverages (30-m resolution) of RMNP and surrounding areas provided by RMNP staff (R. Thomas, RMNP, unpublished data) and created a 400-m buffer around all human-use areas (trails, roads, campsites, and other developed areas) to assess their impact on black bear occurrence. We also selected seven landscape metrics (Table 2) based on their depiction of important landscape factors for bears (Linke et al. 2005) to relate to bear occupancy. We calculated all landscape variables using the Patch Analyst extension (Elkie et al. 1999) in ArcView 3.3.

We related black bear occurrence to cover types and landscape metrics through the use of a 32.2-km^2 sampling window around the camera location and used data collected within this buffer in subsequent analyses. We selected this window size to represent the average home-range size of female black bears in RMNP (Baldwin 2008). All cover types represented the proportion of the window covered by their respective class. Last, we included a year effect in analyses to determine if occupancy varied by year, and we separated camera sites into western and eastern subdivisions of RMNP to assess large-scale differences in precipitation and associated vegetative communities.

For analysis, we used the modeling approach described by MacKenzie et al. (2006) using program PRESENCE (United States Geological Survey, Patuxent Wildlife Research Center, USA; http://www.mbr-pwrc.usgs.gov/software.html) with cover type and landscape variables included as covariates in the analysis. Because the time and date of each black bear visit was recorded on each photo, we were able to use each operational day as a sampling event. However, detection probabilities (p) were low for many sites ($p<0.05$), so we combined trapping nights into 4-day blocks to increase this rate (O'Connell et al. 2006). This yielded three to four survey periods for each site per sample period. For analysis, given some data values >10, we divided all covariates by 10 as a rescaling mechanism (Program PRESENCE ver 4.0; http://www.mbr-pwrc.usgs.

Table 1 Description of cover types used to estimate black bear occupancy for Rocky Mountain National Park, Colorado

Cover type	Description
Herbaceous upland	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Mesic shrublands	Shrublands lining stream banks and valley bottoms
Xeric shrublands	Shrub-dominated communities associated with drier sites
Krummholz	Characterized by stunted limber pine, Engelmann spruce, and subalpine fir at treeline
Dead and down	Characterized by fallen timber from wind, avalanches, or fire
Aspen	Forested site dominated by aspen
Mixed conifer with aspen	Canopy dominated by aspen and mixed conifer species
Riparian mixed conifer	Canopy dominated by spruce/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of 2 or more coniferous species including Engelmann spruce and subalpine fir
Lodgepole pine	Canopy dominated by lodgepole pine
Limber pine	Canopy dominated by limber pine
Ponderosa pine	Canopy dominated by ponderosa pine
Montane Douglas-fir	Canopy dominated by Douglas-fir though ponderosa pine could be codominant
Rock	Characterized by rock, bare soil, or snow
Non-vegetated surface	Included areas covered by roads, trails, and campsites

Table 2 List of landscape metrics and associated descriptions related to black bear occurrence in Rocky Mountain National Park, Colorado

Variable	Description
Patch density	Number of patches/km^2
Edge density	Meters of edge/ha
Total core area index	Measure of the amount of core area on the landscape
Area-weighted mean shape index	Measure of shape complexity
Shannon's diversity index	Measure of relative patch diversity
Shannon's evenness index	Measure of patch distribution and abundance
Interspersion juxtaposition index	Measure of patch adjacency

gov/software/doc/presence/presence.html#covariates). This provided true maximum likelihood estimation, while also facilitating odds ratio interpretation.

For occupancy (Ψ) estimation, we ran all univariate models to determine if they provided substantially more information than the null model [Ψ(.), *p*(.); we held *p* constant for all models]. Only those models with covariates that ranked higher than the null model (i.e., had smaller Akaike's information criterion values corrected for small sample size (AIC_c); Burnham and Anderson 2002) were used in further analyses thereby allowing us to reduce the number of covariates and minimize the chance for spurious results (Baldwin and Bender 2008b). We assessed correlations between remaining covariates using Spearman's ranked test. If variables were correlated at $r_s \geq 0.70$, only the covariate with the lower AIC_c value was included in further analyses to reduce redundancy (Agresti 1996). Once the data set was reduced, we constructed an occupancy model with all remaining variables. We then sequentially removed the variable that contributed the least to the model (as identified by minimal absolute value of β/SE, i.e., stepwise backward-selection approach) one at a time and compared corresponding AIC_c scores after each removal to determine which model resulted in the lowest AIC_c score (Pagano and Arnold 2009). This model was considered the best supported model, and we used maximum rescaled generalized R^2 values (Nagelkerke 1991) to help interpret model fit. We ran 1,000 bootstrap samples and used Pearson's goodness-of-fit test to assess the fit of the global model (MacKenzie and Bailey 2004). We also checked for overdispersion of data ($\hat{c}>1.0$) to determine if adjustments in variance estimates and model selection procedures were needed. We used odds ratios with 85% confidence intervals (CIs) to interpret relationships of habitat factors to bear use (Arnold 2010). We used 85% CIs given that AIC-based model selection approaches support additional variables at $P<0.157$ (Arnold 2010). Finally, we estimated the number of trap sites where bears were present but not detected (i.e., false absences; MacKenzie et al. 2006) using the equation $(1-p)^K$ where K=number of survey replicates.

