FISEVIER

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc



Using non-invasive mark-resight and sign occupancy surveys to monitor low-density brown bear populations across large landscapes



Joshua H. Schmidt ^{a,*}, Kumi L. Rattenbury ^b, Hillary L. Robison ^c, Tony S. Gorn ^d, Brad S. Shults ^{e,1}

- ^a Central Alaska Network, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA
- ^b Arctic Network, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA
- ^c Western Arctic National Parklands, U.S. National Park Service, P.O. Box 1029, Kotzebue, AK 99752, USA
- ^d Division of Wildlife Conservation, Alaska Department of Fish and Game, P.O. Box 1148, Nome, AK 99762, USA
- ^e Western Arctic National Parklands, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA

ARTICLE INFO

Article history: Received 2 August 2016 Received in revised form 12 December 2016 Accepted 10 January 2017 Available online 29 January 2017

Keywords:
Abundance
Brown bear
Den survey
Landscape scale
Mark-recapture
Occupancy
Photographic marks
Population monitoring
Rare species

ABSTRACT

Reliable assessments of low-density carnivore populations such as brown bears *Ursus arctos* are often limited by a lack of sufficient information for strong inference at appropriate scales. Standard approaches often rely on physical marking of individuals or the use of inherently field-intensive hair-snag or distance sampling techniques. Although these tools are very useful, logistical and monetary costs often limit their successful application, particularly in large, remote areas. We developed a novel photographic mark-resight approach using physical characteristics and spatial locations of individual brown bears to temporarily mark individuals over a short revisit interval. We applied this approach along with site-occupancy techniques to evaluate a low-density brown bear population in northwestern Alaska. Based on the mark-resight approach, we estimated there were 420 [95% Crl:274–650] independent and 713 [95% Crl:474–1070] total brown bears in our 19,998km² study area. When expressed as densities, these estimates were consistent with those of other low-density populations from the surrounding area. Estimated den and bear site-occupancy rates were similar, 0.48 [95% Crl:0.37–0.63] and 0.40 [95% Crl;0.28–0.55], respectively. Close congruence among occupancy and abundance estimates supported the robustness of our new mark-resight approach and provided additional metrics for population monitoring. Together, these parallel metrics provide a general framework for monitoring low density populations of brown bears and other rare carnivores when physical marking or intensive survey techniques are impractical.

Published by Elsevier Ltd.

1. Introduction

Estimates of abundance and density are commonly used for monitoring and management of wildlife populations, although these state variables are difficult to measure for rare species (Thompson, 2004). Although many powerful approaches have been used to estimate the abundance and density of large carnivores in a variety of settings and habitats, strong inference is often lacking precisely because individuals are sparsely distributed and difficult to sample (MacKenzie et al., 2005). Mark-resight techniques, often employing radio-collars, are well developed and have been successfully used for many years (e.g., Hein and Andelt, 1995; Miller et al., 1997). Similarly, replicate photographs recorded by spatially distributed camera-traps have been used to 'mark' and subsequently 'resight' individuals based on unique marking patterns (e.g., tigers, Karanth and Nichols, 1998; pumas, Negrões

et al., 2010). Spatially-explicit mark-recapture analytical techniques are then used to estimate population parameters of interest (Royle et al., 2009; Gardner et al., 2010a; Royle et al., 2011). Analogously, DNA samples collected with hair snag traps or other means can also be analyzed in a spatial capture-recapture analytical framework to assess abundance and density (Gardner et al., 2009; Gardner et al., 2010b; Kéry et al., 2011; Russell et al., 2012). Distance sampling approaches have also been used and have the advantage of not requiring the identification of individuals (Becker and Quang, 2009; Becker and Christ, 2015). Each of these approaches can provide useful assessments of population abundance and density, but their implementation can be logistically challenging at large spatial scales.

Capture operations required to physically mark individuals are generally expensive, particularly for species such as brown bears (*Ursus arctos*), often leading to relatively small sample sizes and restricted sampling areas. Alternative approaches such as distance sampling can be conducted over broad areas; however, intensive sampling may be required, sometimes over multiple seasons, in order to acquire sufficient numbers of detections (Becker and Quang, 2009; Reynolds et al., 2011). These requirements have obvious drawbacks when attempting

^{*} Corresponding author.

E-mail addresses: joshua_schmidt@nps.gov, Joshua_Schmidt@nps.gov (J.H. Schmidt).

¹ Current address: Division of Migratory Bird Management, U.S. Fish and Wildlife Service, 1011 East Tudor Road, MS 201, Anchorage, AK, 99,503, USA.

to sample low density bear populations. Spatially-explicit mark-recapture techniques using DNA to identify individuals are often successful even when sample sizes are reduced, but the deployment and collection of traps at the scales necessary for desired inference can be logistically prohibitive (De Barba et al., 2010). Although each of these powerful approaches can be applied successfully in certain situations, high cost or restricted spatial inference may lead to the pursuit of other more easily estimated state variables closely related to abundance and density (e.g., occupancy).

