RESPONSE OF YELLOWSTONE GRIZZLY BEARS TO CHANGES IN FOOD RESOURCES: A SYNTHESIS

Final Report to the Interagency Grizzly Bear Committee

and

Yellowstone Ecosystem Subcommittee

Photo: Ray Paunovich

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Interagency Grizzly Bear Study Team (IGBST)

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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*
CECILY M. COSTELLO, *University of Montana, College of Forestry and Conservation, University Hall, Room 309, Missoula, MT 59812*
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*
DANIEL D. BJORNLIE, *Large Carnivore Section, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520*
MICHAEL R. EBINGER, *University of Montana, College of Forestry and Conservation, University Hall, Room 309, Missoula, MT 59812*
KERRY A. GUNTHER, *Bear Management Office, Yellowstone Center for Resources, Yellowstone National Park, P.O. Box 168, Yellowstone National Park, WY 82190*
MARY FRANCES MAHALOVICH; *U.S. Forest Service; Northern, Rocky Mountain, Southwestern and Intermountain Regions; Forestry Sciences Lab; 1221 South Main Street; Moscow, ID 83843*
DANIEL J. THOMPSON, *Large Carnivore Section, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520*
MEGAN D. HIGGS, *Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717*
KATHRYN M. IRVINE, *U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715*
KRISTIN LEGG, *National Park Service, Greater Yellowstone Monitoring Network, 2327 University Way, Suite 2, Bozeman, MT 59715*
DANIEL B. TYERS, *U.S. Forest Service, 2327 University Way, Suite 2, Bozeman, MT 59715*
LISA A. LANDENBURGER, *U.S. Geological Survey and U.S. Forest Service, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715*
STEVEN L. CAIN, *National Park Service, Grand Teton National Park, P.O. Box 170, Moose, WY 83012*
KEVIN L. FREY, *Bear Management Office, Montana Fish Wildlife and Parks, 1400 South 19th Avenue, Bozeman, MT 59718*
BRYAN C. ABER, *Idaho Department of Fish and Game, 3726 Highway 20, Island Park, ID 83429*
CHARLES C. SCHWARTZ, *U.S. Geological Survey (Emeritus), Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715*

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[1] Corresponding author email: fvanmanen@usgs.gov

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This report contains several references to manuscripts prepared by Interagency Grizzly Bear Study Team authors and others that have been submitted to peer-reviewed journals and were in review or were in preparation for submission at the time of completion of this report. Although reference to such manuscripts is unconventional, we cite these studies because they were designed to address research questions directly related to the central thesis of this project, of which we provide a synthesis here. Release of this support prior to completion of these manuscripts is meant to ensure timely delivery of research findings to support policy and management decisions. However, findings presented here are subject to change pending any revisions that need to be addressed during the peer-review process for each of those manuscripts. Significant changes will require approval of a new product through U.S. Geological Survey's Fundamental Science Practices.

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1. INTRODUCTION

1.1. Legal History

The Yellowstone grizzly bear (*Ursus arctos*) was listed as a threatened species in 1975 (Federal Register 40 FR:31734–31736). Since listing, recovery efforts have focused on increasing population size, improving habitat security, managing bear mortalities, and reducing bear-human conflicts. The grizzly bear population began to recover in the mid-1980s and increased in numbers from approximately 200–350 bears (Eberhardt and Knight 1996) to at least 600 in 2012 (Haroldson et al. 2013). Range expansion occurred concomitantly with the population increase (Schwartz et al. 2002, 2006*b*) and has continued to this date (Bjornlie et al. 2013; Fig. 1). By the end of the 20th century, the U.S. Fish and Wildlife Service (USFWS), the Interagency Grizzly Bear Committee (IGBC; partnership of federal and state agencies responsible for grizzly bear recovery in the lower 48 states), and its Yellowstone Ecosystem Subcommittee (YES; federal, state, county, and tribal partners charged with recovery of grizzly bears in the Greater Yellowstone Ecosystem [GYE]) established that the population had recovered and moved toward delisting. One of the tasks in the 1993 Recovery Plan (USFWS 1993) was the preparation of the Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area detailing management and monitoring plans if and when the population was delisted. A final plan was released in 2007 (USFWS 2007*a*) and the USFWS submitted a final rule to delist the Yellowstone grizzly bear population in March 2007 (USFWS 2007*b*). This delisting rule was challenged and the Federal District Court in Missoula, Montana, issued an order vacating the delisting in September 2009. Protections under the Endangered Species Act were reinstated in March 2010. The USFWS appealed the District Court decision on primary grounds: 1) that regulatory mechanisms after delisting (i.e., the Conservation Strategy) were adequate to ensure that the grizzly population would not decline, and 2) the potential loss of whitebark pine (*Pinus albicaulis*) as a food source would not threaten the Yellowstone grizzly bear population. The 9th Circuit Court of Appeals rendered a decision in November 2011 and reversed the District Court decision regarding the adequacy of protections provided under the Conservation Strategy, but upheld the District Court decision that the USFWS had not sufficiently demonstrated that whitebark pine decline was not a threat to the Yellowstone grizzly bear population. The 9th Circuit Court articulated in detail their concerns regarding each of the arguments made by the USFWS regarding whitebark pine. Specifically, the 9th Circuit Court questioned: 1) the

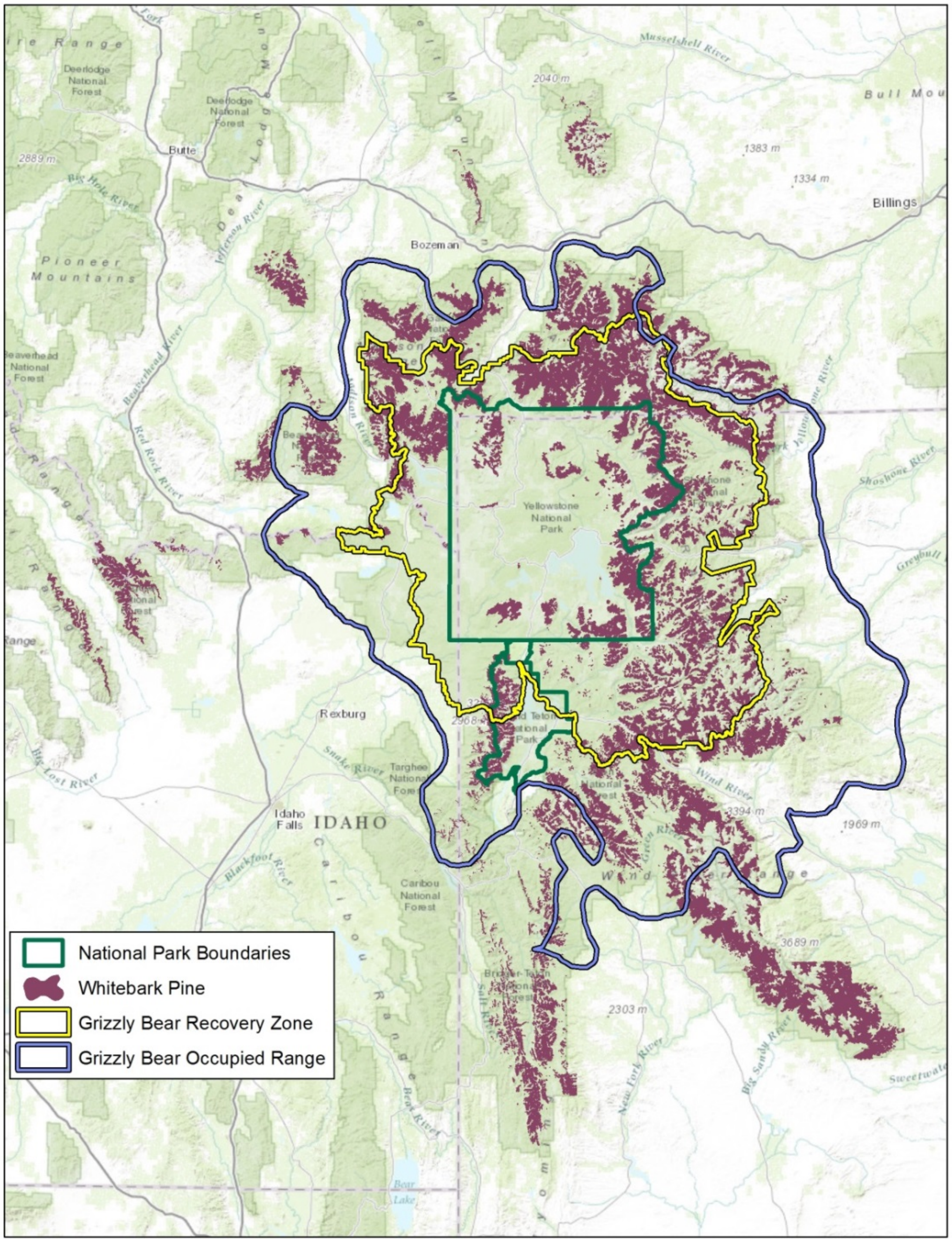

Figure 1. Distribution of whitebark pine, Yellowstone Grizzly Bear Recovery Zone boundary (USFWS 1993), and occupied grizzly bear range in the Greater Yellowstone Ecosystem (Bjornlie et al. 2013). Areas of mapped whitebark pine include stands with various levels of mortality due to mountain pine beetle, blister rust, and fire.

USFWS's statements about the ability of grizzly bears as omnivores to find alternative foods to whitebark pine seeds; 2) particular literature used to support their conclusions; 3) the non-intuitive biological reality that impacts can occur to individuals without causing the overall population to decline; and 4) the validity of the USFWS's comparison with other grizzly populations that have experienced the collapse of whitebark pine in the last century, when the USFWS expressly stated that the Yellowstone grizzly existed in a "unique ecological setting."

The IGBC and YES tasked the Interagency Grizzly Bear Study Team (IGBST) to provide information and further research relevant to the first 3 of these questions. Specifically, the IGBC and YES requested a comprehensive synthesis of the current state of knowledge regarding whitebark pine decline and individual and population-level responses of grizzly bears to changing food resources in the GYE. This research was particularly relevant to grizzly bear conservation given changes in the population trajectory observed during the last decade (Section 1.3).

