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NONINVASIVE GENETIC SAMPLING REVELAS BLACK BEAR POPULATION DYNAMICS DRIVEN BY CHANGES IN FOOD PRODUCTIVITY

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NONINVASIVE GENETIC SAMPLING REVEALS BLACK BEAR POPULATION DYNAMICS DRIVEN BY CHANGES IN FOOD PRODUCTIVITY

By

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Noninvasive genetic sampling reveals black bear population dynamics driven by changes in food productivity

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I conducted research on the demography of a harvested north Idaho black bear (*Ursus americanus*) population to determine the underlying dynamics of changes in population abundance, to determine how much these dynamics were driven by variation in food productivity, and to evaluate how these processes could influence inferences based on mark-recapture analysis. In cooperation with Idaho Department of Fish and Game and the USDA Forest Service, I used barb-wire corrals to collect black bear DNA during 2003-2006 in the Purcell Mountains of Idaho. We analyzed these DNA samples to determine the number of uniquely identified individuals in each year, N_u. I used a combination of both genetic and mark-recapture analyses to evaluate the sources of variation in N_u over the four years and to what extent this variation was driven by changes in productivity of foods on the landscape. Specifically, I investigated deviations of Hardy-Weinberg equilibrium and genetic substructure in relation to changes in abundance, and whether variation in vital rates were a function of changing berry productivity in the study area. I found a heterozygote deficiency and detected genetic substructure indicating I sampled ≤ 4 subpopulations within the same area over the four years (a Wahlund Effect). My mark-recapture analyses suggest this pattern was probably in response to landscape changes in summer berry abundance. My results suggest important variation in population dynamics driven by changes in food productivity, which should be considered when using mark-recapture analyses to monitor population trends for black bears.

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INTRODUCTION

Temporal variation in the dynamics and abundance of animal populations is of great interest to conservationists and wildlife managers. Demographics of animal populations vary temporally due to gains or losses through the biological processes responsible for population change: births, immigration, deaths, and emigration. The causes of changes in theses vital rates can be due to a variety of abiotic and biotic factors, among them environmental conditions and management actions. Populations are managed under 3 general guidelines: control, conservation, and sustained yield (Caughley 1977) and to determine if a population is meeting these management objectives, monitoring is necessary.

Managed populations of harvested and endangered species are monitored over time to determine if a population is meeting management goals, to detect an incipient or undesirable change, and to identify a response to natural perturbations and management actions (Goldsmith 1991). Inconclusive or ambiguous population monitoring results can have large impacts on effective management of a species, especially if monitoring results fail to detect a change in population abundance or if monitoring results suggest a change in abundance that is not real (Elzinga et al. 2001). Monitoring is often achieved through relative abundance indices and estimates of abundance (Gibbs et al. 1998). A positive linear relationship between an index and actual abundance is often assumed but is generally untested, thus changes in an index may not reflect true changes in abundance (Gibbs 2000). Although indices are not always reliable and lack estimates of precision, they are commonly used because they are relatively easy to obtain and inexpensive to collect (Gibbs 2000). By contrast, obtaining estimates of abundance requires a large

expenditure of time and resources; they are generally more reliable than indices, however, because they incorporate a probability of detection to account for unobserved animals (Williams et al. 2002).

The relatively recent development of noninvasive genetic sampling and microsatellite genotyping coupled with mark-recapture analysis has allowed estimates of abundance in rare or elusive species (Taberlet and Bouvet 1992, Foran et al. 1997, Palsbøll et al. 1997, Kohn et al. 1998, Woods et al. 1999). Monitoring through noninvasive sampling is advantageous for species with low densities or secretive behavior because the animal does not have to be captured or observed to gain necessary abundance information, contrary to traditional methods. Genetic sampling is commonly used to estimate population size through mark-recapture analyses or to describe patterns in population genetics (e.g., genetic variation, effective population size, etc.; Schwartz et al. 2006*a*). Combining mark-recapture estimates with descriptions of population genetics provides a more complete understanding the population dynamics than either method alone. This combined information facilitates a comprehensive interpretation of monitoring results, thus improving effective management of a species.

Black bears (*Ursus americanus*) are an important game species of North America (Garshelis 1990) and effective monitoring of black bear populations is necessary to make sound management decisions and to ensure persistence (Miller 1990, Garshelis 1993, Pelton 2000, Garshelis and Hristienko 2006). Monitoring bear populations, however, is challenging because bears are difficult to observe due to the dense forest habitat they often occupy, their low densities, and their secretive and solitary behavior (Pelton et al. 1978, Harris 1986, Woods et al. 1999, Rice et al. 2001). Estimating population

abundance using mark-recapture analyses is one of the most objective methods to monitor and manage bear populations (Garshelis 1990). Noninvasive genetic sampling coupled with mark-recapture analysis has become a popular method used by management agencies to monitor bears because it allows relatively larger samples sizes to be collected (Mowat and Strobeck 2000) and may violate fewer assumptions of mark-recapture models than traditional methods (Woods et al. 1996), providing increased precision and accuracy for estimates.

Violation of critical mark-recapture model assumptions about equal catchability and population closure (demographic and geographic), however, are issues that challenge both noninvasive genetic sampling and traditional mark-recapture methods. Bias in population estimates caused from violation of assumptions can significantly affect inferences on population trend and consequently, effective management. Bears can exhibit variation in capture probabilities, often violating the assumption of equal catchability. Responses of bears to traps can vary depending on the availability of natural food resources, which can change during the period of a mark-recapture study (Harris 1986). Bears that have been trapped may also exhibit a behavioral response due to prior trap history (e.g. a trap happy or trap shy response; Otis et al. 1978). Capture probabilities for bears can also vary depending upon a bear's sex, age, individual behavior and/or other biological attributes (Harris 1986). Demographic closure can be assumed generally for bears if the duration of the study is no longer than 6-10 weeks (Mowat and Strobeck 2000). Because bears have large home ranges that often overlap with study area boundaries, the assumption of geographic closure is difficult to meet (Harris 1986). Specifically, temporary migrations on and off the study area (i.e.,

violation of the assumption of geographic closure) can affect estimates of capture probability directly, often causing bias in survival and population estimates (Pollock et al. 1990). The degree of geographic closure violations may vary from year to year for bears depending upon the availability and distribution of food resources, which can make monitoring bears through mark-recapture estimates difficult.

Understanding the dynamics of bear populations is essential to accurately interpret monitoring results; e.g., the composition of a sampled black bear population can be highly transient, particularly if a large proportion of observed bears are dispersers or temporary immigrants. For populations of black bears, vital rates vary strongly with productivity of food. 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 Cowen 1971, Rogers 1976, Rogers 1993). When food resources are scarce, survival and reproduction in black bears can be reduced substantially (Jonkel and Cowen 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, Garshelis 1989, Pelton 1989).