Site-occupancy modeling approaches (MacKenzie et al., 2002, 2006) are a common alternative for monitoring populations of rare species when approaches for estimating abundance are not feasible. Siteoccupancy surveys are often more practical logistically and provide useful information directly related to abundance (MacKenzie et al., 2005; Tempel and Gutierrez, 2013). Identification of individuals is not required, but rather the detection/non-detection of the species of interest at each site is used to estimate detection probability and the proportion of the sites that contain ≥1 individual. For species that are rare or otherwise difficult to detect, signs (e.g., tracks, feces, dens) may be used as an alternative to the direct detection of individuals to provide inference to the population of interest (Stanley and Royle, 2005; Karanth et al., 2009; Hines et al., 2010; Long et al., 2011; Wilson and Schmidt, 2015). The logistical efficiency of occupancy surveys can often be used to increase spatial inference, providing information at the landscape scale that would be impossible if more intensive methods were used (Karanth et al., 2011). Interestingly, multi-metric monitoring approaches that exploit the inferential benefits of both occupancy and abundance estimation are less well developed. In many cases, occupancy and abundance data could be collected simultaneously for little additional cost. If properly designed, parallel site-occupancy and abundance surveys could be used to provide more comprehensive inference useful for managers of species occurring at low densities.

Brown bears often occur at low densities presenting many challenges for sampling. Collar-mark-resight (e.g., Miller et al., 1997), DNA mark-recapture (Solberg et al., 2006; Boulanger et al., 2008; Kendall et al., 2008), or distance sampling approaches are the most commonly employed methods for assessing brown bear populations, although, costs often limit the successful application of such field methods in large, remote areas. Unfortunately, such areas often support large components of the overall population important for conservation and management. The desire to assess and manage populations occurring in large, remote areas can lead to the pursuit of abundance estimates despite high risk of poor estimator performance due to low sample sizes (Reynolds et al., 2011). Occupancy methods require less data than abundance approaches, tend to be more precise, and can provide important trend information. However, occupancy surveys in continuous habitat require careful consideration of plot size and individual movements during the revisit period (Efford and Dawson, 2012). Abundance information, while generally more difficult to obtain, is often relied on for management, particularly for harvested species. We propose that the collection of both occupancy and abundance information may provide a tractable solution to the problem of monitoring and managing bears and other rare species in a variety of settings.

Here we introduce a novel non-invasive mark-resight survey approach, applied concurrently with site-occupancy and sign surveys, to estimate abundance and site-occupancy rates for a low density brown bear population in northwestern Alaska. Our primary objectives were to: 1) estimate den site-occupancy, 2) estimate bear site-occupancy, and 3) estimate brown bear abundance and density. We show that each data type provides information useful for addressing unique monitoring and management goals and strengthens overall conclusions. We expect our approach could be used to improve monitoring of brown bears throughout much of their range, in addition to being broadly applicable to other rare carnivore species.

2. Material and methods

2.1. Study area

Our study area encompassed a 19,998 km² area of the central Seward Peninsula in western Alaska, USA (Fig. 1). The terrain ranges from flat tussock-tundra, to rolling hills and steep rugged terrain in the Bendelaben and Kigluaik Mountains. Woody vegetative cover is generally sparse in northern areas of tussock tundra, consisting primarily of willow (*Salix* spp.) thickets along riparian corridors. Shrub patches become more common in the southern portion of the study area where alder (*Alnus* spp.) is also present. Areas of spruce (*Picea* spp.) forest are restricted to the extreme southeast portion of the study area. Black bears do not generally occur on the central Seaward Peninsula, so all observations of bears and bear sign were assumed to be related to brown bears. Brown bears occur throughout the area in all habitat types, although densities are generally greater further south.

2.2. Sampling design

We used a systematic sampling design to provide uniform coverage over the entire area and to minimize movement of bear groups between sampled units during the survey period (Fig. 1). We began by generating a systematic grid of 31 km² cells across the entire study area. Individual cells represented potential sampling subunits. Our choice of cell size was based on anticipated bear densities (1–2 bear groups/subunit) based on past work (Miller et al., 1997) and the expected amount of time required to adequately search each subunit (≤1 h). We selected groups of 4 adjacent cells, regularly spaced throughout the area, to form 48 primary sampling units each consisting of 4 subunits (Fig. 1). Spacing between primary units (i.e., >11 km) was intended to be large enough to minimize the probability that an individual bear could be observed in adjacent units on the same or separate days. As much as was practical, we surveyed groups of primary units in sequence to further avoid the potential effects of movement of individual bears among units between days.

2.3. Field methods

Aerial surveys were conducted in both 2013 and 2015 and were timed to coincide with the end of den-emergence, just prior to leafout of the woody vegetation (i.e., late May/early June). A single pilot and observer formed a 'team' given the task of searching subunits for bears. Each day pairs of teams were assigned 2 primary units (8 subunits) to survey. Each of the 2 teams independently searched each subunit for bear groups (i.e., 2 independent visits, one by each pilotobserver team) using a tandem seat fixed-wing aircraft. Teams were instructed to search each subunit thoroughly for bears with the guideline of attempting to spend ≤1 h of search time in each subunit. Pilots were free to choose the search pattern as long as the entire subunit was covered (see online Appendix; Fig. A1). Subunits were searched sequentially so that the second team covered each subunit completed by the first team within 4 h, minimizing the possibility of bears moving into or out of a given subunit between visits. The separation in time and differences in flight patterns helped address the potential problem of incomplete availability (e.g., Laake et al., 2008; Wilson et al., 2014). In 2015, teams were also instructed to search for and record observations of bear dens. Up to 8 teams conducted surveys each day, and units were generally surveyed from north to south to further limit the possibility of individual bear groups from being detected in >1 unit due to movements between days.

