



Research Article

Density Dependence, Whitebark Pine, and Vital Rates of Grizzly Bears

FRANK T. VAN MANEN,¹ U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715, USA

MARK A. HAROLDSON, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715, USA

DANIEL D. BJORNLIE, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520, USA

MICHAEL R. EBINGER,² College of Forestry and Conservation, University Montana, University Hall, Room 309, Missoula, MT 59812, USA

DANIEL J. THOMPSON, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520, USA

CECILY M. COSTELLO, College of Forestry and Conservation, University Montana, University Hall, Room 309, Missoula, MT 59812, USA

GARY C. WHITE, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA

ABSTRACT Understanding factors influencing changes in population trajectory is important for effective wildlife management, particularly for populations of conservation concern. Annual population growth of the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem, USA has slowed from 4.2–7.6% during 1983–2001 to 0.3–2.2% during 2002–2011. Substantial changes in availability of a key food source and bear population density have occurred. Whitebark pine (*Pinus albicaulis*), the seeds of which are a valuable but variable fall food for grizzly bears, has experienced substantial mortality primarily due to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak that started in the early 2000s. Positive growth rates of grizzly bears have resulted in populations reaching high densities in some areas and have contributed to continued range expansion. We tested research hypotheses to examine if changes in vital rates detected during the past decade were more associated with whitebark pine decline or, alternatively, increasing grizzly bear density. We focused our assessment on known-fate data to estimate survival of cubs-of-the-year (cubs), yearlings, and independent bears (≥ 2 yrs), and reproductive transition of females from having no offspring to having cubs. We used spatially and temporally explicit indices for grizzly bear density and whitebark pine mortality as individual covariates. Models indicated moderate support for an increase in survival of independent male bears over 1983–2012, whereas independent female survival did not change. Cub survival, yearling survival, and reproductive transition from no offspring to cubs all changed during the 30-year study period, with lower rates evident during the last 10–15 years. Cub survival and reproductive transition were negatively associated with an index of grizzly bear density, indicating greater declines where bear densities were higher. Our analyses did not support a similar relationship for the index of whitebark pine mortality. The results of our study support the interpretation that slowing of population growth during the last decade was associated more with increasing grizzly bear density than the decline in whitebark pine. Grizzly bear density and its potential effect on vital rates and population trajectory warrant consideration for management of the grizzly bear population in the Greater Yellowstone Ecosystem. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS demographic change, density dependence, Greater Yellowstone Ecosystem, grizzly bear, *Ursus arctos*, vital rates, whitebark pine decline.

The trajectory of a wildlife population is the collective manifestation of vital rates (e.g., survival and fecundity), which are broadly governed by the life-history characteristics of a species (Cole 1954). Changes in the population

trajectory are a direct consequence of variation in age-specific vital rates, which, in turn, are influenced by a combination of ecological processes (Caughley 1977). Given sufficient time, population growth progresses most wildlife populations toward a relatively steady density through the interaction between population processes and available resources, with environmental variation superimposing random fluctuations over time (Caughley and Sinclair 1994:54). Populations are ultimately limited by availability or access to non-consumable (e.g., space, nest sites) or consumable resources (Caughley and Sinclair

Received: 4 September 2014; Accepted: 26 September 2015

¹E-mail: fvanmanen@usgs.gov

²Present address: U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715, USA.

1994). Understanding these relationships and how they influence the population trajectory can be insightful for wildlife managers and has important implications for mortality management. An informed management response to a reduction in population growth would be different if a change in trajectory was caused primarily by a decline in food resources versus a population experiencing density-dependent effects indicative of a population reaching carrying capacity.

Concepts related to population limitation and regulation have garnered particular interest from brown bear (*Ursus arctos*) managers as bear densities have increased in several recovering populations in Europe and the continental United States over the past 3 decades (Schwartz et al. 2006a, Kindberg et al. 2011, Mace et al. 2012, Chapron et al. 2014). McLellan (1994) suggested that food availability is likely the ultimate factor limiting brown bear populations but argued that this is a function of social behavior influencing access to food resources and level of energy expenditure in most instances, rather than a limitation of food biomass itself. Similarly, Miller et al. (2003) indicated that differences in body mass among Alaskan brown bear populations were most parsimoniously explained by each population's proximity to carrying capacity rather than differences in their habitat quality. Zedrosser et al. (2006) reported that body size of adult female brown bears was positively associated with abundance and availability of food, but that it may be constrained by competition for food at greater population densities. Density may influence vital rates directly through mechanisms such as infanticide by adult males (Swenson et al. 1997, Wielgus and Bunnell 2000). Miller et al. (2003) suggested that variation in cub survival and litter size was mostly influenced by proximity to carrying capacity, with some additional influence from environmental variation and stochastic events.

When a population is nearing carrying capacity, regulatory mechanisms are expected to affect vital rates and population growth. When that same population also experiences a change in abundance of food resources, it is difficult to isolate which factors may be affecting population growth most. However, when individual-level data on resource loss and population density are available, the relative strength of association with changing vital rates would be indicative of factors that may be acting more strongly on a particular population. Such studies require substantial, longitudinal datasets. Recent changes in the population trajectory of the grizzly bear population in the Greater Yellowstone Ecosystem (GYE) provided a unique opportunity to investigate these relationships. During 1983–2001, the estimated annual rate of population growth (λ) was between 4.2% and 7.6% (Harris et al. 2006) but declined to between 0.3% and 2.2% based on 2002–2011 data (Interagency Grizzly Bear Study Team [IGBST] 2012:34). Independent from these population projections, annual estimated numbers of unique females with cubs-of-the-year (cubs; Knight et al. 1995, Keating et al. 2002) corroborated a change in the population trajectory. Change-point analyses indicated this likely occurred around 2001 (M. Higgs, Montana State University, unpublished data).

One hypothesis for the slowing of population growth is based on substantial decline of an annually variable, high-calorie fall food source for grizzly bears, seeds of whitebark pine (*Pinus albicaulis*). Previous studies have reported associations between annual whitebark pine cone production and survival of independent bears (Haroldson et al. 2006), fecundity (no. F cubs/breeding-age F/yr; Schwartz et al. 2006a), movements (Blanchard and Knight 1991), and frequency of management actions (Mattson et al. 1992, Blanchard and Knight 1995, Gunther et al. 2004). Starting in the early 2000s, whitebark pine experienced widespread mortality primarily from mountain pine beetle (*Dendroctonus ponderosae*) infestations and, to a lesser degree, from fire and white pine blister rust (*Cronartium ribicola*) infection (Gibson 2007). Based on monitoring transects established in the GYE as part of the Interagency Whitebark Pine Monitoring Program, an estimated 27% (95% CI = 18–36%) of whitebark pine trees >1.4 m tall (all age classes) died during 2008–2013 (Greater Yellowstone Whitebark Pine Monitoring Working Group 2014). Observed cumulative mortality was 37% for trees >10 cm and \leq 30 cm diameter at breast height (DBH) and 72% for trees >30 cm DBH. By 2013, 72% of 176 monitored transects had evidence of beetle infestation (Greater Yellowstone Whitebark Pine Monitoring Working Group 2014). On transects monitored annually for whitebark pine cone production (Blanchard 1990), 75% of 190 mature, cone-bearing sample trees died between 2002 and 2014, with most mortality occurring prior to 2010 (Haroldson 2014).

Given that the grizzly bear population in the GYE experienced robust growth from the early 1980s through late 1990s, an alternative hypothesis for slowing population growth among grizzly bears in the GYE is that population density factors may be affecting vital rates. Eberhardt (1977, 2002), for example, hypothesized that population regulation in long-lived vertebrates is largely a function of density-dependent survival among younger age classes (i.e., cub and yearling survival for grizzly bears), which may be followed by changes in reproductive rates and, finally, adult survival.

There is substantial spatial heterogeneity within the GYE with respect to whitebark pine mortality and grizzly bear density (Bjornlie et al. 2014b). Therefore, we sought to obtain inference regarding how spatial and temporal variation in whitebark pine decline and grizzly bear density were associated with grizzly bear survival and reproductive parameters. If resource effects from whitebark pine mortality were more influential, we hypothesized that a decline in these vital rates would be greatest among those bears that resided in areas where mortality of whitebark pine was high. Alternatively, if population density effects were more influential, we predicted that vital rates would decrease as relative density of grizzly bears increased spatially and temporally among individuals.

STUDY AREA

Our study area comprised occupied grizzly bear range in the GYE (50,280 km² by 2010; Bjornlie et al. 2014a) and included Yellowstone National Park, Grand Teton National

Park, portions of 5 adjacent national forests, and state and private lands in Montana, Wyoming, and Idaho. The GYE consists of a high-elevation plateau surrounded by 14 mountain ranges with elevations $>2,130$ m, and contains the headwaters of 3 continental-scale rivers. Summers are short and most average annual precipitation (50.8 cm) falls as snow. Vegetation transitions from low-elevation grasslands through conifer forests at mid-elevations, reaching alpine tundra around 2,900 m. Within occupied grizzly bear range, the area of mapped whitebark pine is approximately 7,090 km² (14%; Landenburger et al. 2008) within a narrow elevation range of 2,500–3,060 m (Mahalovich 2013). Detailed descriptions of the geography, climate, and vegetation appear in Mattson et al. (1991) and Schwartz et al. (2006c).

