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Abstract: We evaluated the efficiency of an extension of a single season capture–mark–recapture (CMR) population estimation method, a closed-capture robust-design model, to monitor trends in population size, apparent survival, and temporary emigration rates over a 5-year period for a low-density population of American black bears (*Ursus americanus*) in north central Utah, USA. We also used robust-design Pradel models to estimate finite rate of population change and recruitment. We identified individual bears through genetic analysis of tissue samples collected non-invasively at scent-lured sampling sites. Although the population was relatively small ($\hat{N} = 15\text{–}22$), the Huggins robust-design model provided precise estimates of abundance (CV = 8–14%) and female apparent survival (CV = 9%). Apparent survival for females ($\phi = 0.80$, SE = 0.07) was 2.2x higher than for males ($\phi = 0.36$, SE = 0.12; $P = 0.003$). In contrast, temporary emigration was 40.8x higher for males ($\gamma'' = 0.58$, SE = 0.24) than for females ($\gamma'' = 0.004$, SE = 0.06; $P = 0.024$). Data were insufficient to estimate probability of staying for either sex. From the Pradel model, finite rate of population change was similar for males and females ($\lambda = 1.05$, SE = 0.12 for females; $\lambda = 1.11$, SE = 0.16 for males), but recruitment was 3.0x higher for males ($f = 0.75$, SE = 0.17) than for females ($f = 0.25$, SE = 0.10; $P = 0.013$). Population size appeared to be stable or slightly increasing over the 5-year period. This noninvasive CMR study provided relatively efficient, precise estimates of a low-density black bear population on a small study site. We recommend using robust-design closed-capture models if samples are taken over multiple years; in addition to population size, apparent survival, movement, recruitment, and finite population change can be estimated, providing timely insights into population trends and the mechanisms driving them.

Key words: American black bear, apparent survival, DNA profiling, emigration, Huggins capture–mark–recapture, microsatellites, population estimate, Pradel model, robust design, *Ursus americanus*, Utah

Genetic analyses of tissue have been used in capture–mark–recapture (CMR) models to estimate population size and density for American black bears (*Ursus americanus*; Boerson et al. 2003, Tredick et al. 2007, Immell and Anthony 2008, Tredick and Vaughan 2009, Clark et al. 2010) and brown bears (*U. arctos*; Woods 1999, Mowat and Strobeck 2000, Boulanger et al. 2004, Proctor et al. 2010). Although studies on brown bears have used multiple-year sampling (for example, see Boulanger et al. [2004]), with the exception of Clark et al. (2010), black bear studies have focused on single-year sampling frames and produced limited insight into mechanisms driving population change over time. Using DNA from hair samples, we evaluated the expansion of a single-season CMR population estimation method to multiple years (i.e., closed-capture robust-design or temporal symmetry formulations) to monitor trend in population size (λ), apparent survival, and temporary emigration for a small population of black bears in north central Utah, USA. Our overarching objective was to determine whether this relatively inexpensive approach would provide accurate enough estimates from which to make meaningful management decisions.
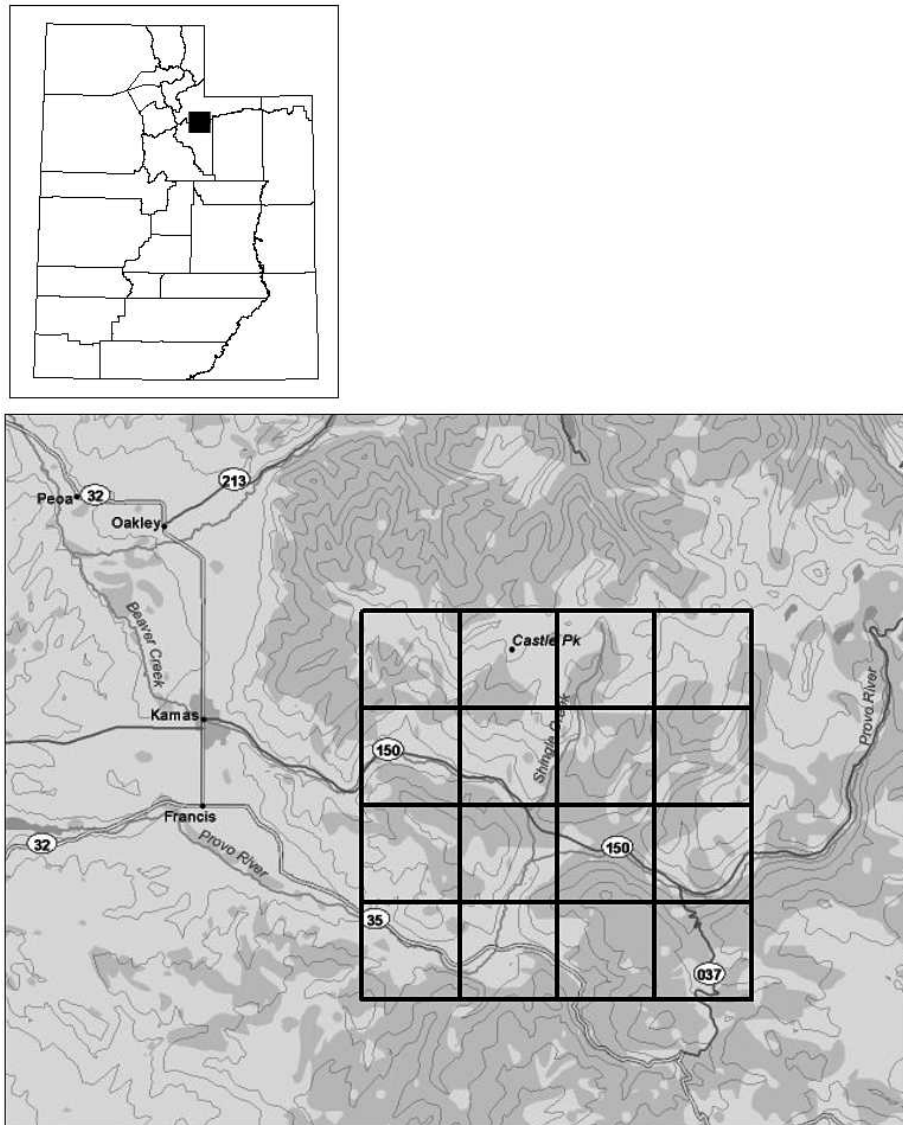
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Fig. 1.   Location of capture–mark–recapture study area grid for American black bears near Kamas, in north central Utah, USA, 2004–08.