Once we determined the best model, we estimated male and female black bear density separately by relating occupancy (divided by 2 to separate by sex) values to average home-range size and overlap (the proportion of each individual bears home range that was overlapped by any radio-collared bears) for males [mean 95% MCP home-range size=68.0 km^2 (SE=16.5); overlap of 95% MCP home ranges=0.108 (SE=0.062); Baldwin 2008] and females [mean 95% MCP home-range size=32.2 km^2 (SE=5.0); overlap of 95% MCP home ranges=0.325 (SE=0.050); Baldwin 2008] using:

$$\text{minimum density} = (\Psi/2) \times 100\ \text{km}^2/[\text{HRS} \times (1-\text{HRO})]$$

where HRS = home-range size and HRO = percentage of home-range overlap (modified from Augeri et al. 2006). We estimated density separately for males and females given that home-range size and overlap can vary substantially between male and female black bears (Pelton 2003). We then combined these values to estimate total black bear density/100 km^2. We constructed 90% CIs for density estimates using parametric bootstrapping that incorporated error from occupancy, home-range size, and home-range overlap estimates (Bender et al. 1996). Although we did not have home-range size and overlap information for all black bears in RMNP, we had information for the majority of black bears residing east of the continental divide, which was where all but two radio-collared bears were captured. Therefore, we felt that estimates of overlap were accurate. Nonetheless, estimates of population size were potentially biased low given the potential for greater home-range overlap.

Last, we used regression (Zar 1999) to relate CPUE to density estimates for all studies we were able to locate for black bears in the USA that provided information on CPUE for actual captures (not camera-trapping) and reported densities of <20 bears/100 km^2 (Table 3). We defined CPUE as the number of unique black bears physically captured/1,000 trap nights; density estimates (excluding cubs) were derived through different methods including Bowden's estimator, Lincoln–Peterson estimator, minimum number known, modified Peterson estimator, and population reconstruction (Table 3). We would have preferred utilizing studies that used the same method for estimating density, but such standardization was not possible given the limited number of studies. Such variation may weaken results but should not over-inflate model fit. All inputs were log-transformed to represent a curvilinear relationship (Romain-Bondi et al. 2004), and residual plots were checked to assess outliers.

Table 3 List of studies and locations used to relate CPUE (number of unique bears captured/1,000 trap nights) to density (bears/100 km^2) of black bears

Study	Location	CPUE	Density[a]
This study	Colorado	6.9	1.4
Grogan and Lindzey 1999	Wyoming	22.4	2.5
Orlando 2003; Brown 2004	Florida	16.9	2.9
Harter 2001	South Carolina	21.7	5.7
Costello et al. 2001	Western New Mexico	42.3	9.4
Cunningham and Ballard 2004	Arizona	43.8	12.9
Frost 1990	Utah	29.1	12.9
Costello et al. 2001	Northern New Mexico	48.2	17.0
Kasworm and Manley 1988	Montana	38.9	17.4

[a] Density estimators included: Bowden's estimator = Grogan and Lindzey (1999); Lincoln–Peterson estimator = Kasworm and Manley (1988) (excluding cubs), Harter (2001), and Brown (2004); minimum number known = Frost (1990), current study; modified Peterson estimator = Cunningham and Ballard (2004); population reconstruction = Costello et al. (2001)

We constructed an initial model without RMNP included to predict bear density estimates for our study site, and a second model including RMNP (using minimum number known densities) to see whether inclusion of RMNP data affected model performance.

