



Research Article

# Body and Diet Composition of Sympatric Black and Grizzly Bears in the Greater Yellowstone Ecosystem

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**ABSTRACT** The Greater Yellowstone Ecosystem (GYE) has experienced changes in the distribution and availability of grizzly bear (*Ursus arctos*) food resources in recent decades. The decline of ungulates, fish, and whitebark pine seeds (*Pinus albicaulis*) has prompted questions regarding their ability to adapt. We examined body composition and diet of grizzly bears using bioelectrical impedance and stable isotopes to determine if 1) we can detect a change in diet quality associated with the decline in either ungulates or whitebark pine, and 2) the combined decline in ungulates, fish, and pine seeds resulted in a change in grizzly bear carrying capacity in the GYE. We contrasted body fat and mass in grizzly bears with a potential competitor, the American black bear (*Ursus americanus*), to address these questions. Grizzly bears assimilated more meat into their diet and were in better body condition than black bears throughout the study period, indicating the decline in ungulate resources did not affect grizzly bears more than black bears. We also found no difference in autumn fat levels in grizzly bears in years of good or poor pine seed production, and stable isotope analyses revealed this was primarily a function of switching to meat resources during poor seed-producing years. This dietary plasticity was consistent over the course of our study. We did not detect an overall downward trend in either body mass or the fraction of meat assimilated into the diet by grizzly bears over the past decade, but we did detect a downward trend in percent body fat in adult female grizzly bears after 2006. Whether this decline is an artifact of small sample size or due to the population reaching the ecological carrying capacity of the Yellowstone ecosystem warrants further investigation. © 2013 The Wildlife Society.

**KEY WORDS** American black bear, bioelectrical impedance, body condition, body mass, diet, grizzly bear, stable isotopes, Yellowstone.

Grizzly bears (*Ursus arctos*) are opportunistic omnivores (Schwartz et al. 2003) and feed on an array of animals and plants. The Greater Yellowstone Ecosystem (GYE) contains large populations of ungulates and winter-killed elk (*Cervus elaphus*) and bison (*Bison bison*) are primary spring foods for 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 use carcasses throughout the active season and, since reintroduction of gray wolves (*Canis lupus*), usurp wolf kills (MacNulty et al. 2001, Ballard et al. 2003, Gunther and Smith 2004). 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 ( $\delta^{15}\text{N}$ ) in grizzly bear hair 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 meat is a nutritional buffer in years of poor whitebark pine (*Pinus albicaulis*) cone production (Mattson 1997, Felicetti et al. 2003). In contrast, diets of American black bears (*Ursus americanus*) in the GYE

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are composed mostly of vegetative material in the form of grasses, forbs, and fruits, with animal matter coming principally from insects (Fortin et al. 2013; S. Cain, National Park Service, unpublished data). Ungulates are consumed by black bears but the frequency of use is substantially less than use by grizzly bears (Fortin et al. 2013).

Ungulate numbers in the GYE likely have declined in the past decade. The bison population in the park has fluctuated largely because of a removal program directed at brucellosis (*Brucella abortus*) management (Cross et al. 2010b). Approximately 40% of the park's bison population was removed in 2008 (Cross et al. 2010a). Elk numbers on the northern range, in the Madison-Firehole, and in the Gallatin Canyon have declined, but elk numbers from some herds east of the national park either remained constant or increased (Creel 2010, Cross et al. 2010a). Competition for the ungulate resource among predators has increased because of a threefold increase in grizzly numbers since the 1970s and growth of the reintroduced wolf population from 31 individuals in 1995 to 376 individuals in 31 packs by 2006 (Schwartz et al. 2006, Barber-Meyer et al. 2008, Creel 2010).

Spawning cutthroat trout (*Oncorhynchus clarkii*) were a primary food source for grizzly bears from mid-May through July from tributary streams to Yellowstone Lake (Reinhart and Mattson 1990), but this fish population has declined from whirling disease (*Myxobolus cerebralis*) and non-native lake trout predation (*Salvelinus namaycush*; Koel et al. 2003). Currently, the cutthroat trout population is estimated to be <10% of historical numbers (Koel et al. 2005) and Fortin et al. (2013) found biomass of cutthroat trout consumed by grizzly bears and black bears declined by 70% and 95%, respectively, between 1997 and 2007.

When available, seeds from whitebark pine are a favored food during late summer and autumn for grizzly bears (Mattson et al. 1991). Bears obtain seeds by raiding red squirrel middens (*Tamiasciurus hudsonicus*; Kendall 1983, Mattson and Reinhart 1997). Whitebark pine, a masting species that produces a seed crop every 2–3 years, has been shown to positively influence cub production following years of good seed production, and contribute to reduced survival during years of poor seed production, particularly in areas of the GYE affected by humans (e.g., high road density, developed areas; Mattson et al. 1992; Schwartz et al. 2006, 2010).

Whitebark pine has been attacked by white pine blister rust (*Cronartium ribicola*) and mountain pine beetles (*Dendroctonus ponderosae*), the latter having caused the greatest mortality (Greater Yellowstone Whitebark Pine Monitoring Working Group 2006, Gibson 2007). Cumulative mortality of whitebark pine trees used to index cone production was high from 2002 to 2009 (70%; Haroldson and Podruzny 2010), but the trend in mortality of whitebark trees has slowed in recent years (73% cumulative mortality in 2012; Haroldson and Podruzny 2013). Concern about the potential threat of whitebark pine decline on the Yellowstone grizzly bear prompted a challenge to the 2007 delisting of this population from the Endangered Species Act, which ultimately resulted in reinstatement of its threatened status in March 2010.

In contrast to the GYE, grizzly bears in the Flathead Valley of Canada, where they are sympatric with black bears, fed almost exclusively on plant matter (McLellan 2011). As suggested by several others (Welch et al. 1997, Apps et al. 2004, Mattson et al. 2005), McLellan (2011) felt that black bears in the Flathead had a competitive advantage over grizzly bears because the lower energy requirements associated with their smaller body mass allowed black bears to accumulate greater percent body fat on a low-protein diet of small, dispersed fruits (primarily huckleberry [*Vaccinium membranaceum*] and buffaloberry [*Shepherdia canadensis*]). Supporting this hypothesis, black bears had a greater percentage of body fat compared with grizzly bears (McLellan 2011).