METHODS

Capture and Handling

We used similar procedures for collection and analysis of demographic data as documented by Schwartz et al. (2006d) but extended the dataset from 1983–2001 to 1983–2012. We used culvert (i.e., box traps) or Aldrich leg-hold snares to capture bears (Blanchard 1985). Since 1997, bear capture and handling procedures were reviewed and approved by the Animal Care and Use Committee of the United States Geological Survey; procedures conformed to the Animal Welfare Act, and to United States government principles for use and care of vertebrate animals in testing, research, and training. Grizzly bear captures were conducted under United States Fish and Wildlife Service Endangered Species Permit (Section [i] C and D of the grizzly bear 4[d] rule, 50 CFR17.40 [b]) and additional research permits for the national park units and 3 states. We livecaptured bears in frontcountry (road access) and backcountry (no road access) settings within and outside national parks and wilderness areas. Except for dependent offspring, we fitted captured grizzly bears with radio transmitters (very high frequency [VHF] or global positioning system [GPS]; Telonics, Inc., Mesa, AZ). Adults were radiocollared, whereas independent subadults were instrumented with expandable collars, collars with programmable releases, glue-on transmitters, or ear transmitters. When we fitted radio collars on bears, we used a biodegradable canvas spacer to ensure collar drop. All transmitters were equipped with a motion sensor that reduced pulse rate if stationary for 4–5 hours, allowing for detection of mortalities and shed collars.

Analyses

Key determinants of bear population dynamics are survival of adult females, cubs, and yearlings, and reproductive output. Therefore, we examined the following parameters to test our hypotheses: 1) independent bear survival (≥ 2 years old; known-fate model), 2) cub and yearling survival (nest survival model for daily survival), and 3) reproductive transition probability of females (multi-state live-encounter model of transition from no offspring to cubs).

Independent survival.—We typically began telemetry monitoring of independent bears in early April and

concluded in late November but did not routinely monitor bears intensively during the denning season. We conducted telemetry flights every 7–14 days to determine bear status (i.e., alive, dead). Upon receiving a stationary mortality signal, we investigated potential bear mortalities within 2 weeks. We classified fates as unresolved in those instances where no collar or carcass was found, or certainty of the individual's fate was unknown.

We estimated survival of independent bears by following the known-fate procedures of Haroldson et al. (2006) in Program MARK (White and Burnham 1999). We coded bears as either alive, dead, or censored each month. An individual's encounter history began the month and year it was first captured and concluded the month and year it was censored or died. During the active season (Apr–Nov), we considered a bear alive during a gap in telemetry data if we knew it was alive before and after the data gap. If the gap exceeded 60 days during the active season, we censored bears for the appropriate months. We classified bears as alive during the denning months if they were alive the previous October or November and they emerged from dens wearing a functional radio collar. We censored bears with unknown fates (Haroldson et al. 2006). We used the results of Schwartz et al. (2010) to develop a base model to estimate survival of independent-aged bears and included capture status (research or management [conflict] bear), sex, quadratic function of age ($\text{age} + \text{age}^2$), proportion of locations in secure habitat (areas ≥ 4.05 ha that were >500 m from open or gated roads; U.S. Fish and Wildlife Service 2007), proportion of locations in developed areas, and season (denning vs. active).

Dependent young survival.—We defined dependent offspring as bears in their first (cub) and second year (yearling) of life because they remain with their mothers during these periods. We determined their fate from visual observations of family groups during ground monitoring or aerial telemetry flights of radio-collared females. We were able to document mortality in a few instances, but in all other cases, we assumed that cubs or yearlings died when they were no longer observed with their mother or when their mother died. We followed procedures of Schwartz et al. (2006b) to estimate cub and yearling survival using the nest survival model of Dinsmore et al. (2002) in Program MARK. Encounter histories were based on 3 dates: 1) the first date a female with young was seen (day i), 2) the last date young were known to be present with their mother (day j), and 3) the last date the mother was monitored (day k). For young that survived the monitoring interval, day k equaled day j . In cases where dependent offspring died, k was the first date of observation of the mother without young.

We estimated survival of dependent offspring for 3 time periods. The first period represented the cub stage and spanned the period between the date of our first observation of a litter of cubs following den emergence in spring (22 Apr) and the date of our last cub observation prior to den entry (18 Nov; 211 days). The second period was winter denning, which was from 19 November to 17 April (150 days). The third period represented the yearling stage and spanned the

dates of our first and last observations of a litter of yearlings (18 Apr to 3 Nov; 199 days). We estimated daily survival rates (DSR) for each time period. For the entire cub period, we calculated the survival rate as DSR_{cub}^{211} , whereas survival for the yearling (yrl) period was based on DSR_{yrl}^{199} .

Survival of individual offspring within a litter may not be independent, which may lead to overdispersed data that can bias the variance of estimates, although not the estimates themselves (Schmutz et al. 1995). Therefore, we used a data bootstrap procedure similar to the analyses of Bishop et al. (2008) by bootstrapping on unique litters, but used bootstrapping to perform model selection rather than estimation of the amount of overdispersion. We used simulation procedures in Program MARK to obtain model estimates for each of 5,000 bootstrap resamples of unique litters. We used the 5,000 resamples to calculate median beta coefficients.

Reproductive transition.—We used the method of Schwartz and White (2008) to estimate the likelihood that a radio-marked female ≥ 3 years old would transition between different reproductive states based on visual observations from telemetry flights. At least 2 consecutive years of observations are required to document a reproductive transition. In any given year, a female may be in one of the following states: no young (N), with cubs (C), with yearlings (Y), or with 2 year olds (T), resulting in 10 potential reproductive transitions that are biologically feasible (Schwartz and White 2008). For our analysis, we were primarily interested in the transition from no offspring in 1 year to cubs the following year (i.e., N to C). For females with no offspring, the only alternative transition is to no offspring again, thus, this transition provides an effective measure of how reproduction may be affected by population density or whitebark pine decline. We used the multi-state model in Program MARK that assumes first-order Markovian transitions (i.e., the next transition is conditional on the current state only) to estimate transition rates. Fecundity varies by age because of reproductive maturation and senescence, a relationship closely fit by a quadratic curve, so we included age ($\text{age} + \text{age}^2$) of individual females in our base model for the N to C transition (Schwartz and White 2008).

Testing for time trend.—To determine if changes in vital rates over time were associated with grizzly bear density or whitebark pine mortality, it was important to fit a covariate for time trend to each model to detect whether vital rates changed and, if so, when and how they changed. We tested 8 temporal covariates to capture plausible scenarios of vital rate changes (Supplementary Fig. S1), including a linear trend (T_{lin}), 4 quadratic splines (starting in 1983 [T_{q1983}], 1991 [T_{q1991}], 1996 [T_{q1996}], and 2001 [T_{q2001}], respectively; value range = 0.001–0.900), 2 sigmoidal trends (inflection points around 1995 [T_{sig1}] and 2000 [T_{sig2}], respectively; value range = 0–1.0), and a binary covariate (T_{period}) that split the 30-year study period into 1983–2001 and 2002–2012, the second representing the period of slowed population growth documented by IGBST (2012). We also included a model with no time trend in each analysis. We determined which temporal covariate had the most support

based on the global model for each vital rate using Akaike's Information Criterion with a second-order correction for small sample size (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2002). We used the most supported temporal covariate to develop a model set for hypothesis testing.

Hypothesis testing.—We examined whether changes in vital rates over time were associated with either whitebark pine decline or grizzly bear density. To do so, we assigned covariate values to the encounter histories of individually marked bears based on annual, spatially explicit indices of whitebark pine decline and grizzly bear density. Potential effectiveness of the indices as covariates was contingent on detecting variation through space and time.

We derived the grizzly bear density index (Bjornlie et al. 2014b) using capture, telemetry, and life-history data for 870 bears involved in >1,800 captures during 1975–2012. We spatially reconstructed individual bears' extent of use, as represented in a lifetime activity range, and temporally extruded these activity ranges each year from the age of independence (≥ 2 years of age) through the known or estimated year of death. The lifetime activity range was defined by the mean lifetime activity radius of telemetry locations, collected approximately every 10–14 days during the active season, from the center of activity (Bjornlie et al. 2014b; $\gamma_{\text{male}} = 24.3$ km, $\gamma_{\text{female}} = 12.8$ km; based on 80th percentile to exclude outliers). We restricted data to known-aged individuals (cementum annuli aging) that were captured for research or management purposes. We explicitly accounted for any management bears that established a new range after transport by recalculating their activity centers. We overlaid each lifetime activity range on a grid of 14- × 14-km cells (196 km²), approximating the annual home-range size of female bears (IGBST, unpublished data). For each grid cell, the density index in a given year was the sum of proportional overlap of all lifetime activity ranges for bears present during that year (Bjornlie et al. 2014b). We assumed lifetime activity-range estimates were representative of years prior to first capture. Grid cells that were completely covered by an activity range received a value of 1 for that individual. For cells partially covered by an activity range, the contribution to the density index was based on its proportional coverage. Our derivation of this index has several caveats. First, the density index is based on bears that were captured and although capture effort is distributed spatially and temporally throughout the ecosystem, differences in capture effort may cause biases. Therefore, we tested if the density index was correlated with capture effort (1996–2012) by evaluating the correlation between the change in capture effort (cumulative no. trapnights of current and preceding years/grid cell) and change in bear density at the grid-cell level. The large extent of the study grid resulted in many uninformative cells with zero density and zero capture effort and we excluded them from this evaluation. Furthermore, 29% of cells with non-zero cumulative density values for the time series were cells where there was no capture influence (i.e., capture index = 0) for the entire time period. These cells were not solvable in terms of correlations and were excluded. Of the remaining cells ($n = 250$), we