Study area

The study was conducted within the Heber-Kamas Ranger District of the Uinta-Wasatch-Cache National Forest, 9.6 km east of Kamas, in Summit County, Utah (Fig. 1). Portions of the Beaver, Yellow Pine, Slate, Shingle, North and South Forks of the Provo, and Soapstone drainages flowed through the study area, where elevation ranged from 2,195 to 3,050 m.

Two major plant communities existed in the study area: the montane forest zone (1,830–2,900 m) and the sub-alpine forest zone (2,500–3,300 m). Dominant trees in the montane zone were lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and Gamble oak (*Quercus gambelii*). The understory was composed of manzanita (*Arctostaphylos patula*), Oregon grape (*Mahonia repens*), snowberry (*Symphoricarpos oreophilus*), and grouse whortleberry (*Vaccinium scoparium*). The sub-alpine zone was dominated by mixed stands of Engelmann spruce (*Picea engelmannii*), sub-alpine fir (*Abies concolor*), and lodgepole pine,
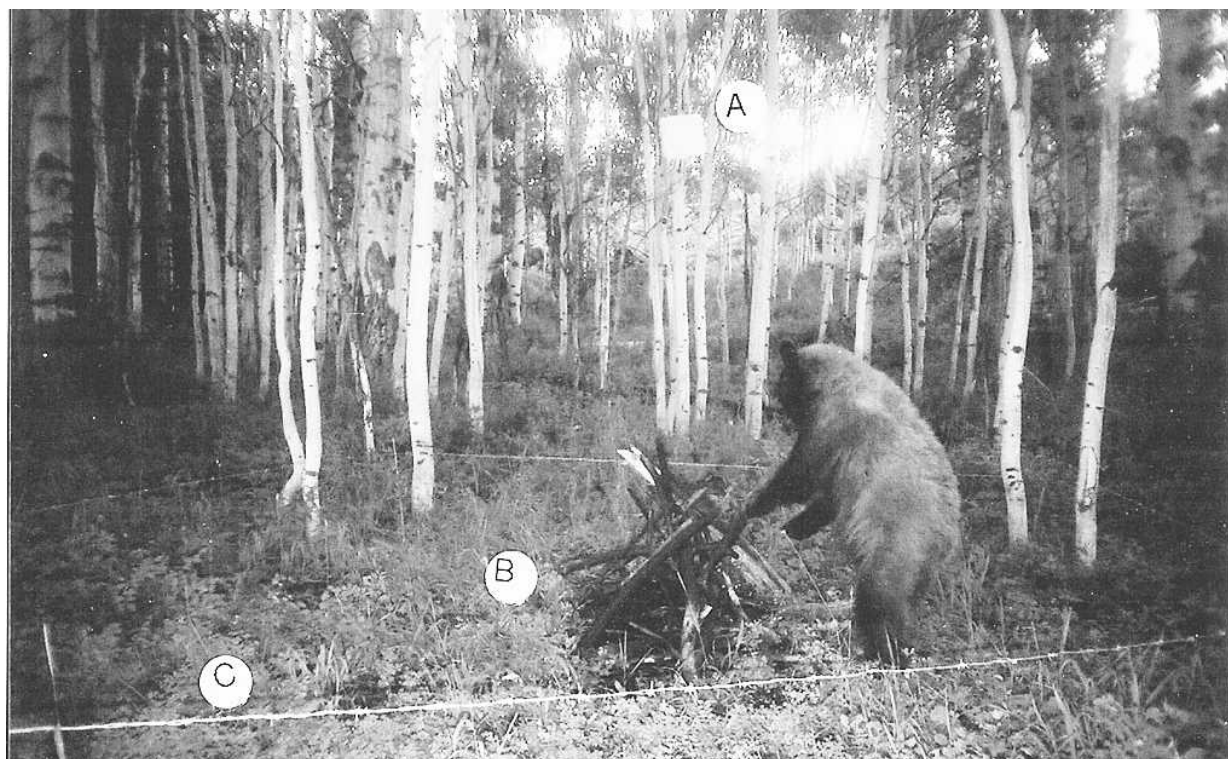
Fig. 2. Hair sampling site (HSS) design with black bear present near Kamas, in north central Utah, USA: (A) Carpet, 15 cm x 15 cm soaked in liquid scent. (B) Pile of logs, sticks and forest litter coated with liquid scent. (C) 4-point barbed wire hair, 50 cm high.

with scattered stands of Douglas fir. Wet meadows and large talus slopes were found at the highest elevations (Wasatch-Cache National Forest 1994).

The bear population inhabiting our study area was subjected to limited public hunting during spring and fall seasons where harvest is controlled by restricting the number of hunters. In addition to hunting, bears die from depredation control actions by state officers, motor vehicle accidents, and natural causes. There were 9 reported deaths of bears in the 640 km^2 hunting unit that includes the study area during the 5 years of study, including 5 bears (all males) that were hunter killed and 4 bears (2 males, 1 female, 1 unreported gender) that were killed for depredation.

Methods

We collected tissue from individual bears by collecting their hair, including hair follicles, on barbed wire. Hair sampling sites (HSS) were distributed systematically in a grid-like fashion across the study area. In 2004, we first established a series of 25 HSS 3.2 x 3.2 km grid cells that totaled 259 km^2, overlaid on a standard USGS 7.5 min topographic map (Fig. 1). In the first year of study (2004), the grid was divided into 25 square cells, each 3.2 km x 3.2 km (10.4 km^2) in size. Analysis of the 2004 data revealed that recapture probabilities were excessively high and bears were recaptured at multiple locations. We concluded that sampling intensity could be reduced without substantial loss of data. Therefore, we used the 2004 perimeter boundaries in 2005–08, but divided the grid into 16 larger cells measuring 4.0 km x 4.0 km each, or 16.19 km^2 in area, and established a HSS in each cell.