Results

Minimum number known

We totaled 3,617 trap nights (2003=934, 2004=1,222, 2005=860, 2006=601) resulting in 16 total captures (2003=8, 2004=1, 2005=4, 2006=3) of 14 individual black bears [eight females (four adult, four subadult); six males (four adult, two subadult)]. Of these captures, 14 were in snares, and one each in culvert and wire box traps. Although we exerted greater trapping effort in the western portion of the park (western: 2003=0, 2004=1,019, 2005=619, 2006=392, and total=2,030 trap nights; eastern: 2003=934, 2004=203, 2005=241, 2006=209, and total=1,587 trap nights), the total number of captures was greater in eastern RMNP (west=3, east=13). This yielded one black bear capture per 676.7 and 132.3 trap nights for the western and eastern portions of RMNP, respectively, for a total of one capture per 241.1 trap nights for the entire park. The bear captured in the cage trap was excluded from CPUE values as no measurable effort was expended on our part (incidental capture by D. Hunter, United States Geological Survey, Fort Collins, CO, USA).

We operated cameras for 2,608 days (850, 868, and 890 days in 2004, 2005, and 2006, respectively) resulting in visual identification of a minimum of 11 additional black bears from 14 total bear visits (2004=4, 2005=7, 2006=3) to seven sites in the western portion of RMNP and ten total visits (2004=1, 2005=5, 2006=4) to seven sites in the eastern portion of the park (Fig. 1). This yielded one visit per 89.1 and 131.8 camera nights for western and eastern RMNP, respectively, for a total of one visit per 108.7 camera nights.

Although the largest number of individuals captured occurred in the eastern portion of RMNP (12 eastern, two western), the distribution of photographed individuals was similar (six eastern, five western). Two collared black bears were harvested, and two other mortalities of collared individuals from unknown causes resulted in a minimum number of 21 individuals (15 on the eastern side, six on the western side). Two of these black bears were photographed on the periphery of the park (<1 km from boundary) and were not subsequently observed again; they may not have extensively used park property so we reduced the minimum number known value by 1 (half of 2) to account for this probability. Based on location and physical descriptions of

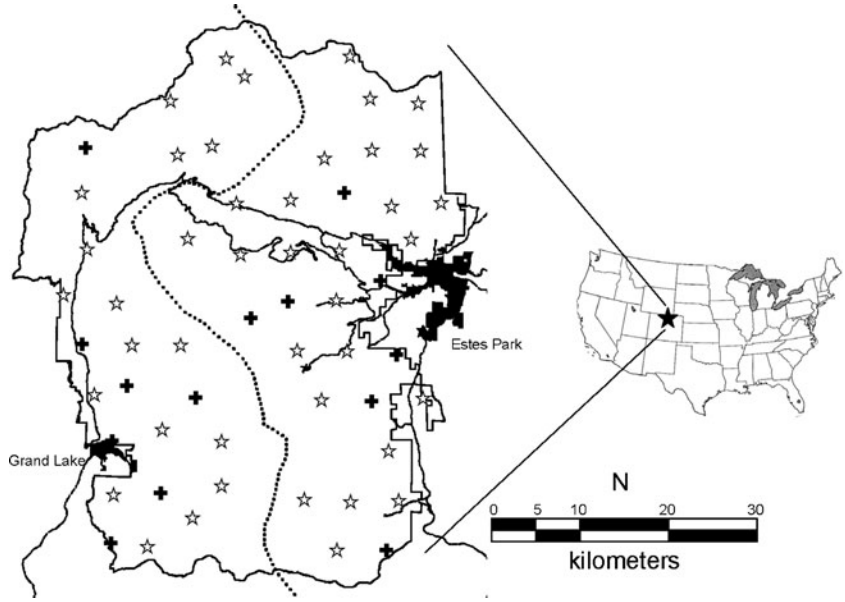

Fig. 1 Map depicting camera locations operated from 2004 to 2006 to detect bear presence in Rocky Mountain National Park (RMNP), Colorado. Camera locations with bear visits are depicted by *crosses*, while those without bear visits are marked with *stars*. The *dotted line* demarcates the western and eastern subdivisions of RMNP, the *dashed lines* represent park roads and highways, while *dark areas* represent towns

black bears given in visitor reports, it was likely there were another one to two bears on both the western and eastern portions of the park resulting in a total population size of 20–24 black bears. It should be noted that this estimate assumed no additional mortality during the sampling period. However, annual survival was high during our study [adults=0.96 (SE=0.04), subadults=0.83 (SE=0.14); Baldwin and Bender 2009b], so additional mortalities should have been minimal. Therefore, we assumed 22 individuals in the population, which resulted in a density estimate of 1.35 bears/100 km^2 in RMNP (range=1.23–1.48 bears/km^2).