detected little correlation between the rate of change of the cumulative capture index and that of the density index: the distribution of correlation coefficients for these 250 cells approached a normal distribution with a mean near 0 ($\bar{x} = 0.07$; $\sigma = 0.28$; Bjornlie et al. 2014b). The second caveat is that the initial and ending years from 1975 to 2012 underestimated density relative to the middle years of this period. This is unavoidable because we could not include bears that might have been captured prior to 1975 and forecast into the future, nor bears that might be captured in the future (i.e., post-2012) and back-cast to the present. The average age of first capture is approximately 5 years so this time lag was not a concern for the starting year of 1983 because of capture effort during 1975–1982. However, for the ending years, underestimation of the density index started around 2007. Therefore, we ended the density index in 2006 and used autoregressive integrated moving average ARIMA (1,1,1) forecasting. We accounted for drift (i.e., $d > 0$) and based projections on the previous 5 years of density information (2002–2006) to project trends forward from 2007 through 2012 on a cell-by-cell basis (i.e., 960 time-series projections). We validated the density index using data from standardized observation flights conducted twice annually by IGBST since 1998 in 28 Bear Observation Areas (BOAs). All independent-aged bears (≥ 2 years old) were counted individually. For females with offspring, we only counted the mother. Using BOAs as the sampling unit, we calculated correlation coefficients to test if bear observation rates were positively associated with the density index. We ended the period for validation in 2006 because of the aforementioned time lag for sampling bears. For the 1998–2006 period, the mean density index was positively correlated with mean log-transformed counts of bear groups/hour/1,000 km² within BOAs ($r = 0.725$, $P < 0.001$, $n = 28$; Bjornlie et al. 2014b). Assuming that changes in observation rates over time are a product of the number of bears in BOAs, these results support the efficacy of the index to track relative changes in bear density. Over time, the bear density index showed an expanding pattern due to population expansion and increasing index values in core areas of the ecosystem, reflecting increasing bear density (Supplementary Fig. S2). Additional details on the development and evaluation of this index are provided by Bjornlie et al. (2014b).

With the exception of a single year (2009; Macfarlane et al. 2013), no annual data existed to derive an individual covariate of whitebark pine decline. Therefore, we developed a spatially explicit, annual index of whitebark pine mortality. Normalized Difference Vegetation Index (NDVI) data derived from MODIS satellite imagery (250-m resolution) have been effectively used to model insect-induced tree mortality (Verbesselt et al. 2009) so we developed a similar approach to estimate change in healthy whitebark pine canopy. Our area of analysis followed an existing whitebark pine distribution map (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011) that was also used by Macfarlane et al. (2013), which included mixed and pure stands. Whitebark pine in the GYE is most commonly found with lodgepole pine (*Pinus contorta*),

Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) as associates, and occurs as a climax species in pure stands only on the most exposed sites (Arno and Hoff 1989). Whitebark pine cones are indehiscent and grizzly bears obtain $>90\%$ of seeds by raiding red squirrel (*Tamiasciurus hudsonicus*) cone caches (Kendall 1983, Mattson and Reinhart 1997). Greatest red squirrel densities occur in mixed, mature conifer stands, where food supply is more consistent (Mattson and Reinhart 1994, Podruzny et al. 1999). Within mapped whitebark pine, we selected pixels with $\geq 50\%$ canopy cover (2001 National Land Cover Database; Homer et al. 2007) to ensure that we measured changes for pixels that were mostly forested. For each year, we used 5 composite scenes (16 days each; late Jul through mid-Oct) to calculate a weighted mean annual value of NDVI for each grid cell. We weighted each pixel using the 16-bit binary coded Quality Assurance (QA) science datasets (SDS) included in the MODIS products (Solano et al. 2010). Using the Vegetation Indices (VI) pixel reliability parameter (bits 2–5 of the QA-SDS dataset), we converted the 11 classes of binary data to an interval-scaled (range = 1–11) weighting factor for each pixel in each composite scene. Because our primary interest was to detect mortality of whitebark pine rather than inter-annual variation in reflectance from other sources (e.g., precipitation), we used a robust piecewise constant signal denoising algorithm (Little and Jones 2011) to reduce annual variation. Finally, using 2000 as the reference year, we calculated change in the reflectance value of each grid cell for each year. We used 2000 as the reference year because the most recent outbreak of mountain pine beetle began in 1999–2000 with peak beetle activity around 2009 (Mahalovich 2013). Consequently, 2001 was the first year during which this index showed negative values among sampled bears. Several sources of uncertainty likely were propagated in this index, as is common with remote sensing data (Lechner et al. 2012). Among the 3 sources of uncertainty addressed by Lechner et al. (2012; classification scheme uncertainty, spatial scale, classification error), our index was least sensitive to classification scheme uncertainty because we used continuous NDVI data, rather than discrete classes. Regarding spatial scale, uncertainty associated with the index at the observation scale of a pixel decreased substantially as we aggregated pixel values to our analysis scale of a lifetime activity range (Bian and Butler 1999), as described subsequently. We could not quantify classification error because it was not feasible to groundtruth this retrospective index because of the dynamic changes that have occurred in whitebark pine stands. Therefore, we used 2009 data from Macfarlane et al. (2013) to qualitatively assess our index (Supplementary Fig. S3). Besides reflecting the effects of mountain pine beetle, our index also detected changes due to other sources of mortality, such as forest fires. The index showed fine-scale, gradual changes in whitebark pine stands for many areas, likely reflecting a spreading pattern of local outbreaks of mountain pine beetle, with a few areas showing larger-scale, abrupt changes indicative of forest fires (Supplementary Fig. S3).

To measure the indices for bear density and whitebark pine mortality as a covariate value for each bear, we first estimated lifetime centers of activity of individual bears. We calculated the mean activity radius for females and males and then applied that distance to each individual's activity center to measure the mean annual value of each index based on grid cells within that area. We proportionally adjusted the weight for grid cells that fell on the perimeter. Additionally, for the index of whitebark pine mortality, we weighted the index according to the proportion of whitebark pine cover type (Landenburger et al. 2008) for cells with >50% tree cover (Homer et al. 2007) available for each bear. In other words, severe mortality and high proportion of the whitebark pine cover type combined to produce the lowest indices, indicative of the most severe decline. Conversely, values were close to 0 for bears with little whitebark pine in their activity range and varied only slightly with change in whitebark pine cover.

We developed a suite of models to test our research hypotheses using AIC_c . For each vital rate, our model set included a base model as previously described, a model with the top-supported temporal covariate only, and models with either the index of bear density or the index of whitebark pine mortality. Finally, to test each vital rate with grizzly bear density or whitebark pine mortality changing as a function of the temporal covariate, we included models with interaction terms for 1) the temporal covariate and grizzly bear density index and 2) the temporal covariate and whitebark pine index. For survival of independent bears, we also included a term for sex. Because cub and yearling survival were based on bootstrapping, we performed model selection using the median AIC_c and ΔAIC_c values based on the 5,000 resamples of each model. We used model averaging to graphically show relevant relationships of estimated vital rates and model covariates. In testing our research hypotheses, our focus was on the relationships represented by the model parameters, rather than estimation of each vital rate. Vital rate estimates from our analyses are not fully comparable with those provided by Schwartz et al. (2006d) and IGBST (2012) because we used model averaging, different covariates, and data from a different time period.

RESULTS

The indices for grizzly bear density and whitebark pine mortality showed considerable variation among individual bears (grizzly bear density index: $\bar{x} = 13.9$, $SD = 5.6$, range = 0–29.2; index of whitebark pine mortality: $\bar{x} = -0.022$, $SD = 0.050$, range = -0.380–0 [more negative numbers reflect greater mortality]) through time (Fig. 1). The mean annual density index for sampled bears increased from approximately 9 early in the study period to over 16 toward the end, with a concomitant increase in variation (Fig. 1A). The whitebark pine index indicated that the number of bears affected and the extent of whitebark pine loss increased rapidly after the year 2000, with annual means ranging from -0.070 to 0 (Fig. 1B). Among sampled bears, we found little evidence of a correlation between these 2 indices for the entire time period ($r = -0.048$, $P = 0.039$, $n = 1,872$), or after the year 2000, the period of whitebark

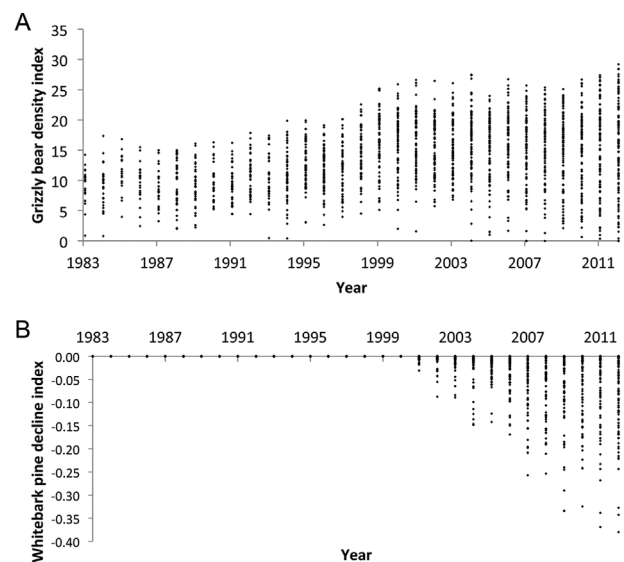


Figure 1. Mean index values for (A) grizzly bear density and (B) whitebark pine mortality associated with lifetime activity ranges of independent-aged (≥ 2 years) grizzly bears sampled in the Greater Yellowstone Ecosystem, USA, 1983–2012.

pine decline ($r = 0.098$, $P = 0.001$, $n = 1,063$). Thus, these indices provided useful measures of local changes experienced by individual bears over time and across a wide gradient of conditions in the GYE.