When a bear den was observed, the location of the den was recorded and the subunit was classified as 'occupied' by bear dens. Although photographs were taken of many dens, identification of individual dens was not always possible due to high den density which caused observer swamping in some areas. In addition, spatial locations often lacked

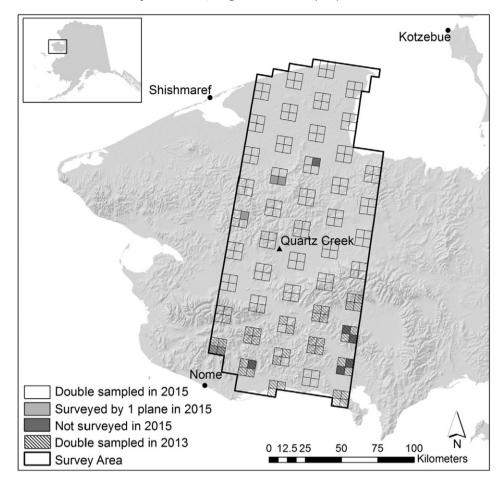


Fig. 1. Map of the study area on the central Seward Peninsula, Alaska showing the location of primary sample units (big squares) and subunits (smaller squares within each unit).

sufficient precision to unambiguously determine the identity of dens in close proximity to one another. Therefore we consolidated den observation data to 'dens detected' (i.e., 1) or 'dens not detected' (i.e., 0) at the level of the subunit. Clearly limiting observation efforts to dens determined to be 'fresh' and increasing efforts to accurately record spatial locations and photographs for each fresh den, may resolve these problems in future applications.

When a bear group was detected, the observer took multiple highresolution photographs of the group, recorded the spatial location using a GPS unit, and noted any distinguishing characteristics of the group (e.g., pelage color) or location (e.g., on a kill) that may aid in subsequent identification. The number of individuals in the group and their apparent ages (i.e., cubs versus adults) were also recorded. At the end of each day, paired teams compared sighting locations, photographs, and field notes for each subunit surveyed to determine which unique bear groups were detected by each team. The photographs and spatial locations were used as temporary uniquely identifiable 'marks' allowing positive identification of individuals over the short interval between visits (Fig. A2). Sightings of groups differing in size (e.g., sows with cubs vs. single bears) were easily resolved. Single bears observed in approximately the same location were potentially more difficult, although the combination of differences in physical characteristics (e.g., coloration, apparent size) and spatial location allowed us to determine whether two detections represented the same or different individuals (Fig. A3). Because bears are solitary in nature and occurred at low densities within our study area, it was highly unlikely that > 1 group of the same size and physical characteristics would be detected at the same location during revisits. While we were confident in our ability to distinguish among bear sightings and assumed misidentification errors did not occur, it is possible that such errors could be formally addressed (e.g., Yoshizaki et al., 2009; Morrison et al., 2011). The detection/non-detection records of each group were used to create sighting histories for analysis. These data were also consolidated to ≥ 1 bear detected/not detected at the subunit level to allow us to estimate bear site-occupancy in addition to abundance using the same dataset. This allowed us to directly compare estimates of den site-occupancy, bear site-occupancy, and bear abundance.

2.4. Analysis

2.4.1. Den site-occupancy

We used a site-occupancy modeling approach to estimate the probability of a den occurring within each subunit (i.e., 'den site occupancy'). Available covariates were limited, so we used random effects to address variation in detection and occupancy probabilities. Unmodeled heterogeneity in capture probability is known to cause estimator bias (Link, 2003), so we assumed that detection probability varied at the smallest scale possible (i.e., the subunit), to provide the most flexibility in accounting for heterogeneity in the detection process. Sources of heterogeneity in detection may have included different numbers of dens occurring in each subunit (i.e., Royle and Nichols, 2003) or variation in vegetative cover or sighting conditions. We assumed that den siteoccupancy varied at the primary unit level, to account for autocorrelation among subunits within each primary sampling unit and other sources of heterogeneity such as habitat type that may have caused site occupancy probabilities to differ among primary units. While den site occupancy also may have varied among adjacent subunits, we included the random term at the primary unit level to avoid parameter

identifiability issues. Our basic model can be written as:

$$y_{ij} \sim Bernoulli(z_i * p_{ij})$$
 $z_i \sim Bernoulli(\Psi_i)$
 $logit(p_{ij}) = e.subunit_i$
 $logit(\Psi_i) = e.unit_i$

The observed occupancy state y at each subunit i during each visit j was the product of the true occupancy state of the subunit, z_i , and the probability of detecting occupancy in an occupied subunit during a particular visit, p_{ij} . We modeled p_{ij} and Ψ_i as functions random effects at the level of the survey subunit, $e.subunit_i$, and primary unit, $e.unit_i$, respectively. We did not include any covariates because our main objective was to address overall heterogeneity in p_{ij} and Ψ_i to produce unbiased estimates of site occupancy, however, specific covariates could be included when available. To estimate the total number of subunits containing bear dens, we summed across the true occupancy states, z_i , to calculate the number of surveyed cells that were occupied and then divided this value by the proportion of the total survey area covered. Estimates were not produced for 2013 because den site occupancy information was collected in 2015 only.