The differences in diets and body fat among bear species between the GYE and the Flathead suggest that the competitive advantage of 1 bear species over the other may depend on the quality and ability to defend foods. Because the GYE has experienced changes in some of the high-quality foods, we were interested in what potential impacts these might have on grizzly bear food habits and body condition. We focused on 2 issues: 1) is there a change in diet quality associated with the decline in either ungulates or whitebark pine, and 2) has the combined decline in fish, ungulates, and pine nuts resulted in a change in the carrying capacity of the GYE for grizzly bears. We do not specifically address changes in availability of cutthroat trout in this paper because the decline in this food has been addressed in previous works by Haroldson et al. (2005) and Fortin et al. (2013).

To evaluate the impact of the decline in ungulate numbers on the 2 bear species, we hypothesized the following. If the decline in ungulate numbers has reduced their consumption, we would expect to detect a decline in  $\delta^{15}\text{N}$  during 2000–2010. Because grizzly bears can dominate and defend meat in the form of ungulate carcasses until fully consumed, we would also expect that grizzly bear diets would contain more meat than diets of black bears, and large grizzly bear males would have  $>\delta^{15}\text{N}$  signatures than smaller females and subadults over this same time period (Welch et al. 1997, Rode et al. 2001, Robbins et al. 2007). Alternatively, adult males might be the first to show a decline in either  $\delta^{15}\text{N}$  or body condition associated with the decline in ungulates because adult males are more predatory than other ages and sexes (Fortin et al. 2013). Fortin et al. (2013) also found that male grizzly bears in the Yellowstone Lake area made little use of false-truffles (*Rhizopogon* spp.), which could compound interpretation of  $\delta^{15}\text{N}$  signatures, so males may be a sensitive indicator of decline in ungulate resources. Because insects comprise a more substantial source of animal matter in diets of black bears than grizzly bears, we would expect no change in  $\delta^{15}\text{N}$  among black bears during the period of ungulate decline because we are not aware of coinciding insect declines. We further hypothesized that if grizzly bears are still capable of obtaining sufficient amounts of meat, they would be fatter than black bears and therefore at a competitive advantage because of the influence of body condition on reproduction (Robbins et al. 2012).

To evaluate the decline in whitebark pine on grizzly bears, we hypothesized the following. If the decline in whitebark pine seeds has reduced diet quality of grizzly bears (e.g., root, foliage, and meat cannot serve as alternative, high-quality foods), we would expect to detect a difference in body fat levels in autumns of good seed production versus autumns of poor seed production. Alternatively, if roots, foliage, and meat serve as high-quality alternative foods in the absence of whitebark pine seeds in autumn, we would expect body condition in grizzly bears is unrelated to whitebark pine seed production. If high-quality alternative foods were available in years of low whitebark pine production, we likewise would hypothesize that fat levels in bears would not have declined over the past decade (i.e., declines in pine seed crops have not resulted in a net decline in body condition over time).

To determine if changing food resources (fish, ungulates, and whitebark pine) are affecting or beginning to affect carrying capacity of grizzly bears in the GYE, we focused on 2 issues: the relative difference in diet and condition between black and grizzly bears during 2000–2010 and particularly in years with good and poor crops of whitebark pine seeds. Because the number of grizzly bears has increased in the GYE over the past 3 decades (Interagency Grizzly Bear Study Team [IGBST] 2012), and most available habitat is now occupied (Bjornlie et al. 2013), the population may be approaching ecological carrying capacity ( $K$ ). This idea was supported by Boyce et al. (2001) and Schwartz et al. (2006), who observed evidence of density dependence in juvenile survival and cub production. We explored a suite of alternative hypotheses that focus on the state of the grizzly bear population relative to carrying capacity. Because little is known regarding when density-dependent phenomena may manifest themselves in bear populations (i.e., along the gradient of  $0.5K$  to  $K$ ), our hypotheses reflect a relative scale. If the population is well below  $K$  (i.e., not affected by food), we hypothesized that grizzly bear mass and body condition would remain constant over the period of food decline. We would not expect to see a decrease in the amount of meat in the diet over time (i.e., ungulate resource are abundant enough to meet dietary needs) and the lack of change would be consistent among cohorts. In a second scenario, the grizzly bear population is much closer to  $K$ , either as a result of an increasing bear population or decline of  $K$  because of the decline of whitebark pine seeds, ungulates, and fish, and alternative foods are not high enough in quality and availability to meet the population needs. If this is the case, we hypothesized we would see a decline over time in grizzly bear body condition, mass, and the proportion of meat in the diet because available resources per bear would decrease. We also hypothesized that these effects would be most distinct among subadults and adult females that could not defend an ungulate carcass against adult males. Additionally, if the declines of ungulates, fish, and seeds of whitebark pine were sufficient to reduce  $K$  in the GYE for grizzly bears, we predicted the environment would become more suitable for black bears (e.g., similar to Flathead Valley) and therefore black bears would have better body condition than grizzly bears.

## STUDY AREA

At the time of our study, grizzly bears occupied approximately 50,280 km<sup>2</sup> in the GYE (Bjornlie et al. 2013). Our study area essentially coincided with occupied grizzly bear range and included Yellowstone and Grand Teton National Parks, portions of 6 adjacent national forests, plus state and private lands in Montana, Wyoming, and Idaho. Grizzly bears and black bears were sympatric throughout this region. All 3 states had black bear hunting seasons. Yellowstone grizzly bears were protected under the Endangered Species Act for most of our study period (2000–2010) and were not hunted during a short interval (2007–2009) in which the population was delisted. The GYE is 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. Detailed descriptions of the geography, climate, and vegetation appear in Schwartz et al. (2006).

Rasker (1991) included the 20 surrounding counties in the definition of the GYE because of the strong ecological and socioeconomic linkages between public and private lands within the area. Gude et al. (2007) used this area because development regulations were implemented at the county level. The area encompassed 145,635 km<sup>2</sup> with public and tribal lands making up 68% of the region. Land ownership was divided among private lands (32%), United States Department of Agriculture Forest Service (32%), Bureau of Land Management (19%), National Park Service (7%), Tribal Lands (5%), and state lands, wildlife refuges, and other federal lands (5%; Gude et al. 2007).