Our analysis of survival of independent bears was based on 1,872 annual encounter histories of 645 individual bears. Among the 8 temporal covariates we tested, period (T_{period} ; 1983–2001 vs. 2002–2012) had the most support ($AIC_c = 1,128.62$; AIC_c weight [w_i] = 0.54; Supplementary Table S1); the second and third most supported models were based on no time trend and a quadratic trend, but both had much less support ($\Delta AIC_c = 2.40$, $w_i = 0.16$ and $\Delta AIC_c = 3.34$, $w_i = 0.10$, respectively). Therefore, we used T_{period} as the temporal covariate to test our hypotheses. We did not fit an interaction term for this covariate because the interaction was inherent in the whitebark pine covariate: statistical support for the whitebark pine covariate would indicate it occurred during the latter period of 2002–2012. The model with T_{period} ($\hat{\beta} = 0.847$, 95% CI = 0.297–1.398), sex ($\hat{\beta} = 0.467$, 95% CI = -0.040–0.973), and $T_{\text{period}} \times$ sex interaction ($\hat{\beta} = -0.690$, 95% CI = -1.468–0.089; Supplementary Table S2) had the most support ($w_i = 0.34$; model A5; Table 1), followed by a model ($\Delta AIC_c = 1.05$, $w_i = 0.20$; model A2; Table 1) with sex ($\hat{\beta} = 0.183$, 95% CI = -0.204–0.569; Supplementary Table S2) and T_{period} only ($\hat{\beta} = 0.522$, 95% CI = 0.128–0.916; Supplementary Table S2). There was some evidence of greater survival during the 2002–2012 period, primarily among males (Fig. 2). We detected little support for an association of independent bear survival with the indices for grizzly bear density or whitebark pine mortality or their interaction with period ($\Delta AIC_c > 1.90$; Table 1).

We used 326 encounter histories for offspring of 116 females to estimate survival for the cub and yearling periods;

Table 1. Model-selection results to test association of 4 vital rates of grizzly bears with time trends, spatially and temporally explicit indices of whitebark pine mortality (WbPmort) and grizzly bear density (GBdensity), and their interactions, Greater Yellowstone Ecosystem, USA, 1983–2012. We examined the following parameters: survival of independent-aged grizzly bears (≥ 2 yrs), survival of cubs-of-the-year (cub) and yearlings (yrl), and reproductive transition from no offspring to cubs.

Model no. and model description	AIC _c ^a	Δ AIC _c ^b	w_i^c	K ^d	Dev ^e
Independent survival ^f					
A5 {base + sex + T _{period} + sex × T _{period} }	1,128.04	0.00	0.34	10	1,108.02
A2 {base + sex + T _{period} }	1,129.08	1.05	0.20	9	1,111.07
A6 {base + sex + T _{period} + GBdensity}	1,129.93	1.90	0.13	10	1,109.91
A7 {base + sex + T _{period} + WbPmort}	1,130.20	2.16	0.12	10	1,110.18
A8 {base + sex + T _{period} + GBdensity + T _{period} × GBdensity}	1,130.56	2.52	0.10	11	1,108.53
A4 {base + sex + WbPmort}	1,131.81	3.77	0.05	9	1,113.80
A3 {base + sex + GBdensity}	1,132.81	4.77	0.03	9	1,114.79
A1 {base + sex}	1,133.97	5.93	0.02	8	1,117.96
Cub and yearling survival ^g					
B7 {cub(GBdensity + T _{q2001} + GBdensity × T _{q2001}), yrl(GBdensity + T _{sig1} + GBdensity × T _{sig1})}	697.42 (53.84) ^h	0.00 (4.14) ^h	0.95 ⁱ	8	681.42 (53.84) ^h
B5 {cub(GBdensity + T _{q2001}), yrl(GBdensity + T _{sig1})}	705.75 (53.03)	7.59 (9.40)	0.02	6	693.75 (53.03)
B8 {cub(WbPmort + T _{q2001} + WbPmort × T _{q2001}), yrl(WbPmort + T _{sig1} + WbPmort × T _{sig1})}	705.76 (53.50)	7.68 (10.49)	0.02	8	691.37 (53.54)
B6 {cub(WbPmort + T _{q2001}), yrl(WbPmort + T _{sig1})}	708.83 (53.42)	10.74 (10.76)	<0.01	6	696.83 (53.42)
B2 {cub(T _{q2001}), yrl(T _{sig1})}	710.44 (52.94)	12.23 (12.13)	<0.01	4	702.44 (52.94)
B3 {cub(GBdensity), yrl(GBdensity)}	725.95 (53.64)	28.70 (14.34)	<0.01	4	717.95 (53.64)
B4 {cub(WbPmort), yrl(WbPmort)}	732.18 (53.12)	34.26 (17.76)	<0.01	4	724.18 (53.12)
B1 {cub(), yrl(.)}	733.30 (53.27)	35.70 (17.77)	<0.01	2	729.30 (53.27)
Reproductive transition from no offspring to cubs ^j					
C7 {base + T _{sig1} + GBdensity + T _{sig1} × GBdensity}	6,196.19	0.00	0.44	13	6,169.26
C1 {base}	6,198.08	1.89	0.17	10	6,177.53
C2 {base + T _{sig1} }	6,198.79	2.61	0.12	11	6,176.13
C3 {base + GBdensity}	6,199.78	3.60	0.07	11	6,177.12
C4 {base + WbPmort}	6,199.99	3.80	0.07	11	6,177.32
C6 {base + T _{sig1} + WbPmort}	6,200.07	3.88	0.06	12	6,175.28
C5 {base + T _{sig1} + GBdensity}	6,200.90	4.71	0.04	12	6,176.11
C8 {base + T _{sig1} + WbPmort + T _{sig1} × WbPmort}	6,201.84	5.66	0.03	13	6,174.92

^a Akaike's Information Criterion adjusted for small sample size.

^b Difference in AIC_c compared with lowest AIC_c model.

^c AIC_c model weight.

^d No. model parameters.

^e Model deviance.

^f Base model was modified from Schwartz et al. (2010) and included trap status (research or management bear), age, age², secure habitat, developed area, and season (denning vs. active); time trend modeled as a binary variable (T_{period}: 1983–2001 [period 1] vs. 2002–2012 [period 2]).

^g Time trend for cubs and yearlings modeled as quadratic spline starting in 2001 (T_{q2001}) and sigmoidal function (T_{sig1}), respectively.

^h Median value based on 5,000 bootstrap resamples; standard deviation in parentheses.

ⁱ AIC_c weights based on median Δ AIC_c values of the 8 models from the 5,000 resamples.

^j Base model included age and age² for the transition of no young to cubs; time trend modeled as a sigmoidal function (T_{sig1}).

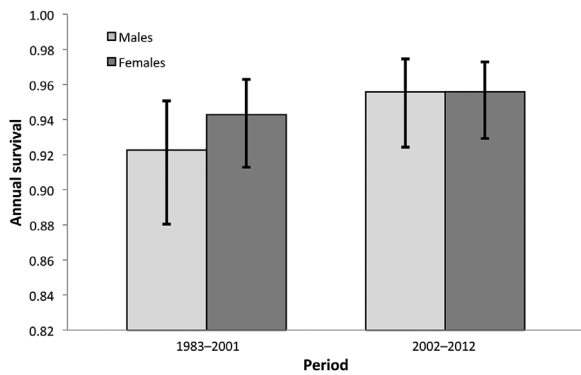


Figure 2. Predicted annual survival and 95% confidence intervals (vertical lines) of independent-aged (≥ 2 years) grizzly bears in the Greater Yellowstone Ecosystem, USA, by period (1983–2001 and 2002–2012). Predictions based on model-averaged estimates. Covariate values in the base model were set at their mean (age = 8.4 years [M and F], proportion of locations in secure habitat = 0.82, proportion of locations in developed area = 0.13).