2.4.2. Bear site-occupancy

We also fit occupancy models to the bear observation data, consolidated at the level of the subunit. We converted observations of individual bear groups into 1's and 0's representing the detection of ≥ 1 bear group, or no detections within a subunit, respectively. Our bear site occupancy model was structurally similar to our den site-occupancy model and can be written as:

$$egin{aligned} y_{ijk}^* &\sim Bernoulli\Big(z_{ik}^* * p_{ij}^*\Big) \ \\ z_{ik}^* &\sim Bernoulli\Big(\Psi_{ik}^*\Big) \ \\ logit\Big(p_{ij}^*\Big) &= e.subunit_i^* \ \\ logit\Big(\Psi_{ik}^*\Big) &= int_{yr}^* + e.unit_i^* \end{aligned}$$

The notation and model structure generally follows that of the den site-occupancy model, however, we use the superscript * to indicate that parameters are not shared between the two models. We again included random effects at the subunit and primary unit levels to address heterogeneity in detection and occupancy probabilities, respectively. The only structural difference between the den and bear group occupancy models was that Ψ_{ik}^* was assumed to vary between years, k, as modeled by a year-specific intercept, int_{yr}^* . We assumed that the probability of detecting bear site-occupancy was the same among years, but that occupancy differed between 2013 and 2015. Because we covered only a limited area in 2013, we restricted our presentation and interpretation of bear site-occupancy to 2015 only. However, we included the 2013 data to aid in the estimation of detection probability under the assumption that the detection process was similar among years.

2.4.3. Abundance

We used a mark-resight double-observer model for analyzing the capture histories of individual bear groups. Because we expected that each subunit contained only 1–2 bear groups on average, we augmented the data from each surveyed subunit with 4 additional 00 capture histories (i.e., at least double the expected number of groups) representing potential but undetected bear groups prior to analysis (i.e., data augmentation; Royle, 2009). We then estimated how many

of these potential groups actually were present but undetected in each subunit. A subsequent sensitivity analysis augmenting the data with 6 additional capture histories produced nearly identical results, indicating that augmenting by 4 was adequate (results not shown). We formulated our mark-resight model in a structure analogous to our occupancy models, although here the sample unit is the potential bear group, l, rather than the subunit. Using similar notation, this model can be written as:

$$y_{jkl}^{A} \sim Bernoulli\left(z_{k}^{A}*p_{kj}^{A}\right)$$
 $z_{kl}^{A} \sim Bernoulli\left(\Psi_{kl}^{A}\right)$
 $size_{kl} \sim Poisson(mean.size_{kl})$
 $logit\left(p_{kj}^{A}\right) = e.subunit_{k}^{A}$
 $logit\left(\Psi_{kl}^{A}\right) = int_{yr}^{A} + e.unit_{k}^{A}$
 $log(mean.size_{kl}) = size.int$
 $\hat{N}_{k} = sum\left(z_{kl}^{A}*size_{kl}\right)$

Note the components of this model are indexed by visit, i, year, k, and potential group, *l*. The superscript *A* indicates parameters are specific to the abundance model and are not shared with either occupancy model. We add an additional submodel representing group size, size_{kl}, represented by a single intercept term, size.int. The estimated total number of bears present in the sampled units in each year, \hat{N}_k , is derived by summing the true states, z_{kh}^A of all potential groups after multiplying each group by average group size based on the observed data. The total number of bears was then estimated by dividing the estimated number of bears within the sampled area by the proportion of the total study area that was sampled. Group size information was subdivided into 2 categories for analysis: independent bears (cubs excluded) and total bears (cubs included). Analyses for independent bears and total bears were conducted separately, although the 2 data sets were fit to the same model. This separation allowed direct comparison with historical estimates (i.e., Miller et al., 1997) and also provided a separate assessment of the adult population which may be of more interest for management. We again included the 2013 data for the purpose of aiding in the estimation of detection probability but did not present or interpret 2013 abundance estimates.

All 3 analyses were conducted in a Bayesian framework and were fit in OpenBUGS (Thomas et al., 2006). We used compact priors for intercept terms on the logit scale, N(0,10), and weakly informative priors on standard deviation of random effects, U(0.1,10). We limited the prior distributions of these random effects terms to be slightly above 0, assuming that there was some heterogeneity in both detection and occupancy at the subunit and unit levels, respectively. Restricting the bounds in this way increased model identifiability, thereby preventing the precision of the random effects terms from tending to ∞ and dramatically improving convergence. Without this restriction, all variation could theoretically be attributed to either the detection or occupancy process, an unlikely scenario leading to unrealistic parameter estimates. Sensitivity analysis indicated that the exact choice of weakly informative priors on the random effects terms had little impact on final results. We ran 2 independent Markov chains for 20,000 to 60,000 iterations, depending on the model, discarding the initial iterations as burn-in. We used the Gelman-Rubin diagnostic (Brooks and Gelman, 1998) and a visual inspection of the chains to assess convergence. We also calculated the Bayesian p-value (Gelman et al., 2004) for each analysis to assess model fit.

3. Results

During 2013, we surveyed 42 of 191 subunits in the southern portion of the survey area twice between June 2-5 (Fig. 1). We detected 27 unique bear groups in 17 of the surveyed subunits. Poor weather conditions prevented completion of a full survey. In 2015, we surveyed 181 of 191 subunits twice and 4 subunits only once between May 19–29 (Fig. 1). The average time interval between revisits to subunits was 1.2 h. During 2015, we detected 58 unique bear groups in 41 subunits and observed bear dens in 56 subunits. Of the 85 total bear groups observed, 22 were detected by both teams. In 2015, the average distance moved between revisits for groups observed by both teams was 1.1 km. Up to 8 pilot-observer teams conducted surveys each day, and survey effort totaled approximately 406 h of flight time in 2015. The average number of sightings per hour of flight time was approximately 0.18 groups, translating to roughly 1.4 bear group detections for the average pilot-observer team during a full 8 h day. The estimated total cost of the project was approximately \$145,000, excluding staff salaries. Compared to the cost estimates presented by Miller et al. (1997), we estimate our costs were < 10% that of a hypothetical collar mark-resight project with inference to the same study area.