Differing behavior of male and female black bears can also influence population dynamics strongly. Females generally exhibit less movement and smaller home ranges than males (Pelton 2000) which can result in increased survival (Bunnell and Tait 1985, Kasworm and Thier 1994). During years of food scarcity, however, the behavior of males and females becomes less disparate, where females increase their movements and are more readily attracted to human food sources (Noyce and Garshelis 1997). Males

also have greater natal dispersal distances than females; with subadult males often dispersing long distances to establish their home range and subadult females establishing home ranges within or near their mother's home range (Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Moyer et al. 2006). These dispersal patterns of black bears can be also influenced and potentially restricted by landscape gradients and anthropogenic factors (Cushman et al. 2006, Schwartz et al. 2006*b*).

I conducted research on the demography of a harvested north Idaho black bear population, to determine the underlying dynamics of changes in population abundance, to determine how much these dynamics were driven by variation in food productivity, and to evaluate how these processes could influence inferences based on mark-recapture analysis. In cooperation with Idaho Department of Fish and Game and the USDA Forest Service, I used barb-wire corrals to collect black bear DNA (Woods et al. 1999) in a mark-recapture framework during 2003-2006 in the Purcell Mountains of Idaho. We analyzed these DNA samples to determine the number of uniquely identified individuals in each year, N_u. I used a combination of both mark-recapture and genetic analyses to evaluate the sources of variation in N_u over the four years and to what extent this variation was driven by changes in productivity of foods on the landscape.

To explore how variation in abundance of important food species for black bears might have contributed to variation in N_u, I used mark-recapture analyses to associate vital rates with measures of productivity of foods important to black bears in northern Idaho. Black bears in the Pacific Northwest rely heavily on soft mast plant species which have inherently variable abundances and distributions from year to year (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Beecham and Rohlman 1994). Specifically, in

northern Idaho, huckleberries are the most important food resource and other berry producing plants, such as buffaloberry, serviceberry, and mountain ash are also important (Beecham and Rohlman 1994). Thus, I evaluated how productivity of each of the four berry species contributed to variation in vital rates. I calculated productivity in different ways: 1) summed productivity over all species, to evaluate contribution of overall berry productivity, 2) productivity of individual species, to account for potentially strong variation in contributions among species, and 3) productivity of species in the summer (mid-July to mid-September; huckleberries, buffaloberry and serviceberry) and fall (mid-September to mid-November; den entrance: mountain ash) to account for seasonal effects. High values for any of these measures could increase survival and reproduction and reduce emigration and immigration; low values would have the opposite effect.

I used the Pradel model (Pradel 1996) in program MARK (White and Burnham 1999), which offers a technique to estimate and model the vital rates of a population in an ecological and biological context through the use of covariates (Franklin 2001, Boulanger et al. 2004*a*). The Pradel model estimates apparent survival, which includes both mortality and emigration, and recruitment rate, which include both births and immigration. I hypothesized that apparent survival would decrease during low berry years due to increased mortality and emigration. For recruitment, I hypothesized that a low berry year would decrease recruitment through reduced births or would increase recruitment through increased immigration.

To gain additional insights into the sources of variation in N_u, I used genetic analyses to estimate effective population size (N_e; number of breeding adults; Schwartz et al. 1998), deviations from Hardy-Weinberg (HW) proportions (observed vs. expected

heterozygosity; Robertson and Hill 1984), and the genetic structure of the population (i.e., spatial variation in allele frequencies between demes or subpopulations). I estimated N_e and compared estimates to N_u to determine whether or not the variation in abundance was consistent. I calculated deviations of HW proportions, which can provide important insights into the mating system, social behavior, or population genetic structure of the northern Idaho black bear population (Allendorf and Luikart 2007). I evaluated whether spatial genetic structure existed and compared it to N_u to determine if bears from spatially structured subpopulations influenced the patterns of abundance I observed. I then combined both genetic and mark-recapture analyses to fully understand the cause of temporal variation in N_u and how it may influence my estimates of population trend.

STUDY AREA

The study area was located in the Purcell Mountains of the Idaho Panhandle National Forest of Idaho, USA, encompassing approximately 400 km^2 of forested land and a large river system. Approximately three sides of the study area were bordered 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* Nutt.), 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 (*Abies lasiocarpa*) and mountain hemlock (*T. mertensiana)* dominated elevations above 1,300 m. Understory vegetation primarily consisted of thinleaf huckleberry (*Vaccinuim membranaceum*), 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

In cooperation with the Idaho Department of Fish and Game (IDFG) and USDA Forest Service, 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 to evenly distribute efforts across the study area from 2003-2006 (White et al. 1982). We placed hair trap stations systematically within 2.6 km^2 cells in years 2003 and 2004. From 2005-2006, 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 km^2) than previous years to reduce logistical constraints. The duration of primary sampling periods were approximately 6-12 weeks in all four years, conducted during the summer when births were nonexistent and bear mortality was low. Within each primary sampling period was ≥ 1 secondary sampling period(s) (i.e., trapping sessions) that were each ≤ 14 days in length. The length of trapping sessions was conducive to assume demographic closure within primary sampling periods and prevent DNA degradation of hair samples from weather exposure.

Hair trap stations consisted of a single strand of 4-pronged barbed wire wrapped around ≥ 3 trees about knee height (45-50 cm; Woods et al. 1999). We placed a pile of decayed wood in the center of the corral where we applied a mixture of liquefied fish, cow blood, and glycerine as a long-distance lure, but that did not give investigating bears a food reward. Every 14 days, we examined each hair trap thoroughly for hairs on each

barb and on the ground (when hair fell off barbed wire). We considered hairs collected from each barb a single sample and placed it in a centrifuge tube or coin envelope with approximately 10 ml of silica desiccant. After hair collection, we burned each barb that had snared hair to prevent future DNA contamination.

Individual Genetic Analysis

The Rocky Mountain Research Station (RMRS) Wildlife Genetics Laboratory analyzed hair samples we collected. They analyzed black bear samples at 9 microsatellite markers: *G1A, G10D, G10B* (Paetkau and Strobeck 1994)*, G10H, G10J, G10M, G10X, UarMu59* (Paetkau et al. 1998) *and Msut-2* (Kitahara et al. 2000). They identified species, individual identity, and gender in each sample with sufficient DNA. Laboratory methods followed procedures found in Schwartz et al. 2006*b*. Extensive error-checking was conducted to minimize genotyping error (i.e., allelic dropout and false alleles) due to variable quantities and qualities of DNA in noninvasive genetic samples. Each DNA sample was analyzed twice (2003 samples were analyzed once) and program DROPOUT (McKelvey and Schwartz 2004, McKelvey and Schwartz 2005) was used to detect genotyping errors and identify loci and samples with probable error (Schwartz et al. 2006*b*). If genotyping errors were detected by DROPOUT, problem samples were analyzed additional times until no errors were detected in the dataset. A 28.1% overestimate of unique genotypes resulted prior to error-checking measures (Schwartz et al. 2006*b*).