118 of these records represented mortalities. Time trend analyses for cub survival indicated the best fit for quadratic models, with most support for a quadratic time trend starting in 2001 (T_{q2001} ; $AIC_c = 741.60$; $w_i = 0.41$; Supplementary Table S1), followed by a quadratic time trend starting in 1996 (T_{q1996} ; $\Delta AIC_c = 1.09$; $w_i = 0.24$). We chose T_{q2001} as our temporal covariate. For yearling survival, the best fit was evident for a sigmoidal time trend over the study period (T_{sig1} ; $AIC_c = 746.08$; $w_i = 0.64$; Supplementary Table S1), followed by a model with the second sigmoidal function (T_{sig2} ; $\Delta AIC_c = 3.37$; $w_i = 0.12$). Therefore, we applied T_{sig1} to the yearling period to develop our model set for hypothesis testing. Results of the 5,000 bootstrap resamples indicated greatest support for a model that included the time trends, bear density index, and their interactions (median $AIC_c = 697.42$; $w_i = 0.95$; model B7; Table 1). For cub survival, parameter estimates for the bear density index (median $\hat{\beta} = 0.014$, 95% CI = -0.047 – 0.075) and time trend (median $\hat{\beta} = 10.189$, 95% CI = -8.721 – 29.099) had confidence intervals that overlapped 0, but there was evidence of a $T_{q2001} \times$ bear density interaction (median $\hat{\beta} = -1.242$, 95% CI = -2.227 to -0.256 ; Supplementary Table S2). Model-averaged estimates of cub survival showed the effect of the interaction, with a decline of cub survival starting in 2001 and more so in areas with greater index values for bear density (Fig. 3A). For yearling survival, parameter estimates did not indicate an interaction effect for $T_{sig1} \times$ bear density (median $\hat{\beta} = 0.388$, 95% CI = -0.165 to 0.941), although there was some evidence of a decline in yearling survival based on the time trend covariate T_{sig1} (median $\hat{\beta} = -7.089$, 95% CI = -14.327 to 0.150 ; Model B7, Supplementary Table S2). Model-averaged estimates of yearling survival indicated this decline occurred during the 1990s (Fig. 3B). The model with whitebark pine, time trend, and their interaction was the third-ranked model but had little support (median $\Delta AIC_c = 7.68$; $w_i = 0.02$; model B8; Table 1); only the parameter estimates for time trend did not bound 0 in the 95% confidence intervals (cubs: median

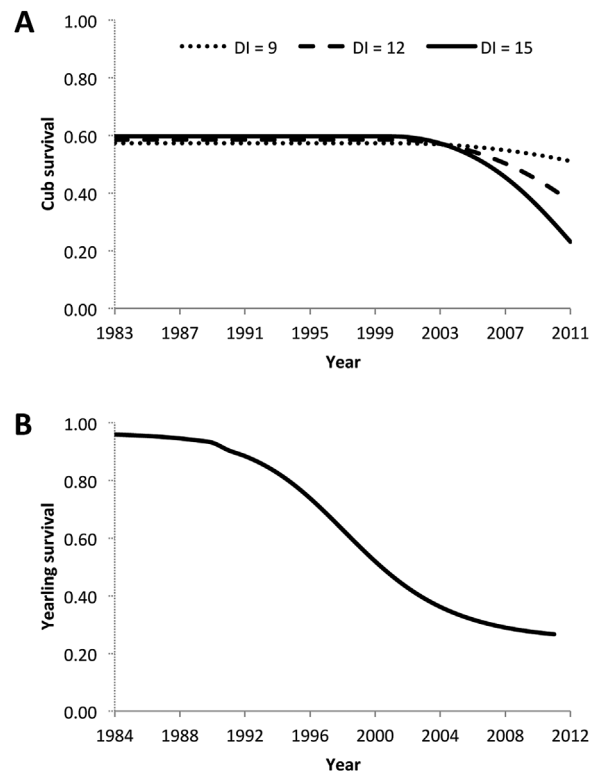


Figure 3. Predicted survival rate of grizzly bear cubs-of-the-year (cub) and yearlings, Greater Yellowstone Ecosystem, USA, 1983–2012. Predictions based on model-averaged estimates. (A) Survival rate during 211-day cub period and grizzly bear density index (DI). Time trend was based on quadratic spline starting in 2001. The 3 levels of the grizzly bear density index ($DI = 9, 12, \text{ or } 15$) reflect range of density conditions experienced by sampled bears during the study period, with generally greater values as the study period progressed. We set the covariate value for the index of whitebark pine mortality at a value of -0.04 . (B) Survival rate during 199-day yearling period. Time trend was based on sigmoidal function. We set the covariate for bear density at a value of 12 and the covariate for the index of whitebark pine mortality at a value of -0.04 , approximating conditions experienced by sampled bears during the early 2000s.

$\hat{\beta} = -14.328$, 95% CI = -20.935 to -7.720 ; yearlings: median $\hat{\beta} = -2.101$, 95% CI = -3.802 to -0.399 ; Supplementary Table S2). The evidence ratio between the equivalent, competing models with temporal interactions ($E_{B7,B8}$) was 46.6 in favor of the model based on the grizzly bear density index (B7) versus the whitebark pine index (B8; Table 1).

Finally, we estimated reproductive transitions based on 185 encounter histories of 156 females (377 transitions, of which 199, 101, 58, and 19 started in the N, C, Y, and T states, respectively). Among the temporal covariates we tested, the sigmoidal time trend T_{sig1} had slightly more support ($AIC_c = 6,196.86$; $w_i = 0.28$; Supplementary Table S1) than the binary covariate of T_{period} ($\Delta AIC_c = 0.16$, $w_i = 0.25$) and T_{sig2} ($\Delta AIC_c = 0.80$, $w_i = 0.18$). Therefore, we used T_{sig1} as the temporal covariate to test our hypothesis. The most supported model had an AIC_c weight of 0.44 (model C7; Table 1) and included T_{sig1} ($\hat{\beta} = 3.048$, 95% CI = 0.080 – 6.017), grizzly bear density index ($\hat{\beta} = 0.257$, 95% CI = 0.045 – 0.468), and their interaction ($\hat{\beta} = -0.321$, 95% CI = -0.570 to -0.072 ; Supplementary Table S2). The

second- and third-ranked models had less support ($\Delta AIC_c = 1.89$, $w_i = 0.17$ [model C1] and $\Delta AIC_c = 2.61$, $w_i = 0.12$ [model C2], respectively; Table 1) and contained the base model and the covariate for T_{sig1} ($\hat{\beta} = -0.580$, 95% CI = -1.544 – -0.384), respectively (Supplementary Table S2). Based on the 2 competing models with the temporal interactions (models C7 and C8; Table 1), the evidence ratio $E_{C7,C8}$ indicated 16.9 times greater support for a grizzly bear density association with transition probability compared with the index for whitebark pine mortality. Model-averaged estimates showed the probability of reproductive transition from no offspring to cubs declined during the 1990s, which was more pronounced in areas with greater population densities (Fig. 4).

DISCUSSION

The vital rate that generally has most influence on the population trajectory in grizzly bear populations is survivorship of adult females, followed by reproductive rates and juvenile survival (Eberhardt et al. 1994, Garshelis et al. 2005, Harris et al. 2006). However, as Mitchell et al. (2009) reported for American black bears (*Ursus americanus*), high variance of juvenile survival and recruitment may have a greater influence on variation of population growth than adult female survival (Harris et al. 2011). In the GYE, survival of independent-aged females was high and did not change during the study period and thus did not contribute to slowing of population growth. Survival of dependent-aged bears declined, however, and was negatively associated with population density, particularly for cubs (Fig. 3A). Decline in cub survival was evident beginning in the early 2000s and was associated more strongly with increasing grizzly bear density than reduced availability of whitebark pine. Cub survival is a

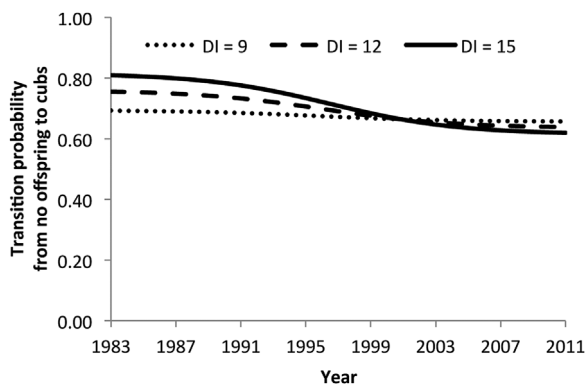


Figure 4. Predicted probability of reproductive transition of female grizzly bears from having no offspring to having cubs-of-the-year (cub) and relationship with grizzly bear density index (DI), Greater Yellowstone Ecosystem, USA, 1983–2012. Predictions based on model-averaged estimates. Time trend was based on sigmoidal function. The 3 levels of the grizzly bear density index ($DI = 9, 12, \text{ or } 15$) reflect range of density conditions experienced by sampled bears during the study period, with generally greater values as the study period progressed. We set the covariate for age at the mean value for sampled females (8.4 years). We set the covariate value for the index of whitebark pine mortality at -0.04 , approximating conditions experienced by sampled bears during the early 2000s.

potential density-dependent factor contributing to population regulation among bear populations and we explore 2 potential causes for the grizzly bear population in Yellowstone: intraspecific killing and interference competition.

Intraspecific killing may function as a density-dependent effect on cub survival, although different biological mechanisms have been proposed (Miller 1990, Swenson et al. 2001, Wielgus et al. 2001, Miller et al. 2003, McLellan 2005). McLellan (1994) reported 57 cases of intraspecific killing of brown bears, and cubs were the victim in 44% of instances, followed by adult females (12%), several of which were killed while protecting their cubs. The latter was documented ($n = 2$) for the first time in areas with high bear densities in Yellowstone National Park in May 2012 (IGBST, unpublished data). For the GYE, we hypothesize that a connection exists between increased survival of independent-aged males (Fig. 2; IGBST 2012) and increased mortality of cubs as a function of bear density during the last decade of the study period (Fig. 3A). Indeed, most of our observations of males killing cubs have occurred in recent years (IGBST, unpublished data).