## METHODS

### Trapping and Handling

Members of the Interagency Grizzly Bear Study Team (IGBST) have captured bears for research and monitoring since the 1970s. We used data from bears captured during 2000–2010. 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)), Yellowstone National Park Research Permit YELL-00073, and Grand Teton National Park Research Permit GRTE 1990-Sci-0003. We used culvert traps or Aldrich leg-hold snares to capture bears (Blanchard 1985). We conducted trapping in both front- (road access) and backcountry (no road access) settings within and outside national parks and wilderness areas. Although some bears were captured where they were in conflict with humans, we only included bears trapped for research and monitoring

purposes because we wanted to make inferences to wild bears in the GYE. Beginning in 2000, we also marked a sample of black bears, mainly from the range of the northern Yellowstone elk herd, around Yellowstone Lake, and within Grand Teton National Park.

### Body Composition

We weighed all bears with an Artech Model 20210-2K s-beam load cell (Artech Industries, Inc., Riverside, CA) and a 4406 indicator (A&D Co., Ltd., Tokyo, Japan). We measured body composition by bioelectrical impedance (Quantum II, RJL Systems, Clinton Township, MI) following procedures outlined by Farley and Robbins (1994) and detailed by Hilderbrand et al. (1998). We placed each bear on a tarp prior to bioelectrical impedance analysis measurements to prevent erroneous readings because of electric conductivity with the ground. We determined total body water and body lipid content using equations for black and brown bears following Farley and Robbins (1994).

We obtained our samples from 4 cohorts: subadult and adult males and females of each species. We defined age class for black bears as subadults (2–3 years old) and adults ( $\geq 4$ ), whereas grizzly bear subadults were 2–4 years old and adults were  $\geq 5$  old. We treated whitebark pine cone production as a continuous variable as discussed by Schwartz et al. (2006:14), but we also classified whitebark pine seed crop into good or poor years based on the percent of trees producing above (good) or below (poor) the overall median count of cones/tree on transects monitored annually throughout the GYE (Haroldson et al. 2004). A mountain pine beetle outbreak began around 2003 in the GYE. To account for the potential decline in cone production, we modified the median cone count by multiplying it by the proportion of live trees remaining on transects. For example, if our median count was 22 cones/tree and the proportion of dead trees was 70%, we adjusted the cone count to 6.6 ( $22 \times 0.3$ ). We contrasted differences using univariate analysis of variance (ANOVA; GLM, SPSS 15.0, SPSS, Inc., Chicago, IL) and linear regression. We normalized proportional data using an arcsine transformation prior to statistical analyses (McDonald 2009) and back transformed values for presentation here.

### Stable Isotopes

All samples were analyzed by the Stable Isotope Core Laboratory at Washington State University. We prepared and analyzed all tissues (hair, red blood cells, and plasma) as per Felicetti et al. (2003). We lyophilized and homogenized red blood cells and serum samples, whereas hair samples were cleaned with deionized water to remove extraneous matter and washed with a 2:1 mixture of chloroform/methanol to remove lipids. We ground and homogenized a 15-mg representative portion of each clean hair sample using a wig-l-bug, which used a ball mill. We weighed 0.6-mg samples into tin boats for nitrogen analysis. We used an ECS 410 (Costech Analytical, Valancei, CA) elemental analyzer interfaced with a Delta Plus XP (Thermo-Finnigan, Bremen, Germany) mass spectrometer to analyze all samples via continuous flow–isotope ratio mass spectrometry (Fry

et al. 1992). The laboratory performed instrument stability checks and made necessary calibrations prior to all analyses. Samples and reference material were prepared to yield signals of the same amplitude, to account for bias. In addition, blind reference material was analyzed with samples as a check of the normalization. In this case, an independent protein standard, B-2155, (Elementar microanalysis) yielded mean delta values of 6.00‰ (5.94‰ actual)  $\delta^{15}\text{N}$ . We reported isotopic signatures as parts per thousand (‰) relative to  $N_{\text{air}}$  ( $\delta^{15}\text{N}$ ) using the internationally distributed standards USGS (U.S. Geological Survey) 32, 25, and 26. Our analytical error was estimated at  $\pm 0.1\%$ . We estimated the proportion of plant and animal matter in the assimilated diets using  $\delta^{15}\text{N}$  (nitrogen) for each unique bear.

We used nitrogen isotope values of food items derived by Fortin et al. (2013) for plants ( $-1.02 \pm 2.45\%$ ) and meat ( $4.07 \pm 0.68\%$ ). Fortin et al. (2013) used a weighted mean for meat based on percentage intake of the various meat sources from Mealey (1975), and we used that weighted mean here. They chose MixSIR for their mixing model because it accounted for variation among source isotopic signatures and fractionations (Semmens and Moore 2008). They excluded false truffles and insects from mixing models because of the unknown nature and digestibility of nitrogen bound in non-protein chitin (Cork and Kenagy 1989, Claridge and Cork 1994, Noyce et al. 1997, Claridge et al. 1999, Swenson et al. 1999). We used fractionation values of  $4.5 \pm 0.5\%$  for plants and  $4.0 \pm 0.1\%$  for meat (Robbins et al. 2005, Florin et al. 2011).

For each species, we contrasted the isotopic signature for sex, cohort (subadult and adult males and females), season (defined differently for each tissue), and year using data from 2000 to 2010. Although our age criteria for classifying subadults and adults differed by 1 year for grizzly bears and black bears, these criteria are based on reproductive maturity and thus provide valid comparison of isotopic signatures between the 2 species. We had adequate data for May–October and May–September for grizzly and black bears, respectively. Following the methods similar to Felicetti et al. (2003), we considered 2 seasons for hair based on observations of the timing of the annual molt among Yellowstone bears. We treated samples collected during May–June as being produced during the preceding year and to represent that year's diet. We considered hair collected in August–October as being produced during the current year and reflecting the current year's diet. We binned hair isotope data into spring and autumn seasons, excluding hair collected during July because we could not ascertain its age with certainty. We treated season for serum and blood clot samples (red blood cells) monthly, recognizing that serum reflected the isotopic signature of the foods consumed during the preceding 10–14 days and red blood cells that of foods consumed during the previous 3 months (Hilderbrand et al. 1996).

