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Density Dependence, Whitebark Pine Decline, and Changing Vital Rates of Yellowstone Grizzly Bears

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ABSTRACT Understanding potential factors influencing changes in population trajectory is important for effective wildlife management, particularly for populations of conservation concern. Recent evidence suggests annual population growth of the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem 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 over the past 15 years. Whitebark pine (*Pinus albicaulis*), the seeds of which are a valuable but variable fall food for grizzly bears, has experienced substantial tree mortality primarily due to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak that started in the early 2000s. Concurrent with changes in food resources, the grizzly bear population has reached high densities in some areas and has continued to expand, now occupying >50,000 km². 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 also 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 impact as individual covariates. Models indicated moderate support for an increase in survival of independent male bears over the period 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 lesser rates evident during the last 10–15 years. Cub survival and, to a lesser degree, 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 impact. The results of our study support the interpretation that slowing of population growth during the last decade is associated more with increasing grizzly bear density rather than a function of whitebark pine decline.

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

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The trajectory of a wildlife population is the collective manifestation of vital rates, such as 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 moves most wildlife populations towards 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 either by availability or access to non-consumable (e.g., space, nest sites) or consumable resources (Caughley and

Sinclair 1994). Understanding these relationships and how they influence the population trajectory can be insightful for wildlife managers. For example, management response to a reduction in population growth may be different if a change in trajectory was primarily caused by a decline in food resources versus a population reaching carrying capacity.

Concepts related to population limitation and regulation have garnered particular interest from brown bear managers as bear densities of several recovering populations in northern Europe and the continental U.S. have increased over the past 3 decades (e.g., Schwartz et al. 2006d, Kindberg et al. 2011, Mace et al. 2012). A better understanding of these population processes could have important implications for harvest management, for example. McLellan (1994) suggested that food likely is the ultimate factor limiting brown bear populations, but argued 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 populations' proximity to carrying capacity rather than differences in their habitat quality. Zedrosser et al. (2006) found that body size of adult female brown bears was positively associated with abundance and availability of food but 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 were 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 impact vital rates and population growth. When that same population also experiences a change

in abundance of food resources, it is difficult to isolate which factor(s) 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 which factor(s) may be acting more strongly on a particular population. Such studies require substantial, longitudinal datasets. Recent changes in the population trajectory of the Greater Yellowstone Ecosystem (GYE) grizzly bear population 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). Based on change-point analyses of trend in number of females with cubs-of-the-year, the trajectory likely changed around 2001 (M. Higgs, Montana State University, unpublished data).

One hypothesis for the slowing of population growth is based on substantial decline of a temporally variable but valuable fall food source for grizzly bears, whitebark pine (*Pinus albicaulis*). Previous studies have demonstrated associations between whitebark pine cone production and survival of independent bears (Haroldson et al. 2006), fecundity (number of female cubs/female bear/yr; Mattson et al. 1992, 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 from mountain pine beetle infestation (*Dendroctonus ponderosae*), fire, and white pine blister rust (*Cronartium ribicola*) infection, with mountain pine beetle the greatest causative mortality factor (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). For repeatedly monitored trees, observed cumulative mortality was 37% for trees >10 cm and ≤ 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), 74% of 190 mature, cone-bearing sample trees died between 2002 and 2013 (Haroldson 2013).

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

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 variation in whitebark pine decline and grizzly bear density were associated with 4 vital rates: survival of independent bears (≥ 2 yrs), cub and yearling survival, and female reproductive transition from no offspring to cubs. If resource effects from whitebark pine mortality were more influential, we hypothesized a decline in these vital rates would be greatest among those bears that reside 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.

STUDY AREA

Our study area was comprised of occupied grizzly bear range in the GYE (50,280 km² by 2010; Bjornlie et al. 2014a) and included Yellowstone and Grand Teton National Parks, portions of 6 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 greater than 2,130 m, and contains the headwaters of 3 continental-scale rivers. Summers are short with most average annual precipitation (50.8 cm) falling 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 to 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 conducted trapping in both frontcountry (road access) and backcountry (no road access) settings within and outside national parks and wilderness areas.