Each HSS was created by stringing a single strand of 4-point barbed wire 50 cm above ground level around ≥4 trees; the wire was stapled to tree trunks for support, and the HSS circumferences ranged from 26–28 m (Fig. 2). A 1-m high pile of woody debris (sticks, logs, forest litter) was placed in the center of each HSS, and 1 liter of scent-lure was poured on the pile. In addition, a 15 cm x 15 cm scent-soaked square of carpet was suspended 2–3-m

Table 1. Scent lure used, number of new bear visits (NBV; initial captures), total bear visits (TBV; total captures), and scent lure rank based upon field capture data for black bears in Kamas study area, Utah, USA, 2004–08.

| | Session[a] | | | | | | | | | | | |
| | 1 | | | 2 | | | 3 | | | 4 | | |
Year	Scent	NBV	TBV	Scent	NBV	TBV	Scent	NBV	TBV	Scent	NBV	TBV
2004	FO	7	7	AO	5	9	FAS	1	5	CB	0	5
2005	FO	8	8	AO	6	9	FAS	0	6	CB	1	3
2006	FO	4	5	AO	6	8	FO	2	5	AO	2	4
2007	AO	11	11	FAS	2	6	FO	2	6	UCO	2	5
2008	FAS	14	14	BO	3	7	FO	1	5	AO	2	7

[a]FO = fish oil (NBV = 24, TBV = 35); AO = anise oil (NBV = 32, TBV = 48); FAS = fatty acid scent (NBV = 17, TBV = 31); BO = banana oil (NBV = 3, TBV = 7); CB = cattle blood (NBV = 1, TBV = 8); UCO = used cooking oil (NBV = 2, TBV = 5).

high, directly above the debris pile on a wire stretched between 2 perimeter trees (Proctor 1995, French et al. 1996). We arbitrarily applied one of 6 liquid scent-lures (anise oil, fish oil, banana oil, cattle blood, used cooking oil, fatty acid scent) to each site, maintaining the same scent-lure at that site during the 14-day sampling session, but changing the scent-lure following each session to maintain novelty for bears (Table 1). Different combinations were used to determine preference (if any), keep interest high and unique during the 5-year study, reduce trap shyness (Boulanger et al. 2008), and minimize bias in population estimates due to individual heterogeneity (Ebert et al. 2010). The use of liquid scent-lures provided an incentive for bears to investigate HSSs without providing a food reward, thus discouraging repeated visits at individual sites within individual 14-day monitoring periods (i.e., encounter sessions). The wire barbs collected the bears' hair as they rubbed against the wire strand while crossing over or under the wire to reach the lure.

We constructed and baited HSSs 2 weeks prior to our first collection visit. Beginning in June of each

Table 2. Hair samples collected, number, and percent assigned to individual bears, new individuals sampled, and total individuals sampled for a study of black bears in Kamas study area, Utah, USA, 2004–08.

Year	Total hair samples	Samples assigned to individuals	%	New individuals M	New individuals F
2004	180	43	24	5	8
2005	144	47	33	5	5
2006	135	42	31	5	1
2007	111	60	54	5	2
2008	139	63	45	7	4
Total	709	255	36	27	20

year, our study included 4 consecutive (14-day) encounter sessions, collecting all hair found each time (Table 2). We arbitrarily selected and marked a barb on each HSS as the starting point for numbering all barbs on the HSS wire and then counted and numbered barbs sequentially along the wire in a clockwise fashion to define the location of each hair sample. The barb number was used to identify each hair sample collected. The entire hair tuft from each barb was considered an individual sample; each was pulled by hand and placed in a separate paper envelope. Black bear and human DNA will not cross contaminate (D. Paetkau, Wildlife Genetics International, Nelson, British Columbia, Canada, personal communication, 2011). However, prior to hair removal we rubbed our hands with an ethyl alcohol-based personal antimicrobial wipe to remove as much dirt, oil, and bear DNA from other HSS as possible under field conditions. Each envelope was labeled with an identification number specifying year, HSS, session number, and barb number, and was stored in a desiccation chamber. Following hair collection, we removed all residual hairs from each barb by burning with a butane-fueled lighter.

Hair samples were analyzed by Wildlife Genetics International laboratory, using QIAGEN DNeasy Tissue kits (Qiagen, Germantown, Maryland, USA) to extract DNA from each sample with a minimum of 1 guard hair follicle, or 5 under-fur follicles. Up to 10 guard hair follicles or 30 under-fur follicles were extracted per sample. Individual identification was established by analyzing >6 microsatellite markers that had a mean observed heterozygosity of at least 0.78 in the study population (G10J, G10B, G1D, G10L, G10M, G10X). When possible, G10H, MU59, G10P were also analyzed from samples to

strengthen identification of individuals (Paetkau et al. 1998). Samples were sequenced using an ABI Prism 310 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA), and data were analyzed using Genescan and Genotyper software (Perkin-Elmer, Applied Biosystems, Foster City, California, USA). PCR conditions were a 75 sec initial denaturation at 94°C for 15 sec, 54°C for 20 sec, and 72°C for 1 min. To avoid error-prone samples of lower quality, individual identity was only assigned for samples that produced strong, typical (e.g., balanced peak heights), diploid (i.e., not mixed) data for all 6 primary markers (Paetkau 2003). Error-checking was based on selective re-analysis of similar pairs of genotypes following the protocol of Paetkau (2003). After error-checking there were no pairs of genotypes that mismatched at just 1 marker ('1MM-pairs'), the category within which most errors are found, and the 2 pairs that mismatched at 2 markers had been shown to be reproducibly different when replicated. The high variability and paucity of similar genotypes indicate that the chance of having sampled 2 bears with the same multilocus genotype was negligible (Paetkau 2003). Once individual identity was established for all of the samples with identifiable 6-locus genotypes, a single sample from each individual was selected for gender analysis using the amelogenin marker (Ennis and Gallagher 1994). Hair samples could be identified to sex but were not used for age. Although studies with hair collected on 50-cm high barbed wire detected substantial portions of cub and yearling brown bears (Kendall et al. 2009), due to the smaller stature of black bear cubs living on our study area we assume that we only detected bears that were ≥1 yr old.

After the genetic results were received from the lab and individuals were identified for each year's collection, a first encounter history was developed. Although multiple samples might be recorded for an individual bear within each 14-day encounter session, we only recorded a single capture/bear for the session. Capture histories were constructed for each bear encountered during the study with sex as a group covariate; there were 4 encounters/year, each representing a 14-day session. We used a Huggins robust-design model implemented in Program MARK (White and Burnham 1999, White 2008) in which secondary trapping occasions (i.e., the 4 encounters/yr, assumed to be demographically closed) were used to estimate probability of capture (p), probability of recapture (c), and population size

(N). The longer interval between the primary capture trapping sessions (here, approximately 10 months) was sufficiently long that gains (birth and immigration) and losses (death and emigration) could occur. Thus, between closed-capture sessions, robust-design closed-capture models estimate apparent survival (ϕ; animal survives to $t + 1$, given alive at t and in the super-population); temporary emigration (γ'', the probability of being off the study area or unavailable for capture during the primary trapping session t, given that the animal was present during the primary trapping session ($t - 1$), and survived to trapping session t); and probability of remaining outside the sample (γ', the probability of being off the study area or unavailable for capture during primary trapping session t given that the animal was not present on the study area during primary trapping session ($t - 1$) and survived to trapping session t). Population size was a derived parameter in the Huggins model (Huggins 1991), which uses log-based confidence intervals that incorporate the minimum number of bears known to be alive on the study area (White et al. 2001).