1.2 Changes in Whitebark Pine and Other Grizzly Bear Foods

Grizzly bears are opportunistic omnivores (Schwartz et al. 2003) and feed on an array of animals and plants. Seeds from whitebark pine are a frequent food for grizzly bears during mid-August through late September and, occasionally, in spring when seed production in the previous fall was high (Mattson et al. 1991). Whitebark pine is a masting species and grizzly bear consumption of seeds is associated with this natural cycle of good and poor years of cone production. Seeds may comprise 50–80% of fall scat volume of some bears when cone production is good, but only trace amounts when cone production is low (Kendall 1983, Mattson et al. 1991). Grizzly bears obtain virtually all (>90%) seeds by excavating middens of red squirrels (*Tamiasciurus hudsonicus*; Kendall 1983, Mattson and Reinhart 1997). 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. 2006*a*), movements (Blanchard and Knight 1991), and frequency of management actions (Mattson et al. 1992, Blanchard and Knight 1995, Gunther et al. 2004). Cone crop failures influence foraging behaviors that may increase vulnerability to human-caused mortality. When whitebark pine production is poor, grizzly bears tend to use lower elevations (Blanchard and Knight 1991, Mattson et al. 1992), where the risk of bear-human conflict is greater and survival is less (Schwartz et al. 2010). Starting in the early 2000s, whitebark pine experienced widespread tree mortality because of mountain pine beetle (*Dendroctonus ponderosae*), wildland fire, and white pine blister rust (*Cronartium ribicola*), with mountain pine beetle having caused the greatest mortality (Gibson 2007). Because whitebark pine was the focus of the 9th Circuit Court ruling in November 2011, we provide a detailed synthesis of the current state of knowledge of these impacts in a subsequent chapter.

Yellowstone grizzly bears have been identified as one of the most carnivorous interior populations in North America (Jacoby et al. 1999, Mowat and Heard 2006). Isotopic nitrogen ($\delta^{15}N$) in grizzly bear hair samples suggested that meat provided 45% and 79% of the protein in the annual diets of adult females and adult males, respectively, during 1977–1996 (Jacoby et al. 1999), and provided evidence for meat as an important nutritional buffer in years of poor whitebark pine cone production (Mattson 1997, Felicetti et al. 2003). The GYE contains large populations of ungulates and winter-killed elk (*Cervus elaphus*) and bison (*Bison bison*) are important spring foods to bears (Green et al. 1997, Mattson 1997). Grizzly bears prey on elk calves during late May through early July (Gunther and Renkin 1990, Fortin et al. 2013) and, to a lesser extent, on older elk throughout the year (Mattson 1997). Bears opportunistically scavenge carcasses throughout the active season and commonly usurp kills of other predators, such as cougars (*Puma concolor*; Murphy et al. 1998) and, since their reintroduction in 1995, gray wolves (*Canis lupus*; MacNulty et al. 2001, Ballard et al. 2003, Gunther and Smith 2004). Ungulate remains left by hunters also provide grizzly bears with meat and bears are attracted to areas outside of national parks when these remains become available during fall (Haroldson et al. 2004).

Some ungulate populations in the GYE have experienced changes during the past decade, whereas others have not. The bison population in the park has fluctuated largely because of a removal program directed at brucellosis (*Brucella abortus*) management (Cross et al. 2010*b*). Approximately 40% of the park's bison population was removed in 2008 (Cross et al. 2010*a*), but numbers rebounded to near previous levels by 2012 (Geremia et al. 2012, Interagency Bison Management Plan 2012). Elk numbers on the northern range, in the Madison-Firehole, and Gallatin Canyon have declined but elk numbers from some herds east of Yellowstone National Park either remained constant or increased (Creel 2010, Cross et al. 2010*a*). Competition for the ungulate resource has increased due to an approximate 3-fold increase in grizzly numbers since the 1970s and growth of the reintroduced wolf population from 31 individuals in 1995 to a minimum of 463 in the GYE in 2012 (USFWS et al. 2013).

Prior to the 1990s, spawning cutthroat trout (*Oncorhynchus clarkii*) were a valuable food for grizzly bears residing near the tributary streams to Yellowstone Lake from mid-May through

July (Reinhart and Mattson 1990), but this fish population has declined from non-native lake trout predation (*Salvelinus namaycush*), whirling disease (*Myxoblus cerebralis*), and prolonged droughts (Koel et al. 2003, 2005). The cutthroat trout population is estimated to be <10% of historical numbers (Koel et al. 2005) and biomass of cutthroat trout consumed by grizzly bears and American black bears (*Ursus americanus*) in this region declined by 70% and 95%, respectively, between 1997 and 2007 (Fortin et al. 2013).

1.3 Changes in Grizzly Bear Vital Rates and Population Growth

During 1983–2001, the estimated annual rate of population growth (λ) was between 4.1% (using a conservative assumption that unresolved fates of independent females represented mortality) and 7.6% (censoring data of independent females with unresolved fates; Schwartz et al. 2006*d*). Under the Revised Demographic Criteria for the Grizzly Bear Recovery Plan (USFWS 2007*c*) the IGBST is required to perform a Demographic Review if the population trajectory of females with cubs-of-the-year (F_{COY}) over all years since 1983 showed evidence of a change. In 2011 this occurred for the first time since 2007 (Haroldson 2012) and the IGBST re-evaluated fecundity and survival of cub, yearling, and independent grizzly bears in the GYE for 2002–2011. These analyses did not include data from Schwartz et al. (2006*d*) but used a consistent analytical approach (see IGBST 2012:32 for 2 exceptions). Projections for 2002–2011 showed annual population growth rates were 0.3% (unresolved fates assumed to represent mortality) and 2.2% (unresolved fates censored), thus indicating a slowing of population growth compared with 1983–2001 (IGBST 2012:34). The primary cause of the slower growth during 2002–2011 was lower annual survival rates among cubs (estimate declined from 0.640 during 1983–2001 to 0.553 during 2002–2011) and yearlings (from 0.817 during 1983–2001 to 0.539 during 2002–2011; IGBST 2012:33). Based on change-point analyses of trend in number of F_{COY}, the change in trajectory likely started around 2000 or 2001 (M. Higgs, Montana State University, unpublished data). We note that Harris et al. (2007) estimated that under current monitoring protocols a scenario in which annual population growth stabilized (i.e., $\lambda = 1.0$) would be detectable after 7 or 8 years. The detection of this slowing of population growth at around 10 years is consistent with this prediction.

2. PROJECT OBJECTIVES

Our overall project objectives were to 1) document the current status and trend of whitebark pine in the GYE based on available literature, recent monitoring data, and expert assessments; and 2) investigate potential impacts of whitebark pine decline and changes in other food resources on Yellowstone grizzly bears. We addressed the first objective through collaboration with the Greater Yellowstone Whitebark Pine Monitoring Working Group, which was coordinated through the National Park Service Inventory and Monitoring Program (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011), and by commissioning a comprehensive report on the future status of whitebark pine (Mahalovich 2013). We approached our second objective by developing a comprehensive set of research questions that addressed potential impacts of changing food resources on grizzly bears at the individual and population level. Based on the knowledge that the population trajectory of the Yellowstone grizzly bear population showed robust growth through the late 1990s, and thus increasing bear densities, but a slowing of population growth since the early 2000s (IGBST 2012), we also investigated potential impacts of resource declines versus density-dependent effects on population growth. Density-dependence may operate through factors that influence population growth as a function of population density (e.g., survival may decrease as number of animals per unit area increases). Key demographic analyses referenced in the final USFWS delisting rule (USFWS 2007*b*), and in the District and Circuit Court decisions following litigation, were based on the period 1983–2001 (e.g., Schwartz et al. 2006*d*), ending at the onset of the period of whitebark pine decline. We thus focused our analyses on the time period of ~2000–2012 but also used data prior to 2000 as a baseline for comparison for several analyses.

3. CURRENT STATUS AND TREND OF WHITEBARK PINE

3.1 Whitebark Pine Ecology

Whitebark pine is a slow-growing, long-lived, stone pine of the western United States and southwestern Canada, distributed in coastal mountain ranges from British Columbia to California and the Rocky Mountains from Alberta to Wyoming. Whitebark pine occupies high-elevation sites characterized by poorly developed soils, snowy winter conditions, and extremely wind-swept exposures. Whitebark pine is most commonly found mixed with other conifers, where it is a long-lived, seral dominant (Arno and Hoff 1989). In the GYE, primary associates are lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). On the harshest sites, whitebark pine is a climax species occurring in pure stands or in association with subalpine fir (Arno and Hoff 1989). Within the 50,280 km^2 of occupied grizzly bear range in the GYE (Bjornlie et al. 2013), whitebark pine occurs on approximately 7,090 km^2 (14%; Fig. 1) within a narrow elevation range of approximately 2,500 to 3,060 m (Mahalovich 2013).

The large, edible seeds of whitebark pine are a food source for various birds and mammals, including Clark's nutcrackers (*Nucifraga columbiana*), red squirrels, American black bears, and grizzly bears (Lorenz et al. 2008). They are a high-energy food, containing approximately 11% carbohydrates, 21% protein, and 60% fat by weight (Lanner and Gilbert 1994). Cones of whitebark pine are indehiscent, meaning that they do not split open to scatter seeds when mature. Seed dispersal is achieved by the harvest and caching of seeds by wildlife species, most notably the coevolved mutualist Clark's nutcracker. To ensure that some seeds survive to germinate, whitebark pine has evolved a masting strategy whereby populations synchronize their reproduction to periodically produce cone crops large enough to satiate seed consumers (Lorenz et al. 2008). In the GYE, large cone crops occur every 1 to 4 years, averaging every 2 years (Haroldson 2013).

There is some evidence that whitebark pine has been declining since the early 1900s, in response to several natural and human-related causes (Kendall and Keane 2001). Whitebark pine is a fire-adapted, moderately shade-intolerant, pioneer species that often colonizes after disturbance. Except on the most extreme sites, where it usually out-competes less hardy species, whitebark pine is generally replaced over time by more shade-tolerant species, such as subalpine fir. Fire suppression has been implicated as an agent responsible for the successional replacement of whitebark pine by more shade-tolerant species (Arno 1986, Brown et al. 1994, Keane at al. 1994, Murray et al. 2000, Keane 2001). However, other studies revealed little change in fire frequency in subalpine forests (Sherriff et al. 2001, Buechling and Baker 2004, Larson and Kipfmueller 2012), with subalpine fir establishment occurring well before modern fire suppression (Larson et al. 2009). Although fire is beneficial to the long-term persistence of whitebark pine, large-scale wildfires can reduce whitebark pine populations and cone production in the short-term. If post-fire whitebark pine regeneration is compromised by other factors, wildfires have the capacity to contribute to overall decline.

Mountain pine beetle is a native, cambium-feeding insect that can cause widespread mortality in all pine species in western North America, including whitebark pine. Pine bark beetles are found as far south as Mexico and occur as far north as British Columbia. Pine bark beetles typically attack large, mature trees and kill those trees with inner bark thick enough to support larvae (Perkins and Roberts 2003, Larson 2011). Episodic outbreaks occur every 20–40 years and cover extensive areas, with an average duration of 12–15 years. Outbreaks can cause up to 60% overall tree mortality and 80% to 90% mortality among larger trees (Raffa et al. 2008). The most recent outbreak, which began in the early 2000s, has caused mortality within millions of hectares across the Rocky Mountains (Raffa et al. 2008). The severity of the current outbreak is attributed to warmer winters at higher elevations allowing for increased beetle survival and reproduction (Logan and Powell 2001, Logan et al. 2010, Dooley 2012).