Analyses

Key determinants of bear population dynamics are survival of adult females, survival of cubs and yearlings, and reproductive output. Therefore, we examined the following parameters to test our hypotheses: 1) independent bear survival (≥ 2 yrs 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 during the denning season. We conducted telemetry flights every 7–14 days to determine bear status (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 (unresolved fate) each month of the active season (April–November). 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, 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 in data exceeded 2 months during the active season, we censored bears for those months. Bears with unknown fates were censored (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 (age + age²), proportion of locations in secure habitat (areas ≥ 4.05 ha that are >500 m from open or gated roads), proportion of locations in developed areas, and season (denning vs. active).

Dependent Young Survival.—We defined dependent offspring as bears in their first (cub-of-the-year) and second year (yearling) of life, as they remain with their mothers during these periods. We determined their fate from visual observations during ground monitoring or aerial telemetry flights. We were able to document mortality in a few instances but in all other cases we assumed that cubs or yearlings had 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) (for young that survived to be yearlings, j was the starting day of their second winter of hibernation); 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 the spring (22 April) and the date of our last cub observation prior to den entry (18 November; 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 (from 18

April to 3 November; 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 described by 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 median AIC_c and ΔAIC_c values based on the 5,000 resamples of each model to perform model selection.

Reproductive Transition — We used the method of Schwartz and White (2008) to estimate the likelihood that a radiomarked 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 of no offspring in one year to a reproductive state with cubs the following year (i.e., N to C). 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 1st-order Markovian transitions (i.e., the next transition is conditional on the current state only) to estimate transition rates. Because fecundity is correlated with age, our base

model included a quadratic covariate for age ($\text{age} + \text{age}^2$) of individual females for the N to C transition (Schwartz and White 2008).

Hypothesis Testing.—Whitebark pine decline started during the early 2000s and although the outbreak may have waned in recent years, substantial mortality occurred between 2003 and 2009 (Haroldson 2013, Greater Yellowstone Whitebark Pine Monitoring Working Group 2014). We examined whether changes in vital rates over time were associated with either whitebark pine decline or grizzly bear density. We assigned covariate values to the encounter histories of individually marked bears based on spatiotemporal indices of whitebark pine decline and grizzly bear density and time trend.

The grizzly bear density index was derived from telemetry locations and life-history of captured bears and was created by back- and forecasting lifetime activity ranges to indicate the presence of individuals in the population through space and time (Bjornlie et al. 2014b). The density index in a given year was the sum of proportional overlap of all lifetime activity ranges present during that year, as calculated for 14- × 14-km grid cells. The index of whitebark pine decline was a spatiotemporal estimate of change in healthy whitebark pine canopy, as derived from NDVI (normalized difference vegetation index) data based on MODIS satellite imagery (250- × 250-m grid cells) and using 2000 as the reference year (M. Ebinger, University of Montana, unpublished data). Consequently, 2001 was the first year during which this index showed negative values among sampled bears. To measure these indices 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 were partially outside that area. For the

index of whitebark pine decline, we weighted the index according to the proportion of whitebark pine cover type (Landenburger et al. 2008) for cells with >50% tree cover (U.S. Geological Survey 2001) available for each bear. Potential effectiveness of the indices as covariates was contingent on capturing sufficient variation through space and time. The indices 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 impact: $\bar{x} = -0.022$, $SD = 0.050$, range = -0.380 –0 [more negative numbers reflect greater impact]) and also reflected changes over time. The mean annual index of grizzly bear density associated with sampled individuals ranged from 8.9 to 16.4, whereas the mean annual index of whitebark pine impact ranged from 0 to -0.070 .

Temporal covariates were crucial to our analyses to determine if changes in vital rates were associated with grizzly bear density or whitebark pine impact. To assess this we first fit different temporal covariates for each of the vital rate analyses to determine which covariate was most supported. We tested 8 temporal covariates, including a linear trend, 4 quadratic splines (starting at 1, 10, 15 and 20 years into the study period, respectively; value range = 0.001–0.900), 2 sigmoidal trends (inflection points around 1995 and 2000, respectively; value range = 0–1.0), and a binary covariate that split the 30-year study period into 1983–2001 and 2002–2012, the second representing the period of slowed population growth (IGBST 2012). 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.

We developed a suite of models to test our research hypotheses based on 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 impact. Finally, to test each vital rate with grizzly bear density or whitebark pine impact 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 index for whitebark pine impact. For survival of independent bears, we also included a term for sex. We used model averaging to graphically show relevant relationships among 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. Because we used model averaging, different covariates, and data from a different time period, estimates presented here are not fully comparable with those provided by Schwartz et al. (2006d) and IGBST (2012).