A second, density-related cause for lower survival among dependent-aged (i.e., cubs and yearlings) bears may be interference competition. As population density increases, interference competition has the potential to constrain the feeding efficiency of some individuals, particularly subordinate individuals such as juveniles (Rutten et al. 2010, López-Bao et al. 2011). Breed et al. (2013) suggested that reduced foraging efficiency of young-of-the-year gray seals (*Halichoerus grypus*) in Nova Scotia, Canada resulted in reduced survival at greater densities, which likely explained the slowing of population growth they observed. Unlike exploitation competition, when food supplies are depleted with increasing population density, interference competition can arise even when food is plentiful, as Gende and Quinn (2004) demonstrated for brown bears on Chichagof Island, Alaska. At the extreme, interference competition can cause starvation among less-competitive individuals even in the absence of food depletion (Goss-Custard et al. 2001). If conspecifics are potentially predatory, as in brown bears, increased vigilance may further affect foraging efficiencies at higher population densities, as generally observed in predator-prey systems (St. Juliana et al. 2011). There is ample evidence for interference competition among brown bear populations. Although McLellan (1994) identified food as the ultimate factor limiting brown bear populations, he noted that bear consumption rarely reduces food biomass to levels where foraging efficiency is compromised. Instead, he suggested that foraging is more likely impaired at high densities by social behaviors such as displacement, increased vigilance, and increased energy expenditure from social stress. Older bears, particularly adult males, are usually dominant at productive feeding sites by virtue of their larger body size. Subordinate juveniles and females with dependent young may avoid areas used by adult males and several authors have suggested this serves to reduce the risk of intraspecific predation (Wielgus and Bunnell 1994, Mattson and Reinhart 1995, Ben-David et al. 2004, Rode et al. 2006).

Such avoidance can incur a nutritional cost. Nevin and Gilbert (2005), for example, found that females with cubs reduced energy intake by 37% when selecting sub-optimal habitats in a salmon-rich environment. Similarly, Steyaert et al. (2013) suggested a food-for-safety trade-off exists among female brown bears with cubs in Sweden that may have its origins in avoiding intraspecific predation.

Our study was not designed to determine whether population density acted more directly (i.e., intraspecific killing) or indirectly (i.e., interference competition) on cub survival. We speculate both processes may play a role in the GYE but only have supporting evidence for intraspecific killing based on investigations of mortality (IGBST, unpublished data). We lack the ability to directly assess the nutritional costs of interference competition on cub body condition because we rarely captured females with cubs and avoided handling them when we did. However, percent body fat of females exerts a strong influence on body condition of newborns (Robbins et al. 2012) and thus provides a useful indicator of this effect. Although data presented in Schwartz et al. (2014) indicated a possible decline in percent body fat among fall captures of adult females during 2007–2010, additional data and analyses since that time provided no evidence of a decline in percent body fat during the period of whitebark pine decline (IGBST 2013:19–20).

Yearling survival also declined, but this decline was not explicitly associated with whitebark pine mortality or population density. The decline in yearling survival began during the 1990s and thus prior to the onset of whitebark pine decline. Cubs tend to be more susceptible to intraspecific killing than yearlings (McLellan 1994), which may explain why we did not observe an interaction for the change in yearling survival with bear density. However, power to detect an interaction effect may have been limited by the smaller number of records contributing to estimation of yearling survival compared with cub survival.

Our study provided moderate evidence that the probability of reproductive transition from no offspring to cubs declined during the 1990s, prior to whitebark pine decline, and that this decline was greater in areas with higher bear densities (Fig. 4). The increase in adult female densities where survival is high may be linked with reproductive suppression through interference competition within female hierarchies (Gende and Quinn 2004, Støen et al. 2006). As discussed previously, a greater number of adult males due to their increased survival since the early 2000s may also have contributed to interference competition.

The changes we observed in survival of dependent young and reproductive transition are consistent with the documented slowing of estimated annual population growth since the early 2000s (IGBST 2012). Lower cub survival, in particular, may have been an important contributor to reduced population growth. The observed reduction in cub survival from an estimated 0.64 ± 0.087 (SE) during 1983–2001 to 0.55 ± 0.064 during 2002–2011 (IGBST 2012) would have reduced annual population growth, from 1.076 to 1.049. A study of Scandinavian brown bears similarly demonstrated that an observed difference in cub

survival (S_0), between 2 study areas with ($S_0 = 0.85$ – 1.00) and without ($S_0 = 0.58$ – 0.61) harvesting of adult males, could reduce annual population growth from 1.18 to 1.14 (Swenson et al. 1997). Recent analyses on that same population further indicated relatively high elasticity of the cub survival parameter on population growth (Gosselin et al. 2015).

Density-dependent changes in life-history traits are more likely to occur when populations are near carrying capacity (Caughley 1977; Fowler 1981a,b) and the research of Miller et al. (2003) supports this notion for brown bears. Our findings are consistent with Schwartz et al. (2006b), who predicted based on 1983–2001 data that population density may influence cub and yearling survival as density reaches carrying capacity in different portions of the GYE, such as inside Yellowstone National Park. Of course, population changes mediated by density may be linked with food resources and carrying capacity of the environment (Miller 1990). Thus, there is the possibility that decline of whitebark pine and other resources (e.g., cutthroat trout [*Oncorhynchus clarkii*] around Yellowstone Lake; Haroldson et al. 2005, Teisberg et al. 2014) reduced carrying capacity, which, through increased exploitation competition for high-energy foods, could have reduced cub survival and reproductive transitions in a density-dependent fashion. This effect would be difficult to separate from that of interference competition we discussed previously. If bears were responding to a decline in carrying capacity, however, we would have expected home-range size and movements to have increased (McLoughlin et al. 2000), bears to have relied on lower-energy food resources (McLellan 2011), and body condition to have declined as a consequence (Rode et al. 2001, Robbins et al. 2004, Zedrosser et al. 2006). To date, there is little support for these conditions in the Yellowstone Ecosystem: female home ranges have decreased in size and are less variable in areas with greater bear densities (Bjornlie et al. 2014b), daily movement rates and daily activity radii have not changed for either sex during fall (Costello et al. 2014), bears continue to use high-quality foods (Fortin et al. 2013), and body mass has not declined (Schwartz et al. 2014). As we discussed previously, percent body fat among adult females has not declined since the early 2000s (IGBST 2013, Schwartz et al. 2014) and, regardless, this effect would be consistent with either interference or exploitation competition and would not explain the changes in vital rates that occurred much earlier than the declines in foods. Current evidence indicates bears showed a functional response to declines in whitebark pine (Costello et al. 2014) and cutthroat trout (Fortin et al. 2013) and compensated for the loss of these particular foods through diet shifts (Schwartz et al. 2014).

Previous studies linking grizzly bear survival rates to production of whitebark pine seeds largely attributed the effect to a behavioral response to the annual variation in this food. When seed production was high, bears were more likely to use high elevations where the potential for human-caused mortality was lower (Mattson et al. 1992, Blanchard and Knight 1995). Haroldson et al. (2006) also detected this

effect in their models and estimated that annual survival among non-conflict bears was 0.947, 0.957, and 0.965 after years with median whitebark pine cone counts of 0 (no crop), 7.5 (average), and 15 (high), respectively; a greater effect was observed among conflict bears with corresponding survival rates of 0.818, 0.850, and 0.874, respectively. This annual variation is not inconsistent with a long-term, stable trend in survival, as we observed among independent bears. In fact, recent analyses indicate annual cone production is still associated with the annual frequency of grizzly bear mortalities during 2000–2012 (IGBST 2013:24). Even heavily affected stands may contain surviving trees that produce cone crops and grizzly bear use of whitebark pine seeds in such stands has been observed (Orozco and Miles 2013), although Costello et al. (2014) detected a downward trend in fall selection of whitebark pine habitats during 2000–2012. Thus, on an annual basis, good whitebark pine cone production may still have a positive effect on survival of independent bears. However, we found no evidence of a longer term downward trend in survival of independent bears associated with the decline of this food.

Similar to our results, previous studies have not shown that annual variation in whitebark pine cone production was a strong correlate for cub and yearling survival (Schwartz et al. 2006*b*). Schwartz et al. (2006*a*) observed an association between fecundity and the annual index of whitebark pine cone production; however, they detected a much stronger relationship with an index of minimum population size than whitebark pine cone production, which supports our findings and interpretation that bear density is associated with long-term changes in reproduction.

Data from our study support the hypothesis that slowing of population growth of grizzly bears in the GYE is a function of increasing grizzly bear density rather than the decline of a high-calorie fall food resource, whitebark pine. This interpretation is reinforced by recent findings of Gosselin et al. (2015), who suggested that the behavior of individuals and social biology of brown bears can have pronounced effects on population growth. Although multiple lines of evidence support the interpretation of a bear density effect, alternative explanations exist beyond the ones we explored here. First, cub and yearling survival may have declined because of reduced body condition unrelated to whitebark pine or bear density. However, as we mentioned previously, a decline in female body condition would likely be a precursor to decline in offspring condition and we have not observed a decline in female percent body fat. Second, with the reintroduction of gray wolves (*Canis lupus*) in 1995–1996, we cannot dismiss the potential role of wolf predation on cubs and yearlings but with only 4 incidents observed since 2001 (Gunther and Smith 2004; IGBST, unpublished data), we do not regard this as a substantial source of cub or yearling mortality and have no empirical evidence to support this hypothesis. Finally, as with any study, sampling variation could have affected our results, but this could only explain our findings if there was a distinct trend in sampling variation over the course of our study, for which we have no evidence.