White pine blister rust was inadvertently introduced into to North America in 1910 near Vancouver, British Columbia. The first infections of whitebark pine were observed in the 1920s and since then it has spread throughout whitebark pine range (Hoff and Hagle 1990). Blister rust can cause canopy dieback, reproductive failure, and tree mortality. Damaged trees can survive for years with severely diminished cone production (Tomback and Achuff 2010). All age classes of whitebark pine are susceptible to blister rust, particularly seedlings and saplings. By limiting reproduction and reducing seedling survival, blister rust can reduce natural regeneration (Smith et al. 2008). Among regions of the northern Rocky Mountains, and among sites within some regions, blister rust prevalence in whitebark pine ranges from 0% to 100% (Kendall and Keane 2001, Kinloch 2003, Helmbrecht et al. 2007, Smith et al. 2008). The greatest rust infection levels are in northwestern Montana, where the fungus was introduced in the 1920s (McDonald and Hoff 2001). This area is also home to the most rust-resistant whitebark pine populations (Mahalovich et al. 2006). Long-term site monitoring indicates mortality rates from blister rust averaged 2.1% per year in western Montana (Keane and Arno 1993) and 3% per year in the Canadian Rockies (Smith et al. 2013).

3.2 Fire History

There is uncertainty regarding the importance of the role of fire suppression in the GYE. Fire history studies of GYE subalpine forests have consistently shown that the 300- to 450-year fire interval have been controlled by climate and by changes in the fuel complex as a result of succession, and that 20th-century fire suppression has likely had little impact on the dynamics of these higher-elevation forests (Romme 1982, Barrett 1994, Meyer and Pierce 2003, Whitlock et al. 2003).

During the summer of 1988, extensive fires burned in the GYE, which ultimately affected approximately 2,500 km^2. The extent of these fires was chiefly a consequence of low fuel moisture conditions caused by a drought and sustained high winds (Renkin and Despain 1992, Turner et al. 2003, Schoennagel et al. 2004). Although severe, the 1988 fires were similar to fires that occurred during the 1700s and earlier (Schoennagel et al. 2004), possibly the very fires that led to the establishment of many extant whitebark pine stands. Within Yellowstone National Park, 240 km^2 of whitebark pine forest burned, representing 28% of the total area of whitebark pine forest present around 1972 (Renkin and Despain 1992). Thus, this event represented a substantial short-term loss of whitebark pine, particularly of mature, cone-producing trees. As such, the decline of whitebark pine observed during the 2000s is not the first disruption of this food source experienced by the GYE grizzly population since its listing in 1975.

In the long-term, the fire-induced regeneration brought about by the large-scale 1988 fires may represent an instance of the successional reestablishment of this pioneer species. Regenerating whitebark pine seedlings appeared in burned stands as early as 1991–1993 (Tomback et al. 2001) and seedlings and recruited saplings persist and increase to the present day. On revisited sites, density of whitebark pine stem regeneration increased during 1990–2001 on Henderson Mountain and Mount Washburn in Yellowstone National Park (Tomback et al. 2011), and during 1998–2008 in the Absaroka Beartooth Wilderness of the Gallatin National Forest (Tyers et al., in prep.).

Whitebark pine trees are capable of producing cones at 20–30 years of age, although large crops do not typically occur until 60–80 years of age (Day 1967, Krugman and Jenkinson 1974, McCaughey and Tomback 2001). Therefore, trees established 20–22 years ago are likely on the verge of cone production. Availability of this potential cone resource by grizzly bears will depend on its harvest by red squirrels and previous studies suggest that squirrels will likely use these regenerating stands. Although mature conifer forest represents the highest quality habitat (Patton and Vahle 1986, Ransome and Sullivan 1997), red squirrels are known to use disturbed and fragmented forests (Sullivan and Moses 1986, Thompson et al. 1989, Bayne and Hobson 2000, Haughland and Larsen 2004, Russell et al. 2010), even causing damage to regenerating stands (Sullivan 1987). Squirrel use of open forest habitats is encouraged by availability of downed logs (Carey 2000, Bakker 2006), which typically are plentiful in post-fire stands. Finally, the 1988 fires created a spatially complex mosaic of unburned and burned patches, encompassing a wide range of burn severities (Christensen et al. 1989, Turner et al. 2003). This post-fire heterogeneity may facilitate use of regenerating stands by squirrels residing in neighboring mature stands.

3.3 White Pine Blister Rust and Mountain Pine Beetle

The first reported outbreak of mountain pine beetle in whitebark pine in the GYE began around 1925 (Furniss and Renkin 2003). The majority of whitebark pine was infested by 1937, and by 1942, mountain pine beetle was no longer considered a problem (Despain 1990). The next major epidemic occurred from 1969 to 1985, characterized by overlapping outbreaks with 1980 attributed as the peak year (U.S. Department of Agriculture 2012*a*, *b*, *c*; Olliff et al. 2013).

The most recent outbreak of mountain pine beetle began around 2000. Based on U.S. Forest Service aerial detection surveys, peak mountain pine beetle activity occurred in 2009 (U.S. Department of Agriculture 2012*a*, *b*, *c*). Coincident with that peak year, Macfarlane et al. (2013) used an aerial survey called the Landscape Assessment System (LAS) to assess pine beetle-caused mortality of whitebark pine across its distribution in the GYE. Results combining photo-inventoried and interpolated mortality levels indicated that 46% of the whitebark pine distribution showed severe mortality, 36% showed moderate mortality, 13% showed low mortality, and 5% showed trace levels of mortality. Sixteen of the 22 major mountain ranges experienced widespread, moderate to severe mortality. Locations with colder microclimates, such as the central core of the Wind River Range and the Beartooth Plateau, showed low levels of mortality and were identified as refugia from the beetle outbreak.

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 2013*b*). For tagged trees, observed cumulative mortality was 37% for trees >10 cm and ≤30 cm DBH (diameter at breast height) and 72% for trees >30 cm DBH (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013*b*). By 2013, 72% of 176 monitored transects had evidence of beetle infestation (Greater Yellowstone Whitebark Pine

Monitoring Working Group 2013*b*). 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). Most mortality was observed between 2003 and 2009. Evidence suggests the current outbreak is waning (Haroldson and Podruzny 2013, Haroldson 2013, Greater Yellowstone Whitebark Pine Monitoring Working Group 2013*b*, Hayes 2013, Olliff et al. 2013), however, occasional irruptions may be expected at smaller scales over the next 3–8 years. Based on the 2002–2012 data, there are no indications of back-to-back outbreaks as in the 1969–1985 mountain pine beetle infestations (Mahalovich 2013).

Blister rust was first identified within the GYE in 1937 in the Bear Creek drainage of the Gallatin National Forest (Kendall and Asebrook 1998). Blister rust is a cool, moist weather disease (Van Arsdel et al. 1965, Van Arsdel 1967) and infection rates tend to be higher on the western side of the continental divide (Smith et al. 2008). Prevalence of rust infection is more limited in drier and colder environments as found in the GYE (Kendall and Keane 2001). Based on transects in the GYE monitored for whitebark pine health, current infection levels average 20–30% with no change in infection rate; spatial variation likely reflects geographic differences in microclimate (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013*a*, *b*). Consistent with earlier research (Berg et al. 1975), blister rust infection decreases at higher elevations (Mahalovich 2013). Infection and mortality rates decrease rapidly as a function of tree size (Mahalovich 2013). Model-estimated, 2-year mortality rates for trees infected with blister rust were 5–30% among trees <10 cm DBH to 0–1% among larger trees (Irvine et al., in review). Based on artificial inoculations, current blister rust resistance in the GYE is estimated at 9–28%, meaning that the trees can tolerate the presence of infection without succumbing to mortality (Mahalovich et al. 2006; Mahalovich, in prep.). The family heritability for rust resistance in the GYE is moderate (0.70–0.72; range = 0–1.0), indicating whitebark pine can favorably respond to selection and breeding (Mahalovich et al. 2006, Mahalovich, in prep.). Infection levels and mortality will likely not increase unless a virulent strain of rust is introduced, a wave year of infection occurs, or localized micro-climatic changes once again favor the infection cycle.

Several researchers found a relationship between rust infection and beetle infestation (Six and Adams 2007, Larson 2011, Bockino and Tinker 2012), suggesting the presence of both agents might increase risk of mortality. This was confirmed, but only in smaller trees, based on the whitebark pine health monitoring transects in the GYE. Mountain pine beetle was most important in explaining probability of tree mortality, but an additive effect of severe blister rust infection and pine beetle attack was evident for trees <20 cm DBH (Irvine et al., in review).

Reduced densities of mature trees resulting from mortality due to pine beetle, blister rust, and fires, in combination with stand isolation, have the capacity to reduce cone production and regeneration (Rapp et al. 2013). Despite these recent events in the GYE, surveys of natural regeneration indicate a mixture of seedling and sapling natural regeneration is currently present. Estimates of 550–2,450 trees per acre were obtained on survey sites on the Gallatin and Bridger-Teton National Forests, where the majority of trees were in the 20–40-year-old age class, indicating regeneration since the pine beetle outbreaks of the 1970s and 1980s. In addition, 2- and 3-year-old seedlings were also observed, indicating regeneration following the 2009 masting event at the height of the pine beetle outbreak (Mahalovich 2013). Recruitment of new trees has also been observed on the 176 GYE transects of the Interagency Whitebark Pine Monitoring Program: during 2008–2013, >8,700 trees ≤1.4 m tall were observed and recruitment of >400 newly tagged trees >1.4 m tall was documented (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013*b*). The majority of trees added were ≤2.5 cm DBH and this size class has experienced a net increase of approximately 25% (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013*a*).

3.4 Future Outlook

Increasing temperatures may increase the lower elevational limits of whitebark pine above the tallest peaks in some ecosystems (Bartlein et al. 1997, Warwell et al. 2007, Schrag et al. 2008). Models relating projected climate to its current geographical distribution have predicted dramatic decreases in whitebark pine over the next 50 years, although range reduction would be less likely in the GYE than other locales (Warwell et al. 2007, McDermid and Smith 2008). These models did not consider the potential interactive effects of climate change, mountain pine beetle, blister rust, and fire regimes on future sustainability of whitebark pine. Climate change may exacerbate the impacts of pine beetle and blister rust (Keane et al. 2012). The severity of the current outbreak of mountain pine beetle likely was worsened by warmer winter temperatures facilitating establishment and expansion of beetle populations at higher elevations (Logan and Bentz 1999, Logan and Powell 2001, Logan et al. 2003, Campbell et al. 2011, Preisler et al. 2012). A warmer climate may accelerate the spread of blister rust, particularly at higher elevations (Koteen 2002, Larson 2011), although more arid conditions may slow its spread (Geils et al. 2010). Wildfires are expected to increase in frequency and size as climate changes (Ryan 1991, Brown et al. 2004, Running 2006, Keeton et al. 2007), and this could potentially benefit whitebark pine. Loehman et al. (2011) demonstrated that whitebark pine could be maintained in Glacier National Park if increases in large, stand-replacement fires create large, competition-free areas.