RESULTS

For survival of independent bears, our analysis was based on 1,872 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] = 0.65); the second most supported model was based on a quadratic time trend starting in 2001, but it had less support ($\Delta AIC_c = 3.34$, $w_i = 0.12$). Therefore, we used T_{period} as the temporal covariate to test our hypothesis. Because the index of whitebark impact used the year 2000 as the reference year, 2001 was the first year during which this index showed negative values among sampled bears. Therefore, we did not fit an interaction term for this covariate because the interaction was inherent in the whitebark pine impact covariate: statistical support for the whitebark pine impact covariate would indicate it occurred during the latter period of 2002–2012. The model with T_{period} ($\hat{\beta} = -0.16$, 95% CI = -0.28 to -0.03), sex ($\hat{\beta} = 0.47$, 95% CI = -0.04 to 0.97) and $T_{\text{period}} \times \text{sex}$ interaction ($\hat{\beta} = -0.69$, 95% CI = -1.47 to 0.09) had the most support ($w_i = 0.34$; model

A5; Table 1a;), followed by a model ($\Delta AIC_c = 1.05$, $w_i = 0.20$; model A2; Table 1a) with sex ($\hat{\beta} = 0.18$, 95% CI = -0.20 to 0.57) and T_{period} only ($\hat{\beta} = 0.52$, 95% CI = 0.13 to 0.92). We detected little support for an association of independent bear survival with the indices for grizzly bear density or whitebark pine impact or their interaction with period ($\Delta AIC_c > 1.90$; Table 1a). Of the covariates in the model set of Table 1a (not considering the covariates of the base model), all model-averaged parameter estimates had 95% CIs that included zero, although there was some evidence of greater survival during the 2002–2012 period (T_{period} : $\hat{\beta} = 0.608$, 95% CI = -0.063 to 1.278), primarily among males (Fig. 1).

We used 326 encounter histories for offspring of 116 females to estimate cub and yearling survival; 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} ; $w_i = 0.41$), followed by a quadratic time trend starting in 1997 (T_{q1997} ; $\Delta AIC_c = 1.09$; $w_i = 0.24$). 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 ($T_{\text{sig}1}$; $w_i = 0.64$), followed by a model with the second sigmoidal function ($T_{\text{sig}2}$; $AIC_c = 3.37$; $w_i = 0.12$). Therefore, we used $T_{\text{sig}1}$ to develop our yearling 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 1b). For cub survival, parameter estimates for the bear density index ($\hat{\beta} = 0.014$, 95% CI = -0.047 to 0.075) and time trend ($\hat{\beta} = 10.189$, 95% CI = -8.721 to 29.099) had confidence intervals that overlapped zero but there was evidence of a $T_{q2001} \times$ bear density interaction ($\hat{\beta} = -1.242$, 95% CI = -2.227 to -0.256). This interaction effect indicated that cub survival declined starting in 2001 and that the decline was greater in areas with greater index values for bear density (Fig.

2a). For yearling survival, the equivalent model (model B7; Table 1b) did not indicate an interaction effect of $T_{\text{sig1}} \times \text{bear density}$ ($\hat{\beta} = 0.388$, 95% CI = -0.165 to 0.941) although there was some evidence of a decline in yearling survival, primarily during the 1990s, based on the time trend covariate T_{sig1} ($\hat{\beta} = -7.089$, 95% CI = -14.327 to 0.150 ; Fig. 2b). The model with whitebark pine impact, time trend, and their interaction was the 3rd-ranked model but had little support (median $\Delta\text{AIC}_c = 7.68$; $w_i = 0.02$; model B8; Table 1b); only the parameter estimates for time trend did not bound zero in the 95% confidence intervals (cubs: $\hat{\beta} = -14.328$, 95% CI = -20.935 to -7.720 ; yearlings: $\hat{\beta} = -2.101$, 95% CI = -3.802 to -0.399). 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 index of whitebark pine impact (B8; Table 1b).

