



Population Ecology

Combined Use of Mark-Recapture and Genetic Analyses Reveals Response of a Black Bear Population to Changes in Food Productivity

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ABSTRACT We used mark-recapture analysis to investigate the dynamics of a black bear (*Ursus americanus*) population in northern Idaho where food availability varies seasonally and annually. We conducted noninvasive genetic sampling (NGS) during 2003–2006 in the Purcell Mountains of Idaho to collect black bear DNA samples for individual identification of bears. We used a combination of both mark-recapture and genetic analyses to evaluate whether variation in vital rates and genetic substructure was a function of changing food productivity in the study area. We found a heterozygote deficiency and detected genetic substructure within a single year, suggesting we sampled multiple subpopulations (a Wahlund effect). Our mark-recapture analyses suggested this pattern was in response to interannual variation in summer berry abundance. This project demonstrated the potential pitfalls of interpreting mark-recapture data over short time periods without ancillary data that can be used to evaluate mechanisms of population change. We found NGS provided information not only for traditional mark-recapture analysis but also complimentary insights into demography gained through genetic analyses. Combining mark-recapture estimates with analyses of population genetics provides a more complete understanding of population dynamics than either method alone, thus improving ecological inferences and effective management. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS black bear, genetic structure, Idaho, mark-recapture, noninvasive sampling, population genetics, Wahlund effect.

The development of noninvasive genetic sampling (NGS) coupled with mark-recapture analysis has allowed estimates of abundance and other population parameters (e.g., vital rates) for rare or elusive species (Taberlet and Bouvet 1992, Palsbl et al. 1997, Woods et al. 1999, Marucco et al. 2009). Noninvasive genetic sampling is advantageous for species with low densities or secretive behavior because animals do not need to be captured or observed to obtain information needed to estimate vital rates, in contrast with many traditional methods. It can also be used to describe patterns in population genetics (Schwartz et al. 2007). Genetic variation and deviations from Hardy–Weinberg (HW) proportions (observed vs. expected heterozygosity; Robertson and Hill 1984) within a population can provide insights (Allendorf and Luikart 2007, Schwartz et al. 2007) into the

mating system (Smith 1987, Elias et al. 2010), population structure (i.e., spatial variation in allele frequencies between demes or subpopulations; Ryman et al. 1979, Kendall et al. 2009, Norén et al. 2011), dispersal patterns and landscape barriers (Funk et al. 2005, Coulon et al. 2008, Vonhof et al. 2008), and social behavior (Morin et al. 1994, Costa-Urrutia et al. 2012).

Black bears are a widespread game species in North America, and effective monitoring of their populations is necessary to make sound management decisions and to ensure persistence (Miller 1990, Garshelis 1993, Pelton 2000, Garshelis and Hristienko 2006). Monitoring of bear populations is challenging because they often occupy dense forest habitat, occur in relatively low densities, and are secretive and solitary (Pelton et al. 1978, Harris 1986, Woods et al. 1999, Rice et al. 2001). Management agencies commonly use NGS coupled with mark-recapture analysis to study and monitor bear populations because the method allows larger sample sizes to be collected than by using traditional capture techniques (Mowat and Strobeck 2000,

Received: 21 June 2011; Accepted: 3 June 2013
Published: 3 October 2013

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Paetkau 2003, Kendall et al. 2009) and may violate fewer assumptions of mark-recapture models than traditional methods (Woods et al. 1999), providing increased precision and accuracy for estimates (Boulanger et al. 2008; Kendall et al. 2008, 2009).

Monitoring bears using periodic mark-recapture estimates can also be challenging because the distribution and abundance of food resources has been found to directly affect growth, survival, reproductive success, and movement rates of black bears (Jonkel and Cowan 1971, Rogers 1976, Rogers 1993, Garshelis and Noyce 2007). When food resources are scarce, survival and reproduction in black bears can be reduced substantially (Jonkel and Cowan 1971, Rogers 1976, Rogers 1993, Beecham and Rohlman 1994), and black bears often respond to wide-spread food scarcities by increasing movement rates and undertaking long-range movements in search of food (Drahos 1951, Garshelis and Pelton 1981, Rogers 1987, Pelton 1989, Garshelis and Noyce 2007). Thus, the composition of a black bear population available for sampling can be highly variable, particularly if a large proportion of observed bears disperse or immigrate temporarily in response to food availability.

We investigated the demography of a harvested population of black bears in relation to interannual variation in food abundance. We used a combination of mark-recapture and population genetic analyses, coupled with patterns of interannual variation in food abundance, to understand the underlying dynamics of the population. Our objectives were to 1) estimate annual vital rates (i.e., apparent survival and recruitment) using mark-recapture analyses, 2) evaluate annual patterns of genetic variation and structure within the population, 3) evaluate how trends in estimates of vital rates and genetic structure could be related to variation in food productivity, and 4) synthesize patterns in vital rates, food productivity, and genetic structure over time to interpret trend for the bear population we observed.

STUDY AREA

The study area was located in the Purcell Mountains of the Idaho Panhandle National Forest of Idaho, USA, encompassing approximately 400 km² of forested land and a large river system. The study area was bordered on 3 sides by state highways. The terrain varied from flat valley bottoms to steep and rugged mountainous slopes, with elevations ranging from approximately 700 m to 2,000 m. Mixed-conifer forests of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) dominated elevations below 1,300 m and Engelmann spruce (*Picea engelmannii*), subalpine fir (*A. lasiocarpa*), and mountain hemlock (*T. mertensiana*) dominated elevations above 1,300 m. Understory vegetation primarily consisted of thinleaf huckleberry (*Vaccinium* spp.), russet buffaloberry (*Shepherdia canadensis*), serviceberry (*Amelanchier alnifolia*), mountain ash (*Sorbus scopulinus*), pacific ninebark (*Physocarpus capitatus*), and oceanspray (*Holodiscus discolor*).

METHODS

Study Design and Mark-Recapture Sampling

We collected black bear hair samples in a robust design framework for mark-recapture analyses (Pollock 1982). We used a systematic grid design of hair trap stations to minimize capture variation and evenly distribute efforts across the study area, 2003–2006 (White et al. 1982). We placed hair trap stations systematically within 2.6-km² cells in 2003 and 2004. In 2005 and 2006, we placed hair trap stations in areas subjectively determined to maximize capture probabilities (forested habitats and >100 m from roads) within larger cells (5.8 km²) because of logistical constraints. The primary sampling periods were 6–12 weeks in all 4 years, conducted during the summer (May–Aug) when births were nonexistent and harvest was not permitted (i.e., when bear mortality was low). Within each primary sampling period, we included ≥1 secondary sampling period (i.e., trapping sessions) that was 11–23 days in length. The length of trapping sessions maximized the likelihood of demographic closure within primary sampling periods and prevented DNA degradation of hair samples from weather exposure. Our hair-trap design and DNA collection protocols were similar to Kendall et al. (2008, 2009).