Given the uncertain future of whitebark pine, active management policies are in place to promote its persistence within the GYE. Federal agencies of the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee have supported the restoration planting of blister rust-resistant seedlings, averaging 95 ha/year (234 acres) during 2000–2013 (Mahalovich and Dickerson 2004, Mahalovich et al. 2006, Schwandt 2006, Schwandt et al. 2010, Mahalovich 2013). These efforts, and various traits of the whitebark pine population within the GYE, all indicate whitebark pine shows promise for being maintained in the subalpine forest. These traits include high levels of genetic diversity, moderate to high heritabilities in key adaptive traits, demonstrated blister rust resistance in some trees, minimal inbreeding, and a generalist adaptive strategy (Richardson et al. 2002; Mahalovich et al. 2006; Mahalovich and Hipkins 2011; Mahalovich 2013, in prep.).

4. GRIZZLY BEAR RESPONSE TO CHANGING FOOD RESOURCES

Our research charge from the IGBC and YES was to address the primary questions posed by the 9th Circuit Court regarding the potential influence of whitebark pine decline on the Yellowstone grizzly bear population. We identified 8 focal topics and posed relevant research questions (hypotheses) accordingly. We chose this multiple-hypothesis framework to strengthen our inference by exploring different types of responses, ranging from the individual to population level: 1) diet diversity; 2) grizzly bear selection of whitebark pine habitat; 3) body condition; 4) animal matter as alternative food sources; 5) changes in movements and home ranges; 6) changing mortality risk due to changing food resources; 7) home-range size as an indicator of density versus resource effects; and 8) relationships between changing vital rates, resource changes, and density dependence. In the following, we present each research question and provide findings from our analyses and literature to examine evidence supporting or refuting each question, which we then synthesize in the Discussion section.

Research Question 1: How diverse is the diet of Yellowstone grizzly bears?

Gunther et al. (in review) examined 44 published papers, 12 books, 4 dissertations, 10 theses, and 66 state and federal agency reports that documented grizzly bear food habits in the GYE during the 122-year period from 1891 through 2012; documentation was most rigorous for the period 1944 through current years. They documented grizzly bear consumption of 234 different foods classified to species, genus, family, or phylum, of which 67% were plants, 15% were invertebrates, and 11% were mammals. Seventy-five taxa were well represented among the various studies, indicating they were consumed frequently. These items included high-caloric foods such as army cutworm moths (*Euxoa auxiliaris*), bison, cutthroat trout, mule deer (*Odocoileus hemionus*), elk, moose (*Alces alces*), and whitebark pine seeds, but also items with lower caloric value (or lower caloric gain/unit effort), such as biscuit root (*Lomatium* spp.), yampa (*Perideridia montana*), clover (*Trifolium* spp.), horsetail (*Equisetum* spp.), ants (*Componotus* spp., *Formica* spp.), and various grass and sedge species.

Spatial and temporal variation in diets is well-documented among grizzly bear populations (e.g., Jacoby et al. 1999). Diets not only vary among years and seasons but are also composed of a mixture of foods within seasons (Rode and Robbins 2000) and among individuals (Edwards et al. 2011). Diets of GYE bears have been documented over a long time period and Gunther et al. (in review) were able to identify broad temporal transitions. Grizzly bears in Yellowstone National Park supplemented their diets of native foods with anthropogenic foods beginning in the 1880s (Schullery 1992) but once park and municipal garbage dumps in the GYE were closed during 1968–1979, consumption of anthropogenic foods decreased and is now limited to occasional, opportunistic occurrences (Gunther et al. 2004).

A second diet shift was restricted to bears in the Yellowstone Lake area (Fig. 1), where consumption of cutthroat trout by grizzly bears likely followed a gradual decline of the trout population that started around the time of the park's establishment and continued into the 1960s (Gresswell and Varley 1988), followed by a temporary rebound during the 1970s and 1980s. As we described previously, a second decline started in the early to mid-1990s and continued into the late 2000s and resulted in a 70% reduction in trout consumption by grizzly bears between 1997–2000 and 2007–2009 (Haroldson et al. 2005, Fortin et al. 2013). Fortin et al. (2013) suggested grizzly bears with home ranges near Yellowstone Lake may compensate for the loss of cutthroat trout by preying more heavily on neonatal elk calves during spring and early summer and incorporating other foods into the annual diet.

Previous studies in the GYE have also demonstrated temporal and spatial variation in foraging patterns and use of whitebark pine seeds. Mattson et al. (1991) reported that annual differences in scat contents were substantial during 1977–1987, and suggested that long-term studies were necessary to adequately document food habits. Fall diets were among the most variable, with whitebark pine seeds found to be a principal food in approximately half of the years, but virtually absent from the diet in other years (Mattson et al. 1991), a pattern consistent with their opportunistic foraging strategy. Additionally, Mealey (1980) recognized regional differences in diets of grizzlies in Yellowstone National Park and identified these geographically unique interactions among bears and their foods as 3 foraging 'economies', including the lake economy described previously, the valley-plateau economy, and the mountain economy. Whitebark pine seeds were identified as a primary food only for the mountain economy. Spatially explicit analyses by Costello et al. (in review) support this concept of diet specialization within the GYE. They found that one third of sampled bears had little or no whitebark pine habitat in their early fall (15 Aug to 30 Sep; 2000–2011) home ranges. These observations occurred before and after the decline of whitebark pine, and were equally divided between good and poor years of whitebark pine cone production. Many of the observed whitebark pine-deficient fall ranges (inside, west, and south of Yellowstone National Park) corresponded well with the locales Mealey (1980) used to describe the valley-plateau economy, namely Hayden, Pelican, and Lamar valleys, along with Cougar Creek Flat. According to Mealey (1980) this economy involved substantial consumption of meat derived primarily from ungulates and rodents, as well as use of roots and corms. For example, this same diet composition was documented in Grand Teton National Park during 2004–2006 (S. Cain, National Park Service, unpublished data), where use of whitebark pine seeds was infrequent, even during years of good production. In this area, whitebark pine use was slightly greater for sympatric American black bears, which are subordinate to grizzly bears. Combined, food habits studies from GYE show that grizzly bears not only display dietary plasticity among individuals and different portions of the ecosystem, but also across seasonal, annual, and decadal time frames.

Research Question 2: Has grizzly bear selection of whitebark pine habitat decreased as cumulative tree mortality increased?

The premise for this question was based on documented fall use of whitebark pine habitat by grizzly bears. We assumed that such habitat use primarily reflected bear excavation of squirrel middens. Analyses by Costello et al. (in review) of >52,000 locations of GPS-collared bears (89 bear years) collected during 2000–2011 estimated that 72% of 60 grizzly bears with whitebark pine habitat in their fall range selected for this habitat during 15 August–30 September. However, general linear regression indicated the strength of selection (as measured by the Manly-Chesson standardized index of selectivity; Manly et al. 1972, Chesson 1978) weakened over the study period, declining from an estimated selection index of 0.69 to 0.50, a difference of 0.19 (95% CI = 0–0.38). The final estimate of 0.50 indicated that, by 2011, grizzly bears used these habitats equal to their availability, thus showing neutral selection (Fig. 2). Costello et al. (in review) found some support for the notion that selection was greater during years of good cone production, and that males were less selective of whitebark pine habitat than females during poor years of cone production. Grizzly bears used whitebark pine habitat on an average of 30 days but many bears repeatedly left and returned during the fall season. Based on quantile regression analysis of 1,779 bear-days of whitebark pine habitat use, Costello et al. (in review) observed no change in dates of use over the study period during years of good cone production. However, during years of poor cone production, onset and duration of use changed over time: bears began using whitebark pine habitat approximately 13.8 days (95% CI = 6.3–20.7) later by the end of the study period (2011), delaying first use from 18 August to 31 August and median date of use from approximately 5 September to 16 September. No change in latest use of whitebark pine habitat was observed in poor or good years.

The shift toward later use of whitebark pine habitat was unexpected. Based on a previous study, we had presumed that increased competition for a declining resource would lead to diminishing returns at an earlier date. In Yellowstone National Park, Haroldson and Gunther (2013) documented differences in the number of fall ‘bear-jams’ (i.e., roadside viewing opportunities for park visitors) relative to annual differences in whitebark pine production during 1990–2004. Among all years, they documented a late-summer decline in the number of bear-jams until the week of 13–19 August. This nadir was followed by a distinct and rapid increase in bear-jams during years of poor whitebark pine production, but a smaller, gradual increase during

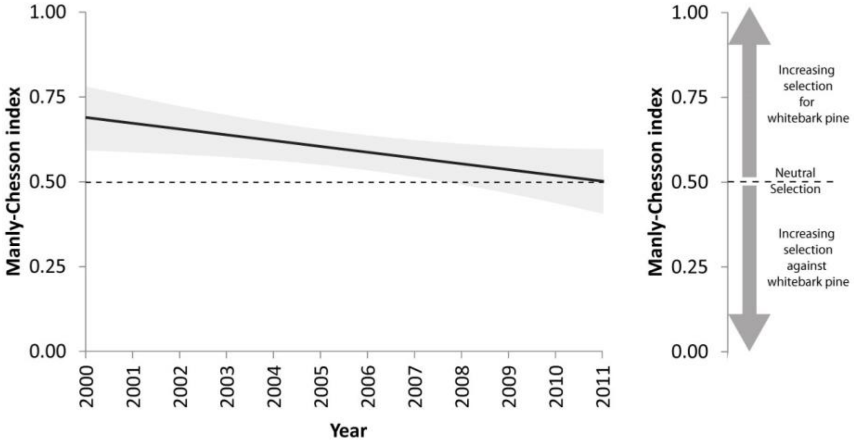

Figure 2. Mean Manley-Chesson index for selection of whitebark pine habitats during 15 August–30 September, 2000–2011, based on 60 GPS-monitored grizzly bears (with >5% whitebark pine habitat present in their fall range), Greater Yellowstone Ecosystem.

years of good whitebark pine production. As high-elevation whitebark pine stands provide few roadside viewing opportunities, this pattern suggests that bears left the more open roadside habitats to begin investigating the availability of whitebark pine seeds at approximately the same time each year, but returned to alternative foods, such as those found in roadside habitats, more quickly when seed abundance was low. The observed delay in use of whitebark pine habitat associated with whitebark pine decline diverges from this pattern.