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 ($w_i = 0.28$) than the binary covariate of T_{period} ($\Delta\text{AIC}_c = 0.16$, $w_i = 0.26$) and T_{sig2} ($\Delta\text{AIC}_c = 0.80$, $w_i = 0.19$). 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 and included T_{sig1} ($\hat{\beta} = 3.048$, 95% CI = 0.080 to 6.017), grizzly bear density index ($\hat{\beta} = 0.257$, 95% CI = 0.045 to 0.468), and their interaction ($\hat{\beta} = -0.321$, 95% CI = -0.570 to -0.072 ; model C7; Table 1c). The 2nd- and 3rd-ranked models had less support ($\Delta\text{AIC}_c = 1.89$, $w_i = 0.17$ [model C1] and $\Delta\text{AIC}_c = 2.61$, $w_i = 0.12$ [model C2], respectively) and contained the base model and the covariate for T_{sig1} , respectively ($\hat{\beta} = -0.580$, 95% CI = -1.544 to 0.384). Based on competing the 2 models with the temporal interactions (models C7 and C8; Table 1c), the evidence ratio indicated 16.9

times greater support for a grizzly bear density association with transition probability compared with the index for whitebark pine impact. However, model-averaged parameter estimates bounded zero in their 95% confidence intervals, although there was some indication for an interaction effect between the grizzly bear density index and the time trend ($\hat{\beta} = -0.141$, 95% CI = -0.428 to 0.145). The T_{sig1} effect indicated the probability of reproductive transition from no offspring to cubs declined during the 1990s, whereas the interaction term suggested this decline was more pronounced in areas with greater population densities (Fig. 3).

DISCUSSION

Among grizzly bear populations, the vital rate that generally has most influence on the population trajectory 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) showed for American black bears (*Ursus americanus*), high variance of juvenile survival and recruitment may have a greater influence on population growth compared with adult female survival (Harris et al. 2011). 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. 2a). Decline in cub survival started in the early 2000s and was associated more strongly with increasing grizzly bear density than reduced availability of whitebark pine. Cub survival is a potential density-dependent factor contributing to population regulation among bear populations and we explore 2 potential causes for the Yellowstone grizzly bear population: 1) intraspecific killing and 2) 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. 1997, 2001;

Wielgus and Bunnell 2000; Wielgus et al. 2001; Miller et al. 2003; McLellan 2005). McLellan (1994) reported 57 cases of intraspecific killing among 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. For the GYE, we hypothesize a connection exists between increased survival of independent-aged males (Fig. 1; IGBST 2012) and increased mortality of cubs as a function of bear density during the last decade of the study period (Fig. 2a). If more killing of cubs by males is contributing to a decline in cub survival, one prediction would be that mortalities occur earlier in the year (i.e., during the breeding season, when males are searching for receptive females [prior to July 15] and cubs are more vulnerable because of smaller size and lower mobility). Indeed, among 69 mortalities that occurred during the cub period, the median date of estimated mortality shifted from August 18 during the first 2 decades of the study period to July 2 during the last decade, when bear densities were greatest.

A second, ultimate cause for lower survival among dependent-aged bears may be interference competition. Experimental studies have shown that, as population density increases, interference competition has the potential to constrain the feeding efficiency of some individuals, particularly subordinate individuals such as juveniles (e.g., López -Bao et al. 2010, Rutten et al. 2010). 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. 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 observed in predator-prey systems (e.g., 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 comes at 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-of-the-year in Sweden that may have its origins in 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 the shift in median mortality date of cubs combined with investigations of mortality by the IGBST (<http://nrmssc.usgs.gov/science/igbst/mort>). Yearling survival also declined but this decline was not explicitly associated with whitebark pine impact 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 detect an interaction for the change in yearling survival with bear density. Indeed, we did not detect a distinct shift in the median date of mortality for yearlings associated with decline in survival ($n = 22$; from July 14 during 1983–1997 to July 4 during 1998–2012) as we did for cubs. Although 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 inference for a population density effect on yearling survival seems limited.

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. 3). Our analyses supported previous observations (IGBST 2012) of a positive trend in independent male survival and these larger males may represent a greater proportion of the population during the last decade of the study period. Analogous to the interpretation of reduced cub survival, the increase in adult male density may be linked with the reduced reproductive transition through 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 a primary contributor to reduced population growth. The observed reduction in cub survival from an estimated 0.638 ± 0.087 (SE) during 1983–2001 to 0.553 ± 0.064 during 2002–2011 (IGBST 2012) would have reduced annual population growth, from 1.074 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 ($S_0 = 0.85\text{--}1.00$) and without ($S_0 = 0.58\text{--}0.61$) harvesting of adult males, could reduce annual population growth from 1.18 to 1.14 (Swenson et al. 1997).