Individual Genetic Analysis

We analyzed black bear samples at 9 microsatellite markers: G1A, G1D, G10B, G10H, G10J, G10M, G10X (Paetkau and Strobeck 1994; Paetkau et al. 1995, 1998), UarMU59 (Taberlet et al. 1997), and Msut-2 (Kitahara et al. 2000). We identified species, individual identity, and sex in each sample that contained sufficient DNA, following laboratory methods in Schwartz et al. (2006). We conducted extensive error checking to minimize genotyping error (i.e., allelic dropout and false alleles) due to variable quantities and quality of DNA in noninvasive genetic samples. We analyzed each DNA sample twice (we initially analyzed 2003 samples once, but many were subject to re-analysis; see Schwartz et al. 2006) and used program DROPOUT (McKelvey and Schwartz 2004, 2005) to detect genotyping errors and identify loci and samples with probable error. If we detected genotyping errors using DROPOUT, we re-analyzed problem samples until we detected no errors in the dataset.

Berry Productivity

To understand contributions of annual variation of food productivity to variation in vital rates, we used fruiting productivity of thinleaf huckleberry, russet buffaloberry, serviceberry, and mountain ash; these species are primary food sources for bears and fruiting varies in abundance and distribution annually (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Beecham and Rohlman 1994). The United States Fish and Wildlife Service (USFWS) has collected data on the production of huckleberries, buffaloberries, and serviceberries since 1989 and of mountain ash since 2001 in the Cabinet-Yaak ecosystem (Kasworm et al. 2008; Fig. 1). The Cabinet-Yaak ecosystem overlapped a portion of our study area; therefore, we assumed the berry production reported by Kasworm et al. (2008) was representative of our study area.

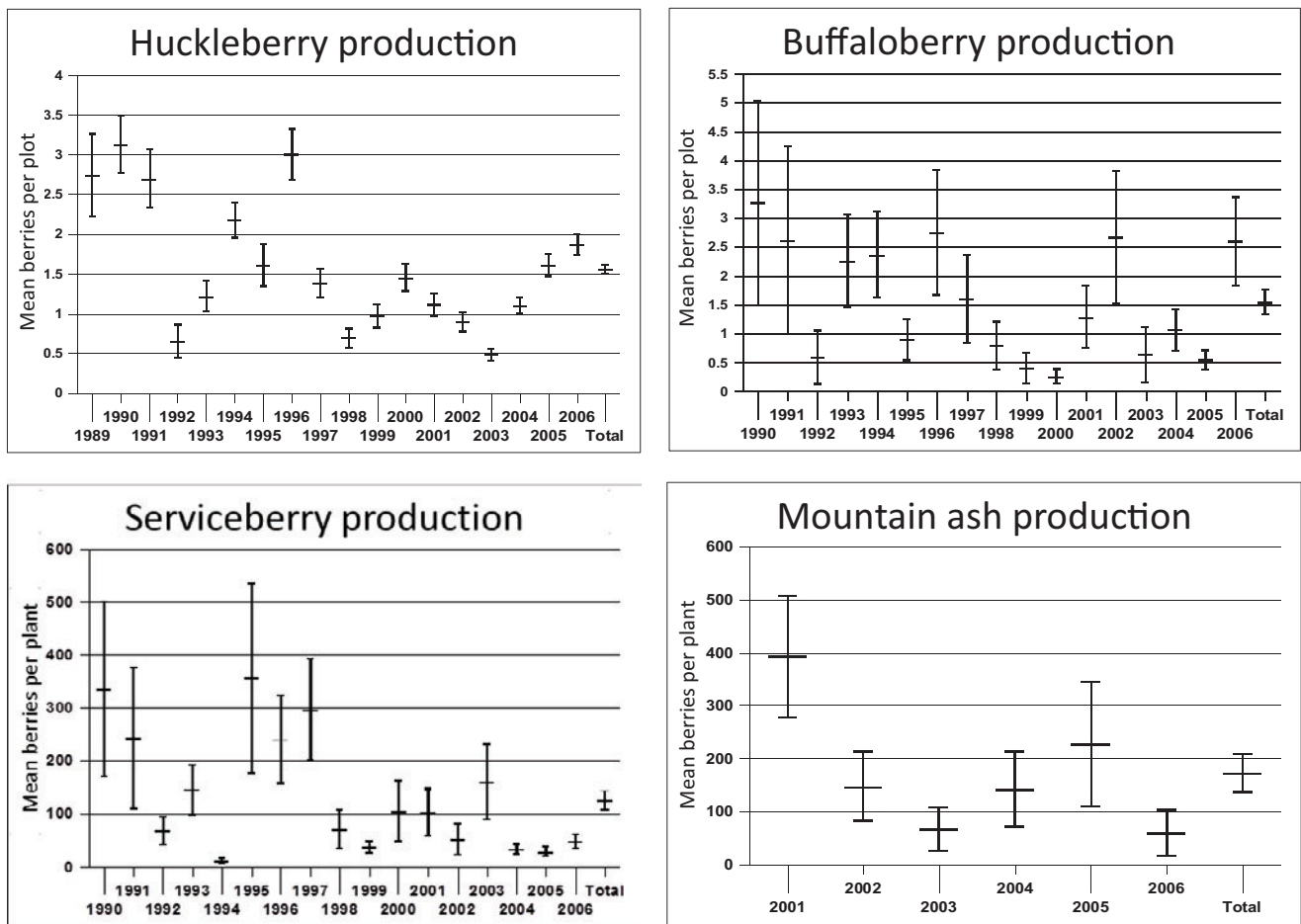


Figure 1. Mean berries per plot and 95% confidence intervals for huckleberries and buffaloberries and mean berries per plant for serviceberries and mountain ash in the Cabinet-Yaak Ecosystem, Idaho and Montana, from 1989 to 2006 (Kasworm et al. 2008).

To estimate production, Kasworm et al. (2008) sampled annual huckleberry and buffaloberry production using line transects placed in homogeneous habitats. They counted all fruits and pedicels within a 0.04-m² frame (2 × 2 decimeter) placed at 1-m intervals. They counted 50 frames containing the desired species on each transect, and if frames did not intercept a portion of the desired plant species, they advanced the frame at 0.5-m intervals. They monitored 16–23 huckleberry and 5 buffaloberry transects each year. Transects were added and removed over the years because of the effect of plant succession on berry productivity. They estimated serviceberry and mountain ash productivity by counting all the berries on marked plants. Ten marked plants were counted at each plot, with 5–7 serviceberry and 3 mountain ash plots sampled over the years. Timing of sampling was adjusted each year to coincide with peak berry ripening (see Kasworm et al. 2008 for more detailed methods).