Whereas further investigation of these patterns is of ecological interest, the findings of Costello et al. (in review) provide conclusive evidence of a behavioral response by grizzly bears to a declining resource. Of course, an important question is if this behavioral response could cause a decline in body condition or whether bears were still able to meet nutritional demands. Therefore, we subsequently investigate trends in body condition of GYE grizzly bears over the last decade and if grizzly bears in the GYE are shifting diets to other food sources.

Research Question 3: Has grizzly bear body condition decreased as whitebark pine declined? During fall, grizzly bears enter a physiological state referred to as hyperphagia (Nelson et al. 1983) during which food intake increases as bears increase fat reserves in preparation for hibernation and, for pregnant females, parturition. Using captive brown bears, Robbins et al. (2012) found evidence for apparent body fat thresholds at the start of hibernation that influence whether females produced cubs. Thus, reduced body condition due to declining food resources could result in population-level effects.

Based on an 11-year dataset (2000–2010) of grizzly bear captures, Schwartz et al. (2013*a*) found that September–October body mass of adult bears (n = 89) and percent body fat of adult and subadults (n = 112) did not differ between years of poor and good whitebark pine production among either sex, nor did they detect annual differences in body mass or body fat over the study period. However, when they analyzed males and females separately, they detected a decline in female percent body fat, primarily after 2006 (Fig. 3), although Schwartz et al. (2013*a*) cautioned that further investigation is needed to determine if the trend in female body fat was real or an artifact of sampling. Data were collected only during September-October and primarily from Yellowstone National Park, so sample sizes were small for this analysis and averaged 2.6 bears/year.

Based on the recommendation of Schwartz et al. (2013*a*), we further investigated female trends in percent body fat by adding 3 years (2011–2013) to their data and performing a post-hoc analysis. Despite the additional 3 years of data, only 2011 resulted in body fat measurements from female captures ($\bar{x}$ = 24.5%, n = 5) during the fall period defined by Schwartz et al. (2013*a*). These additional data were insufficient to statistically confirm or refute the presence of a trend in female body fat during fall. Therefore, we conducted an alternative analysis that included all months during which body fat data were collected to increase sample size and thus the power to detect trends in body condition. The focus of this analysis was the population-level relationship between body fat and the time of year bears were measured. Specifically, we hypothesized that if whitebark pine were impacting female body condition, strength of the positive relationship between body fat and date (Schwartz et al. 2013*a*) would be different during 1) poor whitebark pine production years compared with good years, and 2) the pre-impact versus impact period (i.e., 4 data groups). Because body fat is largely a function of body size, day of year, and age of the individual, we included them as explanatory variables of percent body fat to control for their confounding influence. We excluded cubs and yearlings from this analysis because their body condition is not independent from their mother’s condition. Because of potential body fat measurement biases, we also excluded 10 values from bears that were captured in snares rather than culvert traps. We classified the data into 2 periods based on years prior to the peak of whitebark pine decline (2000–2004) and during and following the peak of decline

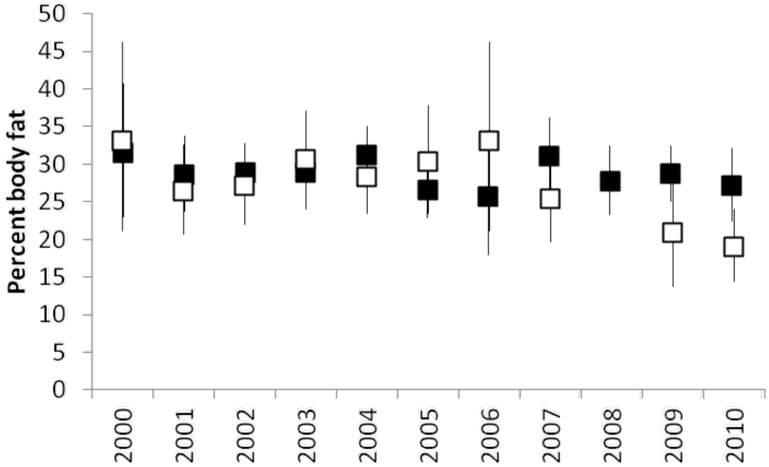

Figure 3. Mean percent body fat (± 95% CI) for 35 female (open symbols) and 77 male (closed symbols) grizzly bears in September and October, 2000–2010, Greater Yellowstone Ecosystem (modified from Schwartz et al. 2013*a*).

(2008–2013). The end of the first period (2004) was defined based on 2005 being the first masting year with >10% mortality of trees on cone-production transects, whereas the second period was defined based on >50% tree mortality. We excluded data from 2005–2007 to prevent confounding influences of this transition period on our primary comparison of pre-impact and impact periods.

Using multiple linear regression, we found no differences in within-year body fat among the 4 data groups ($F_3 = 1.31$, $P = 0.279$), although the distribution of sampling dates, ages, and body sizes were not fully balanced among the data groups. We therefore pooled data by pre-impact and impact period and tested for a period effect. If decline of whitebark pine has impacted body condition, we predicted lower body fat levels throughout the active season (not just during fall; cumulative impacts on body fat would carry over into spring-summer) and a declining relationship between body fat measurements and day of year from the early to later period. Day of year ($\hat{\beta} = 0.003$, SE = 0.001, $P = 0.011$) and body mass ($\hat{\beta} = 0.004$, SE = 0.001, $P < 0.001$) were important predictors of percent body fat. However, the relationship of body fat and day of year did not differ between the 2 periods ($F_1 = 0.40$; $P = 0.496$; Fig 4). Given that finding, we subsequently tested whether body fat levels differed between the 2 periods but found no evidence for this ($F_1 = 1.77$; $P = 0.187$; Fig. 4).

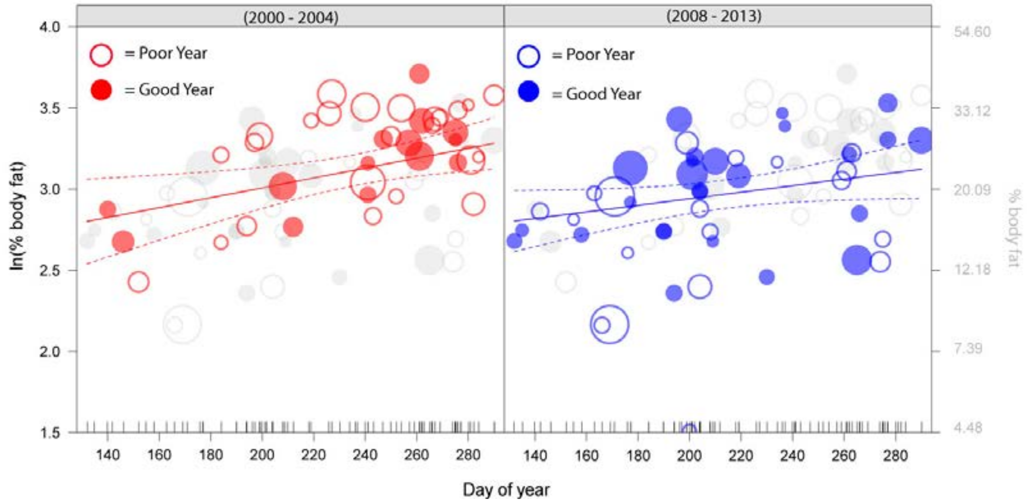

Figure 4. Effect plots and 95% confidence intervals of percent body fat (ln transformed) of female grizzly bears ≥2 years old as a function of day of the year and period, accounting for age and body mass, Greater Yellowstone Ecosystem, 2000–2013. Data values are shown with the size of the circle proportional to the age of the bear. Filled and hollow symbols indicate years of good versus poor whitebark pine cone production. The opposing period's data are shown for reference in light grey in each panel.

Although our analyses showed no difference in the relationship between day of year and percent body fat between the 2 periods, we note a caveat to the interpretation of these data. Research captures of grizzly bears in the Greater Yellowstone Ecosystem are not designed to specifically assess changes in body fat but to mark a geographically balanced set of individuals for long-term monitoring of population vital rates. The stochastic nature of the ages, day of year, and size of individuals captured during any given year and limited sample sizes can contribute to unbalanced datasets. For example, late-season captures of older-aged females have been fewer in recent years (Fig. 4), despite their known presence in the population from telemetry data. In this instance, that potential sampling bias would likely lead to conservative interpretation.

The findings presented here suggest that body condition is not different between poor and good years of whitebark pine production and, given the data obtained to date, has not declined during the period coinciding with the peak of whitebark pine decline. These findings are suggestive of bears obtaining alternative foods, so we subsequently explore evidence of potential diet shifts towards animal matter.

Research Question 4: Has animal matter provided grizzly bears with an alternative food resource to declining whitebark pine?

The premise for this research question was based on the observation that diets of grizzly bears in the GYE have a high content of animal matter among interior populations (Jacoby et al. 1999, Mowat and Heard 2006), primarily in the form of ungulates. Consequently, ungulates may provide an important alternative food for grizzly bears. However, because consumption of meat is already high, such diet shifts may be constrained. Schwartz et al. (2013*a*) used stable isotope analysis of nitrogen and, when accounting for whitebark pine mortality over time, observed greater fall consumption of animal protein during poor versus good years of whitebark pine cone production based on $\delta^{15}N$ in serum (32 F, 59 M; 2000–2010); serum requires only days to weeks to equilibrate with the diet (Hilderbrand et al. 1996). For females 77% (95% CI = 69–84%) of the assimilated nitrogen came from animal matter in poor seed years and 60% (95% CI = 47–72%) in good years, whereas for males these values were 80% (95% CI = 77–84%) and 70% (95% CI = 61–78%), respectively. They concluded that grizzly bears exhibited diet shifts in response to the natural masting cycle of whitebark pine, substituting animal matter for pine seeds in poor seed years and obtaining fat levels in the alternate diet equal to those in good seed years. Additionally, as cumulative tree mortality increased during the study period, the presumable net effect was reduced availability of seeds over time, in both good and poor years, therefore Schwartz et al. (2013*a*) also examined if diet composition changed during 2000–2010. Although they could not measure changes in the assimilation of whitebark pine seeds into bear diets over time ($\delta^{34}S$ isotope has provided confounding results; Schwartz et al., in press), the relative dietary content of meat remained constant based on hair samples (representing previous 6–12 months) and serum samples (representing previous 10–14 days) and increased over the study period for blood clots (representing previous 3 months; Schwartz et al. 2013*a*). Animal matter comprised 44% of assimilated nitrogen in grizzly bear diets based on hair samples (no difference was detected between males and females; Schwartz et al. 2013*a*). We note that colonial insects such as ants and wasps (*Vespula* spp.) can also provide an important source of animal protein but cannot be distinguished from other animal protein in the $\delta^{15}N$ signatures. Ants, for example, are frequently consumed, particularly when other high-quality foods are scarce (Mattson 2001).