Berry Productivity

The United States Fish and Wildlife Service (USFWS) has collected data on the production of huckleberries, buffaloberries, and serviceberries since 1989 and mountain

ash since 2001 in the Cabinet-Yaak ecosystem (Kasworm et al. 2008; Figure 1). Line transects were conducted each year for huckleberry and buffaloberry production, which followed a specific azimuth from the origin of the line through a homogeneous habitat. At 1 m intervals, a 0.04 m^2 frame (2 x 2 decimeter) was used to count all fruits and pedicels within the frame. Fifty frames containing the desired species were counted on each transect and if frames did not intercept a portion of the desired plant species then the frame was advanced at 0.5 m intervals and empty frames were counted. Between 16-23 huckleberry and 5 buffaloberry transects were conducted each year. Transects were added and removed over the years due to the effect of plant succession on berry productivity. Serviceberry and mountain ash productivity was estimated by counting all the berries on marked plants. Ten marked plants were counted at each plot, with the number of plots ranging from 5-7 for serviceberry and 3 plots for mountain ash over the years. Timing of sampling was adjusted each year to coincide with peak berry ripening (Kasworm et al. 2008).

Mark-Recapture Analysis

I 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 driven by changes in food productivity. I used the Pradel model (Pradel 1996) with Huggins closed capture (Huggins 1989, 1991) 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), recruitment rate (f; number of individuals entering the population between time i to i+1 per individual present at time i), capture probability (p), and recapture probability (c) using covariates of food production

(Franklin 2001, Boulanger et al. 2004*b*). Estimates of apparent survival include both mortality and emigration and estimates of recruitment rate include both births and immigration. Estimates of capture probability and recapture probability pertain to the exact sampling period and estimates of apparent survival and recruitment rate correspond to the interval before the given sampling period. I also used the Pradel model to derive estimates of population abundance ($\hat{N}$; $\hat{N}$ = # unique bears/p) each year and realized population growth rate (λ; $\lambda = \varphi_i + f_i$) between years.

I conducted a preliminary analysis to determine if capture and recapture probabilities varied as a function of sex and year. This analysis revealed strong support for variation between sexes, but little support for capture and recapture probabilities varying by year. I was most interested in capture and recapture probabilities varying by year due to varying sample designs and environmental conditions that could have affected capture and recapture probabilities each year. Therefore, I modeled capture probability and recapture probability as nuisance parameters and I used the most biological, parsimonious model of the parameters for analyses of variation in apparent survival and recruitment rates.

The Cabinet-Yaak ecosystem, where berry productivity data was collected, overlaps a portion of the Purcell Mountain study area. Given this proximity; I assumed the berry production would be similar. I standardized the berry abundance data and incorporated six different berry covariates into my mark-recapture candidate model set. I included covariates of each of the four different berry species, a summer berry covariate (huckleberry + buffaloberry + serviceberry), and a total berry covariate (huckleberry + buffaloberry + serviceberry + mountain ash). I modeled apparent survival and

recruitment rate as a function of the prior year's berry abundance. In addition to berry covariates, I considered both sex and time covariates for apparent survival and recruitment rate model building. I included sex as a covariate due to the likely difference in vital rates between sexes and time was included because of the differences in environmental and unidentified conditions each year that could affect vital rates. To determine the effect of each covariate on apparent survival and recruitment parameters, I evaluated beta estimates and their 95% confidence intervals.

I used Akaike Information Criterion adjusted for small sample sizes (AIC_c) to compare models and to select the most parsimonious model (Burnham and Anderson 1998). I considered models with $\Delta AIC_c < 2$ as being supported by the data; I used these models to generate model-averaged estimates of parameters to account for information contained within all supported models. I 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. I 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). I used $QAIC_c$ scores for model selection if overdispersion was detected ($\hat{c} > 1$; Burnham and Anderson 1998).

Population Genetic Analyses

I estimated effective population size (N_e) each year using the linkage disequilibrium method (Program LDN_e; Waples 2006, Waples and Do 2008) to evaluate changes in abundance through changes in allele frequencies and linkage disequilibrium (D), or the non-random association of alleles at different loci. I estimated N_e for each year based on

samples sizes unique to each year (N_{e1}) and on equal sample sizes of 50 (N_{e2}). I compared N_{e1} to N_{e2} to evaluate whether variation in estimates of N_e among years were an artifact of varying sample sizes; if $N_{e1} \approx N_{e2}$, I concluded variation in N_{e1} was not a function of sample sizes. I then compared N_e by year to evaluate observable changes in abundance through changes in D.

I estimated genetic variability within the group of individuals sampled each year using Program GENALEX (Peakall and Smouse 2006) to provide information on changes in abundance through changes in genetic diversity. Specifically, I calculated 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). I also examined the number of private alleles by year, or alleles only observed in a single year. I then compared each estimate of genetic variability by year and examined differences to determine observable changes in population dynamics.

I used Program STRUCTURE (Pritchard et al. 2000, Falush et al. 2003, 2007) to investigate population substructure by year. This program characterizes populations by differing allele frequencies, while minimizing HW deviations and D (Prichard et al. 2000). I 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. This option also allows for improved clustering of closely related populations. I chose to run simulations 50,000 periods before data was collected (burn-in period) and I ran each iteration for 50,000 Markov Chain Monte Carlo (MCMC) repetitions. I ran 10 independent iterations for each population (K) from 1 to 6. The K

with the highest log-likelihood was the most supported, with individuals subsequently divided into K populations. When the most supported K was greater than 1, I used an ad hoc method (ΔK) from Evanno et al. (2005) to identify the most likely K due to greater likelihood variances in STRUCTURE as K increases. I examined the estimated proportion of population membership (Q) of each individual and calculated the mean Q of all individuals for the most supported simulation of K. I calculated the random expectation of Q if membership was equally divided between populations, indicating no population substructure, and then compared the mean Q to the random expectation to determine the presence of population substructure. If mean Q ≈ random expectation of Q, then I would conclude no real population substructure exists. I also examined F_{st} values, a measure of allele frequency divergence, among populations identified. Evaluations of Program STRUCTURE have shown it performs well at assigning individuals to populations with low differentiation among populations ($F_{st} = 0.03$), but F_{st} values must be at least 0.05 to attain a population assignment accuracy rate of 97% (Latch et al. 2006). Therefore, population assignment with F_{st} values far below 0.05 will be considered untrustworthy.

RESULTS

Over the four years the study area ranged from 367 km^2 to 453 km^2 in size; though the general location and relative shape of the study area were largely consistent (Table 1). The location and number of hair trap stations within the study area varied each year, however I analyzed only hair trap stations from areas common to all four years. The total number of capture sessions sampled and total trap days ranged from 1-5 sessions and 1440-5288 days over the four years. A total of 277 (134 females, 140 males, 3 unknown

sex) black bears were identified in the Purcell Mountains over the course of four years. I did not include bears of unknown sex in the mark-recapture analyses because of sex-specific model considerations. N_u each year ranged from 53-156 bears, with 43-66% more bears identified in 2004 than in other years (Table 2; Figure 2). Specifically, there were 53 bears identified in 2003, 156 bears in 2004, 89 bears in 2005, and 70 bears in 2006. A large portion (67%) of bears was captured only once in four years, with 54% of those bears captured during 2004. Recapture rates ranged from 0.16-0.43 over the four years.