Our estimates of den site-occupancy, bear site-occupancy, and independent bear abundance corresponded closely, suggesting similarities in inference and the absence of substantial bias due to misidentification error or lack of closure between revisits (Table 1, Fig. 2). When extrapolated to the entire survey area, we estimated that 328 [95% CrI:251-433] and 272 [95% CrI:191–373] of the 683 total potential subunits (i.e., grid cells) within our study area were occupied by ≥1 den or ≥1 brown bear, respectively (Fig. 2). Correspondingly, estimated abundance for the entire survey area was 420 [95% CrI:274-650] independent and 713 [95% CrI:474–1070] total bears. This translates to each occupied cell containing approximately 1.5 independent bears and 2.6 total bears on average. Precision was greatest for estimates of den occupancy and least for bear abundance (Table 1), as was expected based on higher rates of observation of dens than individual bears and greater data requirements for the mark-resight technique. Detection probabilities were also similar, although the probability of detecting that a subunit was occupied appeared somewhat higher than the probability of detecting an individual bear group (Table 1). With an average of 1.5 independent bears in an occupied subunit, correspondence between detection probabilities was not unexpected. The low number of groups in each occupied subunit suggested that bear site-occupancy would be sensitive to changes in abundance over time as small changes in abundance would be expected to be directly reflected in occupancy rates. Model fit for each analysis was adequate based on the Bayesian p-value (Table 1).

Based on the mark-resight data, our abundance estimates correspond to densities of 21 (95%CrI: 13.7–32.5) independent bears/1000km² and 35.6 (95%CrI: 23.7–53.5) total bears/1000km². Despite important differences in methodology and scale, these density estimates are broadly similar to previous estimates from northwestern

Table 1 Estimates of detection (p), occupancy (Ψ), and abundance (N) of brown bears with 95% credible intervals (in parentheses), measures of goodness-of-fit (GOF) based on the Bayesian p-value, and approximate coefficients of variation (CV) for surveys conducted on the central Seward Peninsula, Alaska. Estimates of p were jointly estimated across years (except for den occupancy), while estimates of Ψ and N are for 2015 only.

	p	Ψ	$N_{independent} \\$	N_{total}	GOF	CV
Den occupancy	0.38	0.48	-	-	0.22	15%
	(0.26-0.53)	(0.37-0.63)				
Bear	0.35	0.40	_	_	0.62	18%
occupancy	(0.20-0.54)	(0.28-0.55)				
Bear	0.33	_	420	713	0.68	23%
abundance	(0.17-0.50)	-	(274-650)	(474–1070)		

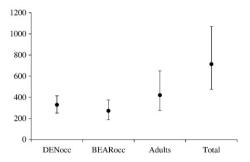


Fig. 2. Estimated number of sample units containing ≥1 brown bear den (DENocc) or ≥1 brown bear group (BEARocc), and the estimated number of independent (Adults) and total (Total) bears within the study area on the central Seward Peninsula, Alaska in 2015. Error bars represent 95% credible intervals.

Alaska (Fig. 3). The precision of our estimates was lower than the previous mark-resight studies, likely because we had fewer revisits to each sample unit. However, our coverage was up to 10 times greater, providing inference to a much larger landscape.

4. Discussion

We found that our photographic mark-resight approach was a logistically feasible and cost effective alternative to more intensive approaches for assessing low-density brown bear populations at large spatial scales. The addition of site-occupancy information added a useful monitoring component directly related to population size, and together our results represent the first rigorous assessment of the brown bear population on the central Seward Peninsula in nearly 25 years. Furthermore, despite obtaining estimates of the state variable of interest (i.e., abundance), the inclusion of site-occupancy estimates had several benefits that may be useful in similar contexts. First, while bear occupancy and abundance estimates were based on the same data, agreement between the den and bear site occupancy results bolstered our conclusion that the abundance estimates were likely appropriate and not substantially biased due to misidentification of individuals. For many species, there may be no existing data with which to assess the validity of new approaches or assess estimator bias. Occupancy metrics, particularly those based on independent datasets (e.g., den surveys), can provide additional lines of evidence leading to increased confidence in new approaches or estimates for little studied populations. Second, occupancy approaches tend to require less data for estimation, resulting in higher precision, providing a useful management tool while

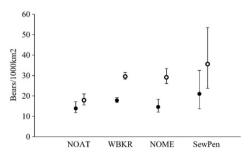


Fig. 3. Estimated brown bear density on the central Seward Peninsula, Alaska (SewPen) in 2015 compared with previous density estimates from previous mark-resight studies in northwestern Alaska including: an area adjacent to Noatak National Preserve (NOAT), the western Brooks Range (WBKR), and a study site north of Nome (NOME). The SewPen study area overlapped the NOME study area. Estimates from the three previous studies are reproduced from Miller et al. (1997). Solid symbols represent densities of independent bears (cubs excluded) and open symbols represent densities of total bears (cubs included). Error bars represent 95% confidence intervals for NOAT, WBKR, and NOME and 95% Bayesian credible intervals for the Seward Peninsula.

additional abundance data are collected over time. Finally, the simultaneous collection of multiple data streams acts as a hedge against insufficient sample sizes for estimating abundance with the precision desired. Rather than defaulting to stand-alone occupancy approaches for rare species, abundance and sign occupancy surveys may be conducted in parallel to increase the amount of information available and support management decisions. This of course requires careful attention to survey design to insure that the objectives and assumptions of each survey method are met. For example, in our study we sized our subunits so that relatively few bear groups would be expected to occur in an occupied subunit. Doing so increases the sensitivity of occupancy as a monitoring tool. The use of multiple metrics can allow greater flexibility in design and potentially increase the utility of many surveys, particularly for rare species such as brown bears.