We performed statistical analyses on nitrogen isotope values using univariate ANOVA (GLM, SPSS 15.0) prior to running MixSIR. We used  $\delta^{15}\text{N}$  as the independent variable and combinations of bear species, cohort, year, season, and

whitebark pine seed production as dependent variables. We tested differences among means with least significant difference tests. Estimates are presented as mean  $\pm$  SE.

## RESULTS

### Body Composition

**Percent body fat.**—We captured and obtained body composition estimates from 316 (95 F, 221 M) grizzly bears and 144 (37 F, 107 M) black bears between May and October, 2000–2010. Grizzly bears were fatter on average (estimated marginal  $\bar{x} \pm$  SE:  $22.5 \pm 0.03\%$ ) than black bears ( $\bar{x} = 18.5 \pm 0.01\%$ ;  $F_{1,448} = 19.35$ ,  $P < 0.001$ ). On an absolute basis, grizzly bears were 4.0% fatter than black bears but based on percentage of body mass were 17.7% fatter. As expected, both species of bears were leaner in spring (Jun, Jul) and fatter in autumn (Sep, Oct;  $F_{5,448} = 18.98$ ,  $P < 0.001$ ; Fig. 1). Both species experienced monthly fat gains from June through October (Fig. 1); no species by month interaction was evident ( $F_{1,448} = 0.61$ ,  $P < 0.693$ ).

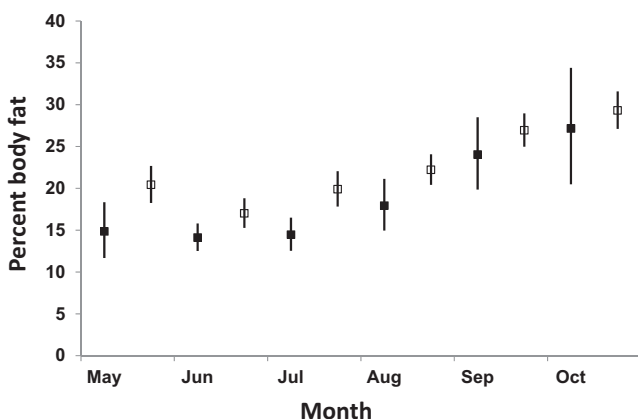
Body fat content differed among black bear age and sex cohorts ( $F_{3,109} = 5.36$ ,  $P < 0.001$ ). Adult females ( $n = 30$ ) were fatter ( $20.2 \pm 0.1\%$ ) than subadult females ( $n = 6$ ;  $8.3 \pm 0.2\%$ ), and adult males ( $n = 74$ ) were fatter ( $18.6 \pm 0.1\%$ ) than subadult males ( $n = 15$ ;  $13.1 \pm 0.1\%$ ). Subadult females and males did not differ ( $P = 0.086$ ) from each other, but the power to detect differences likely was limited by sample size. However, both had less fat than adults of both sexes ( $P = 0.028$ ). Body fat content of adult males and female black bears did not differ ( $P = 0.359$ ). We had adequate data to contrast body fat in black bears among years only for the adult cohorts ( $n = 31$  and 87 for adult females and males, respectively). Body fat content varied among years ( $F_{10,98} = 3.17$ ,  $P < 0.001$ ) during 2000–2010, but not by sex ( $F_{1,98} = 0.758$ ,  $P = 0.386$ ); a sex by year interaction was not significant ( $F_{7,98} = 0.599$ ,  $P = 0.777$ ), and linear regression showed no trend with time ( $R^2 = 0.019$ ,  $F_{1,116} = 2.245$ ,  $P = 0.137$ ; see Fig. S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Body fat content of grizzly bears differed among cohorts ( $F_{3,292} = 7.40$ ,  $P = 0.001$ ). Adult females ( $n = 69$ ) were fatter

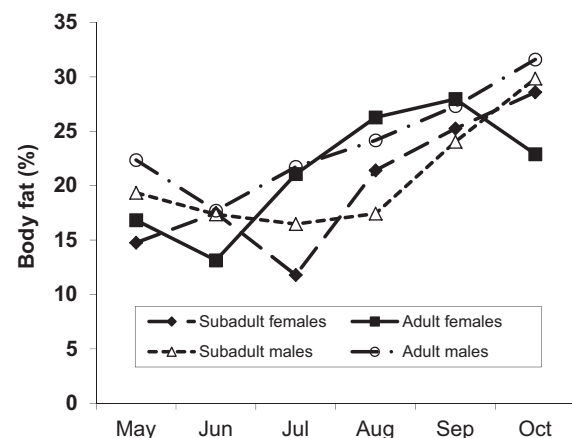
( $23.1 \pm 0.8\%$ ) than subadult females ( $n = 26$ ;  $19.5 \pm 0.7\%$ ), and adult males ( $n = 159$ ) were fatter ( $24.1 \pm 0.8\%$ ) than subadult males ( $n = 62$ ;  $20.1 \pm 0.9\%$ ). Subadult females and males did not differ ( $P = 0.684$ ), but both were less fat than adults of both sexes ( $P \leq 0.010$ ). Adult males and females were not different ( $P = 0.253$ ). Although monthly sample sizes likely were too low to detect statistical differences, adult females and males generally lost fat from den emergence through June, but then gained fat thereafter. Subadult males and subadult females lost fat from den emergence through July and then gained fat thereafter (Fig. 2).