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

Mark-Recapture Analysis

The goodness-of-fit test did not detect overdispersion of recaptures ($\chi^2 = 59.3$, df = 67, P = 0.74), so I used AIC_c for model selection. Few berry covariates appeared to influence apparent survival and recruitment rates indicated by the low number of models that were supported by the data ($\Delta AIC_c < 2$; Table 3). AIC_c model selection indicated that apparent survival and recruitment rates were influenced by sex and summer berry abundance.

Models that considered single berry species or total berry abundance were less supported by the data ($\Delta AIC > 2$). The two most supported models showed that variation in summer berry abundance had a large effect on apparent survival ($\beta_1 = 5.84$, 95% C.I. = 1.74-9.94, $\beta_2 = 4.66$, 95% C.I. = 1.08-8.25). Apparent survival increased as summer berry abundance increased. Variation in summer berry abundance appeared to have an effect on recruitment rates (Model 2; $\beta = 1.75$), however, the 95% confidence interval included zero (95% C.I. = −0.509-4.013).

Model-averaged estimates for female apparent survival show that 9% ($\varphi = 0.91$, SE = 0.08) of females in 2003 died or emigrated before 2004, 58% ($\varphi = 0.42$, SE = 0.06) of females in 2004 died or emigrated before 2005, and 48% ($\varphi = 0.52$, SE = 0.06) of females in 2005 died or emigrated before 2006. Model-averaged parameter estimates for male apparent survival show that 17% ($\varphi = 0.83$, SE = 0.14) of males in 2003 died or emigrated before 2004, 75% ($\varphi = 0.25$, SE = 0.05) of males in 2004 died or emigrated before 2005, and 66% ($\varphi = 0.34$, SE = 0.07) of males in 2005 died or emigrated before 2006. Overall, females had higher apparent survival rates than males (Figure 3).

Model-averaged estimates for female recruitment rate show a 17% ($f = 0.17$, SE = 0.08) increase of new females in 2004 per female alive in 2003, a 10% ($f = 0.10$, SE = 0.04) increase of new females in 2005 per female alive in 2004, and a 13% ($f = 0.13$, SE = 0.05) increase of new females in 2006 per female alive in 2005. Model-averaged parameter estimates for male recruitment rate show a 42% ($f = 0.42$, SE = 0.18) increase of new males in 2004 per male alive in 2003, a 25% ($f = 0.25$, SE = 0.06) increase of new males in 2005 per male alive in 2004, and a 32% ($f = 0.32$, SE = 0.08) increase of new

males in 2006 per male alive in 2005. Overall, males had higher recruitment rates than females (Figure 4).

Model-averaged estimates of population abundance ($\hat{N}$) were 149 (95% C.I. = 96-203) females and 132 (95% C.I. = 68-196) males in 2003, 155 (95% C.I. = 123-188) females and 190 (95% C.I. = 135-245) males in 2004, 81 (95% C.I. = 64-98) females and 81 (95% C.I. = 56-106) males in 2005, and 51 (95% C.I. = 41-62) females and 61 (95% C.I. = 43-78) males in 2006 (Figure 2). Model-averaged estimates for realized population growth rate (λ) were 1.08 (95% C.I. = 0.87-1.29) for females and 1.25 (95% C.I. = 0.79-1.72) for males from 2003-2004, 0.52 (95% C.I. = 0.41-0.62) for females and 0.50 (95% C.I. = 0.37-0.64) for males from 2004-2005, and 0.65 (95% C.I. = 0.51-0.76) for females and 0.66 (95% C.I. = 0.46-0.82) for males from 2005-2006.

Population Genetic Analyses

Estimates of N_{e1} for each year with varying sample sizes ranged from 40.7-155.7 bears during 2003-2006 (Table 4; Figure 2). The highest N_{e1} estimate occurred in 2004, with a 61-74% higher estimate than other years. Estimates of N_{e2} (based on equal samples sizes of 50 individuals among years) yielded a range of N_{e2} estimates similar to varying sample sizes (39.2-170.4), with 2004 again exhibiting the highest estimate.

Observed heterozygosity levels were similar in all years except for 2004, with a 20-26% lower observed heterozygosity than other years (Table 4). Expected levels of heterozygosity under HW equilibrium did not vary significantly from year to year (0.761-0.789). Estimates of F_{is} were comparable in all years except for 2004. Years 2003, 2005, and 2006 did not deviate strongly from HW proportions (F_{is} from –0.004-0.009); however, 2004 had stronger deviations from HW proportions (F_{is} 0.212). In 2004 all loci

had a significant excess of homozygotes, compared to zero or one loci in other years. The number of private alleles identified each year ranged from 0-3 alleles.

The most likely number of populations (K) sampled each year varied from 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. The mean Q in 2006 ranged from 0.829-0.835 with the random expectation if membership was equally divided between populations at 0.5. F_{st} values among populations in 2006 varied from 0.0011-0.1251 with approximately 55% and 45% of individuals in each population. The most likely K in 2004 was 4 populations. The estimated mean Q in 2004 varied from 0.562-0.729 with the random expectation if membership was equally divided between populations at 0.25. F_{st} values among populations in 2004 varied from 0.0431-0.1159 with approximately 25% of individuals in each of the 4 populations.

DISCUSSION

My mark-recapture and population genetic analyses revealed critical changes in population dynamics of northern Idaho black bears took place during 2003-2006; had these changes in dynamics not been identified, inferring population trends accurately from monitoring data would have been difficult. My analyses showed how variation in abundance of important food species for black bears contributed to variation in the number of uniquely identified individuals, N_u, and the underlying dynamics of changes in N_u. My use of combined mark-recapture and genetic analyses resulted in insights into the demography of the bears I studied that would have been impossible to achieve with either analysis alone.

The 3 different measures of population abundance (N_u, $\hat{N}$ and N_e) I estimated all exhibited consistent trends. Estimates of $\hat{N}$ followed the same observed relationship as N_u, and patterns of N_e estimates were comparable to the patterns I observed for N_u in all four years, further corroborating a significant change in abundance took place in 2004 compared to other years. Few bears observed in 2004 were captured more than once in that year, and most bears observed in 2004 were captured only once over the four years, indicating highly transient bears. Consistent patterns among estimates of N and the lack of variation in capture probabilities among years argue strongly that the patterns I observed were not an artifact of sampling.

Mark-recapture analysis revealed the variation in vital rates of northern Idaho black bears was driven by 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 four 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 require for self-maintenance, reproduction, and over-winter 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; i.e., if 1 species has a poor year, good productivity among the other 2 may compensate, which is not possible in the fall where only 1 berry species fruits. In the event that all 3 summer species have poor production, however, bears are likely to make large movements in search of food resources (Drahos 1951, Garshelis and Pelton 1981,

Rogers 1987, Garshelis 1989, Pelton 1989) because they cannot rely on productivity of fall berries alone to ensure over-winter survival.