Occupancy modeling

For univariate occupancy modeling, eight covariates (lodgepole pine, non-vegetated surfaces, rock, mixed conifer, and herbaceous upland cover types; subdivision of RMNP; patch and edge density) increased AIC_c rankings over the null model. However, lodgepole pine was negatively correlated with herbaceous upland (r_s=−0.75), while patch density was negatively correlated with edge density (r_s=−0.92) and the eastern subdivision of RMNP (r_s=−0.72). Given that herbaceous uplands, edge density, and subdivision of RMNP provided less additional information than their correlated counterparts, these covariates were excluded from multivariate analyses.

The best supported occupancy model included lodgepole pine, patch density, non-vegetated surfaces, and mixed conifer and explained 17% of the variance unaccounted for by the null model. Goodness-of-fit simulation models suggested a good fit of the model ($\hat{c}$=0.94, P=0.29). An assessment of the parameter estimates for the top model indicated that occupancy was the greatest at sites with a greater proportion of lodgepole pine [β=0.04 (SE=0.01); odds ratio=1.04 (85% CI=1.02–1.05)] and non-vegetated surfaces [β=0.24 (SE=0.18); odds ratio=1.28 (85% CI=0.99–1.65)], greater patch density [β=0.25 (SE=0.10); odds ratio=1.28 (85% CI=1.12–1.48)], and less mixed conifer [β=−0.008 (SE=0.006); odds ratio=0.99 (85% CI=0.98–1.00)], although non-vegetated surfaces and mixed conifer were not significant covariates in the model given that 85% CIs overlapped with 1. Detection probability for this study was low [p=0.07 (SE=0.02)] and yielded a false-absence rate of 0.75. Using this model, occupancy of RMNP from 2004 to 2006 was 0.46 (SE=0.11). When combined with home-range size and overlap, we determined density estimates of 1.06 female bears/100 km^2 (90% CI=0.69–1.53) and 0.38 male bears/100 km^2 (90% CI=0.24–0.60) for a total of 1.44 bears/100 km^2 (90% CI=0.98–2.04).

Catch per unit effort

Given the possible presence of trap-shy bears in the western portion of the study area (illustrated by large difference for CPUE between western and eastern RMNP from trapping efforts and large disparity between trapping and camera CPUE for western RMNP), we used CPUE (6.9 bears/1,000 trap nights) only from eastern localities for regression analyses. Based on residual plots, we considered the study site in Wyoming (Grogan and Lindzey 1999), an outlier, and excluded it from further analyses [although inclusion of the Wyoming site still resulted in highly significant models (including RMNP: $F_{1,7}$=32.5, P<0.001, R^2=0.82; without RMNP: $F_{1,6}$=17.2, P=0.006, R^2=0.74)]. Resultant models indicated a strong relationship between CPUE and density ($F_{1,6}$=54.0, P<0.001; Fig. 2). The model excluding RMNP also yielded a strong relationship ($F_{1,5}$=17.5, P=0.009; Fig. 2) with predicted density values (1.03 bears/100 km^2, 90% CI=0.27–3.67) relatively comparable to the 90% CI