Grizzly bear body fat content in September and October (i.e., when new crops of whitebark pine seeds were available) did not differ with the annual median counts of whitebark pine cones (range 0–22 cones/tree;  $R^2 < 0.001$ ,  $F_{1,110} = 0.002$ ,  $P = 0.961$ ; see Fig. S2a, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)), when adjusting cone production for recent mortality of whitebark pine trees by mountain pine beetles ( $R^2 = 0.001$ ,  $F_{1,110} = 0.137$ ;  $P = 0.712$ , see Fig. S2b, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)), or when compared between years of good cone production (mean  $\pm$  SE:  $28.0 \pm 0.010$ ) and poor cone production ( $28.1 \pm 0.007$ ;  $t_{110} = -0.104$ ,  $P = 0.276$ ). Grizzly bear body fat content did not differ by year ( $F_{10,91} = 1.34$ ,  $P = 0.221$ ) during 2000–2010, by sex ( $n = 35$  F, 77 M;  $F_{1,91} = 0.88$ ,  $P = 0.350$ ), or sex by year interaction ( $F_{9,91} = 1.17$ ,  $P = 0.323$ ), indicating no change in body condition with time. However, when we split the data by sex, linear regression analyses indicated body fat content of females decreased ( $R^2 = 0.238$ ,  $F_{1,33} = 10.33$ ,  $P = 0.003$ ), but male body fat content did not change ( $R^2 = 0.006$ ,  $F_{1,75} = 0.43$ ,  $P = 0.513$ ; Fig. 3). The change in female body fat content was not consistent for the 2000–2010 period but occurred after 2006.

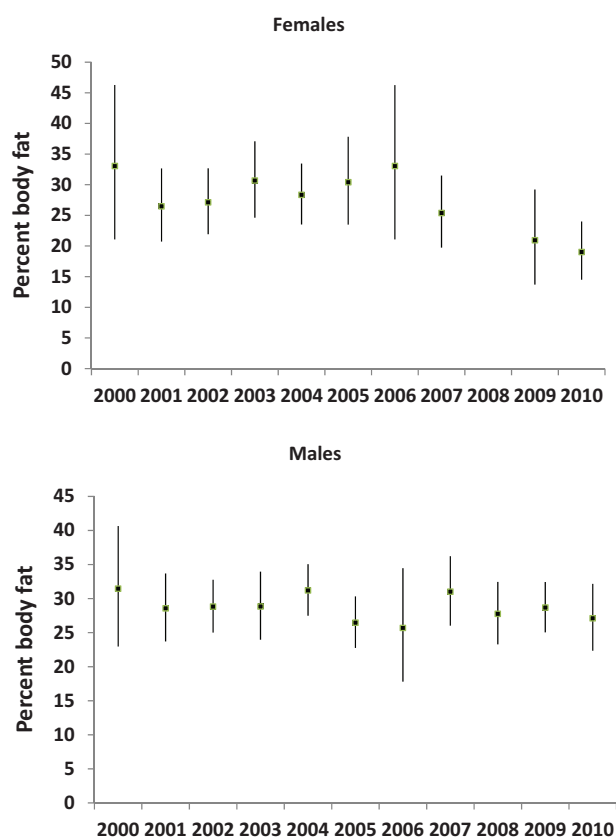
**Body mass.**—Adult female black bears weighed during June–September were heavier ( $69.1 \pm 4.3$  kg) than subadult females ( $45.2 \pm 9.0$  kg), and adult males ( $102.5 \pm 3.1$  kg) were heavier than subadult males ( $56.0 \pm 6.6$  kg;  $F_{3,109} = 27.70$ ,  $P < 0.001$ ). On average, adult males were 1.5 to 2.3 times heavier than the other 3 cohorts. Adult black



**Figure 1.** Percent body fat ( $\pm 95\%$  CI) for black (solid squares) and grizzly (open squares) bears by month in the Greater Yellowstone Ecosystem, 2000–2010.



**Figure 2.** Percent body fat by month for grizzly bear cohorts in the Greater Yellowstone Ecosystem, 2000–2010.



**Figure 3.** Percent body fat ( $\pm 95\%$  CI) for female and male grizzly bears in September and October in the Greater Yellowstone ecosystem, USA, 2000–2010.

bear mass (F:  $n = 28$ ,  $67.0 \pm 4.5$  kg; M:  $n = 81$ ,  $101.4 \pm 2.9$  kg) during the spring and summer (i.e., May to Aug) did not vary annually during 2000–2010 ( $F_{10,90} = 1.90$ ,  $P = 0.056$ ) nor did we find a sex by year interaction ( $F_{7,90} = 1.09$ ,  $P = 0.375$ ).

Mass of adult female grizzly bears between June and September was greater ( $116.7 \pm 4.1$  kg) than subadult females ( $82.1 \pm 7.3$  kg), and adult males ( $189.0 \pm 2.4$  kg) were heavier than subadult males ( $109.6 \pm 4.0$  kg;  $F_{3,292} = 170.80$ ,  $P < 0.001$ ). All 4 cohorts were statistically different from each other ( $P = 0.037$ ). Adult males ranged from 1.6 to 2.3 times heavier than all other age and sex classes. Body masses differed by month ( $P < 0.001$ ), but the cohort by month interactions were not different ( $P = 0.776$ ; see Fig. S3, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Grizzly bear body masses for adult females ( $n = 30$ ,  $134.73 \pm 8.71$  kg) and adult males ( $n = 59$ ,  $207.61 \pm 6.51$  kg) in the fall (Sep–Oct) did not vary annually during 2000–2010 ( $F_{10,68} = 0.236$ ,  $P = 0.991$ ) nor did we find a sex by year interaction ( $F_{9,68} = 0.667$ ,  $P = 0.735$ ). Similarly, spring and summer (May–Aug) grizzly bear body mass did not change during 2000–2010 for either adult females ( $n = 39$ ,  $112 \pm 5.42$  kg) or adult males ( $n = 100$ ,  $182 \pm 3.30$  kg;  $F_{10,117} = 1.19$ ,  $P = 0.305$ ) nor did we find a sex by year interaction ( $F_{10,117} = 0.62$ ,  $P = 0.797$ ). Grizzly bear body mass in fall (Sep and Oct) did not differ between good pine seed years

(F:  $n = 15$ ,  $135.49 \pm 9.97$  kg; M:  $n = 32$ ,  $203.89 \pm 6.83$  kg) and poor years (F:  $n = 15$ ,  $127.79 \pm 9.97$  kg; M:  $n = 27$ ,  $210.64 \pm 7.43$ ;  $F_{1,85} = 0.003$ ,  $P = 0.956$ ) nor did we find a sex by seed year interaction ( $F_{1,85} = 0.695$ ,  $P = 0.407$ ).