Density-dependent changes in life history traits are more likely to occur when populations are near carrying capacity (Caughley 1977; Fowler 1981*a, b*) and the research of Miller et al. (2003) supports this notion for brown bears. Our findings are consistent with Schwartz et al. (2006*b*), 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. 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 increase (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 (Bjornlie et al. 2014*b*), daily movement rates and daily activity radii have not changed for either sex (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). Although Schwartz et al. (2014) provided some evidence that percent body fat may have declined in adult females during

2007–2010, this effect would be consistent with either interference or exploitation competition and would not explain the changes in vital rates that occurred much earlier. Furthermore, current evidence indicates bears showed a functional response to declines in whitebark pine (Costello et al 2014) and cutthroat trout (Fortin et al. 2013), indicating this opportunistic omnivore was able to compensate for the loss of these particular foods. Data from our study support the hypothesis that slowing of population growth of Yellowstone grizzly bears is a function of increasing grizzly bear density rather than the decline of a single valuable fall food resource, whitebark pine.

MANAGEMENT IMPLICATIONS

Our study findings corroborate those of Bjornlie et al. (2014b), 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 in management. If this population is nearing carrying capacity and starting to stabilize, managers should not expect continuation of population growth rates similar to those observed during the 1980s and 1990s, particularly in core areas of the population. In fact, due consideration may be given to the possibility that the population may start exhibiting fluctuations around a long-term mean. Thus, if managers want to maintain a stable population, a new monitoring challenge may be to distinguish 2 potential population trajectory scenarios that would require different management responses: natural oscillations around a stable state, which could include temporary declines, versus a sustained decline.

Current monitoring protocols should be sufficient to detect such 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.

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Animal Care and Use Committee. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Model-selection results to determine association of (a) survival of independent-aged grizzly bears (≥ 2 yrs), (b) survival of cubs-of-the-year (cub) and yearlings (yrl), and (c) reproductive transition, Greater Yellowstone Ecosystem, USA, 1983–2012. Spatially and temporally explicit indices of whitebark pine decline (WbPimpact) and grizzly bear density (GBdensity) and covariates for time trend were used to test research hypotheses.

Model no. and model description	AIC _c ^a	Δ AIC _c ^b	w_i ^c	K ^d	Dev ^e
a. Independent bear survival (base model was modified from Schwartz et al. [2010] and included trap status [research or management bear], age, age ² , 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]])					
A5 {base + sex + T _{period} + sex × T _{period} }	1,128.04	0	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} + WbPimpact}	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 + WbPimpact}	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
b. Cub and yearling survival (time trend for cubs and yearlings modeled as quadratic spline starting in 2001 [T _{q2001}] and sigmoidal function, respectively [T _{sig1}])					
B7 {cub(GBdensity + T _{q2001} + GBdensity × T _{q2001}), yrl(GBdensity + T _{sig1} + GBdensity × T _{sig1})}	697.42 ^f (53.84)	0 ^f (4.14)	0.95 ^g	8	681.42 ^f (53.84)

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(WbPimpact + T _{q2001} + WbPimpact × T _{q2001}), yrl(WbPimpact + T _{sig1} + WbPimpact × T _{sig1})}	705.76 (53.50)	7.68 (10.49)	0.02	8	691.37 (53.50)
B6 {cub(WbPimpact + T _{q2001}), yrl(WbPimpact + 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)	29.70 (14.34)	<0.01	4	717.95 (53.64)
B4 {cub(WbPimpact), yrl(WbPimpact)}	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)

c. Reproductive transition from no offspring (N) to cubs-of-the-year (C) (base model included age and age² for the transition of N to C; time trend modeled as a sigmoidal function [T_{sig1}])

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 + WbPimpact}	6,199.99	3.80	0.07	11	6,177.32
C6 {base + T _{sig1} + WbPimpact}	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} + WbPimpact + T _{sig1} × WbPimpact}	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 Number of model parameters.

^e Model deviance.

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

^g AIC_c weights based on median ΔAIC_c values of the 8 models from the 5,000 resamples.