Mark-Recapture Analysis

We modeled the dynamics of the black bear population through a robust design mark-recapture analysis in Program MARK (White and Burnham 1999) to determine the variation in vital rates that were associated with changes in food productivity. Specifically, we used the Pradel model

(Pradel 1996) to estimate and model apparent survival (ϕ ; probability of survival from time i to $i + 1$ and the probability of remaining in the study area between time i to $i + 1$; includes both mortality and emigration), recruitment rate (f ; number of individuals entering the population between time i to $i + 1$ per individual present at time i ; includes both births and immigration), capture probability (p), and recapture probability (c) using covariates of food production (Franklin 2001, Boulanger et al. 2004). We also used the Pradel model to derive estimates of realized population growth rate ($\lambda = \phi_i + f_i$) among years.

We conducted a preliminary analysis to determine if apparent survival, recruitment rate, and capture and recapture probabilities varied as a function of time (i.e., year), sex of the bear, behavioral response (i.e., $p \neq c$), and additive combinations of covariates (i.e., sex + year). We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to compare models (Burnham and Anderson 2002). We added food productivity covariates to the top models ($\Delta AIC_c < 2$) from these analyses. We fixed the recapture probability in 2003 ($c = 0$) because of a single capture session that year.

We calculated food productivity in 3 different ways: 1) productivity of individual species, to account for potentially

strong variation in contributions among species; 2) productivity of species in the summer (mid-Jul to mid-Sep; when huckleberries, buffaloberry, and serviceberry ripen) and fall (mid-Sep to mid-Nov or den entrance; when mountain ash ripens) to account for seasonal effects; and 3) summed productivity over all species, to evaluate contribution of overall berry productivity.

We standardized the berry abundance data and incorporated 6 different berry covariates into our mark-recapture candidate model set. We modeled apparent survival and recruitment rate as a function of the prior year's berry abundance. We hypothesized that high values for berry abundance could increase survival and reproduction and reduce emigration and immigration; low values would be expected to have the opposite effect. To determine the effect of each covariate on apparent survival and recruitment parameters, we evaluated beta estimates and their 95% confidence intervals.

We used AIC_c to compare models and to select the most parsimonious model; we considered models with $\Delta AIC_c < 2$ to be supported by the data (Burnham and Anderson 2002). We used all supported models to generate model-averaged estimates of parameters. We tested goodness of fit (GOF) to the Cormack-Jolly-Seber (CJS) live encounter model and estimated overdispersion with Program RELEASE (Burnham et al. 1987) for the recapture portion of the encounter history. We estimated overdispersion using the combined χ^2 values and degrees of freedom (df) from tests 2 and 3 in Program RELEASE by $\hat{c} = \chi^2/df$ (Burnham et al. 1987).

Population Genetic Analyses

We used genetic analyses to estimate deviations from HW proportions and to investigate the genetic structure of the population to determine whether annual variation in genetic structure existed. We estimated genetic variability within the group of individuals sampled each year by calculating the observed heterozygosity (H_o ; the proportion of heterozygotes observed in the population), expected heterozygosity (H_e ; the proportion of heterozygotes expected under HW equilibrium), and an inbreeding coefficient (F_{is} ; a measure of departure from expected HW proportions) using Program GENALEX (Peakall and Smouse 2006). We then compared each estimate of genetic variability by year and examined differences and deviations from HW proportions to determine observable changes in population dynamics. We also examined the number of private alleles (i.e., alleles only observed in a single year).

We evaluated whether spatial genetic structure existed for each year using program STRUCTURE (Pritchard et al. 2000; Falush et al. 2003, 2007) to assess if immigration or temporary movement could influence the number of unique individuals observed in a given year. STRUCTURE can be used to evaluate the likelihood of different number of populations (K) in a single sample by minimizing HW deviations and linkage disequilibrium (Pritchard et al. 2000). We used the admixture model, where individuals may have mixed ancestry, and the correlated allele frequencies option, where allele frequencies in different subpopulations are likely

to be similar. We ran STRUCTURE iterations with a burn-in of 50,000 periods and an additional 50,000 Markov chain Monte Carlo (MCMC) repetitions to evaluate K from 1 to 6 (10 iterations per K). We considered the K with the greatest log-likelihood to be the most supported; when the most supported K was >1 , we used an ad hoc method (ΔK) from Evanno et al. (2005) to identify the most likely K . We examined the estimated proportion of population membership (Q) of each individual in each cluster identified for the most supported simulation of K and compared this average Q to the random expectation of Q if membership was equally divided among populations. We also examined F_{ST} values, a measure of population subdivision, among populations identified by STRUCTURE. Evaluations of Program STRUCTURE have shown it performs well at assigning individuals to populations with low differentiation among populations, although F_{ST} values must be at least 0.05 to attain a population assignment accuracy rate of 97% (Latch et al. 2006).

RESULTS

Across years, the study area (i.e., area containing hair traps, buffered by the width of 1 cell) ranged from 367 km² to 453 km² in size, but the location and relative shape of the study area was largely consistent (Table 1; Fig. 2). The number and general location of hair trap stations within the study area also varied each year. The number of trapping sessions sampled and trap days ranged 1–5 sessions and 1,602–5,288 days, respectively, over the 4 years. We identified 277 (134 females, 140 males, 3 unknown sex) black bears in the Purcell Mountains over the study. We did not include bears of unknown sex in the mark-recapture analyses because our models were sex-specific. The number of unique individuals identified each year ranged 53–156 bears, with 75–194% more bears identified in 2004 than in other years (Table 2). We captured a large portion (67%) of bears only once, with 54% of those bears captured during 2004. Recapture rates ranged 0.16–0.43 over the 4 years.

Huckleberry abundance gradually increased during 2003–2006, and the lowest huckleberry abundance in 18 years occurred in 2003 (Fig. 1). Buffaloberry abundance generally increased over the 4 years, except for a drop in abundance in 2005. Serviceberry abundance was relatively high in 2003 and relatively low during 2004–2006. Mountain ash abundance gradually increased 2003–2005 and dropped in 2006. The lowest summer berry abundance (huckleberry + buffaloberry + serviceberry) over the 4 years occurred during 2004 and the highest occurred in 2006. The lowest total berry abundance

Table 1. Mark-recapture sampling design and effort to determine population trend of black bears in northern Idaho, USA, from 2003 to 2006.