Although our methods differed from the collar-based mark-resight surveys conducted in the area previously, our estimates of brown bear abundance and density were strikingly similar to those based on past work in several areas of northwestern Alaska, including an area overlapped by our study area (i.e., Miller and Nelson, 1993; Miller et al., 1997). In general, 95% credible interval coverage contained the point estimates of abundance from previous surveys from the broader area, despite our incorporation of random terms to help address negative bias due to heterogeneity in detection probability (Link, 2003). Because no other recent population data exist for the Seward Peninsula, it is impossible to determine population trajectory over the intervening years, particularly in the context of the doubling of annual harvests between the early 1990's and 2015 (Hughes, 2013). Additional survey information will be required to assess current population trajectory, however, agreement with previous work indicates our estimates are plausible and comparable to what is known about brown bear densities in subarctic Alaska. This is an important development because bear populations are notoriously expensive and difficult to evaluate, resulting in limited population information throughout much of their range. We were also able to make valid inference to an area an order of magnitude larger than would have been possible using existing survey approaches. We expect our survey methodology represents a major development in the assessment of brown bear populations, particularly in open arctic and subarctic habitats where densities are low.

Our successful application of temporary marks in a mark-resight framework is relatively novel in the context of monitoring rare species. We are aware of only one similar application where photographs taken from an aerial survey platform were used to identify individual wild horses *Equus caballus* based on unique color markings (Dawson and Miller, 2008). The primary difference between our method and the Dawson and Miller (2008) approach was that the unique color patterns of wild horses provide more 'permanent' identification that can be reconciled over longer time frames (e.g., days or weeks). In contrast, we relied on variation in brown bear physical characteristics in conjunction with spatial location to ensure positive identification of individuals over a short time period (i.e., hours). Between variation in color, group size, and spatial location, positive identification of individual bear groups was possible over the short revisit interval (e.g., Dean, 1987).

Our estimates are reliant on the assumption that all bears are available to be sampled by at least one team. If some bears remained in their dens or were otherwise unavailable (e.g., sleeping in dense cover during both revisits), our estimates would be negatively biased. We attempted to mitigate these sources of bias through design, specifically by conducting 2 independent surveys so that sighting perspective varied, as well as conducting the survey during the post denning period. When individual movements between revisits are large, the utility and interpretation of resulting occupancy estimates can also become questionable (Efford and Dawson, 2012). Therefore we purposely restricted the time interval between revisits of each subunit to assure that population closure was approximately met and to insure that most groups were near the same location between visits. A small subset of bear groups was detected by the second team either in an adjacent subunit

or just outside the boundary of the subunit where it was initially detected. These groups were assumed to be unavailable to the second team for analysis purposes and indicated that some movement did occur. If bear movements were more common or more extensive than we observed, our estimates of occupancy and abundance would be biased high due to violation of the closure assumption. Failure to recognize an individual group during subsequent visits would also cause positive bias. Based on our observations, the agreement with previous abundance estimates from similar areas, and general agreement with our occupancy metrics, we expect bias was low. In our study area, the relative rarity of bears was actually an advantage because the possibility of encountering a similar bear in the same location between visits was highly unlikely. In higher density populations where misidentification may be a problem or in dense habitats where detection probabilities would be much lower, other survey methods may be preferable. Alternatively, it may be possible to model misidentification error explicitly in some cases (Yoshizaki et al., 2009; Morrison et al., 2011).

The addition of occupancy information and general agreement among occupancy and abundance estimates further increased our confidence in our findings, as well as increasing their utility for management. While bear site-occupancy was directly related to abundance by definition (i.e., based on the same data), the close congruence between our two site-occupancy metrics suggested that bear and den siteoccupancy were also closely related, providing a link among all 3 metrics. This correspondence suggests monitoring and management could be validly based on any of the metrics, depending on objectives. Our results also suggest there is real value in the collection of multiple data types (e.g., both sign and abundance data) related to the same population. When little population information is available, it can be difficult to assess methodological assumptions associated with the field and analytical approaches employed. As we found, additional data streams can provide further assessment of assumptions and bolster confidence in results, particularly for understudied populations. We suggest that a framework leveraging the strengths of each metric for meeting individual objectives could be much more powerful than a program based on occupancy or abundance alone.

Although particularly well suited as a monitoring tool for low-density brown bear populations occurring in open arctic and subarctic habitats, the general approach we describe could be used to monitor a variety of low-density carnivore species with relatively little modification. For example, applications of our particular approach may be extended to other species such as wolves (*Canis lupus*) that exhibit variations in coloration and group size that would facilitate individual group identification over relatively short time intervals. Combined with occupancy metrics, such as tracks or kill sites, photographic mark-resight techniques might be used for population monitoring without reliance on direct marking of individuals. Further development and implementation of reduced-cost field techniques could provide much more extensive information for a variety of populations that are difficult to assess using conventional approaches.