MANAGEMENT IMPLICATIONS

Our study findings corroborate those of Bjornlie et al. (2014*b*), who reported evidence of an inverse relationship between home-range size and the index of grizzly bear population density; they did not observe a relationship between home-range size and availability of live whitebark pine stands. Combined, these studies provide evidence that grizzly bear density may become an increasingly important factor to consider for management of the grizzly bear population in the GYE. The potential role of increased male survival may be of particular interest for mortality management, but further study is needed. Our results suggest that this population is near or at carrying capacity and managers should not expect population growth rates similar to those observed during the 1980s and 1990s in core areas of the population. In fact, consideration should be given to the possibility that the population may start exhibiting fluctuations around a long-term mean. Such oscillations could include short periods of population increases or decreases, which may only be distinguished from sustained increasing or decreasing trends with continued, long-term monitoring. Current monitoring protocols should be sufficient to detect different population trajectories (Harris et al. 2007), but further investigation may be desired to identify additional scenarios and whether new population monitoring approaches may be more effective to adaptively manage the grizzly bear population in the GYE.

ACKNOWLEDGMENTS

We thank pilots S. G. Ard, N. Cadwell, G. E. Hyatt, G. C. Lust, S. T. Monger, K. Overfield, T. N. Schell, A. R. Spencer, D. J. Stinson, D. I. Stradley, R. I. Stradley, C. E. Tyrrel, and B. Warren for conducting observation and telemetry flights. Many people were instrumental in sample collection and analyses and provided miscellaneous support, including C. R. Anderson, C. D. Atkinson, K. T. Bales, J. M. Ball, S. A. Becker, M. J. Biel, B. M. Blanchard, D. W. Blanton, M. J. Boyce, J. E. Brown, M. T. Brusino, S. L. Cain, I. Caudwell, J. G. Clapp, C. C. Clark, B. L. Debolt, S. R. Dewey, C. A. Dickinson, L. R. Ellsbury, K. L. Frey, Z. W. Gregory, R. G. Grogan, K. A. Gunther, C. L. Hendrix, P. A. Hnilicka, C. E. Hockenbary, M. J. Hooker, G. W. Holm, K. D. Inberg, A. Johnson, J. J. Jonkel, J. L. Kershner, L. I. Knox, M. J. Lamoreux, L. A. Landenburger, D. L. Lasseter, S. Lockwood, L. M. Lofgren, C. B. McQueary, N. J. Miles, D. S. Moody, K. E. Orozco, S. R. Podruzny, T. D. Ritter, S. L. Schmitz, B. O. Schleyer, C. Servheen, R. R. Shoemaker, J. F. Smith, K. Smith, B. Snyder, S. C. Soileau, R. L. St. Clair, M. A. Ternent, W. W. Thayer, S. D. Thompson, R. F. Trebelcock, Z. L. Turnbull, M. Urquhart, M. Wegan, C. L. Whitman, J. L. Wilmot, K. R. Wilmot, and D. Wroe. We thank K. K. West for valuable editorial support and J. S. Laufenberg for review of a previous draft of the manuscript as part of the USGS Fundamental Science Practices. We thank former study team leaders R. R. Knight and C. C. Schwartz for their foresight and diligence to establish the long-term datasets that formed

the basis for the analyses presented here. Funds and support for this research were provided by the U.S. Geological Survey, Northern Rocky Mountain Science Center; U.S. Fish and Wildlife Service; Bear Management Office of the Yellowstone Center for Resources at Yellowstone National Park; Grand Teton National Park; U. S. Forest Service; Wyoming Game and Fish Department; Montana Fish, Wildlife and Parks; Idaho Game and Fish; and the Wind River Fish and Game Departments of the Shoshone and Arapaho Tribes. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Arno, S. F., and R. J. Hoff. 1989. Silvics of whitebark pine. General Technical Report INT-253. U.S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide. *Behavioral Ecology* 138:465–474.
- Bian, L., and R. Butler. 1999. Comparing effects of aggregation methods on statistical and spatial properties of simulated spatial data. *Photogrammetric Engineering & Remote Sensing* 65:73–84.
- Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. *Journal of Wildlife Management* 72:1085–1093.
- Bjornlie, D. D., D. J. Thompson, M. A. Haroldson, C. C. Schwartz, K. A. Gunther, S. L. Cain, D. B. Tyers, K. L. Frey, and B. Aber. 2014a. Methods to estimate distribution and range extent of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Society Bulletin* 38:182–187.
- Bjornlie, D. D., F. T. van Manen, M. R. Ebinger, M. A. Haroldson, D. J. Thompson, and C. M. Costello. 2014b. Whitebark pine, population density, and home-range size of grizzly bears in the Greater Yellowstone Ecosystem. *PLoS ONE* 9:e88160.
- Blanchard, B. M. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team, Bozeman, Montana, USA.
- Blanchard, B. M. 1990. Relationships between whitebark pine cone production and fall grizzly bear movements. Pages 362–363 in W. C. Schmidt and K. J. McDonald, compilers. *Proceedings of symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. General Technical Report INT-270, U.S. Department of Agriculture Forest Service, Ogden, Utah, USA.
- Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41–67.
- Blanchard, B. M., and R. R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone Ecosystem. *Journal of Wildlife Management* 59:560–565.
- Breed, G. A., W. D. Bowen, and M. L. Leonard. 2013. Behavioral signature of intraspecific competition and density dependence in colony-breeding marine predators. *Ecology and Evolution* 2:3838–3854.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons, New York, New York, USA.
- Caughley, G., and A. R. E. Sinclair. 1994. *Wildlife ecology and management*. Blackwell, Boston, Massachusetts, USA.
- Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balčiauskas, V. Balys, P. Bedő, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potočnik, P.-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Rysler, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajce, E. Tsingarska-Sedefcheva, M. Vána, R. Veeroja, P. Wabakken, M. Wölff, S. Wölff, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Successful recovery of large carnivores in Europe's human-dominated landscapes. *Science* 346:1517–1519.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- Costello, C. M., F. T. van Manen, M. A. Haroldson, M. R. Ebinger, S. Cain, K. Gunther, and D. D. Bjornlie. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. *Ecology and Evolution* 4:2004–2018.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Eberhardt, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. *Environmental Conservation* 4:205–212.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854.
- Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* 72:360–363.
- Fortin, J. K., C. C. Schwartz, K. A. Gunther, J. E. Teisberg, M. A. Haroldson, and C. T. Robbins. 2013. Dietary adaptability of grizzly bears and American black bears in Yellowstone National Park. *Journal of Wildlife Management* 77:270–281.
- Fowler, C. W. 1981a. Comparative population dynamics in large mammals. Pages 437–455 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. John Wiley and Sons, New York, New York, USA.
- Fowler, C. W. 1981b. Density dependence as related to life history strategy. *Ecology* 62:602–610.
- Garshelis, D. L., M. L. Gibeau, and S. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. *Journal of Wildlife Management* 69:277–297.
- Gende, S. M., and T. P. Quinn. 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82:75–85.
- Gibson, K. 2007. Mountain pine beetle conditions in whitebark pine stands in the Greater Yellowstone Ecosystem, 2006. *Forest Health Protection Report* 06-03, U.S. Forest Service, Missoula, Montana, USA.
- Goss-Custard, J. D., A. D. West, R. A. Stillman, S. E. A. Le V. Dit Durell, R. W. G. Caldow, S. McGroarty, and R. Nagarajan. 2001. Density-dependent starvation in a vertebrate without significant depletion. *Journal of Animal Ecology* 70:955–965.
- Gosselin, J., A. Zedrosser, J. E. Swenson, and F. Pelletier. 2015. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proceedings of the Royal Society of London B* 282:20141840.
- Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee. 2011. Whitebark pine strategy for the Greater Yellowstone Area. http://www.fedgycc.org/wp-content/uploads/2015/06/WBPStrategy_FINAL5.31.11.pdf. Accessed 1 Oct 2015.
- Greater Yellowstone Whitebark Pine Monitoring Working Group. 2014. Summary of preliminary step-trend analysis from the Interagency Whitebark Pine Long-term Monitoring Program—2004–2013: prepared for the Interagency Grizzly Bear Study Team. *Natural Resource Data Series NPS/GRYN/NRDS-2014/600*. National Park Service, Fort Collins, Colorado, USA.
- Gunther, K. A., M. A. Haroldson, K. Frey, S. L. Cain, J. Copeland, and C. C. Schwartz. 2004. Grizzly bear-human conflicts in the Greater Yellowstone Ecosystem, 1992–2000. *Ursus* 15:10–22.
- Gunther, K. A., and D. W. Smith. 2004. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. *Ursus* 15:232–238.
- Haroldson, M. A. 2014. Whitebark pine cone production: 2014. U.S. Geological Survey, Bozeman, Montana, USA. <http://www.nrm-sc.usgs.gov/files/norock/IGBST/2014WBPRReport.pdf>. Accessed 24 Jun 2015.
- Haroldson, M. A., K. A. Gunther, D. P. Reinhart, S. R. Podrutzny, C. Cegelski, L. Waits, T. Wyman, and J. Smith. 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. *Ursus* 16:167–180.
- Haroldson, M. A., C. C. Schwartz, and G. C. White. 2006. Survival of independent grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–42 in C. C. Schwartz, M. A. Haroldson, G. C. White,