Year	Area (km ²)	Traps	Trapping sessions	Trap days	Trap density (traps/km ²)
2003	393	89	1	1,602	0.23
2004	393	89	3	5,288	0.23
2005	453	104	4	4,164	0.23
2006	367	46	5	3,187	0.13

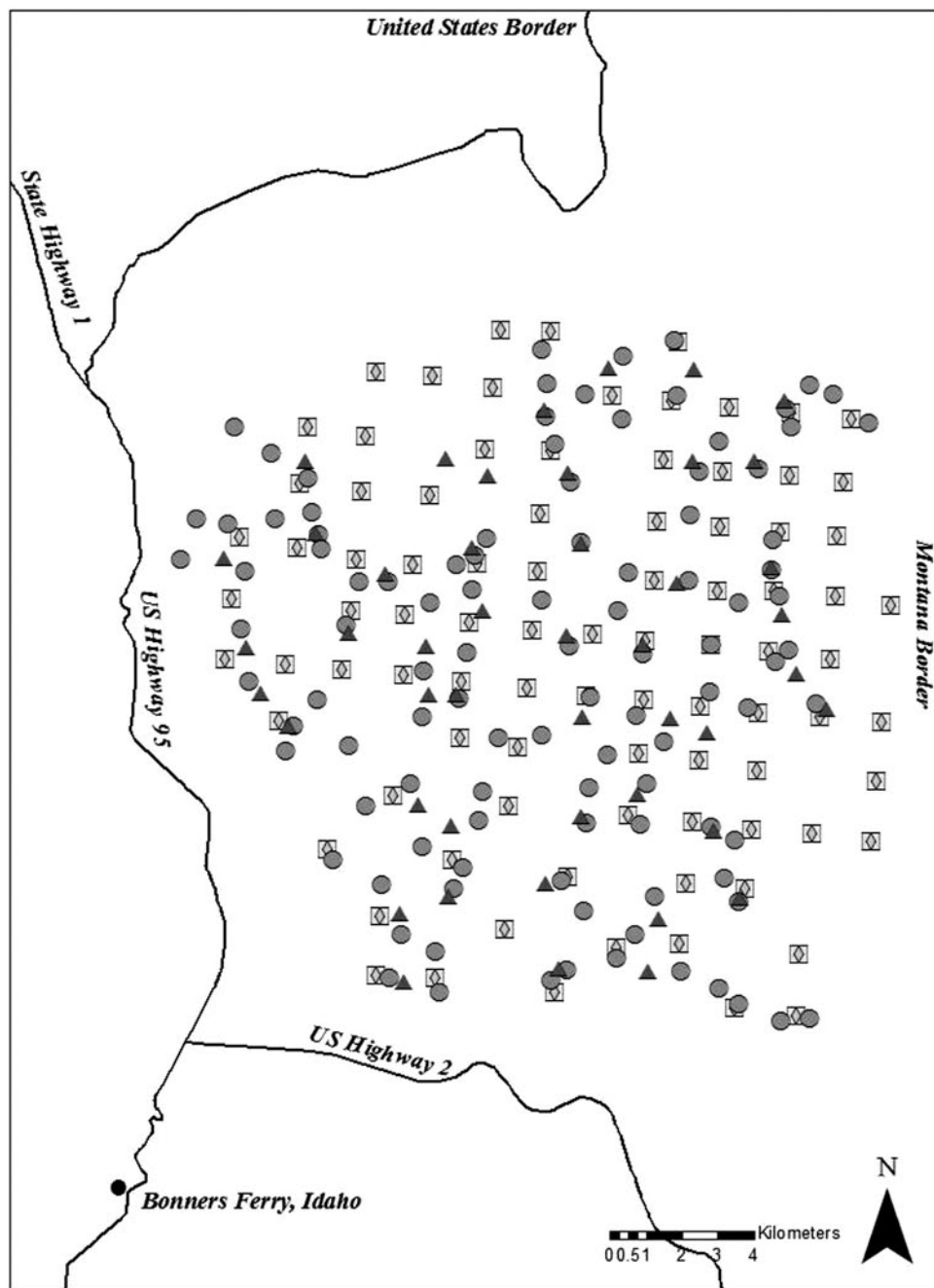


Figure 2. Location of black bear hair-trap stations in 2003 (■), 2004 (◆), 2005 (●), and 2006 (▲) in northern Idaho, USA.

Table 2. Individual genetic analyses of DNA samples using microsatellite markers and recapture events of black bears in northern Idaho, USA, from 2003 to 2006.

Year	No. samples	N_u^a	Females	Males	Unknown sex	Bears captured $>1^b$	Recapture events	Recapture rate ^c
2003	352	53	32	20	1			
2004	383	156	80	74	2	21	25	0.16
2005	328	89	50	39	0	27	38	0.43
2006	266	70	36	34	0	18	26	0.37

^a Number of uniquely identified individuals.

^b 2003 had only a single trapping session (no recaptures).

^c Total number of recapture events divided by N_u .

(huckleberry + buffaloberry + serviceberry + mountain ash) occurred in 2003 and the highest occurred in 2006.

Mark-Recapture Analysis

Our preliminary analyses of apparent survival, recruitment rate, and capture and recapture probabilities revealed strong support for variation among years and between sexes and some support for a behavioral response of capture probabilities. The goodness-of-fit test did not detect overdispersion of recaptures ($\chi^2_{67} = 59.3$, $P = 0.74$). Model selection indicated that apparent survival and recruitment rates were influenced by sex and summer berry abundance of the previous year (Table 3). The 4 best-supported models suggested that variation in summer berry abundance was positively related to apparent survival (AIC_c weighted average $\beta = 3.26$, 95% CI = 1.05–5.47). The top 3 models suggested variation in summer berry abundance also was positively related to recruitment rate (AIC_c weighted average $\beta = 3.36$, 95% CI = 2.11–4.62).

Model-averaged estimates of apparent survival for males and females showed that the largest number of animals died or emigrated between 2004 and 2005 (Fig. 3). Model-averaged recruitment rate estimates for males and females showed that the largest number of new animals entering the population occurred between 2003 and 2004 (Fig. 4). Overall, females had greater apparent survival rates than did

males, and males had greater recruitment rates than did females. Model-averaged estimates (SE) of capture probability for females showed some variation over years, with 0.41 ± 0.032 in 2003, 0.22 ± 0.025 in 2004, 0.24 ± 0.027 in 2005, and 0.22 ± 0.026 in 2006; model-averaged estimates of capture probability for males also varied across years with 0.36 ± 0.029 in 2003, 0.16 ± 0.025 in 2004, 0.17 ± 0.026 in 2005, and 0.16 ± 0.025 in 2006. Overall, females had greater capture probabilities than did males. Model-averaged recapture probabilities did not differ from capture probability estimates (i.e., recapture probability estimates were included in the 95% CI for capture probability). The model-averaged realized population growth estimates for females were 1.99 ± 0.33 in 2003–2004, 0.50 ± 0.05 in 2004–2005, and 0.69 ± 0.07 in 2005–2006; model-averaged realized population growth estimates for males were 3.33 ± 0.82 in 2003–2004, 0.46 ± 0.06 in 2004–2005, and 0.74 ± 0.09 for males in 2005–2006.

Population Genetic Analyses

Observed heterozygosity levels were similar in all years except for 2004, with a 20–26% lower average observed heterozygosity than in other years (Table 4). Expected levels of heterozygosity under HW equilibrium did not vary among years (0.761–0.789). Estimates of F_{is} were comparable in all years except for 2004. Years 2003, 2005, and 2006 did not

Table 3. Model selection results for black bear vital rates influenced by variation in berry productivity in northern Idaho, USA, from 2003 to 2006. Models are ranked from most to least supported based on Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c) from the top model, and Akaike weights (w_i). We also present the number of parameters for each model (K).