We also estimated the finite rate of population change, λ, using the robust-design Huggins full heterogeneity Pradel model (Pradel 1996) using Program MARK. We refer to this as the robust-design Pradel model. Similar to the Huggins robust-design model, we used 4 secondary trapping occasions (during which the population was assumed to be closed) to estimate p, c, and N. During the longer, primary intervals between the secondary periods, apparent survival (ϕ), recruitment rate (f), seniority (γ), and λ can be estimated by the Pradel model. Recruitment rate (f) was the number of new individuals at time $t + 1$ per number of individuals at time t, and included immigration of new recruits from other locations as well as births between 2 closed trapping occasions; γ was the probability that an individual is alive and in the population at time t was also alive and in the population at time $t - 1$. All of the parameters cannot be estimated simultaneously (i.e., it is not possible to estimate ϕ, γ, f, and λ simultaneously) because they are effectively linear functions of each other; estimating any 2 of them can provide estimates of the remaining parameters. We chose a model structure that modeled ϕ and λ directly because these were the parameters in which we were most interested.

We followed the same model selection procedures for the Huggins robust-design model and robust-design

Table 3. Model selection results from mark–recapture analysis for a black bear population in Kamas, Utah, USA, based on data from hair sampling sites set up for 8 weeks during July and August, 2004–08. Analysis used a Huggins closed-capture robust model in Program MARK. Only models with model weights (w_i) > 0.001 are shown.

Model[a]	AIC_c	ΔAIC_c	w_i	Model likelihood	No. parameters
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(\text{sex}) = \gamma''(\text{sex})\}$[b]	499.050	0.000	0.257	1.000	9
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$	500.239	1.189	0.142	0.552	10
$\{p(\text{rankxsex})\ c(\text{rankxsex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$	500.404	1.353	0.131	0.508	12
$\{p(\text{rank})=c(\text{rank})+z\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$	500.488	1.438	0.125	0.487	8
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(.) = \gamma''(.)\}$[b]	501.209	2.159	0.087	0.340	8
$\{p(\text{rank+sex+yr1})\ c(\text{rank+sex+yr1})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$[b]	502.087	3.037	0.056	0.219	12
$\{p(\text{rankxsex})=c(\text{rankxsex})+z\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$[b]	502.088	3.038	0.056	0.219	10
$\{p(\text{rank})=c(\text{rank})+\text{sex}+z\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$	502.516	3.465	0.045	0.177	9
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(\text{sex})\ \gamma''(\text{sex})\}$	502.611	3.561	0.043	0.169	11
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(.)\}$	503.242	4.192	0.032	0.123	9
$\{p(\text{rank})=c(\text{rank})+z\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\ \text{hetero}\}$[c]	504.683	5.633	0.015	0.060	12
$\{p(\text{rank+sex})\ c(\text{rank+sex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\ \text{hetero}\}$[c]	508.191	9.140	0.003	0.010	15
$\{p(\text{rankxsex})\ c(\text{rankxsex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\ \text{hetero}\}$[c]	509.066	10.016	0.002	0.007	17
$\{p(\text{rankcat+sex})\ c(\text{rankcat+sex})\ \phi(\text{sex})\ \gamma'(.)\ \gamma''(\text{sex})\}$	509.371	10.320	0.001	0.006	12
$\{p(\text{rank})\ c(\text{rank})\ \phi(\text{sex+yr})\ \gamma'(\text{sex+yr})\ \gamma''(\text{sex+yr})\}$	511.178	12.128	0.001	0.002	18

[a]Model notation: rankcat = scent lure rank as a categorical variable in which each rank has a unique probability; rankordinal = scent lure rank as an ordinal variable that allowed detection probability to increase but without a linearity assumption (not shown because models with rankordinal had $w_i \leq 0.001$); rank = scent lure rank as a linear trend; yr = year as a categorical variable; t = encounter occasion as a categorical variable (not shown because models with t had $w_i \leq 0.001$); yr1 = first year different due to higher trapping effort; z = additive constant between capture and recapture probabilities; hetero represents a Pledger 2 mixture model to account for trapping heterogeneity; models with the form $\gamma' = \gamma''$ represents random movement, otherwise Markovian movement; w_i = model AIC_c weight.
[b]More parsimonious models for ϕ and λ constructed from the best structures for p and c (within 2 ΔAIC_c units from top model).
[c]Post hoc models with heterogeneity.

Pradel model. We used Akaike's Information Criterion corrected for small sample size (AIC_c) and AIC_c weights to evaluate relative support for each of our candidate models. Models were ranked and compared using AIC_c (Lebreton et al. 1992, Burnham and Anderson 2002) and normalized AIC_c weights (w_i; Buckland et al. 1997, Burnham and Anderson 2002). Models with the lowest AIC_c values were most supported by the data and generally, models <2 AIC_c units of the best model were considered competing models. We used Program MARK to evaluate goodness of fit by estimating overdispersion using a median $\hat{c}$ procedure (White and Burnham 1999). Values of $\hat{c} > 1$ indicate some overdispersion in the data, and the variance is inflated by $\hat{c}$. Had we found overdispersion, we would have used quasi-AIC_c ($QAIC_c$) for model selection (Burnham and Anderson 2002). We model-averaged population and demographic estimates based on their AIC_c weights to account for model selection uncertainty (Burnham and Anderson 2002). All models were used for model-averaged estimates.

We attempted to keep our models simple and model set small because we had a limited data set (i.e., 47 total capture histories). To keep our model set relatively small, we used a 2-phase a priori approach to model development of models by first modeling the nuisance parameters (p and c) in an initial set of models (Anthony et al. 2006, Blakesley et al. 2010, MacKenzie et al. 2010), and by second modeling the demographic parameters.