If grizzly bears are maintaining body condition and shifting diets as suggested by the findings of Schwartz et al. (2013*a*), we hypothesized that the rate of fall carcass use would increase with whitebark pine decline. Ebinger et al. (in prep.) tested this prediction by first developing algorithms using a set of 12 space-time covariates to identify grizzly bear carcass use based on clusters among locations of GPS-collared bears. They subsequently used multinomial logistic regression to classify known bear activities associated with those clusters based on field-truthing (n = 174). Among 5 primary categories of activity (resting, multiple-use, low-biomass carcass, high-biomass carcass, old carcass), Ebinger et al. (in prep.) focused on high-biomass carcasses to test predictions; classification accuracy for this category was 88%. They used the algorithm to identify potential carcass use among 5,413 GPS locations collected during 2002–2011 and developed an index of predicted carcass use by grizzly bears. During September and October that index increased over 2002–2011 ($\hat{\beta}_{year}$= 0.004, SE = 0.001, P = 0.003, R^2 = 0.40), more than doubling from 2002 to 2011. We emphasize that carcass use not only reflects predation, but also involves scavenging ungulates that died from other causes, usurping kills from other carnivores, and use of remains from hunter kills. Observations by Haroldson et al. (2004) indicate the strong motivation and ability of grizzly bears to obtain ungulate resources during the fall hyperphagia period, irrespective of the availability of alternative foods. This is exemplified by the Schwartz et al. (2013*a*) finding that 60% and 70% of assimilated nitrogen came from animal matter, even when whitebark pine cone production was good. Indeed, trends of increased carcass use over time were not evident for June–August monthly analyses (Ebinger et al., in prep.), illustrating the importance of ungulate consumption during fall. We note that Ebinger et al. (in prep.) did not detect a spatial effect due to areas open to hunting, suggesting the increased rate of carcass use was not restricted to multiple-use lands where bears would find hunter-killed ungulate remains. The findings of these studies suggest that animal matter can serve as an alternative fall food to whitebark pine for grizzly bears in the GYE, consistent with the opportunistic foraging strategy of the species. This ability to shift diets is evident in response to annual variation in food resources (e.g., good versus poor years of whitebark pine cone production) but also in response to changes in the distribution and productivity of foods within the GYE over the last decade (e.g., Fortin et al. 2013).

Research Question 5: Have grizzly bear movements increased during the period of whitebark pine decline?

Blanchard and Knight (1991) detected no differences in daily movements of female grizzlies associated with whitebark pine cone production, but did find that male bears moved more during years of poor production. An important question, therefore, is whether the search for diminishing whitebark pine or alternate foods may result in greater movements, potentially increasing their vulnerability to human-caused mortality. For example, greater movements would be expected if the reduction in productive whitebark pine stands required exploitation of more dispersed and distant stands or alternate foods outside their typical use area, as has been observed for American black bears and Asiatic black bears (*Ursus thibetanus*) consuming highly variable oak (*Quercus* spp.) mast (e.g., Garshelis and Pelton 1981, Koike at al. 2012).

Using linear regression, Costello et al. (in review) investigated whether daily or seasonal movements increased during the period of whitebark pine decline. They found no changes in median daily movement distance (*n* = 2,757 locations of 60 bears) between poor or good cone production years, nor over the 2000–2011 study period (median daily movement = 1.4 km [95% CI = 1.2–1.6]). Daily activity radii during fall, a measure of the extent of seasonal movements, were variable (*n* = 2,818 locations; range = 0.1 to 67.5 km) and similarly showed no temporal trend over the study period; the median daily activity radius for males was 3.0 km (95% CI: 0.9–5.1) greater than females but only in years of good cone production. These findings show that fall movements of grizzly bears in the GYE have not changed over the period of whitebark pine decline.

Research Question 6: Has the number of human-caused grizzly bear mortalities increased as whitebark pine resources declined?

When whitebark pine production is poor, grizzly bears tend to use lower elevations (Blanchard and Knight 1991, Mattson et al. 1992). If those lower elevations are in areas with anthropogenic influence, the risk of bear-human conflict is greater and survival is lower (Schwartz et al. 2010). Because relationships between whitebark pine cone production and risk of human-caused grizzly bear mortality have been previously reported (Blanchard 1990, Mattson et al. 1992, Haroldson et al. 2006, Schwartz et al. 2010), Haroldson et al. (in prep.) analyzed patterns in documented, human-caused mortalities during fall (1 Aug to den entrance) for independent-aged (≥2 years) grizzly bears during 2000–2012 (*n* = 172). They sought to determine whether cone production continues to influence numbers of fall human-caused fall bear mortalities, and whether there was evidence for an additive effect from whitebark pine tree mortality. They focused their analysis on 2000–2012 because 1) this was the primary period of whitebark pine decline, and 2) counts of females with cubs-of-the-year (Haroldson et al. 2013) and population projections from vital rates (IGBST 2012) indicated that the population trend was stable to slightly increasing during this period, thus alleviating the need to account for population change in their analysis. Haroldson et al. (in prep.) used Poisson regression with annual count of human-caused fall mortalities as the dependent variable and predictive covariates for cone production, sex, location in or out of the Recovery Zone, and year. They also included interaction terms to determine if effects varied based on cone production or trend over time inside versus outside the Recovery Zone or varied between females and males in poor versus good years of cone production. Their results showed: 1) annual cone production was predictive of human-caused fall mortalities; 2) no evidence of a difference in the annual numbers of fall mortalities between male or female bears; and 3) an increase in annual mortalities over the study period, with most of this increase representing mortalities outside the Recovery Zone (Fig. 5).

Annual mortalities increased during a period when population trend was relatively stable to slightly increasing so an important question is whether this mortality may be additive. Inside the Recovery Zone, where bear survival has historically been linked with whitebark pine cone production, mortality has not increased substantially so effects due to whitebark pine decline seem negligible (Fig. 5). Years of good whitebark pine production are still associated with reduced mortalities inside the Recovery Zone. Mortalities have increased more outside the Recovery Zone, particularly towards the end of the 2000–2012 period. Cumulative mortality of whitebark pine trees observed during 2000–2012 (Haroldson and Podruzny 2013) was correlated with observation year ($r = -0.98$, $P < 0.001$) so whitebark pine decline may be a potential contributor to the increase in human-caused fall mortality. However, the population has also continued to geographically expand its range, increasing 38% from 2004 to 2010, most of which occurred outside the Recovery Zone (Bjornlie et al. 2013). Outside the Recovery Zone, where whitebark pine distribution is more limited and measures to reduce bear-human conflict are less intensive, attributing the observed increase in fall human-caused mortalities solely to whitebark pine decline does not seem warranted. Moreover, effect sizes were small; for example, assuming

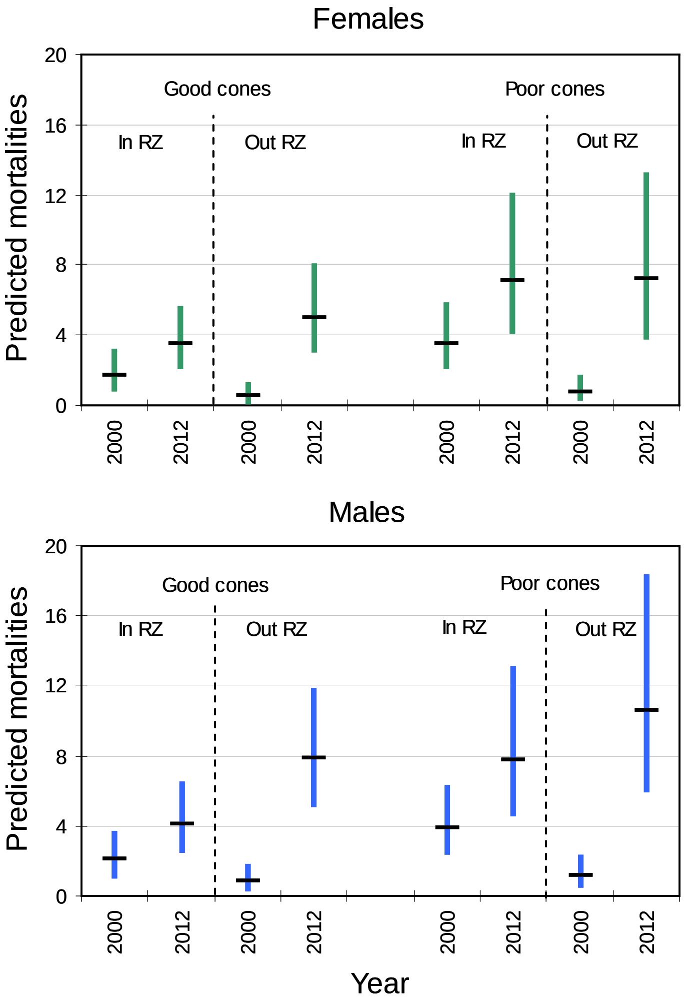

Figure 5. Model-predicted numbers of documented fall (August 1–den entry) human-caused mortalities for females (top) and males (bottom) for the first (2000) and last (2012) year of the study period coinciding with the decline in whitebark pine. Numbers were predicted for inside and outside the Yellowstone Grizzly Bear Recovery Zone (RZ) during years of good (mean median/cones = 14) and poor (mean median cones/tree = 1) whitebark pine production.

the poorest observed cone production (i.e., corresponding with the greatest mortality), the predicted increase in annual number of fall mortalities for female grizzly bears over the period 2000–2012 was 3.5 inside the Recovery Zone and 6.4 outside the Recovery Zone (Fig. 5).

Consistent with these findings, spatial analyses do not indicate grizzly bears selected less-secure habitats as whitebark pine declined. Costello et al. (in review) detected that 78% of 36 grizzly bears, monitored outside of Yellowstone and Grand Teton National Parks during fall 2000–2011, selected for secure habitat (i.e., areas ≥4.05 ha located ≥500 m from roads; IGBC 1998; USFWS 2007*a*). Selection for these lower-risk areas was not associated with selection of whitebark pine habitat. Additionally, using linear regression, they failed to detect a decrease in selection for secure habitat during 2000–2011 (12-year difference = 0.09; 95% CI = -0.08–0.29). As previously reported, Costello et al. (in review) also observed no increase in grizzly bear movement rates over the study period. We note that the analyses of Haroldson et al. (in prep.) and Costello et al. (in review) are distinctly different in that the former involved investigation of human-caused mortalities and included incidents that occurred in areas away from roads, such as conflicts with ungulate hunters. In contrast, inference from Costello et al.'s (in review) analysis was based on areas near roads as a surrogate measure of anthropogenic influence. These findings are not contradictory but merely indicate that bears experiencing loss of whitebark pine in their home ranges are not necessarily exposed to greater risk of conflict or mortality associated with anthropogenic areas. This is an important distinction and addresses one of the more salient questions regarding potentially indirect impacts of whitebark pine decline.