LIST OF FIGURES

Figure 1. Predicted annual survival and 95% confidence intervals (vertical lines) of independent-aged (≥ 2 yrs) grizzly bears in the Greater Yellowstone Ecosystem by period (1983–2001 and 2002–2012). Predictions based on model-averaged estimates of models in Table 1a. Covariate values in the base model were set at their mean (age = 8.4 yrs [males and females], proportion of locations in secure habitat = 0.82, proportion of locations in developed area = 0.13).

Figure 2. Predicted survival rate of grizzly bear cubs-of-the-year and yearlings, Greater Yellowstone Ecosystem, 1983–2012. Predictions based on model-averaged estimates of models in Table 1b. (a) Survival rate during 211-day cub-of-the-year 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, 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 whitebark pine impact 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 whitebark pine impact at a value of -0.04 , approximating conditions experienced by sampled bears during the early 2000s.

Figure 3. Predicted probability of reproductive transition of female grizzly bears from having no offspring to having cubs-of-the-year and relationship with grizzly bear density index (DI), Greater Yellowstone Ecosystem, 1983–2012. Predictions based on model-averaged estimates of models in Table 1c. Time trend was based on sigmoidal function. The 3 levels of the grizzly bear density index (DI = 9, 12, 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 yrs). We set the covariate value for the index of whitebark pine impact at -0.04 , approximating conditions experienced by sampled bears during the early 2000s.

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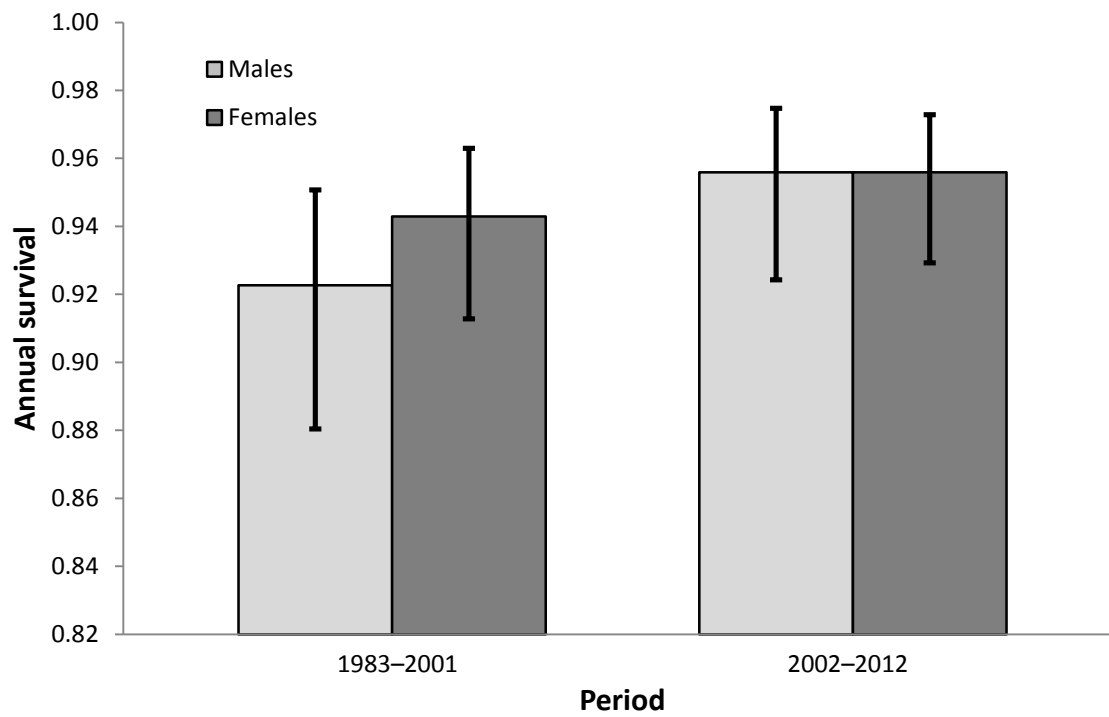