For the Huggins robust-design model, we began with a global model for ϕ, γ'', and γ', which was sex + year for each parameter (the multiplicative model would not converge), and used this structure to fit models for p and c. For p and c, we constructed 8 biologically plausible models that included scent lure rank, sex, encounter occasion, and year. We qualitatively ranked scent lure from 1 to 4 based on previous experience (1 = best, 4 = poorest; Table 1), and used these ranking values in our models. We constructed 3 models to evaluate lures; one that assumed a unique detection probability for each lure (labeled rankcat, Table 3); one that was ordinal and thus allowed detection probability to increase but without the linearity assumption, using a cumulative logit-link (labeled rankordinal, Table 3); and one that fit a linear trend to our rankings (labeled rank, Table 3). We also constructed a model to evaluate

the decrease in sampling intensity (i.e., increase in grid size) after the first year, based on the best model.

Using the best structures for p and c (within 2 ΔAIC_c units from top model) we constructed more parsimonious models for ϕ, γ'', and γ' (Table 3). Because we expected significant dispersal of subadult males, which would be represented by the γ' parameter, in this situation we modeled movement primarily as Markovian (Kendall 2011). However, we also examined 2 candidate models incorporating random movement with the proper movement structure (i.e., not models like γ'(sex) γ''(.), but rather either γ'(sex) γ''(sex) or γ'(.) γ''(.)), based on the top models.

Because of our small sample sizes, we did not initially include heterogeneity models. However, to evaluate its importance we ran the top models (models within 2 ΔAIC_c units from top model) with heterogeneity included using the Huggins–Pledger closed-capture full heterogeneity model with a mixture of 2 capture probabilities (Pledger 2000). Pledger (2000) mixture models model heterogeneity by assigning animals into groups with relatively homogenous capture probabilities. Heterogeneity models were post hoc models that arose from the review process. There were 4 models (Table 3) for which we included heterogeneity; they were 5.6, 9.1, 10.0, and 19.4 ΔAIC_c units lower (respectively from lowest to highest AIC_c) than the same models without heterogeneity. Consequently, we did not include heterogeneity in the remainder of the models used in the analysis.

We summed annual male and female model-averaged estimates of population size (≥ 1 yr old) for total population size; variances were calculated using the delta method (Seber 1982) with model-averaged variances and covariances. We did not attempt to estimate the number of cubs of the year within the study population.

For the robust-design Pradel model, we used the same models for p and c as for the Huggins robust-design model. We began with a global model for ϕ(sex + year) λ(sex + year) because the multiplicative model was poor (>130 ΔAIC_c units from additive model) and used this structure to fit models for p and c. We then mimicked the models from the robust-design analysis as closely as possible for ϕ and λ.

Results

We collected 709 hair samples during the study, of which 255 (36%) were assigned to individual bears

(Table 2). The failure rate was for the most part due to the high quality-control standards employed by the laboratory, and to collection of hair from non-target species (cattle, elk [*Cervus elaphus*], deer [*Odocoileus hemionus*], moose [*Alces alces*], and canid). We excluded 454 samples from analysis due to confounding factors, including 9 that contained hair from >1 bear, 151 that lacked suitable genetic material (initial physical evaluation of the sample revealed too few hairs to process), 255 with insufficient DNA for extraction (failed laboratory's quality control process based on 6 primary markers), and 39 that were from other species and failed during genotyping. We identified 13–23 different bears annually and 47 different bears on the study grid from 2004–08, including 27 individual males and 20 females (Table 2). We identified 4–8 new males and 1–8 new females each year of the study.

We did not detect overdispersion in the data ($\hat{c}$ = 0.90), thus we used AIC_c for model selection and ranking. Huggins closed-capture models with scent lure rank as a linear trend (rank, Table 3) for capture and recapture sessions performed better than models using only encounter occasion ($\Delta AIC_c > 11$ between lowest model with attractant rank and best model using encounter occasion; models with encounter occasions were not shown because $w_i < 0.001$; Table 3). The linear trend of rank also performed better than when individual detection probabilities were assigned to rank or when rank was ordinal (Table 3). There was little difference in capture and recapture probabilities between males and females. For the top 3 models, which had 53% of the model weight, the beta estimates for sex effects were similar; the 95% CIs all overlapped zero considerably (e.g., for top model: $\beta = 0.216$, SE = 0.287, 95% CI = [−0.346–0.779]) as did confidence intervals for model-averaged capture and recapture overlapped for male and female estimates (Fig. 3). Scent lure was a strong effect, with model-averaged capture probabilities varying from 0.17 to 0.56 among the different attractants (Fig. 3).

Model selection results were similar for the Pradel model (Table 4). For both the Huggins robust-design model and the robust-design Pradel model, there were minimal (<2%) differences in demographic estimates by year, so we present a single model-averaged estimate for each sex (Table 5). Additionally, apparent survival estimates were the same for the 2 models. Apparent survival for females was 2.2x higher ($\phi = 0.80$) than for males ($\phi = 0.36$;
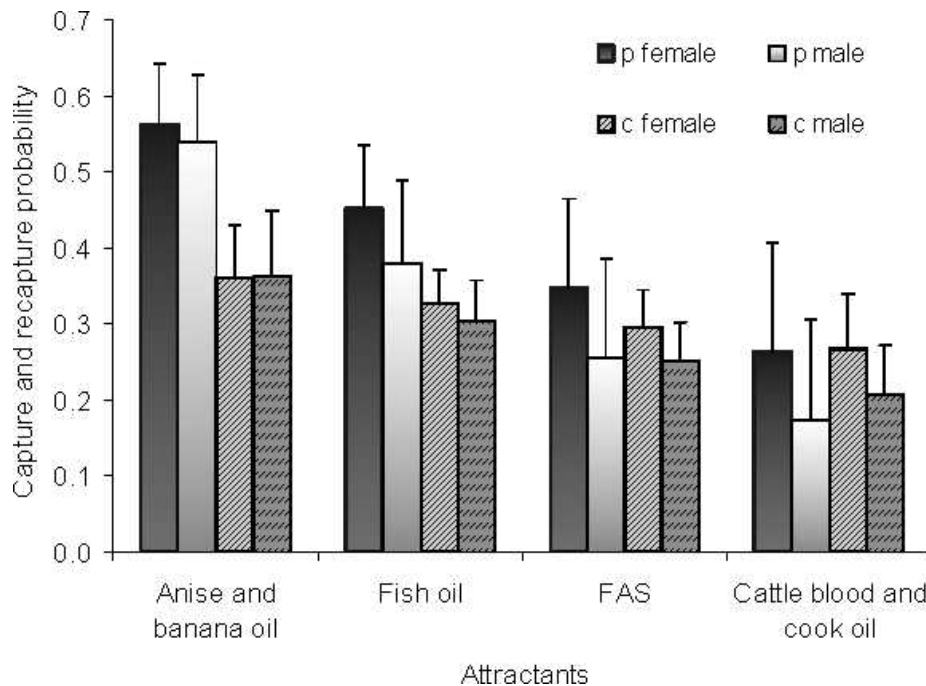
Fig. 3.   Model-averaged estimates of capture (p) and recapture (c) probabilities as a function of attractant and sex for a black bear population near Kamas, Utah, USA, based on data from hair sampling sites set for 8 weeks during Jun–Aug 2004–08. Error bars represent 1 SE.