Apparent survival (ϕ)	Recruitment (f)	Capture and recapture probability (p and c) ^a	K	AIC_c	ΔAIC_c	w_i	Deviance
Sex + summer berries	Sex + summer berries	Sex + year	11	2,362.65	0.00	0.226	2,340.05
Sex + summer berries	Sex + summer berries	Sex ^b	9	2,363.45	0.81	0.151	2,345.05
Sex + summer berries	Sex + summer berries	Sex	8	2,363.87	1.22	0.122	2,347.55
Sex + summer berries	Sex	Sex	7	2,364.37	1.72	0.096	2,350.12
Sex + year	Sex + year	Sex	10	2,364.66	2.01	0.083	2,344.16
Sex + year	Sex + year	Sex ^b	11	2,364.84	2.19	0.075	2,342.25
Sex + year	Sex	Sex	8	2,365.05	2.41	0.068	2,348.73
Sex + year	Sex + year	Sex + year	13	2,365.14	2.49	0.065	2,338.31
Sex + serviceberry	Sex	Sex	7	2,365.36	2.71	0.058	2,351.11
Sex + serviceberry	Sex + serviceberry	Sex ^b	9	2,366.67	4.02	0.030	2,348.26
Sex + serviceberry	Sex + serviceberry	Sex	8	2,367.09	4.44	0.025	2,350.76
Sex + serviceberry	Sex + serviceberry	Sex + year	11	2,373.25	10.60	0.001	2,350.65
Sex + huckleberry	Sex	Sex	7	2,376.19	13.54	0.000	2,361.94
Sex + huckleberry	Sex + huckleberry	Sex + year	11	2,376.47	13.82	0.000	2,353.87
Sex + huckleberry	Sex + huckleberry	Sex	8	2,378.26	15.61	0.000	2,361.93
Sex + huckleberry	Sex + huckleberry	Sex ^b	9	2,378.38	15.74	0.000	2,359.98
Sex + mountain ash	Sex + mountain ash	Sex + year	11	2,379.85	17.20	0.000	2,357.25
Sex + buffaloberry	Sex + buffaloberry	Sex	8	2,380.81	18.16	0.000	2,364.49
Sex + mountain ash	Sex	Sex	7	2,381.28	18.63	0.000	2,367.03
Sex + buffaloberry	Sex + buffaloberry	Sex ^b	9	2,381.93	19.28	0.000	2,363.52
Sex + total berries	Sex + total berries	Sex + year	11	2,382.86	20.21	0.000	2,360.26
Sex + buffaloberry	Sex	Sex	7	2,383.25	20.60	0.000	2,369.00
Sex + mountain ash	Sex + mountain ash	Sex	8	2,383.30	20.65	0.000	2,366.98
Sex + mountain ash	Sex + mountain ash	Sex ^b	9	2,383.89	21.24	0.000	2,365.48
Sex + total berries	Sex	Sex	7	2,388.20	25.55	0.000	2,373.95
Sex + total berries	Sex + total berries	Sex	8	2,390.13	27.48	0.000	2,373.81
Sex + buffaloberry	Sex + buffaloberry	Sex + year	11	2,390.36	27.71	0.000	2,367.76
Sex + total berries	Sex + total berries	Sex ^b	9	2,391.11	28.46	0.000	2,372.70
Constant	Constant	Constant	3	2,404.90	42.25	0.000	2,398.85

^a Capture probability (p) and recapture probability (c) were modeled as equal (i.e., $p = c$) unless otherwise stated.

^b Capture probability (p) and recapture probability (c) were modeled as unequal (i.e., $p \neq c$; behavioral response) but with the same covariate (i.e., sex).

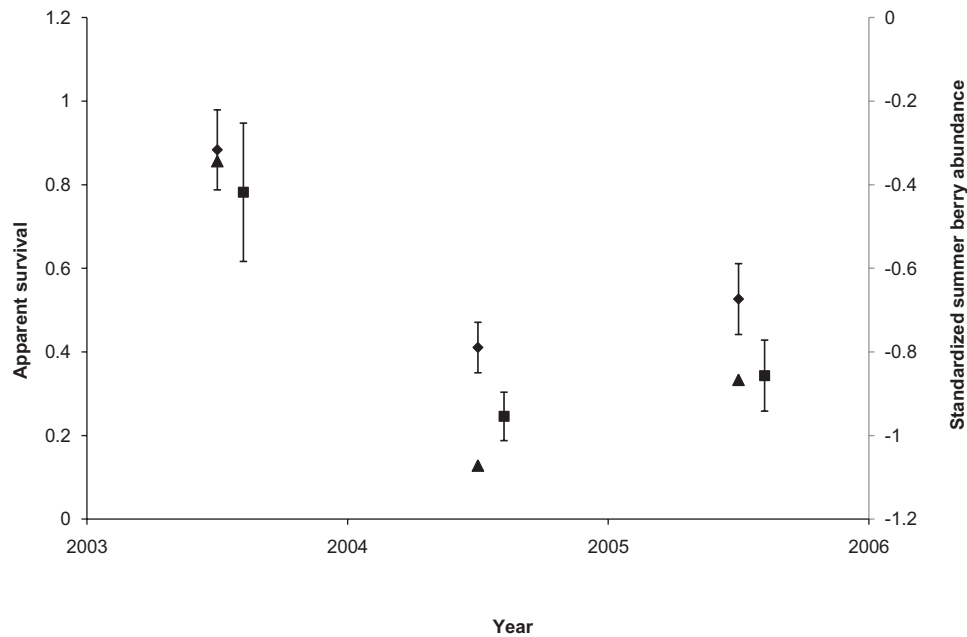


Figure 3. Female (♦) and male (■) model averaged estimates and standard errors for apparent survival of black bears and standardized summer berry abundance (▲) in northern Idaho, USA, from 2003 to 2006.

deviate strongly from HW proportions (F_{is} from -0.004 to 0.009), but we observed a deviation from HW proportions ($F_{is} = 0.212$) in 2004. In 2004, all loci had a significant excess of homozygotes, compared to 0–1 locus in other years. The number of private alleles identified each year ranged 0–3 alleles, with 3 private alleles identified in 2004.

The most likely number of populations (K) sampled each year varied 1–4 populations (Table 4). In 2003 and 2005, the most likely K was 1 population. The most likely K for 2006 was 2 populations, with the mean Q ranging 0.829 – 0.835 . F_{ST} values among populations in 2006 varied 0.0011 –

0.1251 . The most likely K in 2004 was 4 populations, with the mean Q ranging 0.562 – 0.729 , and the random expectation if membership was equally divided among populations was 0.25 . F_{ST} values among populations in 2004 varied 0.0431 – 0.1159 .