Apparent survival estimates decreased from 2003-2004 to 2004-2005 and increased from 2004-2005 to 2005-2006; as I hypothesized, summer berry productivity was correspondingly low in 2004, likely causing increased mortality and emigration during 2004. Relatively higher productivity of summer berries from 2005-2006 likely caused decreased mortality and emigration. The pattern for recruitment was less clear due to uncertainty associated with the estimates (i.e., large standard errors) and no clear pattern of variation over the years. Because of this uncertainty, I was unable to determine if changes in recruitment were due to births or immigration as they pertain to my berry productivity hypotheses. 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, Kasworm and Thier 1994, Kolenosky 1990), large fluctuations observed in the vital rates were likely driven by variation in immigration and emigration rates, not births and deaths.

Predictably for black bears, sex explained variation in the vital rates I observed. Apparent survival for females was higher than for males; I hypothesize this was likely due both to greater survival of females and to stronger fidelity of females to my study area. Bunnell and Tait (1985) showed overall higher survival rates of females than males among 13 black bear populations throughout North America. Numerous black bear studies have observed lower female movements and smaller home ranges compared to males (Jonkel and Cowan 1971, Amstrup and Beecham 1976, Lindzey and Meslow 1977, Reynolds and Beecham 1980, Garshelis and Pelton 1981), indicating stronger site fidelity

by females. By contrast, recruitment was higher for males than for females; I hypothesize this was likely due to greater movements and larger home ranges of males compared to females, which increases the probability males will be recruited into the sampled population.

My analyses of HW deviations, genetic substructure, and the presence of private alleles revealed population dynamics during 2004 differed from other years. I detected no large deviations from expected HW proportions in 2003, 2005, and 2006. By contrast, observed heterozygosity in 2004 differed strongly from expected HW proportions; the presence of more homozygotes than expected suggested an important change in population dynamics for that year. An excess of homozygotes is typically a function of non-random 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). Non-random mating through population subdivision produces an excess of homozygotes at all loci in which the subpopulations differ in allele frequency (Cohen 1990, Allendorf and Luikart 2007). I did not detect genetic substructure in 2003 and 2005, suggesting bears from spatially disjunct subpopulations did not influence the patterns of abundance I observed. I detected 2 possible subpopulations in 2006; the low F_{st} value for 2006 (< 0.05), however, indicated evidence for 2 subpopulations was equivocal. I did detect strong evidence for multiple subpopulations sampled in 2004, indicating that the north Idaho black bear population was not panmictic and bears from spatially structured subpopulations influenced the patterns of abundance I observed. The 3 private alleles, (i.e., alleles only observed in a single year) identified in 2004 further supports the likelihood I sampled

bears originating from relatively far geographic distances that do not normally mate with bears inhabiting my study area.

My results collectively demonstrate the large variation I observed in N_u and vital rates was attributable to temporary immigration. Evidence for a Wahlund effect occurring in 2004 that was driven by variation in food productivity is strongly supported by my results. A Wahlund effect occurs when multiple subpopulations, each within HW proportions are inadvertently sampled together. This results in observed deviations of HW proportions in the sampled population, caused by a greater number of homozygotes than expected due to variation in allele frequencies between subpopulations (Sinnock 1975). The presence of a Wahlund effect in 2004 indicates a large number of immigrant bears moved through the study area that year; results of my mark-recapture analysis indicate these movements were in response to low productivity of food. Given the evidence that the northern Idaho black bear population is not panmictic, berry failures that cause bears to make long distance movements and travel through other subpopulations may be important for maintaining genetic diversity of northern Idaho black bears, provided immigrant bears successfully mate and reproduce. If such movements are temporary foraging forays (i.e., an "occasional sally;" Burt 1943) outside of established home ranges, to which bears ultimately return, then genetic exchange among subpopulations due to such movements may be minimal.

My analyses of population genetics indicate the presence of genetically structured subpopulations of black bears in northern Idaho. 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 natal philopatric and establish

home ranges within or near their mother's home range (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; however, much cost is associated with dispersal (Rogers 1987, Elowe and Dodge 1989, Schwartz and Franzmann 1992). Cushman et al. (2006) showed gene flow among north Idaho black bears was facilitated by contiguous forest cover at mid-elevations and was inhibited by non-forested land cover; and Schwartz et al. (2006*b*) determined that a large, agricultural valley in northern Idaho was not a barrier to gene flow, but that it affected the population's genetic structure.

My results have broad implications for inferring population dynamics of black bears, particularly during years of food scarcities. At face value, estimates of abundance for black bears in my study area from 2003-2006 would suggest large fluctuations in population size, uncharacteristic of species like bears with generally slow population growth (Romanovsky 2002). My analyses showed, however, these fluctuations were due to a temporary change in the distribution of bears, not to population growth driven by increased reproduction and survival. Thus, the increase in abundance I observed in my study area in 2004 was real, but its transient nature would make it inappropriate for inferring population trends or making management decisions. Sampling over multiple years allows outliers, like 2004, to be detected and interpreted accordingly. If my sampling was only conducted during 2004, then my estimate of population size would have been misleading but none of the context needed for reaching this conclusion would have been available. In addition, my interpretation of the variation in N_u would have

likely been incorrect without understanding the influence of food productivity on movements of black bears and subsequent consequences for estimating their abundance.

My results demonstrate the challenges of monitoring black bears using mark-recapture when critical assumptions are violated. The assumption of geographic closure was severely violated in 2004 due to temporary migrations on and off the study area. Violation of the geographic closure assumption negatively affects estimates of capture probability causing estimates of abundance to be positively biased (Otis et al. 1978); such estimates represent the superpopulation of the sampling grid and surrounding area (Kendall 1999). Violation of closure due to temporary emigration (e.g. resident bears temporarily emigrating in search of food) and one entry, one exit (e.g. transient bears) types of movements, however, cause bias of superpopulation estimates (Kendall 1999). Relatively large differences between my estimates of $\hat{N}$ and N_u for 2004 are likely a result of this bias. My results also confirm that the degree of closure violation when sampling black bears can strongly vary due to food productivity, causing biased estimates of population trend. Methods are available to test and correct for geographic closure (Otis et al. 1978, Stanley and Burnham 1999, Boulanger and McLellan 2001) and to determine the effective sampling area (Wilson and Anderson 1985), however no method is likely robust to the degree of violation I observed due to the long distances bears likely traveled in 2004.