### Stable Isotopes

**Hair  $\delta^{15}\text{N}$ .**—We found no difference between hair samples collected in spring or fall for grizzly bears (spring:  $5.35 \pm 0.16\text{‰}$ ; fall:  $5.47 \pm 0.13\text{‰}$ ;  $F_{1,311} = 0.688$ ,  $P = 0.407$ ) or black bears (spring:  $3.92 \pm 0.19\text{‰}$ ; fall:  $3.89 \pm 0.26\text{‰}$ ;  $F_{1,86} = 0.011$ ,  $P = 0.917$ ) because both sampling times included the time period of hair growth. Grizzly bears had greater  $\delta^{15}\text{N}$  values ( $n = 221$ ;  $5.48 \pm 0.13\text{‰}$ ) in hair than black bears ( $n = 94$ ;  $3.97 \pm 0.13\text{‰}$ ;  $F_{1,311} = 100.53$ ,  $P < 0.001$ ). Animal matter comprised approximately 44.4% (95% CI = 40.7–48.3%) of the assimilated nitrogen consumed by grizzly bears and 27.1% (95% CI = 25.1–29.4%) of the assimilated nitrogen consumed by black bears.

For black bears, we found no difference in  $\delta^{15}\text{N}$  values in hair among cohorts ( $F_{3,86} = 0.826$ ,  $P = 0.483$ ), among years ( $F_{9,84} = 1.76$ ,  $P = 0.089$ ), nor in a season by cohort interaction ( $F_{3,86} = 1.029$ ,  $P = 0.384$ ; see Fig. S4, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Values of  $\delta^{15}\text{N}$  averaged  $3.58 \pm 0.52\text{‰}$  for subadult females,  $4.17 \pm 0.17\text{‰}$  for adult females,  $3.98 \pm 0.31\text{‰}$  for subadult males, and  $3.88 \pm 0.13\text{‰}$  for adult males. For grizzly bears, we found no difference in  $\delta^{15}\text{N}$  values in hair among cohorts ( $F_{3,213} = 0.989$ ,  $P = 0.399$ ), among years ( $F_{9,211} = 0.608$ ,  $P = 0.789$ ), nor in a season by cohort interaction ( $F_{3,213} = 0.364$ ,  $P = 0.779$ ). Values of  $\delta^{15}\text{N}$  in grizzly bears averaged  $5.27 \pm 0.27\text{‰}$  for subadult females,  $5.34 \pm 0.20\text{‰}$  for adult females,  $5.39 \pm 0.21\text{‰}$  for subadult males, and  $5.64 \pm 0.12\text{‰}$  for adult males.

We lacked sufficient data for grizzly bears to test for differences in meat consumption relative to the abundance of whitebark pine based on median cone counts, so we binned seed data into poor or good years for our analysis. We contrasted the concentration of  $\delta^{15}\text{N}$  values in hair collected in spring against the abundance of whitebark pine the previous fall under the assumption that spring hair was grown during late summer and autumn of the previous year. Our sample was comprised of 29 females (16 poor and 13 good pine seed years) and 66 males (28 poor and 38 good seed years). We did not detect a difference in  $\delta^{15}\text{N}$  values in hair between years of good and poor seed production for females ( $F_{1,28} = 0.30$ ,  $P = 0.586$ ,  $5.53 \pm 0.24\text{‰}$ ,  $5.25 \pm 0.48\text{‰}$ ) or males ( $F_{1,65} = 0.31$ ,  $P = 0.582$ ,  $5.24 \pm 0.33\text{‰}$ ,  $5.45 \pm 0.23\text{‰}$ ) sampled from 1999 to 2009. Adjusting for whitebark pine tree mortality,  $\delta^{15}\text{N}$  values in grizzly bear hair did not differ between poor and good seed years for females ( $F_{1,28} = 3.69$ ,  $P = 0.066$ ,  $5.76 \pm 0.27\text{‰}$ ,  $4.82 \pm 0.45\text{‰}$ ) or males ( $F_{1,65} = 0.04$ ,  $P = 0.847$ ,  $5.32 \pm 0.31\text{‰}$ ,  $5.40 \pm 0.23\text{‰}$ ).

**Blood clot  $\delta^{15}\text{N}$ .**—Grizzly bear blood clots collected from May through October ( $n = 163$ ) had greater  $\delta^{15}\text{N}$  values ( $6.00 \pm 0.08\text{‰}$ ) than black bear blood clots ( $n = 110$ ,  $3.94 \pm 0.15\text{‰}$ ;  $F_{1,261} = 145.97$ ,  $P < 0.001$ ). Approximately 52.8% (95% CI = 50.1–55.3%) of the assimilated nitrogen



consumed by grizzly bears and 26.9% (95% CI = 24.5–29.6%) consumed by black bears came from animal matter.

For black bears, we lacked sufficient data to contrast cohorts, so we only compared sex. We did not detect a difference in the  $\delta^{15}\text{N}$  values of blood clots between females ( $4.10 \pm 0.28\text{‰}$ ) and males ( $3.90 \pm 0.17\text{‰}$ ;  $F_{1,99} = 0.24$ ,  $P = 0.624$ ). Values of  $\delta^{15}\text{N}$  for blood clots decreased from 2002 through 2008 ( $F_{6,101} = 2.384$ ,  $P = 0.034$ ), suggesting a reduction in the consumption of animal matter (Fig. 4).

For grizzly bears, adult males had greater  $\delta^{15}\text{N}$  values ( $6.29 \pm 0.11\text{‰}$ ) than subadult females ( $5.42 \pm 0.32\text{‰}$ ), adult females ( $5.80 \pm 0.16\text{‰}$ ), and subadult males ( $5.80 \pm 0.17\text{‰}$ ). The 3 latter groups did not differ from each other. Thus, meat content of the assimilated diet was greater in adult males (57.9%, 95% CI = 54.0–62.0%) than in the diet of subadult females (43.6%, 35.0–53.2%), adult females (49.3%, 44.2–54.6%), or subadult males (49.2%, 43.9–54.9%). Values of  $\delta^{15}\text{N}$  in blood clots increased in grizzly bears during 2002–2009 ( $F_{7,154} = 2.508$ ,  $P = 0.018$ ; Fig. 4).