DISCUSSION

Combining mark-recapture estimates with analyses of population genetics allowed for a more complete understanding of the dynamics of the bear population we studied than either method alone did. Our combined results

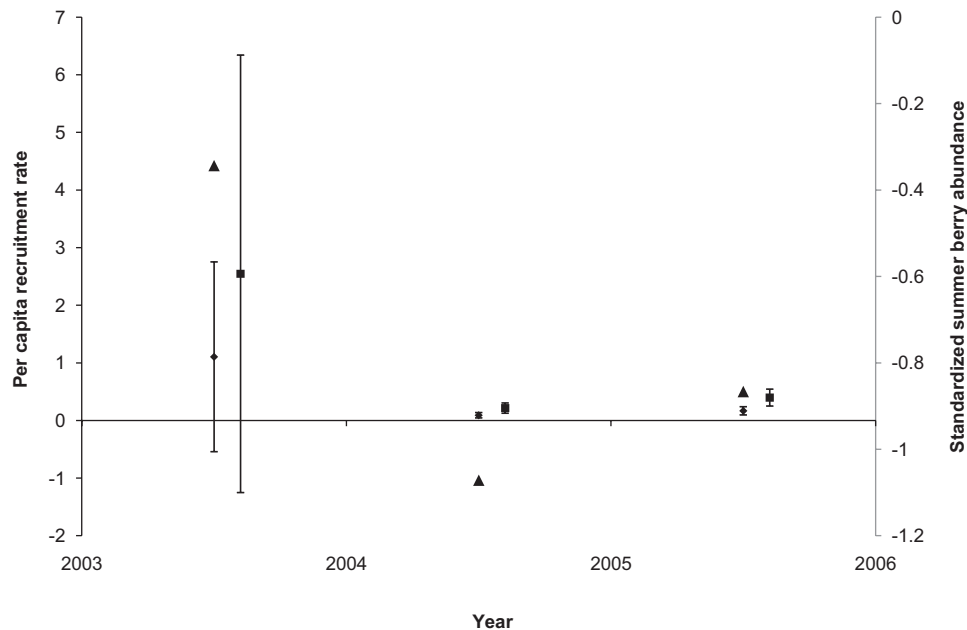


Figure 4. Female (♦) and male (■) model averaged estimates and standard errors for per capita recruitment rate of black bears and standardized summer berry abundance (▲) in northern Idaho, USA, from 2003 to 2006.

Table 4. Genetic variation parameters and number of populations identified for black bears in northern Idaho, USA, from 2003 to 2006.

Year	No. private alleles ^a	H_o^b	H_e^c	F_{is}^d	K^e	ΔK^f
2003	0	0.754	0.761	0.009	1	
2004	3	0.622	0.789	0.212	6	4
2005	1	0.785	0.788	0.004	1	
2006	0	0.780	0.777	-0.004	2	2

^a Number of alleles unique to a single year.

^b Observed heterozygosity.

^c Expected heterozygosity.

^d Inbreeding coefficient [$F_{is} = (H_e - H_o)/H_e$].

^e Most likely number of populations.

^f We used ΔK to calculate most likely K , when $K > 1$.

indicated a large change in population dynamics occurred during our study, and this appeared to be associated with interannual variation in soft mast abundance.

Our mark-recapture analysis revealed variation in vital rates that was associated with variation in food productivity during 2003–2006. Specifically, species that fruit primarily during summer (huckleberry, buffaloberry, and serviceberry) best-explained variation in vital rates over the 4 years. This is likely because summer berries provide the first abundant food source available to bears after they emerge from their dens, and over the course of a year comprise the majority of nutrition bears in northern Idaho obtain for maintenance, reproduction, and overwinter survival (Jonkel and Cowan 1971, Beecham and Rohlman 1994). Further, the presence of 3 berry-producing species in the summer likely reduces variability of overall berry productivity, which is not possible in the fall when only 1 berry species (mountain ash) ripens. In the event that all 3 summer species have poor production, however, bears are likely to make large movements in search of food (Drahos 1951, Garshelis and Pelton 1981, Rogers 1987, Pelton 1989, Garshelis and Noyce 2007) because they cannot rely on productivity of fall berries alone to ensure overwinter survival.

Our apparent survival estimates decreased from 2003–2004 to 2004–2005 and then increased from 2004–2005 to 2005–2006. Consistent with our main hypothesis, summer berry productivity was correspondingly low in 2004, likely causing increased mortality and emigration during 2004. Relatively high productivity of summer berries in 2005–2006 likely caused decreased mortality and emigration. The pattern for recruitment was less clear, because of uncertainty associated with the estimates (i.e., large standard errors) and no clear pattern of variation over years. Given the low reproductive potential and relatively high survival rates of black bears (Jonkel and Cowan 1971, Reynolds and Beecham 1980, Bunnell and Tait 1985, Kolenosky 1990, Kasworm and Thier 1994), large fluctuations observed in the vital rates were almost certainly driven by variation in immigration and emigration rates, not births and deaths.

Our beta estimates suggested summer berry productivity had a positive effect on recruitment, contrary to our hypothesis for years of food scarcity. The relationship we observed is likely due to our limited data for 2003 and how

we modeled variation of berry covariates using a single parameter (i.e., effect on vital rates were constant across time). Using time-varying covariate models (i.e., a separate berry abundance parameter for each year) might have revealed different interannual effects of berry productivity on recruitment, but would have increased the number of model parameters beyond the capacity of our data.

The Pradel model we used is an open population model (i.e., allowing emigration, immigration, births, and deaths), and has 2 primary assumptions: 1) the study area size remains constant, and 2) no permanent trap response exists (Franklin 2001). Because our study area shape changed relatively little over the years, and because bears are wide-ranging animals with large home ranges, we believe violation of the first assumption to the point of bias was unlikely. In addition, the study area size and shape did not change from 2003 to 2004 when we observed the large increase in immigration. With the very small levels of trap response we observed, we believe violation of the second assumption was also unlikely (Franklin 2001). We accounted for the variation in sampling design and effort from 1 year to the next by modeling capture probability by year. We believe the slight changes in sampling durations among years did not bias our results because we captured relatively few bears during extended portions of sampling periods.

Our analyses of HW deviations, genetic substructure, and the presence of private alleles indicated that population dynamics during 2004 differed from other years. In contrast to other years, the observed heterozygosity in 2004 differed strongly from expected HW proportions. The presence of more homozygotes than expected suggested a change in population dynamics. An excess of homozygotes can be a function of nonrandom mating through population subdivision (i.e., the presence of multiple subpopulations sampled within a single population, also known as the Wahlund effect; Wright 1931, Cohen 1990, Allendorf and Luikart 2007). Evidence for genetic substructure was either nonexistent or equivocal in all years except 2004. Detection of genetic substructure in 2004 further provided strong evidence for multiple subpopulations sampled and the presence of a Wahlund effect. This suggests that the northern Idaho black bear population was not panmictic and immigrating bears from spatially structured subpopulations influenced the patterns we observed. The 3 private alleles identified in 2004 further supports the hypothesis that we sampled bears originating from areas relatively distant in 2004; these bears would not typically mate with bears inhabiting our study area.