Wald $Z = 3.020$, $P = 0.003$). In contrast, recruitment was 3.0x higher for males ($f = 0.75$) than for females ($f = 0.25$; Wald $Z = 2.475$, $P = 0.013$). There was no significant difference in finite rate of population change ($\lambda = 1.05$ for females, $\lambda = 1.11$ for males; Wald $Z = 0.315$, $P = 0.753$). Temporary emigration was 40.8x higher for males ($\gamma'' = 0.58$) than for females ($\gamma'' = 0.004$, Wald $Z = 2.257$, $P = 0.024$). We lacked sufficient data to estimate probability of remaining outside the sample for either females ($\gamma' = 0$, 95% CI = 0–1) or males ($\gamma' = 0.29$, 95% CI = 0–0.98).

Population size estimates could not be model averaged for the robust-design Pradel model, so results are presented solely from the Huggins robust-design model. Annual adult population estimates on the study grid ranged from 15 bears in 2004 (95% CI = 12–20 bears) to 22 bears in 2008 (95% CI = 19–26 bears; Table 6). Population size appeared to be stable or slightly increasing over the 5 years of study.

Discussion

Our results suggest that the use of HSSs to collect data and identify individual bears, coupled with multiple capture sessions, holds promise as an efficient approach to monitoring trends in bear population size on low-density Utah populations. Although the bear population size was relatively low, the Huggins robust-design model provided precise estimates of abundance and apparent survival. The coefficient of variation (CV) was ≤14% for population size and ≤9% for female apparent survival estimates. For males, with their lower apparent survival rate, the CV was moderate (27%), although precision would likely increase to acceptable levels (e.g., ≤20%) with additional years or slightly larger population sizes (Kendall et al. 2009).

We note that while precise, it is possible that population size estimates were biased low due to capture heterogeneity. Models with heterogeneity performed poorly. When the 4 top models (models <2 ΔAIC_c from each other) were restructured to include heterogeneity, they were 5.6, 9.1, 10.0, and 19.4 ΔAIC_c units lower than the same model without heterogeneity. It is likely that heterogeneity models did not rise to the top because our capture probabilities were relatively high and sample sizes were small; moreover, based on minimum counts and estimated population sizes, we captured most of

Table 4. Model selection results from mark–recapture analysis for a black bear population in Kamas, Utah, USA, based on data from hair sampling sites in July and August, 2004–08. Results are from a robust-design Pradel model (Huggins configuration) in Program MARK. Only models with model weights (w_i) > 0.001 are shown.

Model[a]	AIC_c	ΔAIC_c	w_i	Model likelihood	No. parameters
{p(rank) c(rank) ϕ(sex) λ(sex)}	0.000	0.289	1.000	0.000	8
{p(sex+rank) c(sex+rank) ϕ(sex) λ(sex)}	0.569	0.218	0.753	0.569	9
{p(sexxrank) c(sexxrank) ϕ(sex) λ(sex) }	0.767	0.197	0.681	0.767	12
{p(sexxrank) = c(sexxrank) ϕ(sex) λ(sex)}	1.849	0.115	0.397	1.849	8
{p(sexxrank) = c(sexxrank)+z ϕ(sex) λ(sex)}	3.608	0.048	0.165	3.608	9
{p(rank) = c(rank)+sex+z ϕ(sex) λ(sex)}	3.859	0.042	0.145	3.859	8
{p(sex+rank) c(sex+rank) ϕ(sex) λ(sex+yr)}	4.658	0.028	0.097	4.658	12
{p(rank+sex) c(rank+sex) ϕ(sex+yr1 = 2) λ(sex+yr)}	4.797	0.026	0.091	4.797	14
{p(sex+rank) c(sex+rank) ϕ(sex+yr) λ(sex+yr)}	7.186	0.008	0.028	7.186	15
{p(sex+rank) c(sex+rank) ϕ(sex+yr) λ(sex+yr)}	7.186	0.008	0.028	7.186	15
{p(rankordinal) c(rankordinal) ϕ(sex) λ(sex)}	7.194	0.008	0.027	7.194	13
{p(sex+rankordinal) c(sex+rankordinal) ϕ(sex) λ(sex)}	7.329	0.007	0.026	7.329	14
{p(rank)=c(rank)+z ϕ(sex+yr) λ(sex+yr)}	9.375	0.003	0.009	9.375	13
{p(rankcat) c(rankcat) ϕ(sex) λ(sex)}	10.422	0.002	0.006	10.422	13
{p(rank) = c(rank)+sex+z ϕ(sex+yr) λ(sex+yr)}	10.540	0.001	0.005	10.540	14
{p(sex+rankcat) c(sex+rankcat) ϕ(sex) λ(sex)}	11.719	0.001	0.003	11.719	12

[a]Model notation: rankcat = scent lure rank as a categorical variable in which each rank has a unique probability; rankordinal = scent lure rank as an ordinal variable that allowed detection probability to increase but without a linearity assumption; rank = scent lure rank as a linear trend; yr = year as a categorical variable; yr1 = first year different due to higher trapping effort, and z = additive constant between capture and recapture probabilities.

the population. Still, it may be that our sample size may have been too small for heterogeneity models to work well, and we recommend future non-invasive genetic sampling studies consider using larger capture grids to sample more bears and reduce the potential for individual heterogeneity to bias the resulting population estimates (Ebert et al. 2010).

Apparent survival rate from the Pradel robust-design model was almost the same as for the robust-design model formulated with γ' and γ''. Female estimates were the same (0.80), whereas male apparent survival was slightly lower for the Pradel version (0.40) than with the γ' and γ'' formulation (0.46). For all estimates, SEs were lower using the

Table 5. Model averaged estimates of demographic parameters for a black bear population in Kamas, Utah, USA, based on data from hair sampling sites set up for 8 weeks during June through August 2004–08.