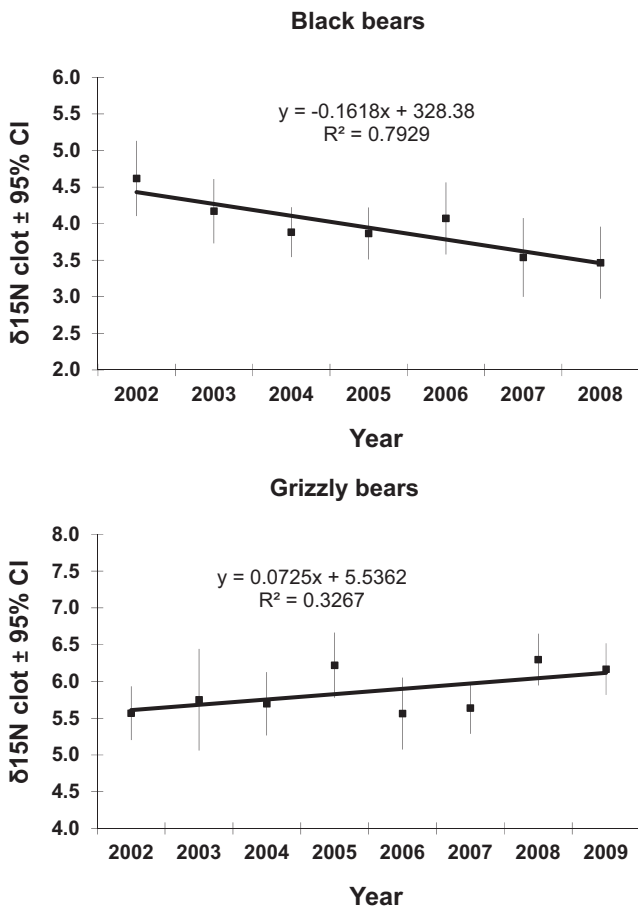
When  $\delta^{15}\text{N}$  values in grizzly bear blood clots were collected in September and October, 2000–2010, we observed no difference in years with whitebark pine seed crops classified as either poor or good years, respectively, for either female ( $n = 24$ ,  $F_{1,22} = 1.272$ ,  $P = 0.272$ ,  $5.32 \pm 0.23\text{‰}$ ,

$4.95 \pm 0.23\text{‰}$ ) or males ( $n = 53$ ,  $F_{1,51} = 1,570$ ,  $P = 0.106$ ,  $6.02 \pm 0.15\text{‰}$ ,  $5.68 \pm 0.14\text{‰}$ ). When we adjusted the seed crops for tree mortality because of mountain pine beetle infestations, we similarly found no difference in  $\delta^{15}\text{N}$  blood clot values for females ( $F_{1,22} = 2.231$ ,  $P = 0.149$ ,  $5.30 \pm 0.18\text{‰}$ ,  $4.80 \pm 0.31\text{‰}$ ) or males ( $F_{1,51} = 0.210$ ,  $P = 0.648$ ,  $5.88 \pm 0.13\text{‰}$ ,  $5.78 \pm 0.18\text{‰}$ ) between poor and good seed years, respectively. We lacked sufficient data for similar tests with black bears.

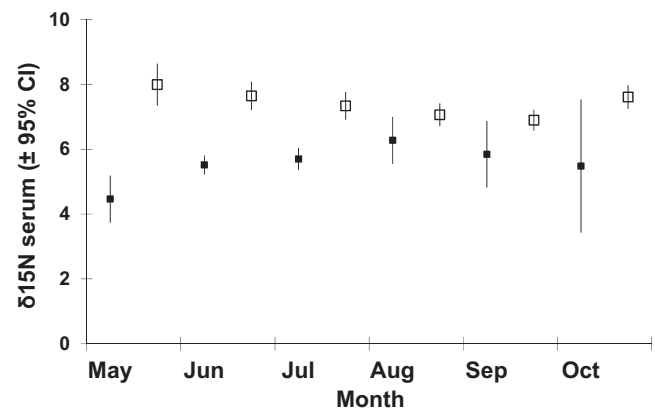
**Serum  $\delta^{15}\text{N}$ .**—Grizzly bears ( $n = 161$ ) had a greater  $\delta^{15}\text{N}$  value ( $7.43 \pm 0.09\text{‰}$ ) in serum collected from May through October than black bears ( $n = 106$ ,  $5.55 \pm 0.216\text{‰}$ ;  $F_{1,255} = 64.19$ ,  $P < 0.001$ ). Serum values of  $\delta^{15}\text{N}$  did not vary by month for either species ( $F_{5,255} = 0.485$ ,  $P = 0.788$ ), but we did observe a species by month interaction ( $F_{1,255} = 4.435$ ,  $P < 0.001$ ; Fig. 5). Approximately 78.2% (95% CI = 75.6–80.7%) of the assimilated nitrogen in grizzly bear serum came from animal matter compared with 45.3% (95% CI = 39.4–52.0%) in black bears.