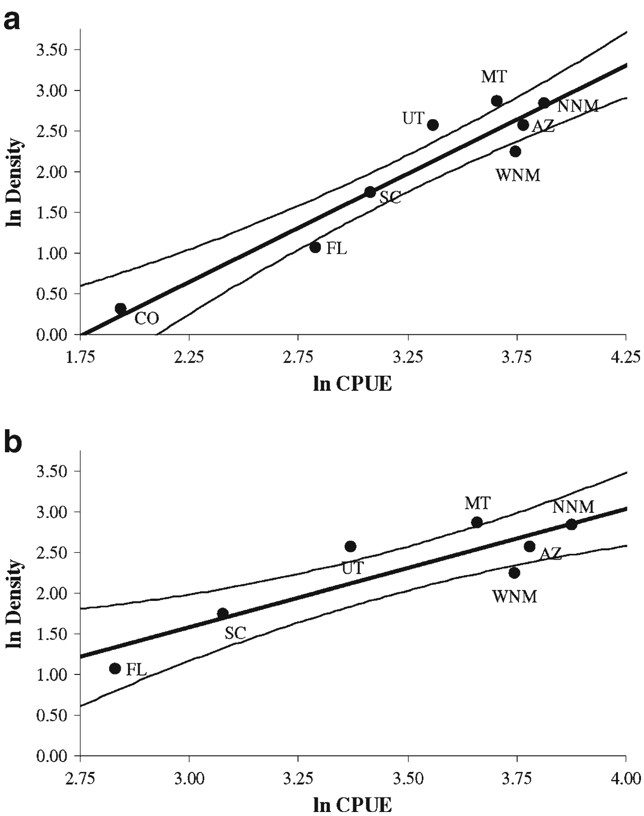

Fig. 2 Regression and 90% CI relating ln catch per unit effort (number of bears captured/1,000 trap nights; CPUE) to ln density (number of bears/100 km^2; density) for eight black bear studies in the USA (*AZ* Arizona, *CO* Colorado, *FL* Florida, *MT* Montana, *NNM* northern New Mexico, *SC* South Carolina, *UT* Utah, *WNM* western New Mexico; see Table 3 for further description): **a** includes CO study site, **b** excludes CO study site. Model equations: **a** $\ln(\text{Density}) = 1.326 \times (\ln[\text{CPUE}]; \text{SE} = 0.347) - 2.337, R^2 = 0.900$ and **b** $\ln(\text{Density}) = 1.451 \times (\ln[\text{CPUE}]; \text{SE} = 0.181) - 2.780, R^2 = 0.777$

derived from the occupancy model. Because we observed a minimum number known (n=14) and subsequent minimum density estimate (0.86 bears/100 km^2), we were able to truncate the lower end of the CPUE CI (90% CI=0.86–3.67). Slope (t=0.39, P=0.704) did not differ between models with and without RMNP.

Discussion

Accurate population and density estimates of black bears are difficult to obtain given the need for intensive sampling and likely violations of assumptions of many approaches (Romain-Bondi et al. 2004). Although total enumeration of a population is often difficult, it may be the best alternative for extremely low-density populations (Beck 1991; McCutchen 1993), particularly when intensive capture efforts are required for estimation of other population parameters (i.e., survival, recruitment, home-range size, etc.). Our minimum number known estimates indicate that RMNP had the lowest density of black bears reported in the literature (1.23–1.48 bears/100 km^2), with this estimate consistent with previous reported minimum known densities for RMNP (1.37–1.52 bears/100 km^2; L. Zeigenfuss, unpublished report) and corroborated by mean estimates from occupancy (1.44 bears/100 km^2) and CPUE (1.03 bears/100 km^2) methods. Although attempting to enumerate the entire population required significant effort, we felt it was the most accurate method given the additional knowledge we obtained about the population (e.g., survival and recruitment rates, nutritional condition estimates, population growth rates, etc.). Moreover, knowing the minimum number of individuals best addresses population persistence, which is the critical question when managing extremely low-density populations.

Detection probabilities were low (p=0.07) for our occupancy modeling approach even after combining four camera nights into a single sampling unit. Detection probabilities between 0.05 and 0.15 can result in less confidence in occupancy estimates than for models with detection probabilities >0.15 given the difficulty in differentiating between sites where bears are poorly detected from sites where they are truly absent (O'Connell et al. 2006). However, our model yielded a density estimate that was very similar to those obtained from minimum number known and CPUE methods and lends credence to this approach. Regardless, accounting for imperfect detection was necessary as adjusted occupancy estimates (Ψ=0.46) were nearly twice as large as naïve estimates (Ψ=0.25) given the large proportion (0.75) of estimated sites where bears were present but not detected. For future studies, incorporating additional sampling locations could increase detection probabilities and would likely reduce the variability of occupancy and detection probability estimates, thereby increasing confidence in this approach.

One of the advantages of the occupancy approach is that when combined with home-range size and overlap, it allows for changes in density to be tracked over time by using a repeated, noninvasive sampling strategy that reduces stress on sampled bears. However, information on home-range size and overlap may not be available for the population in question. Fortunately, for long-term monitoring, using occupancy estimates alone may have advantages over either total enumeration or estimating density. For example, there are circumstances when occupancy rates are density dependent and can serve as a surrogate for density as an indicator of population status (MacKenzie and Nichols 2004; MacKenzie et al. 2006). This approach eliminates the need to estimate home-range size and overlap and thus the uncertainty associated with these measures.

A further advantage of the occupancy modeling approach lies in assessing the relationship between habitat components and occupancy (MacKenzie 2006). For example, bears were observed more frequently at sites with a greater proportion of lodgepole pine. Lodgepole pine stands in RMNP contained a greater proportion of ant sources (e.g., ant mounds, fallen logs, etc.) than all other habitat types combined (Baldwin 2008), with ants constituting the greatest volume of any food source consumed by bears in RMNP (Baldwin and Bender 2009a). Similarly, lodgepole pine was related to historic bear use in RMNP (1984–1991; L. Zeigenfuss, unpublished report). Therefore, it is possible the prevalence of this important food source led to greater occupancy of lodgepole pine stands.