Parameter[a]	Sex	Estimate	SE	95% CI Lower	95% CI Upper	CV (%)
λ	F	1.05	0.12	0.81	1.28	12%
	M	1.11	0.16	0.79	1.43	15%
ϕ	F	0.80	0.07	0.65	0.94	9%
	M	0.36	0.12	0.12	0.60	34%
f	F	0.25	0.10	0.05	0.45	41%
	M	0.75	0.17	0.41	1.09	23%
γ''	F	0.01	0.06	0.00	0.14	451%
	M	0.58	0.24	0.11	1.00	42%
γ'	F	0.00	0.61	0.00	1.00	15058%
	M	0.29	0.35	0.00	0.98	122%

[a]Model notation: λ = finite rate of population growth, ϕ = apparent survival rate, f = recruitment rate, γ'' = temporary emigration, γ' = probability of remaining outside the sample.
[b]Huggins robust-design model was used to estimate γ'' and γ', and robust-design Pradel model was used to estimate λ, ϕ, and f by model averaging done using Program MARK output (Program MARK does not model average for the robust-design Pradel model with the Huggins configuration).

Table 6. Model-averaged estimates of abundance (*N*) for a black bear population near Kamas, Utah, USA, based on data from hair sampling sites set up for 8 weeks during June, July, and August, 2004–08. Results are from an analysis using a Huggins closed-capture robust-design model in Program MARK.

| Year | N | SE | 95% log-based CI | | CV (%) | Proportion female |
			Lower	Upper		
2004	15	2.08	12	20	14	0.60
2005	19	2.48	15	24	13	0.54
2006	15	1.20	13	18	8	0.64
2007	20	2.55	16	26	13	0.57
2008	22	1.75	19	26	8	0.54

Pradel model (which may have been because fewer parameters were estimated). Although the robust-design model evidently worked well for estimating abundance and apparent survival, it may not provide precise estimates of emigration rates for small populations. Temporary emigration had a CV of 38% for males and 290% for females. For males, the lack of precision was due to the small sample size. For example, there were approximately 5–10 male bears using the study area each year, and about half of these ($\gamma'' = 0.57$) temporarily emigrated. Thus, there were only approximately 3–6 bears from which to estimate probability of remaining outside the sample. For females, temporary emigration could not be estimated with precision mainly because the females stayed on the study area, as evidenced by their extremely low temporary emigration ($\gamma'' = 0.03$).

The lower male apparent survival rate may be due to several factors, including legal hunting, where records show selectivity for hunters to kill males. In a black bear population 55 km south of our study, 6 of 10 radiotagged sub-adult males emigrated from that study area and were killed (Pederson et al. 2008). However, our high estimate of male recruitment rate (0.72), which includes immigration as well as recruitment from within, compensated for the low apparent survival rate and resulted in a relatively high estimate of λ (1.11). In contrast, female λ was lower, reflecting a relatively lower recruitment rate (0.26) as well as high female apparent survival. Knowing more about bear movements in the area surrounding HSSs would help identify whether recruitment is coming from within the area or from outside bears moving into the area.

Using both the Huggins and Pradel robust-design models to estimate temporary emigration, population growth rate, and recruitment revealed another interesting finding regarding male movement. The relatively high estimate of male temporary emigration (0.54) coupled with the fact that λ was >1.0 implied that male movement must have been random. That is, if the movement had not been random, then such high emigration would have led to a population decline ($\lambda < 1$). This was supported by our Huggins model selection results; the top model was a random movement model (Table 3). Still, the second best model, only 1.19 ΔAIC_c units below the top model, was a Markovian movement model; this model vagary is likely due to the imprecision of the emigration estimates (Table 4). Because temporary emigration estimates are imprecise, it is difficult to know exactly how movements influence recruitment estimates, and ultimately male and female estimates of λ. Additional monitoring of bear movements is required to answer questions about bear temporary emigration from the study area and would provide insight to λ as well as inform efforts to determine the boundaries of the area truly represented by the HSS grid.

We note that the relatively small size of the study area impacts interpretation of the temporary emigration parameter. Male black bears use large areas; in many regions they use areas larger than this study's capture grid. Therefore, we expected high temporary emigration for males. But, in this situation, temporary emigration is really a measure of whether a male is using the portion of their home range on the study area. We also expected significant dispersal of subadult males, which would be represented by the γ' parameter in this situation. Because our study area was small with a small population size, this parameter was not estimable. However, we are confident that it would be obtainable for larger populations.

We ranked the scent lures from best (1) to worst (4) based on experience, before we began model construction. Out of the 3 models we constructed to evaluate how the lures performed with respect to capture probability, the categorical rank (rankcat)

and ordinal rank (rankordinal) models performed more poorly than the linear trend rank (rank) model. The closest categorical and ordinal rank models were 9.1 and 18.6 ΔAIC_c units from the top model respectively (Table 3). Part of our motivation to use different lures for each trapping session was to ensure we attracted as many bears as possible; we speculated that different bears may prefer different scents and using a wide variety of scents would attract more unique bears. While we detected differences in attraction across the 6 scent lures used in this study, we recommend that future studies restrict scent lure choices to those that bears find most attractive (e.g., anise oil, fish oil, and fatty acid scent) to enhance bear visitation at HSSs.

If multiple years of sampling are to be part of a monitoring protocol, robust-design models require no additional field work beyond what is required for regular closed-capture models. The benefits of a robust design over a traditional mark–recapture design are that apparent survival and temporary emigration rates can be monitored in addition to population size. This is desirable because apparent survival and emigration can provide insight into the mechanisms driving population changes. In addition, apparent survival estimates typically have higher precision than population size, potentially allowing declines to be detected sooner than from population size. Moreover and importantly, apparent survival estimates are not as prone to bias due to capture heterogeneity and do not require population closure. Similarly, population responses to management, such as increased or decreased harvest, can be detected sooner if apparent survival is monitored in addition to population size. The Huggins version of the robust design is especially useful for monitoring as well as testing ecological hypotheses, because individual covariates can be included in the model (White 2008). In theory, individual genotype could eventually be tied to fitness using this approach. Based on our observations and those of Clark et al. (2010), moving from simple closed capture to a robust-design closed capture is highly beneficial for multiple-year studies.

During the 5 years of study, 47 individual bears were encountered at HSSs, of which 27 were males and 20 were females. Our results indicate that females had a stronger affinity to the area than males and a lower mortality rate. This finding is consistent with published reports from elsewhere in black bear range, where males use larger home ranges and move longer distances than females (Pelton 1982, Powell et al. 1997, Pederson et al. 2008).