Research Question 7: Has home-range size increased as grizzly bears sought alternative foods or, alternatively, has home-range size decreased as grizzly bear density increased?

Variability in home-range size among brown bears has been associated not only with different sex and age classes but also availability of food resources and population density. Bears often respond to lower food abundance by increasing the size of their home range to gain access to alternative resources and, conversely, shrink home ranges with increasing food supplies (Powell et al. 1997, McLoughlin and Ferguson 2000, McLoughlin et al. 200l, Dahle and Swenson 2003, Nilsen et al. 2005, Edwards et al. 2013). These relationships have been documented for other solitary species with overlapping home ranges, including experimental manipulations of rodent populations (Taitt 1981, Mares et al. 1982) and field studies of other rodents and large mammals (Saïd et al. 2005, Wauters et al. 2005, Stradiotto et al. 2009). Bears typically respond to increased population density by decreasing their home range, presumably as a reaction to intra-specific social pressures (Dahle and Swenson 2003, Dahle et al. 2006). In addition to the declines in key foods, particularly whitebark pine, grizzly bears in the GYE also experienced increasing population density after several decades of robust population growth (Harris et al. 2006). Therefore, Bjornlie et al. (in review) examined patterns in home-range size of 127 females and 96 males to determine potential associations with resource decline or population density using the period of whitebark pine decline (2007–2012) and a period prior to the decline (1989–1999) as a natural experiment.

Using an annual time step and a coarse spatial scale (14 km × 14 km), Bjornlie et al. (in review) developed a spatially explicit index of bear density based on >1,800 captures of 870 individuals during 1975–2012. The index was based on hind- and forecasting activity ranges of captured bears through time based on their known ages and year of death. For bears whose fates were unknown, they used sex-specific survival probabilities to forecast the annual probability of remaining in the population. The mean density index was positively correlated with mean log-transformed counts of bear groups/hr/1,000 km^2 within Bear Observation Areas monitored by the IGBST ($r = 0.725$, $P < 0.001$, $n = 28$), providing evidence it tracked changes in the population. Bjornlie et al. (in review) measured proportion of whitebark pine habitat in home ranges based on the LAS project, adjusting for tree mortality during the impact period (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011, Macfarlane et al. 2013).
Across the two periods (1989–1999 and 2007–2012), Bjornlie et al. (in review) observed among females: 1) a decrease in home-range size, 2) a decrease in the proportion of whitebark pine in the home range, and 3) an increase in the bear density index within home ranges (Table 1). Among males, they only observed a decrease in the proportion of whitebark pine in the home range (Table 1). Using an information-theoretic framework, they developed a set of models to test associations of home-range size with the individual estimates of density index versus proportion of whitebark pine. Home-range size was not associated with the proportion of whitebark pine in the home range, nor did it increase during the period of whitebark pine decline compared with the earlier period. Home-range size was, however, inversely associated with their index of grizzly bear density, primarily for females (model-averaged $\hat{\beta} = -0.443$, 95% CI = -0.708 to -0.178 for 95% a-local convex hull home range). This effect was observed irrespective of period: in areas where bear densities were high, home ranges tended to be smaller, even during the earlier period when areas with high bear densities were fewer and overall density was lower. Although variation was high, female home-range size decreased with increasing index of bear density and became much less variable (Fig. 6). This inverse relationship between home-range and density is well supported (e.g., Dahle and Swenson 2003). Bjornlie et al. (in review) attributed the stronger relationship among females to philopatry and matrilineal home ranges. Males have much larger home ranges (Schwartz et al. 2003) and may have greater opportunities

Table 1. Sample size (*n*), area (km^2; 95% α-local convex hull method), proportion whitebark pine (WBP; adjusted for tree mortality during impact period), and density index associated with grizzly bear home ranges in the GYE during pre-impact (1989–1999) and impact periods (2007–2012) (modified from Bjornlie et al., in review).

Cohort	Metric	Pre-impact period $\bar{X}$ ± 1 sd	Impact period $\bar{X}$ ± 1 sd	*t*-test[a]
Females	*n*	71	56	
	Home-range size	103 ± 72	81 ± 63	*t* = -2.05, *P* = 0.043
	WBP proportion	0.19 ± 0.18	0.11 ± 0.15	*t* = -2.78, *P* = 0.006
	Density index	13.6 ± 4.2	17.0 ± 6.8	*t* = 3.31, *P* = 0.001
Males	*n*	51	45	
	Home-range size	268 ± 253	309 ± 289	*t* = 0.56, *P* = 0.580
	WBP proportion	0.19 ± 0.18	0.10 ± 0.13	*t* = -2.90, *P* = 0.005
	Density index	13.2 ± 4.8	15.0 ± 5.2	*t* = 1.78, *P* = 0.078

[a] Test results based on log transformation of home-range size and z-score transformation of WBP proportion and density index.

to accommodate effects of increasing densities and resource variation without adjusting home-range area.

The results of Bjornlie et al. (in review) suggest that bear density in the GYE may have a greater influence on home-range size than the availability of whitebark pine. We note, however, that these relationships may be different when overall food supply is considered. Indeed, an alternative explanation for the reduction of female home ranges may be that overall food supply increased. However, data from the GYE do not provide much support for this interpretation. Given that the proportion of live whitebark pine in home ranges declined but home-range size remained the same or decreased, combined with the previously reported lack of evidence of a decline in body condition, alternative resources seem to be available to grizzly bears within their established home ranges.

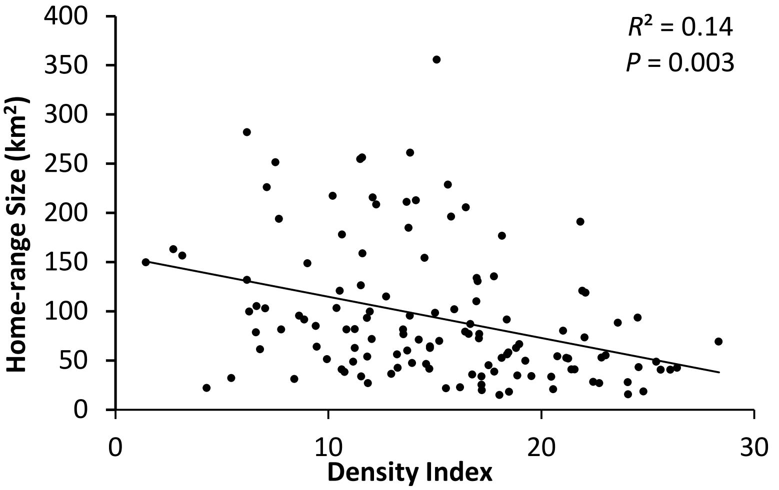

Figure 6. Relationship between home-range size and index of grizzly bear density within home ranges in the Greater Yellowstone Ecosystem, 1989–2012 (modified from Bjornlie et al., in review).

Research Question 8: Are changes in vital rates during the last decade associated more with decline in whitebark pine resources than increases in grizzly bear density?

Changes in a population trajectory are a manifestation of changes in vital rates (e.g., survival, fecundity), which, in turn, reflect the influence of a combination of ecological processes on a wildlife population. Ultimately, availability and access to food resources are determining factors (McLellan 1994).

However, access to food resources may be mediated by density through direct or indirect competition. Zedrosser et al. (2006) found that body size of adult female brown bears was positively associated with food conditions but may be constrained by competition for food at higher densities. Density may also influence vital rates through mechanisms such as infanticide by adult males (Swenson et al. 1997, Wielgus and Bunnell 2000). Although population-level effects due to changes in resources or density-dependent factors are difficult to separate, determining the strength of association with changing vital rates would at least be indicative of which factor(s) may be acting more strongly. Therefore, van Manen et al. (in prep.) investigated whether observed slowing of population growth during the last decade (IGBST 2012) was more strongly associated with an individually based measure of resource decline (i.e., reduction of healthy whitebark pine overstory vegetation), versus an individual estimate of grizzly bear density (i.e., density-dependent effects) associated with a bear's position in the landscape. Key determinants of bear population dynamics are survival of adult females, survival of cubs and yearlings, and the probability of reproductive transition of adult females from having no offspring one year to cubs the following year. Among grizzly bear populations, the parameter that generally contributes most towards 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, high variance of juvenile survival and recruitment compared with adult female survival may have a greater influence on population growth (Harris et al. 2011).

To address this research question, van Manen et al. (in prep.) examined 3 parameters using program MARK (White and Burnham 1999): 1) reproductive transition probability of females (multi-state live-encounter model of transition from no offspring to cubs; $n = 300$ encounter histories), 2) cub and yearling survival (daily survival rate model; $n = 355$ encounter histories), and 3) independent bear survival (≥2 yrs; known-fate model; $n = 1,872$ encounter histories). Change-point analysis indicated the change in annual growth rate of the population occurred around 2001 (M. Higgs, unpublished data), so van Manen et al. (in prep.) defined 2 periods as a covariate (i.e., 1983–2001 and 2002–2012) to account for inherent differences in vital rates; whitebark pine decline coincided with the second period. They examined whether vital rates were associated with whitebark pine decline or grizzly bear density and, if so, if they were different for the 2 periods (interaction effect). Using the spatial and temporal information of individually marked bears, they assigned covariates for each bear in the analysis based on an index of whitebark pine decline, an index of grizzly bear density, and time period. These individual-based covariates were not available for the studies of Schwartz et al. (2006*d*) and enhanced inference regarding factors associated with variation in vital rates. The individual covariates were the index of grizzly bear density used by Bjornlie et al. (in review) and a spatiotemporal index of change in healthy whitebark pine canopy, using 2000 as the reference year (derived from MODIS NDVI [normalized difference vegetation index] satellite data; M. Ebinger, University of Montana, unpublished data). Both indices were measured based on mean values associated with activity radii of annual locations of sampled bears. The indices showed considerable variation among individuals but also reflected changes over time. A suite of models incorporating the above covariates and their interactions were developed and tested.