Inferences of population trend based on estimates of $\hat{N}$, if not clarified by further genetic analysis, would have implied a change in the abundance of bears inhabiting my study area from 2003-2006 that was misleading, potentially leading to inappropriate management decisions. My study showed noninvasive genetic sampling not only

provides information for traditional mark-recapture analysis, but allows additional information into the demographics of the population to be gained through genetic analyses. This is advantageous for sampling rare or elusive species where detailed information and demographic insights are difficult to acquire using traditional techniques. To my knowledge, this is the first study to use noninvasive genetic sampling to gain information about the abundance of a population, but then use the additional information gained from population genetics to determine the cause of an observed outlier.

Management Implications

Monitoring population trend is a main priority for wildlife managers. This project was designed to monitor population trend of black bears and provide implications for trend analysis. Trend analysis is most sensitive to the first and last data points (Humbert et al. submitted). Because 2003 only had a single capture session which likely biased the estimate of abundance, I did not include it in the trend analysis. Apparent trend of two different measures of population abundance (N_u and $\hat{N}$) from 2004-2006 both indicate a decline, however $\hat{N}$ indicates a much steeper decline than N_u. Depending upon the management objective or question the trend of N_u or $\hat{N}$ may be more appropriate. If setting harvest seasons or quotas are the management objective, then the trend of N_u may be a better measure because most of the bears estimated in $\hat{N}$ are not likely available for harvest in that area. If managing bear conflicts is the management objective, then using the trends of $\hat{N}$ may be appropriate. Because bear population dynamics can occur over long periods of time (Garshelis 1993), caution should be exercised when inferring trends over a short-term study such as mine.

My study has implications for designing bear monitoring surveys. First, my study demonstrates the ability of noninvasive genetic sampling to provide information on both abundance and the underlying dynamics of a population. Second, my study demonstrates that years with low food availability can cause significant change in the distribution of bears. Therefore, measures of food productivity should be coupled with abundance data to provide a comprehensive interpretation of monitoring results. If measures of food productivity are not available, then sampling during food scarcities should be avoided to reduce the risk of sampling transient bears. Third, the data I collected in my study showed that with the sample sizes of mark-recapture data achievable with black bears in my study area, small differences in the sampling design (i.e., grid size, density of hair traps) do not appear to influence results. This suggests that sampling at this intensity is robust to small variations in sampling design.

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

Year	Area (km^2)	Traps	Capture sessions	Trap days	Trap Density (traps/km^2)
2003	393	80	1	1440	0.20
2004	393	80	3	5288	0.20
2005	453	104	4	4164	0.23
2006	367	46	5	3187	0.12

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

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 capture session (no recaptures)

[c] Total number of recapture events divided by N_u

Table 3. Model selection results of vital rates influenced by variation in berry productivity based on AIC_c of black bears in northern Idaho, USA, from 2003-2006.

Apparent survival (φ)	Recruitment (*f*)	K	AIC_c	ΔAIC_c	w_i
Sex + Summer Berries	Sex	7	2363.3	0.00	0.315
Sex + Summer Berries	Sex + Summer Berries	8	2363.8	0.51	0.244
Sex + Time	Sex + Time	10	2364.7	1.41	0.156
Sex + Time	Sex	8	2365.1	1.80	0.128
Sex + Serviceberry	Sex	7	2365.4	2.10	0.110
Sex + Serviceberry	Sex + Serviceberry	8	2367.1	3.83	0.046
Sex + Huckleberry	Sex	7	2376.2	12.94	0.000
Sex + Huckleberry	Sex + Huckleberry	8	2378.3	15.00	0.000
Sex + Buffaloberry	Sex + Buffaloberry	8	2380.8	17.56	0.000
Sex + Mountain Ash	Sex	7	2381.3	18.02	0.000
Sex + Buffaloberry	Sex	7	2383.2	19.99	0.000
Sex + Mountain Ash	Sex + Mountain Ash	8	2383.3	20.05	0.000

Sex + Total Berries	Sex	7	2386.6	23.38	0.000
Sex + Total Berries	Sex + Total Berries	8	2388.6	25.34	0.000
Constant	Constant	4	2392.5	29.27	0.000

Table 4. Genetic variation parameters, effective population size, number of populations identified of black bears in northern Idaho, USA, from 2003-2006.

Year	# Private alleles[a]	H_o[b]	H_e[c]	F_{is}[d]	N_e[e]	95% N_e CI	K[f]
2003	0	0.754	0.761	0.009	52.5	37-81	1
2004	3	0.622	0.789	0.212	155.7	113-233	4
2005	1	0.785	0.788	0.004	61.1	47-81	1
2006	0	0.780	0.777	–0.004	40.7	32-58	2

[a] Number of alleles unique in a single year

[b] Observed heterozygosity

[c] Expected heterozygosity

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

[e] Effective population size

[f] ΔK was used to calculate most likely K (population), when $K > 1$.

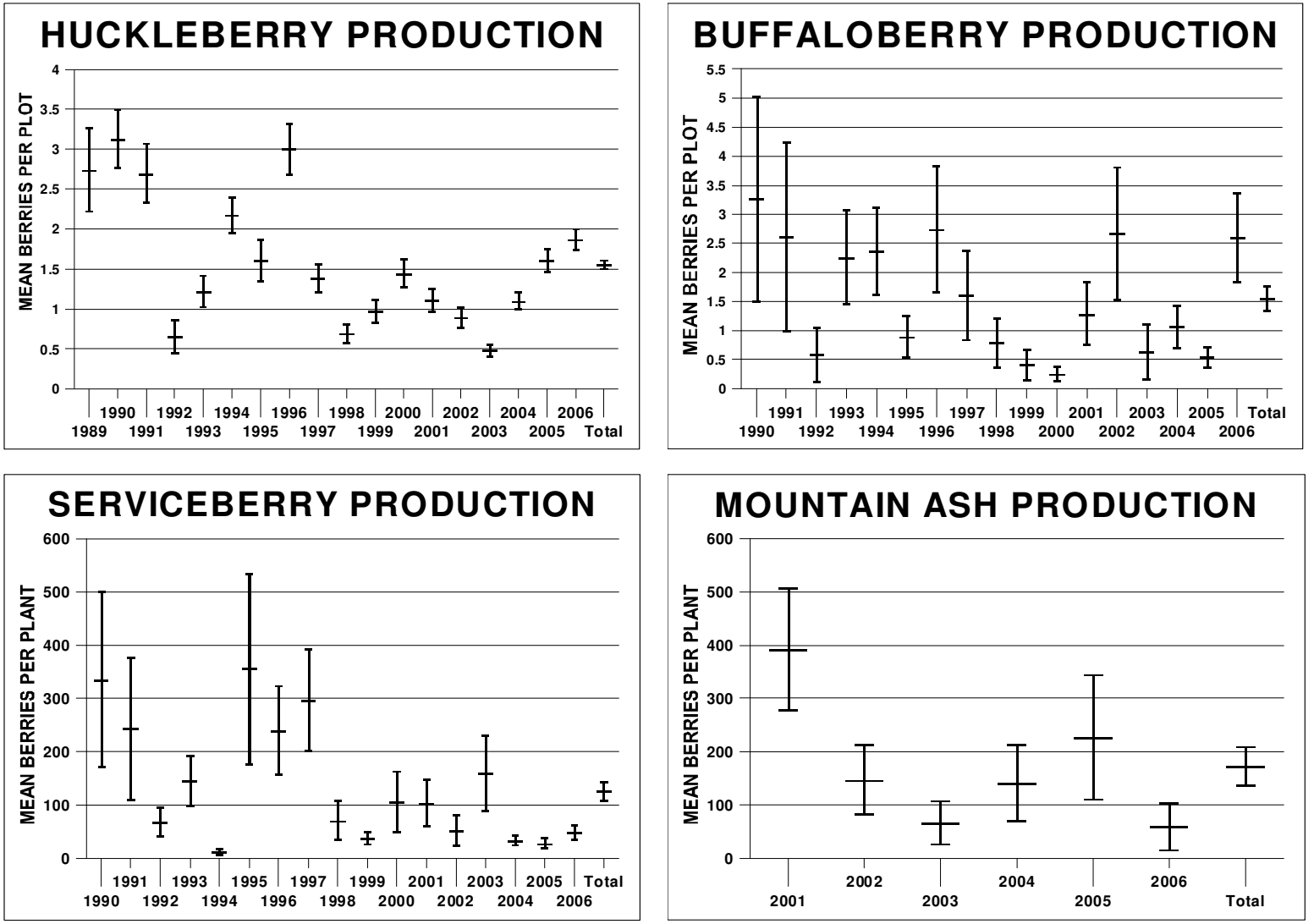
HUCKLEBERRY PRODUCTION
MEAN BERRIES PER PLOT
0
0.5
1
1.5
2
2.5
3
3.5
4
1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 Total
BUFFALOBERRY PRODUCTION
MEAN BERRIES PER PLOT
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 Total
SERVICEBERRY PRODUCTION
MEAN BERRIES PER PLANT
0
100
200
300
400
500
600
1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 Total
MOUNTAIN ASH PRODUCTION
MEAN BERRIES PER PLANT
0
100
200
300
400
500
600
2001 2002 2003 2004 2005 2006 Total