There are also opportunities for extending our basic approach to increase the precision of abundance estimates when appropriate data can be collected. Perhaps the most basic extension would be to borrow detection information across multiple surveys through the use of informed priors when protocols and sighting conditions are similar (e.g., Schmidt and Rattenbury, 2013). We effectively used this principle by assuming detection probabilities were similar between years. The use of prior information in this way increases the precision of all estimates and their sensitivity to changes in population size. The rapid development of integrated modeling approaches also provides a powerful mechanism for combining multiple datasets into a single analysis. Combinations of data from DNA and camera traps (Gopalaswamy et al., 2012; Sollmann et al., 2013b), DNA and occupancy surveys (Chandler and Clark, 2014), and telemetry and camera traps (Sollmann et al., 2013a, 2013c) are 3 such examples. Such combinations improve density estimates over what is possible using either dataset alone. A straightforward extension to our approach for brown bears would be to jointly estimate abundance based on both bear and den abundance data (if available) under the assumption that each adult bear is associated with a single fresh den. This would provide two independent data streams that could be jointly analyzed with direct inference to population abundance (e.g., Blanc et al., 2014). Alternatively, in some areas it would also be possible to jointly estimate detection and abundance using photograph mark-resight data in combination with location information from concurrent telemetry studies. In general, the development of multi-metric surveys, whenever practical, can lead to stronger inference with little extra cost or effort. We broadly encourage the consideration of multi-metric monitoring with the goal of providing multiple supporting data streams, as well as opportunities to more precisely estimate the state variables of interest.

Acknowledgements

Funding for this project was provided by Western Arctic Parklands, the U.S. National Park Service's Arctic Inventory and Monitoring Network, and the Alaska Department of Fish and Game. We thank pilots C. Cebulski, J. Cummings, J. Dau, A. Greenblatt, S. Hamilton, J. Lee, D. Sheldon, E. Sieh, and M. Wade and observers A. Ackerman, B. Dunker, L. Hughes, M. Johnson, A. Lewis, R. Nichols, B. Saito, and C. Sieh. We also thank J. Lawler and 3 anonymous reviewers for helpful comments on an earlier draft of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. National Park Service.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.biocon.2017.01.005.

References

- Becker, E.F., Christ, A.M., 2015. A unimodal model for double observer distance sampling surveys. PLoS One 10, e0136403.
- Becker, E.F., Quang, P.X., 2009. A gamma-shaped detection function for line-transect surveys with mark-recapture and covariate data. J. Agric. Biol. Environ. Stat. 14,
- Blanc, L., Marboutin, E., Gatti, S., Zimmermann, F., Gimenez, O., 2014. Improving abundance estimation by combining capture-recapture and occupancy data: example with a large carnivore. J. Appl. Ecol. 51, 1733-1739.
- Boulanger, J., Kendall, K.C., Stetz, J.B., Roon, D.A., Waits, L.P., Paetkau, D., 2008. Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. Ecol. Appl. 18, 577-589.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. J. Comput. Graph. Stat. 7, 434-455.
- Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. Methods Ecol. Evol. 5, 1351-1360.
- Dawson, M.J., Miller, C., 2008. Aerial mark-recapture estimates of wild horses using natural markings. Wildl. Res. 35, 365-370.
- De Barba, M., Waits, L.P., Genovesi, P., Randi, E., Chirichella, R., Cetto, E., 2010. Comparing opportunistic and systematic sampling methods for non-invasive genetic monitoring of a small translocated brown bear population. J. Appl. Ecol.
- Dean, F.C., 1987. Brown bear density, Denali National Park, Alaska, and sighting efficiency adjustment. Bears: Their Biology and Management. 7, pp. 37-43.
- Efford, M.G., Dawson, D.K., 2012. Occupancy in continuous habitat. Ecosphere 3:32. http:// dx.doi.org/10.1890/ES11-00308.1.
- Gardner, B., Royle, J.A., Wegan, M.T., 2009. Hierarchical models for estimating density from DNA mark-recapture studies. Ecology 90, 1106-1115.
- Gardner, B., Royle, J.A., Wegan, M.T., Rainbolt, R.E., Curtis, P.D., 2010a. Estimating black bear density using DNA data from hair snares. J. Wildl. Manag. 74, 318-325.
- Gardner, B., Reppucci, J., Lucherini, M., Royle, J.A., 2010b. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91, 3376-3383.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis. second ed. Chapman & Hall/CRC, Boca Raton, Florida, USA.
- Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U., MacDonald, D.W., 2012. Density estimation in tiger populations: combining information for strong inference. Ecology 93, 1741-1751.