A greater density of landscape patches was also associated with bear occupancy. Such a patchwork landscape provides a wide diversity of resources for bears, which is likely more important in RMNP than in most other locations given the paucity of abundant food sources in high elevation areas (Beck 1991). Although not a significant covariate in the model, it is interesting to note that non-vegetated surfaces, which are areas covered by roads, trails, and campsites, were positively related to bear occupancy. This is counter to what was observed historically in RMNP (L. Zeigenfuss, unpublished report) but is consistent with more recent observations (Baldwin 2008; Baldwin and Bender 2008a). Bears in RMNP may be habituating to human-use areas and should be closely monitored in the near future.

Relationships between CPUE and density estimates further corroborated minimum number known densities (1.03 vs. 1.35 bears/100 km^2, respectively) and provided a potentially useful tool for monitoring other low-density populations. We found relatively strong relationships between CPUE and density estimates using curvilinear models, similar to Romain-Bondi et al. (2004) for grizzly bears (R^2=0.927) in the North Cascade Ecosystem of Washington and British Columbia, likely because such models fit data better given the curvilinear relationship between home-range size and density for bears (Oli et al. 2002; Pelton 2003; Romain-Bondi et al. 2004).

Moreover, the primary purpose for relating CPUE to density was to establish a method for estimating density when densities are too low to be estimated by other means. Romain-Bondi et al. (2004) estimated density for a small grizzly bear population that was outside the range of data they used to build their CPUE models given that they had little reason to assume relationships did not hold true beyond the sampled range and because the population was too small to be estimated by other methods. Although extrapolation beyond the range of model data should be viewed with caution, models excluding data from our study predicted density estimates consistent with the 90% CI of values derived for RMNP from the occupancy approach. Furthermore, parameter estimates of CPUE models with and without RMNP did not differ, suggesting a robust relationship between density and CPUE among low-density black bear populations and provided additional evidence for the validity of the overall CPUE model. That being said, the effort required to snare black bears in western RMNP was much greater than for camera detection, whereas CPUE values derived from snaring and camera trapping were almost equivalent for eastern RMNP. This suggests substantial trap shyness for black bears in western RMNP, the reason for which is unknown but could be related to increased hunting pressure compared to eastern localities or previous experience with capture techniques. Therefore, unless populations are too small to be estimated by other techniques, we do not recommend using CPUE models as the only approach for monitoring populations, but rather to corroborate estimates derived from other approaches (i.e., occupancy; Jennelle et al. 2002). Ultimately, developing predictive models from more rigorously controlled studies (e.g., occupancy modeling, mark/recapture through hair snaring) with standardized protocols for estimating density and CPUE would likely result in a stronger relationship and warrants further investigation particularly given the limited funding available for such research and inventory projects.

Management implications

Inventorying and monitoring ultra low-density bear populations is very difficult or impossible using traditional mark–recapture approaches (Romain-Bondi et al. 2004). However, the utilization of alternative approaches may provide the opportunity to inventory such populations. In this study, we used a combination of trapping, remote-triggered cameras, and National Park visitor sighting information to enumerate the minimum number of black bears in RMNP. Next, we utilized these same remote-triggered cameras through occupancy modeling to develop a statistically robust estimate of density. Lastly, we developed a CPUE model from trapping data to help corroborate these findings. Results from our study provided consistent mean density values (1.03–1.44 bears/100 km^2), thus providing confidence in our estimates. It is this use of corroborative techniques that we feel is a key concept to consider when inventorying low-density populations given that monitoring such a small number of wide-ranging individuals is substantially impeded by minimal encounter opportunities.

Because of limitations in funding for research and management projects for black bears and other wildlife species, it is important to maximize the outputs obtained from such studies. For example, habitat use can be determined from occupancy modeling (e.g., Baldwin and Bender 2008b). Alternatively, radiotransmitters can be placed on trapped individuals to assess survival, recruitment, movement and activity patterns, and habitat use (e.g., Baldwin 2008; Baldwin and Bender 2008a, 2009b, 2010). This information can be combined with simultaneously derived density assessments to develop a management plan, ultimately providing a stronger use of research and management funds for managing the target species

(Nichols and Williams 2006). We encourage others to consider a similar approach when monitoring and managing other low-density populations.

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