Figure 1.

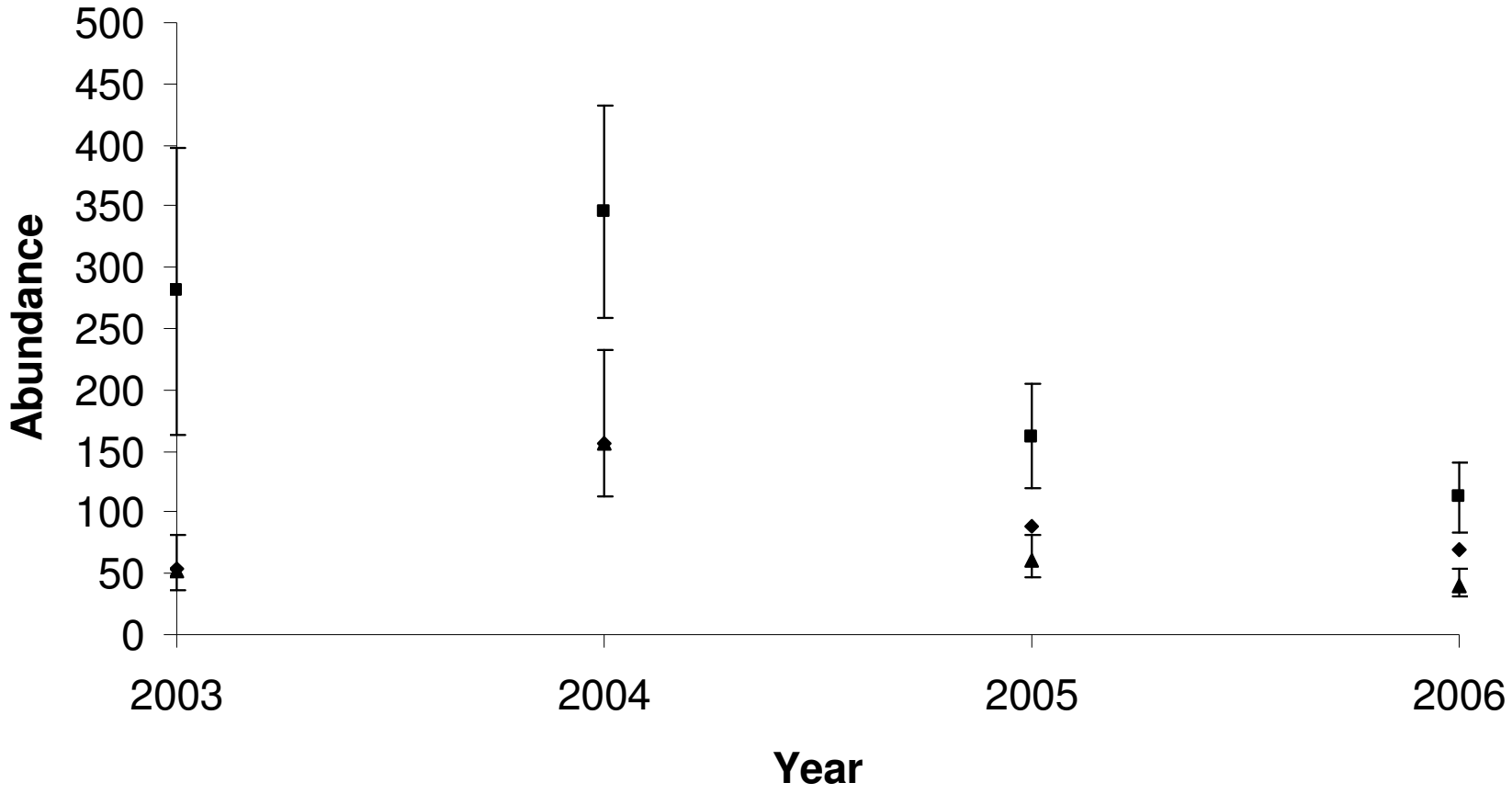
500
450
400
350
300
250
200
150
100
50
0
Abundance
2003
2004
2005
2006
Year

Figure 2.