- Hein, E.W., Andelt, W.F., 1995. Estimating covote density from mark-resight surveys. J. Wildl, Manag. 59, 164-169.
- Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Samba Kumar, N., Karanth, K.U., 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecol. Appl. 20, 1456-1466.
- Hughes, L., 2013. Unit 22 brown bear management report. Brown bear management report of survey and inventory activities 1 July 2010–30 June 2012. In: Harper, P., McCarthy, L.A. (Eds.), Species Management Report ADF&G/DWC/SMR-2013-4. Alaska Department of Fish and Game, Juneau, pp. 266–278.
 Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic
- captures and recaptures. Ecology 79, 2852-2862.
- Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U., Christensen, N.L., 2009. Patterns and determinants of mammal species occurrence in India, J. Appl. Ecol. 46, 1189-1200
- Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., MacKenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. J. Appl. Ecol. 48, 1048-1056.
- Kendall, K.C., Stetz, J.B., Roon, D.A., Waits, L.P., Boulanger, J.B., Paetkau, D., 2008. Grizzly bear density in Glacier National Park, Montana. J. Wildl. Manag. 72, 1693-1705.
- Kéry, M., Gardner, B., Stoeckle, T., Weber, D., Royle, J.A., 2011. Use of spatial capturerecapture modeling and DNA data to estimate densities of elusive animals. Conserv. Biol. 25, 356-364.
- Laake, J., Dawson, M.J., Hone, J., 2008. Visibility bias in aerial survey: mark-recapture, linetransect or both? Wildl. Res. 35, 299-309.
- Link, W.A., 2003. Nonidentifiability of population size from capture-recapture data with heterogeneous detection probabilities. Biometrics 59, 1123-1130.
- Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J., Buzas, J.S., 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landsc. Ecol. 26, 327-340
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248-2255.
- MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K., Bailey, L.L., 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86, 1101-1113
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Burlington, MA, USA.
- Miller, S.D., Nelson, R.R., 1993. Brown bear—a brown bear density and population estimate for a portion of the Seward Peninsula, Alaska. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration. Final Report, Project W-23-4 and W-23-5.
- Miller, S.D., White, G.C., Sellers, R.A., Reynolds, H.V., Schoen, J.W., Titus, K., Barnes Jr., V.G., Smith, R.B., Nelson, R.R., Ballard, W.B., Schwartz, C.C., 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildl. Monogr. 133, 3-55
- Morrison, T.A., Yoshizaki, J., Nichols, J.D., Bolger, D.T., 2011. Estimating survival in photographic capture-recapture studies: overcoming misidentification error. Methods Ecol. Evol. 2, 454-463.
- Negrões, N., Sarmento, P., Cruz, J., Eira, C., Revilla, E., Fonseca, C., Sollmann, R., Tôrres, N.M., Furtado, M.M., Jácomo, A.T.A., Silveira, L., 2010. Use of camera-trapping to estimate puma density and influencing factors in central Brazil. J. Wildl. Manag. 74,
- Reynolds, J.H., Thompson, W.L., Russell, B., 2011. Planning for success: identifying effective and efficient survey designs for monitoring. Biol. Conserv. 144,
- Royle, J.A., 2009. Analysis of capture-recapture models with individual covariates using data augmentation. Biometrics 65, 267-274.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84, 777-790.
- Royle, J.A., Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., 2009. A hierarchical model for estimating density in camera-trap studies. J. Appl. Ecol. 46, 118-127.
- Royle, J.A., Magoun, A.J., Gardner, B., Valkenburg, P., Lowell, R.E., 2011. Density estimation in a wolverine population using spatial capture-recapture models. J. Wildl. Manag. 75,
- Russell, R.E., Royle, J.A., Desimone, R., Scwartz, M.K., Edwards, V.L., Pilgrim, K.P., McKelvey, K.S., 2012. Estimating abundance of mountain lions from unstructured spatial sampling. J. Wildl. Manag. 76, 1551-1561.
- Schmidt, J.H., Rattenbury, K.L., 2013. Reducing effort while improving inference: estimating Dall's sheep abundance and composition in small areas. J. Wildl. Manag. 77, 1048-1058
- Solberg, K.H., Bellemain, E., Drageset, O.-M., Taberlet, P., Swenson, J.E., 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (Ursus arctos) population size. Biol. Conserv. 128, 158-168.
- Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B.T., Simons, T.R., Pollock, K.H., O'Connell, A.F., 2013a. A spatial mark-resight model augmented with telemetry data, Ecology 94, 553-559,
- Sollmann, R., Torres, J.M., Furtado, M.M., de A. Jacomo, A.T., Palomares, F., Roques, S., Siveira, L., 2013b. Combining camera-trapping and noninvasive genetic data in a spatial capture-recapture framework improves density estimates for the jaguar. Biol. Conserv. 167, 242-247.
- Sollmann, R., Gardner, B., Chandler, R.B., Shindle, D.B., Oronato, D.P., Royle, J.A., O'Connell, A.F., 2013c. Using multiple data sources provides density estimates for endangered Florida panther. J. Appl. Ecol. 50, 961–968. Stanley, T.R., Royle, J.A., 2005. Estimating site occupancy and abundance using indirect de-
- tection indices. J. Wildl. Manag. 69, 874-883.

- Tempel, D.J., Gutierrez, R.J., 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conserv. Biol. 27, 1087–1095.
- torial species, the California spotted owl. Conserv. Biol. 27, 1087–1095.

 Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS Open. R News 6, 12–17.

 Thompson, W.L., 2004. Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters. Island Press, Washington, USA.

 Wilson, T.L., Schmidt, J.H., 2015. Scale dependence in occupancy models: implications for estimating bear den distribution and abundance. Ecosphere 6:168. http://dx.doi.org/10.1890/ES15-00250.1.
- Wilson, T.L., Schmidt, J.H., Thompson, W.L., Phillips, L.M., 2014. Using double-observer aerial surveys to monitor nesting bald eagles in Alaska: are all nests available for detec-
- rial surveys to monitor nesting bald eagles in Alaska: are all nests available for detection? J. Wildl. Manag. 78, 1096–1103.

 Yoshizaki, J., Pollock, K.H., Brownie, C., Webster, R.A., 2009. Modeling misidentification errors in capture-recapture studies using photographic identification of evolving marks. Ecology 90, 3–9.