Management implications

Our noninvasive CMR-DNA study provided relatively efficient and reasonably precise estimates of a low-density black bear population on a small study site. We recommend using robust-design closed-capture and robust-design Pradel models if samples are taken over multiple years because in addition to population size, apparent survival, movement, recruitment, and finite population change rates can be estimated. Repeated periodic sampling efforts should provide managers with timely insights into population trends and the mechanisms driving them.

Acknowledgments

Literature cited

Anthony, R.G., E.D. Forsman, A.B. Franklin, D.R. Anderson, K.P. Burnham, G.C. White, C.J. Schwarz, J.D. Nichols, J.E. Hines, G.S. Olson, S.H. Ackers, L.S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, K.M. Dugger, K.E. Fehring, T.L. Fleming, R.P. Gerhardt, S.A. Gremel, R.J. Gutiérrez, P.J. Happe, D.R. Herter, J.M. Higley, R.B. Horn, L.L. Irwin, P.J. Loschl, J.A. Reid, and S.G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs 163.

Blakesley, J.A., M.E. Seamans, M.M. Conner, A.B. Franklin, G.C. White, R.J. Gutiérrez, J.E. Hines, J.D. Nichols, T.E. Munton, D.W.H. Shaw, J.J. Keane, G.N. Steger, and T.L. McDonald. 2010. Population dynamics of spotted owls in the Sierra Nevada, California. Wildlife Monographs 174.

Boersen, M.R., J.D. Clark, and T.L. King. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. Wildlife Society Bulletin 31:197–207.

Boulanger, J., B.N. McLellan, J.G. Woods, M.F. Proctor, and C. Strobeck. 2004. Sampling design and bias in DNA-based capture–mark–recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

———, G.C. White, M. Proctor, G. Stenhouse, G. Machutchon, and S. Himmer. 2008. Use of occupancy models to estimate the influence of previous live captures on DNA-based detection probabilities of grizzly bears. Journal of Wildlife Management 72: 589–595.

Buckland, S.T., K.P. Burnham, and N.H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53:603–618.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: A practical information theoretic approach. Springer, New York, New York, USA.

Clark, J.D., R. Eastridge, and M.J. Hooker. 2010. Effects of exploitation on black bear populations at White River National Wildlife Refuge. Journal of Wildlife Management 74:1448–1456.

Ebert, C., F. Knauer, I. Storch, and U. Hohmann. 2010. Individual heterogeneity as a pitfall in population estimates based on non-invasive genetic sampling: A review and recommendations. Wildlife Biology 16: 225–240.

Ennis, S., and T.F. Gallagher. 1994. PCR based sex determination assay in cattle based on the bovine Amelogenin LOCUS. Animal Genetics 25:425–427.

French, S.P., M.G. French, and R.H. Ward. 1996. A pilot study to develop a non-invasive method of marking grizzly bears for population size estimation and determine genetic diversity. Yellowstone Grizzly Foundation, Evanston, Wyoming, USA.

Huggins, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.

Immell, D., and R.G. Anthony. 2008. Estimation of black bear abundance using a discrete DNA sampling device. Journal of Wildlife Management 72:324–330.

Kendall, K.C., J.B. Stetz, J.B. Boulanger, A.C. MacLeod, D. Paetkau, and G.C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–17.

Kendall, W. 2011. The robust design. Pages 15-1–15-50 in E. Cooch and G.C. White, editors. Program MARK: A gentle introduction. http://www.phidot.org/software/mark/docs/book/, accessed 26 December 2011.

Lebreton, J.-D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

MacKenzie, D.I., M.E. Seamans, R.J. Gutierrez, and J.D. Nichols. 2010. Investigating the population dynamics of California spotted owls without marked individuals. Journal of Ornithology. DOI 10.1007/s10336-010-0544-6.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling and mark–recapture analysis. Journal of Wildlife Management 64:183–193.

Paetkau, D., G.F. Shields, and C. Strobeck. 1998. Gene flow between insular coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283–1292.

———. 2003. An empirical exploration of data quality on DNA-based population inventories. Molecular Ecology 12:1375–1387.

Pederson, J.C., S.B. Bates, and J.T. Flinders. 2008. Black ghosts of the forest. A Utah bear study. Tri Quest Book Services, Orem, Utah, USA.

Pelton, M.R. 1982. Black bear. Pages 504–514 in J.A. Chapman and G.H. Feldhammer, editors. Wild mammals of North America. John Hopkins University Press, Baltimore, Maryland, USA.

PLEDGER, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. Biometrics 56:434–442.

POWELL, R.A., J.W. ZIMMERMAN, AND D.E. SEAMAN. 1997. Ecology and behavior of North American black bears: Home ranges, habitat and social organization. Chapman and Hall, London, UK.

PRADEL, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

PROCTOR, M. 1995. DNA fingerprint from black bear hair as a basis for a mark recapture population estimate. Okanangan University College, British Columbia, Canada.

———, B. MCLELLAN, J. BOULANGER, C. APPS, G. STENHOUSE, D. PAETKAU, AND G. MOWAT. 2010. Ecological investigations of grizzly bears in Canada using DNA from hair, 1995–2005: A review of methods and progress. Ursus 21:169–188.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. Edward Arnold, London, England, UK.

TREDICK, C.A., M.R. VAUGHAN, D.F. STAUFFER, S.L. SIMEK, AND T. EASON. 2007. Sub-sampling genetic data to estimate black bear population size: A case study. Ursus 18:179–188.

———, AND ———. 2009. DNA-based population demographics of black bears in coastal North Carolina and Virginia. Journal of Wildlife Management 73:1031–1039.

WASATCH-CACHE NATIONAL FOREST. 1994. Wasatch-Cache National Forest vegetation. USDA, US Forest Service, Salt Lake City, Utah, USA.

WHITE, G.C., AND K.P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study Supplement 46:120–138.

———, ———, AND D.R. ANDERSON. 2001. Advanced features of Program Mark. Pages 368–377 in R. Field, R.J. Warren, H. Okarma, and P.R. Sievert, editors. Wildlife, land, and people: Priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.

———. 2008. Closed population estimation models and their extensions in program MARK. Environmental and Ecological Statistics 15:89–99.

WOODS, J.G., D. LEWIS, D. PAETKAU, B.N. MCLELLAN, M. PROCTOR, AND C. STROBECK. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.