Our population genetics results indicate the presence of genetically structured subpopulations of black bears in northern Idaho. The ecology of black bears and the habitats they occupy in northern Idaho suggest genetic divergence among geographically proximate subpopulations is likely. Female black bears are natally philopatric (Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Moyer et al. 2006), resulting in low levels of female-mediated gene flow. Male black bears have high dispersal rates, resulting in high levels of male-mediated gene flow.

Dispersal, however, is very costly (Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1992).

The mark-recapture and population genetic results together demonstrated that the variation in the number of unique individuals observed and vital rates were likely attributable to temporary immigration in response to low food productivity. These results have broad implications for inferring population dynamics of black bears, particularly during years of food scarcity. At face value, vital rate estimates for black bears in our study area 2003–2006 would suggest large fluctuations in the population, uncharacteristic of species such as bears with generally slow population growth (Romanovsky 2002). Our analyses showed, however, that these fluctuations were likely due to a temporary change in the distribution and movement patterns of bears, not to population growth driven by increased reproduction and survival. Thus, the increase in the population we observed in our study area in 2004 was probably real, but its transient nature would make it inappropriate for inferring population trends and thus of questionable usefulness for management. Sampling over multiple years allowed the detection and appropriate interpretation of anomalous patterns, such as those we found for 2004.

Our results demonstrated the challenges of monitoring black bears using mark-recapture methods when critical assumptions are violated, particularly if our data were used to estimate population abundance, which is the information most often desired by managers. The assumption of geographic closure was likely violated in 2004 because of temporary migrations on and off the study area. Violation of the geographic closure assumption would negatively affect estimates of capture probability, causing estimates of abundance to be positively biased (Otis et al. 1978); such estimates would ultimately represent the superpopulation of the sampling grid and surrounding area (Kendall 1999). Violation of the closure assumption caused by completely random movements on and off the study area will give unbiased superpopulation estimates (Kendall 1999). If temporary emigration or immigration (e.g., bears temporarily emigrating or immigrating in search of food) and permanent 1 entry, 1 exit (e.g., transient or dispersing bears) types of movements occur, however, then superpopulation estimates will be biased (Kendall 1999). Our results also confirm that the degree of closure violation when sampling black bears can strongly vary because of food productivity, causing biased estimates of population trend. Methods are available to test and correct for geographic closure violation (Otis et al. 1978, Wilson and Anderson 1985, Stanley and Burnham 1999, White and Shenk 2001, Efford et al. 2004); no method, however, is likely robust to the degree of violation we observed because of the long distances bears may have traveled in 2004.

MANAGEMENT IMPLICATIONS

Our project was in part designed to monitor population trend of black bears in northern Idaho and to provide implications for trend analysis. We found that inferences of population trend based on estimates of λ , if not clarified by further

genetic analysis, would have implied a change in the abundance of bears inhabiting our study area 2003–2006 that was misleading, potentially resulting in inappropriate management decisions. Our study also demonstrated that years with low food availability can cause significant changes in the distribution of bears; coupling measures of food productivity with abundance data may therefore be needed to provide a comprehensive interpretation of monitoring results. If measures of food productivity are not available, then sampling during suspected food scarcities is best avoided to reduce the risk of sampling transient bears. Because of the bear population dynamics we observed, we suggest caution should be exercised when inferring trends over a short-term study such as ours; reliable estimates of trend for black bear populations require long-term monitoring.

ACKNOWLEDGMENTS

We thank the Idaho Department of Fish and Game for financial and logistical support of this project, as well as the many people who helped deploy and check hair-trapping stations used in this study. We also thank personnel from the Wildlife Genetics Laboratory at the United States Forest Service Rocky Mountain Research Station for their meticulous and thorough work on the genetic analyses. We are particularly grateful for helpful and thought-provoking reviews of this work by F. Allendorf, R. Waples, J. Boulanger, and 2 anonymous reviewers. Use of trade names does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Allendorf, F. W., and G. Luikart. 2007. Conservation and the genetics of populations. Blackwell Publishing, Malden, Massachusetts, USA.
- Beecham, J. J., and J. Rohlfman. 1994. A shadow in the forest: Idaho's black bear. University of Idaho Press, Moscow, Idaho, USA.
- Boulanger, J., S. Himmer, and C. Swan. 2004. Monitoring of grizzly bear population trends and demography using DNA mark-recapture methods in the Owikeno Lake area of British Columbia. *Canadian Journal of Zoology* 82:1267–1277.
- Boulanger, J., K. C. Kendall, J. B. Stetz, D. A. Roon, L. P. Waits, and D. Paetkau. 2008. Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. *Ecological Applications* 18:577–589.
- Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. *Arctic* 38:316–323.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5.
- Cohen, J. E. 1990. DNA fingerprinting for forensic identification: potential effects of data interpretation of subpopulation heterogeneity and band number variability. *American Journal of Human Genetics* 46:358–368.
- Costa-Urrutia, P., C. Abud, E. R. Secchi, and E. P. Lessa. 2012. Population genetic structure and social kin associations of Franciscana dolphin, *Pontoporia blainvillei*. *Journal of Heredity* 103:92–102.
- Coulon, A., J. W. Fitzpatrick, R. Bowman, B. M. Stith, C. A. Makarewicz, L. M. Stenzler, and I. J. Lovette. 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida scrub-jay (*Aphelocoma coerulescens*). *Molecular Ecology* 17:1685–1701.
- Drahos, N. 1951. Notes on bears. *New York State Conservationist* 7:14–18.