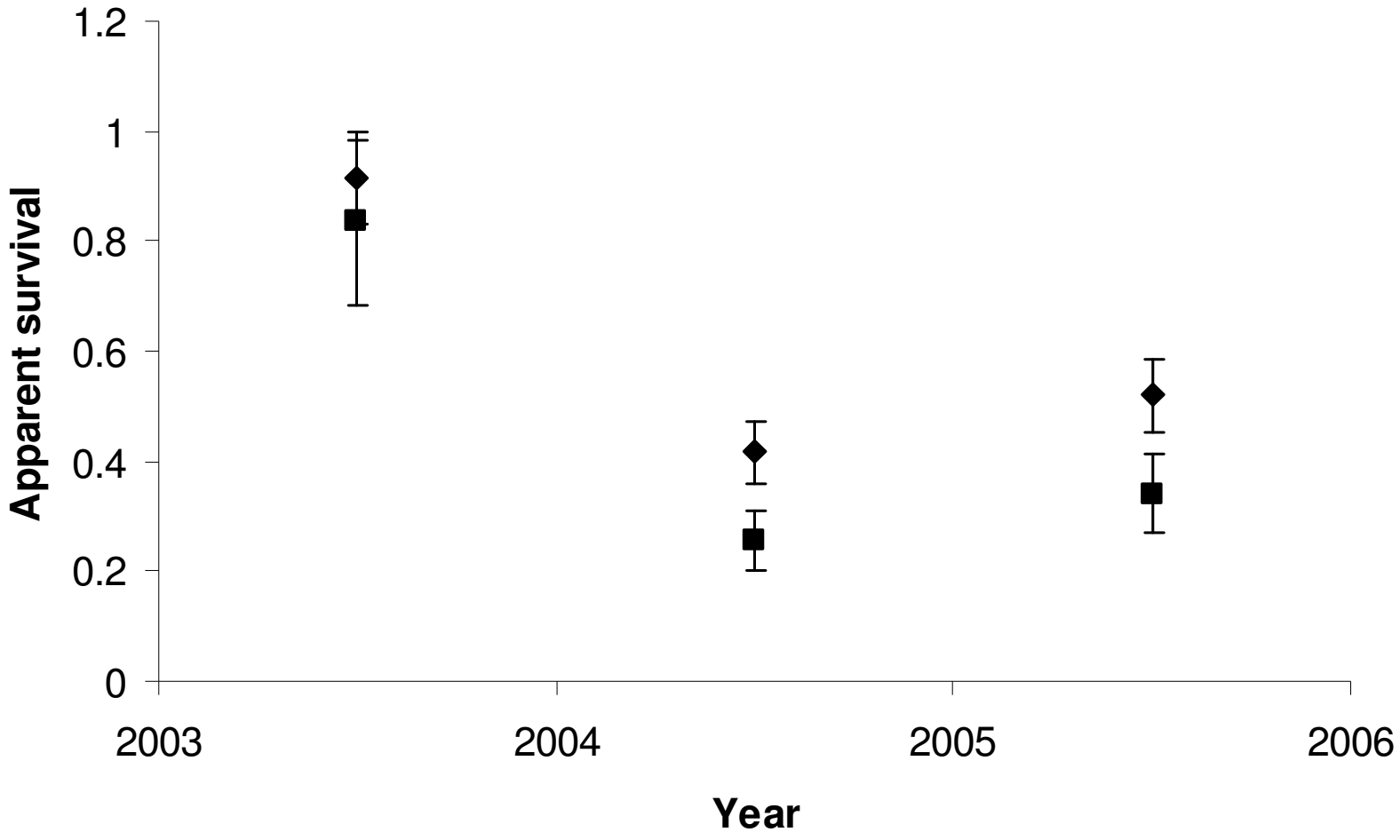

Figure 3.

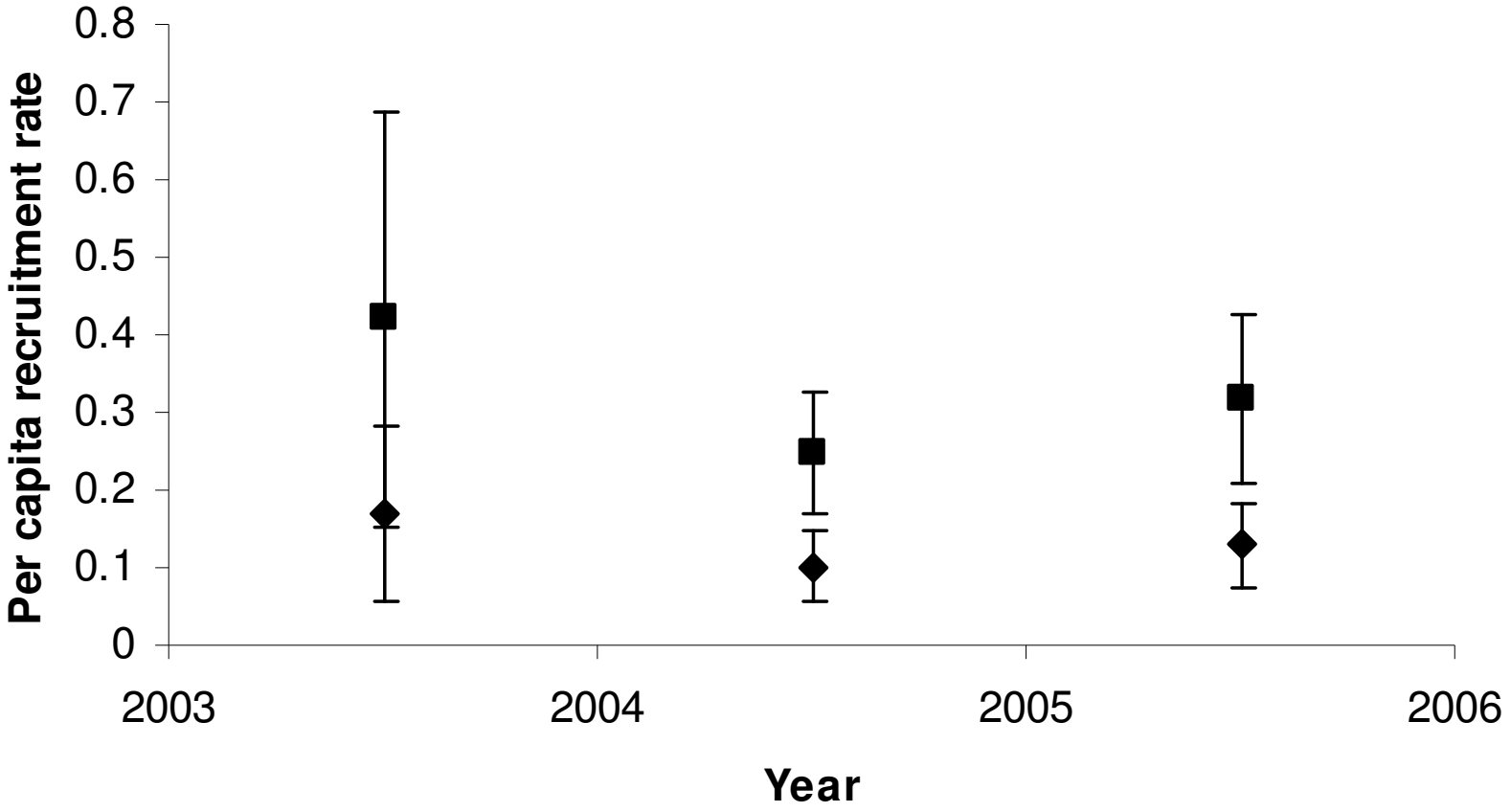
Per capita recruitment rate
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2003
2004
2005
2006
Year

Figure 4.