Fig. 1

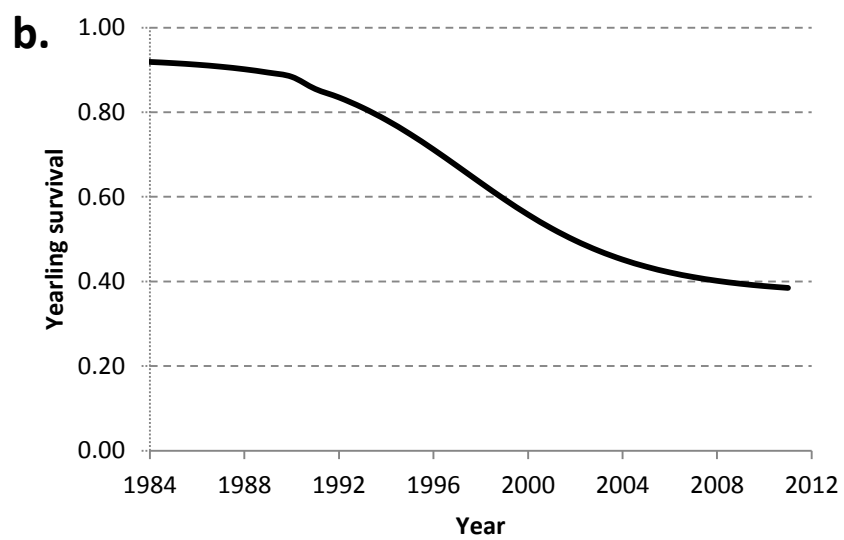
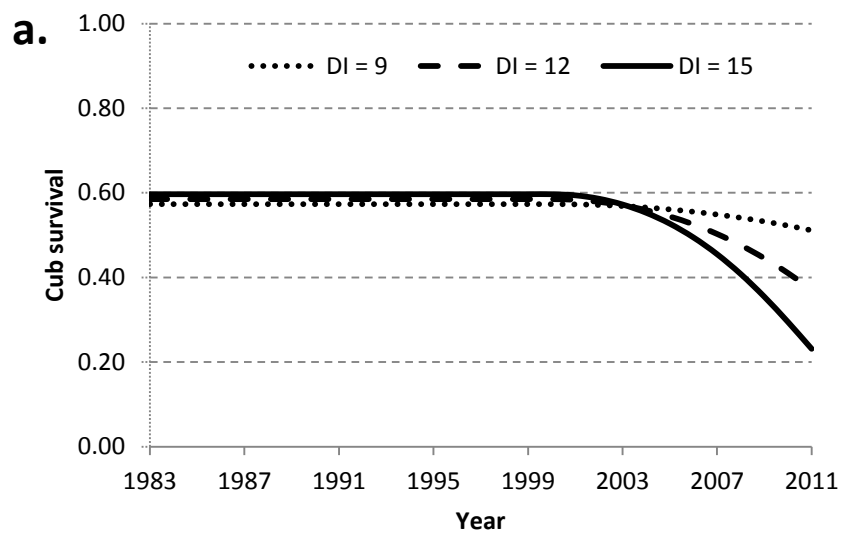


Fig. 2

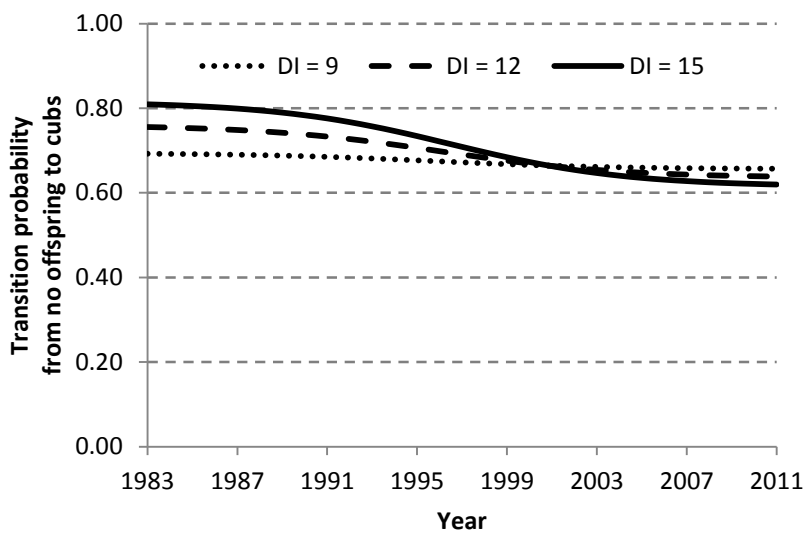


Fig. 3