- Efford, M. G., D. K. Dawson, and C. S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation* 27:1:217–228.
- Elias, J., S. Dorn, and D. Mazzi. 2010. Inbreeding in a natural population of the gregarious parasitoid wasp *Cotesia glomerata*. *Molecular Ecology* 19:2336–2345.
- Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:962–968.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* 14:2611–2620.
- Falush, D., M. Stephens, and J. K. Pritchard. 2003. Inference of population structure: extensions to linked loci and correlated allele frequencies. *Genetics* 164:1567–1587.
- Falush, D., M. Stephens, and J. K. Pritchard. 2007. Inference of population structure using multilocus genotype data: dominant markers and null alleles. *Molecular Ecology Notes* 7:574–578.
- Franklin, A. B. 2001. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Pages 290–296 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century*. The Wildlife Society, Bethesda, Maryland, USA.
- Funk, W. C., M. S. Blouin, P. S. Corn, B. A. Maxell, D. S. Pilliod, S. Amish, and F. W. Allendorf. 2005. Population structure of Columbia spotted frogs (*Rana luteiventris*) is strongly affected by the landscape. *Molecular Ecology* 14:483–493.
- Garshelis, D. L. 1993. Monitoring black bear populations: pitfalls and recommendations. *Western Black Bear Workshop* 4:123–144.
- Garshelis, D. L., and H. Hristienko. 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. *Ursus* 17:1–7.
- Garshelis, D. L., and K. V. Noyce. 2007. Seeing the world through the nose of a bear—diversity of foods fosters behavioral and demographic stability. Pages 139–163 in T. E. Fulbright and D. G. Hewitt, editors. *Wildlife science: linking ecological theory and management application*. CRC Press, Boca Raton, Florida, USA.
- Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smokey Mountains National Park. *Journal of Wildlife Management* 45:912–925.
- Harris, R. B. 1986. Grizzly bear population monitoring: current options and considerations. University of Montana Forest and Conservation Experiment Station, Miscellaneous Publication No. 45, Missoula, Montana, USA.
- Jonkel, C. J., and I. McT. Cowan. 1971. The black bear and the spruce-fir forest. *Wildlife Monographs* 27:1–57.
- Kasworm, W. F., H. Carriles, T. G. Radandt, and C. Servheen. 2008. Cabinet-Yaak grizzly bear recovery area 2007 research and monitoring progress report. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- Kasworm, W. F., and T. J. Thier. 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. *International Conference of Bear Research and Management* 9:223–230.
- Kendall, K. C., J. B. Stetz, J. 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, K. C., J. B. Stetz, D. A. Roon, L. P. Waits, J. Boulanger, and D. Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. *Journal of Wildlife Management* 72:1693–1705.
- Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80:2517–2525.
- Kitahara, E., Y. Isagi, Y. Ishibashi, and T. Saitoh. 2000. Polymorphic microsatellite DNA markers in the Asiatic black bear *Ursus thibetanus*. *Molecular Ecology* 9:1661–1686.
- Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. *International Conference on Bear Research and Management* 8:385–392.
- Latch, E. K., G. Dharmarajan, J. C. Claubitz, and O. E. Rhodes, Jr. 2006. Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conservation Genetics* 7:295–302.
- Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southeastern Washington. *Journal of Wildlife Management* 41:413–425.
- Marucco, F., D. H. Pletscher, L. Boitanai, M. K. Schwartz, K. Pilgrim, and J.-D. Lebreton. 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the Western Alps. *Journal of Applied Ecology* 46:1003–1010.
- McKelvey, K. S., and M. K. Schwartz. 2004. Providing reliable and accurate genetic capture-mark-recapture estimates in a cost-effective way. *Journal of Wildlife Management* 68:453–456.
- McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes* 5:716–718.
- Miller, S. D. 1990. Population management of bears in North America. *International Conference on Bear Research and Management* 8:357–373.
- Morin, P. A., J. J. Moore, R. Chakraborty, L. Jin, J. Goodall, and D. S. Woodruff. 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265:1193–1201.
- 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.
- Moyer, M. A., J. W. McCown, T. H. Eason, and M. K. Oli. 2006. Does genetic relatedness influence space use pattern? A test on Florida black bears. *Journal of Mammalogy* 87:255–261.
- Norén, K., L. Carmichael, E. Fuglei, N. E. Eide, P. Hersteinsson, and A. Angerbjörn. 2011. Pulses of movement across the sea ice: population connectivity and temporal genetic structure in the arctic fox. *Oecologia* 166:973–984.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12:1375–1387.
- Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- 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.
- Paetkau, D., and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bear populations. *Molecular Ecology* 3:489–495.
- Palsbll, P. J., J. Allen, M. Bérube, P. J. Clapham, T. P. Feddersen, P. S. Hammond, R. R. Hudson, H. Jrgensen, S. Katona, A. H. Larsen, F. Larsen, J. Lien, D. K. Mattlia, J. Sigurjonsson, R. Sears, T. Smith, R. Sponer, P. Stevick, and N. Oien. 1997. Genetic tagging of humpback whales. *Nature* 388:767–769.
- Peakall, R., and P. E. Smouse. 2006. GenAlex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Pelton, M. R. 1989. The impacts of oak mast on black bears in the southern Appalachians. *Proceedings of the Workshop: Southern Appalachian Mast Management*. University of Tennessee, Knoxville, Tennessee, USA.
- Pelton, M. R. 2000. Black bear. Pages 389–403 in S. Demarais and P. K. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Pelton, M. R., B. Cardoza, B. Conley, C. Dubrock, and J. Lindzey. 1978. Census techniques and population indices. *Proceedings Eastern Workshop on Black Bear Research and Management* 4: 242–252.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multi-locus genotype data. *Genetics* 155:945–959.
- Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. *International Conference on Bear Research and Management* 4: 181–190.
- Rice, C. G., J. Rohlman, J. Beecham, and S. Pozzanghera. 2001. Power analysis of bait station surveys in Idaho and Washington. *Ursus* 12:227–236.
- Robertson, A., and W. G. Hill. 1984. Deviations from Hardy-Weinberg proportions: sampling variances and use in the estimation of inbreeding coefficients. *Genetics* 107:703–718.

- Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Transactions of the North American Wildlife and Natural Resource Conference* 41:431–438.
- Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97.
- Rogers, L. L. 1993. The role of habitat quality in the natural regulation of black bear populations. *Proceedings of Western Black Bear Workshop* 4: 95–102.
- Romanovsky, Y. E. 2002. Life history variation within a taxon: a comparative analysis of birds and mammals. *Zhurnal Obshchei Biologii* 63:371–381.
- Ryman, N., F. W. Allendorf, and G. Ståhl. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout (*Salmo trutta*). *Genetics* 92:247–262.
- Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56:426–431.
- Schwartz, M. K., S. A. Cushman, K. S. McKelvey, J. Hayden, and C. Engkjer. 2006. Detecting genotyping errors and describing American black bear movement in northern Idaho. *Ursus* 17:138–148.
- Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22:25–33.
- Smith, P. J. 1987. Homozygous excess in sand flounder, *Rhombosolea plebeia*, produced by assortative mating. *Marine Biology* 95:489–492.
- Stanley, T. R., and K. P. Burnham. 1999. A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6:197–209.
- Taberlet, P., and J. Bouvet. 1992. Bear conservation genetics. *Nature* 358:197.
- Taberlet, P., J.-J. Camarra, S. Griffin, E. Uhres, O. Hanotte, L. P. Waits, C. Dubois-Paganon, T. Burke, and J. Bouvet. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Molecular Ecology* 6:869–876.
- Vonhof, M. J., C. Strobeck, and M. B. Fenton. 2008. Genetic variation and population structure in big brown bats (*Eptesicus fuscus*): is female dispersal important? *Journal of Mammalogy* 89:1411–1420.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study Supplement* 46:120–138.
- White, G. C., and T. M. Shenk. 2001. Population estimation with radio marked animals. Pages 329–350 in J. J. Millspaugh and J. M. Marzluff, editors. *Design and analysis of radio telemetry studies*. Academic Press, San Diego, California, USA.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Wildlife Management* 66:13–21.
- Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging free ranging black and brown bears. *Wildlife Society Bulletin* 27:616–627.
- Wright, S. 1931. The evolution of Mendelian populations. *Genetics* 16:97–159.

Associate Editor: Scott McCorquodale