Using an information-theoretic analysis framework, van Manen et al. (in prep.) found most support for a reproductive transition model that included period, density index, and a period × density interaction (Akaike's Information Criterion [$\mathrm{AIC_c}$] weight = 0.57) and a period-only model ($\mathrm{AIC_c}$ weight = 0.22); models with terms for whitebark pine impact had $\Delta\mathrm{AIC_c}$ values ≥2.93 and thus received less support. The probability of reproductive transition from no offspring to cubs declined from 1983–2001 (period 1) to 2002–2012 (period 2), and was a function of increasing density. Similarly, they found most support for a cub and yearling survival model that included period, density index, and a period × density interaction ($\mathrm{AIC_c}$ weight = 0.65) and a period-only model ($\mathrm{AIC_c}$ weight = 0.27); models with terms for whitebark pine impact had $\Delta\mathrm{AIC_c}$ values ≥5.31 and thus had little support. Cub survival was associated with the bear density index and this relationships changed from 1983–2001 to 2002–2012, with cub survival declining during the latter period. The analyses of van Manen et al. (in prep.) further indicated the association of lower cub survival with density was most distinct starting around the year 2001 (Fig. 7). Finally, for survival of independent bears, van Manen et al. (in prep.) only observed an effect due to period, corresponding with greater male survival during 2002–2011, which was documented previously (IGBST 2012), but no association with density or whitebark pine decline. These demographic results support the interpretation that slowing of population growth during the last decade may be more associated with increasing grizzly bear density and not simply a direct function of whitebark pine decline.

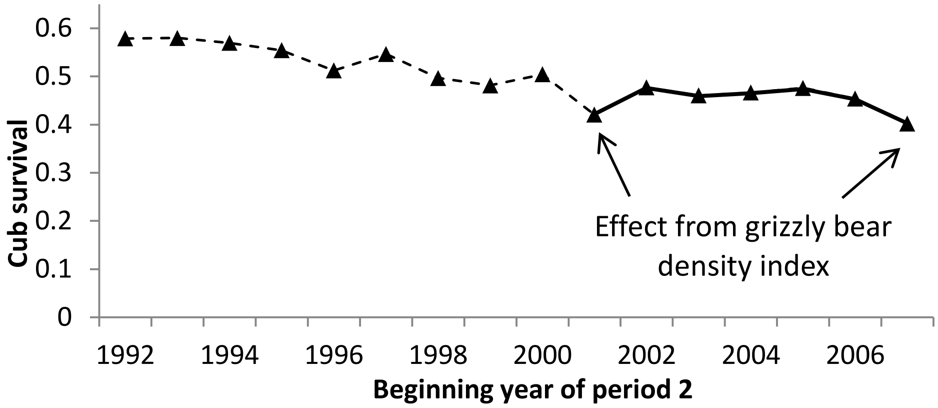

Figure 7. Annual cub survival of grizzly bears in the Greater Yellowstone Ecosystem as a function of varying time periods to determine when the relationship between cub survival and bear density changed during 1983–2012 (van Manen et al., in prep.). An early (period 1) and late period (period 2) were defined and were varied for this analysis (e.g., the value for year 1992 reflects cub survival for period 1992–2012, the value for year 1993 reflects 1993–2012, and so on). Starting in 2001, cub survival was lower for period 2 compared with period 1 due to an interaction with the bear density index.

5. DISCUSSION

Numerous studies provide evidence of considerable ecological plasticity among bears in general (e.g., Stirling and Derocher 1990, Yeakel et al. 2013) and brown bears in particular (Van Daele et al. 2012). Diet plasticity is central to the evolutionary strategy of brown bears, which allows them to occupy a wide range of the world's biomes (Schwartz et al. 2013*b*) and may, in part, explain why brown bears occupy the greatest diversity of habitats of the 8 bear species in the world (Schwartz et al. 2003). Our recent studies of grizzly bears in the GYE support similar diet diversity and ecological plasticity. Yellowstone grizzly bears exhibit substantial diet breadth seasonally and spatially. We found that historically and contemporarily a sizeable proportion of Yellowstone grizzly bears occupy areas with little or no whitebark pine habitat and thus exhibit variation in primary food resources in their diets. Yellowstone grizzly bears have also demonstrated the ability to successfully shift major food items in their diet as availability changes (Gunther et al., in review). In response to reduced availability of whitebark pine, Yellowstone grizzly bears exhibited reduced selection of whitebark pine habitat over the past decade in addition to a shorter and delayed duration of use during poor cone production years. This response presumably reflects a reduction in midden excavation by grizzly bears, which was also documented after the extensive 1988 fires (Podruzny et al. 1999). As an alternative to whitebark pine consumption, grizzly bears seem to have increased consumption of animal matter and other foods. Stable isotope analyses of samples collected 2000–2010 (Schwartz et al. 2013*a*) and analyses of carcass use (Ebinger et al., in prep.) support an increase in consumption of animal matter coinciding with the period of reduced use and selection of whitebark pine habitat. In the apparent transition of grizzly bears reducing use of whitebark pine seeds and shifting to other foods, movements and home-range size did not increase, the latter actually declining for females (Table 1). Additionally, whitebark pine availability was not associated with home-range size, but rather home-range size was more closely linked with bear density (Bjornlie et al., in review). Recent analyses suggest that foods available in the GYE are adequate to maintain body condition at levels prior to whitebark pine decline. Furthermore, recent analyses of demographic rates (IGBST 2012) do not indicate a decline in fecundity (m_x) during the last decade (2002–2011; $\overline{m}_x$ = 0.29, 95% CI = 0.23–0.35) compared with 1983–2001 ($\overline{m}_x$ = 0.32, 95% CI = 0.28–0.36). Thus, this body of new work conducted in the GYE suggests that grizzly bears continue to access food resources sufficient to maintain individual productivity, even in the face of whitebark pine decline

At the population level, we addressed whether bears may become more vulnerable to mortality in less secure habitat areas due to whitebark pine decline, based on observations by Schwartz et al. (2010) that grizzly bears move to lower elevations during poor whitebark pine years. The analyses of Haroldson et al. (in prep.) indicate whitebark pine cone production is still associated with reduced human-caused mortalities in fall for independent-aged grizzly bears (Fig 5). They also provided evidence that the increase in mortalities has been small for both sexes inside the Recovery Zone during 2000–2012. Outside the Recovery Zone, mortalities have been increasing at a faster rate. Whether this may be due to effects of whitebark pine decline or to expansion of occupied grizzly bear range into locales where landscapes are less suitable for long-term occupancy is difficult to ascertain. The lack of a distinct mortality trend inside the Recovery Zone, where availability of whitebark pine habitat is greater, provides support for the latter explanation. The increase in number of mortalities was small and was not apparent in survival estimates of independent-aged bears during 2002–2011: annual survival for subadults (2–4 years; both sexes) and adult (≥5 years) females was 0.95, showing no change from 1983–2001, whereas adult male survival actually increased from 0.87 during 1983–2001 to 0.95 during 2002–2011 (Haroldson et al. 2006, IGBST 2012).

Demographic analyses indicated a decline in cub survival and the probability of reproductive transition during 2001–2012 are associated with an index of grizzly bear density rather than availability of whitebark pine (van Manen et al., in prep.). Eberhardt (1977) 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. Indeed, evidence exists that cub survival is a potential density-dependent factor in population regulation among bear populations, although different mechanisms have been proposed by which density-dependence affects cub survival (Miller 1990; Swenson et al. 1997, 2001; Wielgus and Bunnell 2000; Wielgus et al. 2001; Miller et al. 2003; McLellan 2005). Results of van Manen et al. (in prep.) are consistent with suggestions by Schwartz et al. (2006*a, c*), who postulated based on 1983–2001 data that density-dependence may affect reproductive output and cub and yearling survival among GYE grizzly bears. Observed changes in vital rates (IGBST 2012) are consistent with the observed slowing of estimated annual population growth since the early 2000s. Lower cub survival, in particular, may have been a primary contributor to reduced population growth. The observed reduction in cub survival from an estimated 0.640 during 1983–2001 to 0.553 during 2002–2011 would have reduced annual population growth, from 1.074 to 1.049 (van Manen et al., in prep.). 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).

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. Of course, population changes mediated by density dependence may be linked with resources and carrying capacity of the environment. Thus, there is the possibility that decline in the whitebark pine resource reduced carrying capacity, which, in turn, could have affected cub survival and reproductive transitions. If that had occurred, however, we would have expected home-range size to increase, bears to have relied on lower-quality food resources, and body condition to have declined. There is little support for these conditions to date in the Yellowstone Ecosystem.

Finally, our research demonstrates that a paradigm shift may be in order with regard to the significance of whitebark pine as a food resource for grizzly bears in the GYE. Whereas whitebark pine is used extensively by bears when available, we note the long-documented history of intra-population variation in feeding strategies (i.e., diet specialization). The simple concept of the 3 feeding economies of Mealey (1980) still largely applies to occupied grizzly bear range in the GYE. Whitebark pine is, and has historically been, absent from the home range or diet of a sizable portion of the Yellowstone grizzly population (Mealey 1980; Costello et al., in review). Even in areas where whitebark pine is available, it is not consistently used every year due to stochastic nature of masting events (e.g., 8 out of 20 years prior to 2000 had cone counts representative of good production years). We speculate the historic emphasis on whitebark pine resulted in part from the fact that it is an easily measured resource compared with most other grizzly bear diet items. Because of extensive whitebark pine data we have gained substantial knowledge about its ecological role for grizzly bears in the GYE. Combined, the findings of studies presented here do not indicate strong dependence among GYE grizzly bears on whitebark pine seeds but rather, where and when available, the inclusion of this food as a component of a diverse and dynamic diet.

6. CONCLUSIONS

Whitebark pine is a diminished resource for grizzly bears in the GYE, but bears whose habitat overlaps with whitebark pine continue to forage on pine seeds when available. Despite evidence that the current mountain pine beetle outbreak is waning and that effects from blister rust are limited and manageable, the long-term future of whitebark pine remains uncertain in light of climate change. However, evidence from the analyses presented here suggests that whitebark pine decline has had no profound negative effects on grizzly bears at the individual or population level. The findings of analyses presented here indicate that the Yellowstone grizzly bear population has shown notable resilience in the face of decline of whitebark pine and natural stochasticity of other food resources within the GYE. Grizzly bears obtained sufficient alternative foods through diet shifts and have maintained body mass and percent body fat over time. Based on extensive demographic analyses completed to date, we have not observed a decline in the Yellowstone grizzly bear population but only a slowing of population growth since the early 2000s (IGBST 2012, Haroldson et al. 2013, Higgs et al. 2013), possibly indicating the population is near carrying capacity. Evidence from demographic analyses indicates that the change in population trajectory was more associated with grizzly bear density, primarily through reduced cub survival and reproductive transition, rather than whitebark pine decline. Finally, the number of fall mortalities increased during 2000–2012 but effect sizes seem small and were not apparent in survival estimates of independent-aged bears for that period. Therefore, the increase in number of mortalities is unlikely to have affected population growth.

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