- R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, editors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Harris, R. B., C. C. Schwartz, M. A. Haroldson, and G. C. White. 2006. Trajectory of the Yellowstone grizzly bear population under alternative survival rates. Pages 44–55 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. Temporal, spatial and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Harris, R. B., C. C. Schwartz, R. D. Mace, and M. A. Haroldson. 2011. Study design and sampling intensity for demographic analyses of bear populations. *Ursus* 22:24–36.
- Harris, R. B., G. C. White, C. C. Schwartz, and M. A. Haroldson. 2007. Population growth of Yellowstone grizzly bears: uncertainty and future monitoring. *Ursus* 18:168–178.
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerron, J. N. VanDriel, and J. Wickman. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing* 73:337–341.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Interagency Grizzly Bear Study Team. 2012. Updating and evaluating approaches to estimate population size and sustainable mortality limits for grizzly bears in the Greater Yellowstone Ecosystem. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana, USA. [http://nrmisc.usgs.gov/files/norock/IGBST/GYEGBMortWksRpt2012\(2\).pdf](http://nrmisc.usgs.gov/files/norock/IGBST/GYEGBMortWksRpt2012(2).pdf). Accessed 30 Nov 2013.
- Interagency Grizzly Bear Study Team. 2013. Response of Yellowstone grizzly bears to changes in food resources: a synthesis. Report to the Interagency Grizzly Bear Committee and Yellowstone Ecosystem Subcommittee. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana, USA. http://nrmisc.usgs.gov/research/igbst/GBFSR_Refs. Accessed 2 Mar 2015.
- Keating, K. A., C. C. Schwartz, M. A. Haroldson, and D. Moody. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Ursus* 13:161–174.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. *International Conference on Bear Research and Management* 5:166–173.
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114–123.
- Knight, R. R., B. M. Blanchard, and L. L. Eberhardt. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23:245–248.
- Landenburger, L. A., R. L. Lawrence, S. R. Podruzny, and C. C. Schwartz. 2008. Mapping regional distribution of a single tree species: whitebark pine in the Greater Yellowstone Ecosystem. *Sensors* 8:4983–4994.
- Lechner, A. M., W. T. Langford, S. A. Bekessy, and S. D. Jones. 2012. Are landscape ecologists addressing uncertainty in their remote sensing data? *Landscape Ecology* 27:1249–1261.
- Little, M. A., and N. S. Jones. 2011. Generalized methods and solvers for noise removal from piecewise constant signals. I. Background theory. *Proceedings of the Royal Society A* 467:3088–3114.
- López-Bao, J. V., F. Palomares, A. Rodríguez, and P. Ferreras. 2011. Intraspecific interference influences use of prey hotspots. *Oikos* 120:1489–1496.
- Mace, R. D., D. W. Carney, T. Chilton-Radandt, S. A. Courville, M. A. Haroldson, R. B. Harris, J. J. Jonkel, M. Madel, T. L. Manley, C. C. Schwartz, C. Servheen, J. S. Waller, and E. Wenum. 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *Journal of Wildlife Management* 76:119–128.
- Macfarlane, W. W., J. A. Logan, and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. *Ecological Applications* 23:421–437.
- Mahalovich, M. F. 2013. Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem. Future status of whitebark pine: blister rust resistance, mountain pine beetle, and climate change. Report 2470 RRM-NR-WP-13-01, U.S. Department of Agriculture Forest Service, Northern Region, Missoula, Montana, USA. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3792945.pdf. Accessed 26 Feb 2015.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69:1619–1629.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56:432–442.
- Mattson, D. J., and D. P. Reinhart. 1994. Bear use of whitebark pine seeds in North America. Pages 212–220 in W. C. Schmidt and F.-K. Holtmeier, compilers. Proceedings of the international workshop on subalpine stone pines and their environment: the status of our knowledge. U.S. Forest Service General Technical Report INT-GTR-309, Ogden, Utah, USA.
- Mattson, D. J., and D. P. Reinhart. 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behavior and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. *Canadian Journal of Zoology* 73:2072–2079.
- Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926–940.
- McLellan, B. N. 1994. Density-dependent population regulation of brown bears. Pages 15–24 in M. Taylor, editor. Density-dependent population regulation of black, brown, and polar bears. *International Conference on Bear Research and Management, Monograph Series* 3.
- McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16:141–156.
- McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 89:546–558.
- McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* 14:39–60.
- Miller, S. D. 1990. Impact of increased bear hunting on survivorship of young bears. *Wildlife Society Bulletin* 18:462–467.
- Miller, S. D., R. A. Sellers, and J. A. Keay. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- Mitchell, M. S., L. B. Pacifici, J. B. Grand, and R. A. Powell. 2009. Contributions of vital rates to growth of a protected population of American black bears. *Ursus* 20:77–84.
- Nevin, O. T., and B. K. Gilbert. 2005. Measuring the cost of risk avoidance in brown bears: further evidence of positive impacts of ecotourism. *Biological Conservation* 123:453–460.
- Orozco, K. E., and N. J. Miles. 2013. Use of diminished whitebark pine resources by adult female grizzly bears in Togwotee Pass, Spread Creek, and Mt. Leidy in the Bridger Teton National Forest, Wyoming, 2012. Pages 45–47 in F. T. van Manen, M. A. Haroldson, and K. West, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2012*. U.S. Geological Survey, Bozeman, Montana, USA.
- Podruzny, S. R., D. P. Reinhart, and D. J. Mattson. 1999. Fire, red squirrels, whitebark pine, and Yellowstone grizzly bears. *Ursus* 11:131–138.
- Robbins, C. T., M. Ben-David, J. K. Fortin, and O. L. Nelson. 2012. Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy* 93:540–546.
- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15:161–171.
- Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* 133:70–80.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62–71.
- Rutten, A. L., K. Oosterbeek, J. van der Meer, S. Verhulst, and B. J. Ens. 2010. Experimental evidence for interference competition in oyster-catchers, *Haematopus ostralegus* I. Captive birds. *Behavioral Ecology* 21:1251–1260.
- Schmutz, J. A., D. H. Ward, J. S. Sedinger, and E. A. Rexstad. 1995. Survival estimation and the effects of dependency among animals. *Journal of Applied Statistics* 22:673–681.

- Schwartz, C. C., J. K. Fortin, J. E. Teisberg, M. A. Haroldson, C. Servheen, C. T. Robbins, and F. T. van Manen. 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 78:68–78.
- Schwartz, C. C., M. A. Haroldson, and S. Cherry. 2006a. Reproductive performance of grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. Pages 18–23 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, editors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006b. Survival of cub and yearling grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Pages 25–31 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, editors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006c. Study area and methods for collecting and analyzing demographic data on grizzly bears in the Greater Yellowstone Ecosystem. Pages 9–17 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, editors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74:654–667.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006d. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., and G. C. White. 2008. Estimating reproductive rates for female bears: proportions versus transition probabilities. *Ursus* 19:1–12.
- Solano, R., K. Didan, A. Jacobson, and A. Huete. 2010. MODIS vegetation index user's guide (MOD13 series). Version 2. University of Arizona, Tucson, USA.
- Steyaert, S. M. J. G., C. Reusch, S. Brunberg, J. E. Swenson, K. Hackländer, and A. Zedrosser. 2013. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biology Letters* 9:20130624.
- Støen, O.-G., A. Zedrosser, P. Wegge, and J. E. Swenson. 2006. Socially induced delayed primiparity in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 61:1–8.
- St. Juliana, J. R., B. P. Kotler, J. S. Brown, S. Mukherjee, and A. Bouskila. 2011. The foraging response of gerbils to a gradient of owl numbers. *Evolutionary Ecology Research* 13:869–878.
- Swenson, J. E., F. Sandegren, S. Brunberg, and P. Segerström. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- Teisberg, J. E., M. A. Haroldson, C. C. Schwartz, K. A. Gunther, J. K. Fortin, and C. T. Robbins. 2014. Contrasting past and current numbers of bears visiting Yellowstone cutthroat trout streams. *Journal of Wildlife Management* 78:369–378.
- U.S. Fish and Wildlife Service [USFWS]. 2007. Final conservation strategy for the grizzly bear in the Greater Yellowstone Area. Interagency Conservation Strategy Team, Missoula, Montana, USA. http://www.fws.gov/mountain-prairie/species/mammals/grizzly/Final_Conservation_Strategy.pdf. Accessed 3 Mar 2015.
- Verbesselt, J., A. P. Robinson, C. Stone, and D. Culvenor. 2009. Forecasting tree mortality using change metrics derived from MODIS satellite data. *Forest Ecology and Management* 258:1166–1173.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study Supplement* 46:120–138.
- Wielgus, R. B., and F. L. Bunnell. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405–413.
- Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* 93:145–154.
- Wielgus, R. B., F. Sarrazin, R. Ferriere, and J. Clobert. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98:293–303.
- Zedrosser, A., B. Dahle, and J. E. Swenson. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510–518.

Associate Editor: Jamie Sanderlin.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article at the publisher's website.