Values of  $\delta^{15}\text{N}$  in black bear serum collected in June ( $5.49 \pm 0.18\text{‰}$ ), July ( $5.76 \pm 0.19\text{‰}$ ), August ( $6.23 \pm 0.39\text{‰}$ ), and September ( $6.01 \pm 0.62\text{‰}$ ) did not differ ( $F_{3,89} = 1.19$ ,  $P = 0.317$ ) nor did it differ between females ( $6.02 \pm 0.32\text{‰}$ ) and males ( $5.72 \pm 0.23\text{‰}$ ;  $F_{1,89} = 0.616$ ,  $P = 0.435$ ). We did not observe a month by sex interaction ( $F_{3,89} = 0.301$ ,  $P = 0.824$ ). Values of  $\delta^{15}\text{N}$  in black bear serum did not vary during 2002–2008 ( $F_{6,98} = 1.96$ ,  $P = 0.078$ ; see Fig. S5, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). For grizzly bears, we lacked sufficient data to compare cohorts, so we only contrasted  $\delta^{15}\text{N}$  values as a function of sex among months (May–Oct). Values of  $\delta^{15}\text{N}$  in serum varied by month ( $F_{5,149} = 4.73$ ,  $P < 0.021$ ) and between the sexes ( $F_{3,149} = 4.73$ ,  $P = 0.031$ ; Fig. 6). We did not find a month by sex interaction ( $F_{5,149} = 0.76$ ,  $P = 0.584$ ). However,  $\delta^{15}\text{N}$  serum values did not change from 2000 to 2009 ( $F_{9,151} = 1.32$ ,  $P = 0.232$ ; see Fig. S6, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

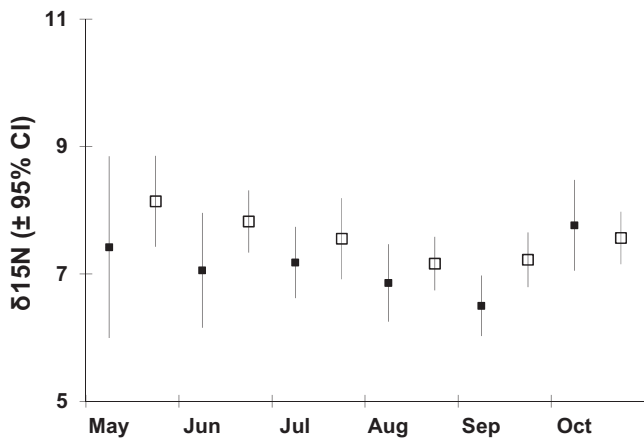
Values of  $\delta^{15}\text{N}$  in grizzly bear serum for good or poor whitebark pine seed years (based on median cone counts during 1999–2009) did not differ in either females ( $n = 32$ ;



**Figure 4.** Concentration ( $\text{‰} \pm 95\%$  confidence interval) of stable isotope nitrogen ( $\delta^{15}\text{N}$ ) in blood clots collected annually from black and grizzly bears in the Greater Yellowstone Ecosystem, USA, 2002–2009.



**Figure 5.** Concentration ( $\text{‰}$ ) of the stable isotope nitrogen ( $\delta^{15}\text{N}$ ) in blood serum collected monthly from black bears (solid square) and grizzly bears (open square) in the Greater Yellowstone Ecosystem, USA, 2000–2010.



**Figure 6.** Concentration (‰) of stable isotope nitrogen ( $\delta^{15}\text{N}$ ) in blood serum collected monthly from female (solid squares) and male (open squares) grizzly bears in the Greater Yellowstone Ecosystem, USA, 2000–2010.

$F_{1,31} = 0.60$ ,  $P = 0.443$ ) or males ( $n = 59$ ;  $F_{1,58} = 1.61$ ,  $P = 0.209$ ). When adjusting for whitebark pine tree mortality,  $\delta^{15}\text{N}$  values differed in both females ( $F_{1,31} = 5.32$ ,  $P = 0.028$ ) and males ( $F_{1,58} = 6.78$ ,  $P = 0.012$ ). Mean ( $\pm$  SE)  $\delta^{15}\text{N}$  values in female serum were  $7.32 \pm 0.26$  in poor and  $6.37 \pm 0.33$  in good seed years. Values for males were  $7.59 \pm 0.14$  in poor seed years and  $6.91 \pm 0.24$  in good years. Approximately 76.8% (95% CI = 68.6–83.9%) of the assimilated nitrogen in female grizzly bear serum came from animal matter in poor seed years, compared with 59.6% (95% CI = 47.4–71.8%) in good years. For males, approximately 80.4% (95% CI = 76.9–83.7) of their assimilated nitrogen came from animal matter in poor seed years and 69.7% (95% CI = 60.9–77.9) in good years. We could not test for differences in  $\delta^{15}\text{N}$  serum values of black bears for poor and good whitebark pine seed years because we did not have an adequate sample.

## DISCUSSION

Our results indicate that grizzly bears are meeting their nutritional requirements in the face of declining whitebark pine, cutthroat trout, and ungulates (Table 1). As expected, adults of both species were heavier and fatter than subadults and body fat increased from spring through autumn. Subadults took longer in the spring after hibernation to regain body condition than adults. Percent body fat among grizzly bears in the GYE was greater on average than black

bears, a finding contrary to that of McLellan (2011) in the Flathead valley of Canada, where bears eat mainly vegetation and berries and meat consumption among grizzly bears was limited to subadult (9%) and adult (22%) males. Our findings were much more similar to studies of sympatric black and brown bear populations in south-central Alaska (Belant et al. 2006) and the Kenai Peninsula (Fortin et al. 2007). Differences in meat content between assimilated grizzly bear diets (44%, 53%, 78% for hair, blood clot, and serum) and black bear diets (27%, 27%, and 45% for hair, blood clot, and serum) in our study were not as distinct as those of Belant et al. (2006) (brown bear: 75–84%; black bear: 27–30%; keratin and blood samples) and Fortin et al. (2007) (brown bear: 80%; black bear: 16%; hair samples); salmon (*Oncorhynchus* spp.), rather than terrestrial meat, represented a large proportion (67–83%) of the assimilated meat in diets of those brown bears and may explain the greater difference. Besides greater assimilation of salmon in diets of brown bears, Belant et al. (2006) also observed lower percent body fat for black bears compared with brown bears during years when spawning numbers of salmon were below average. They concluded that brown bears constrained black bear access to a high-quality food, resulting in reduced body condition of black bears. Similarly, our observations of body fat and meat assimilation infer that grizzly bears in the GYE have a competitive advantage over black bears and the decline in ungulate resources has not affected grizzly bears. These conclusions are further supported by our  $\delta^{15}\text{N}$  signatures in hair indicating that assimilated grizzly bear diets contained more meat than black bear diets, adult grizzly bear males showed greater use of meat resources than females or subadult males, and the constant (hair, serum) or increasing (blood clots)  $\delta^{15}\text{N}$  of grizzly bear samples over the study period.

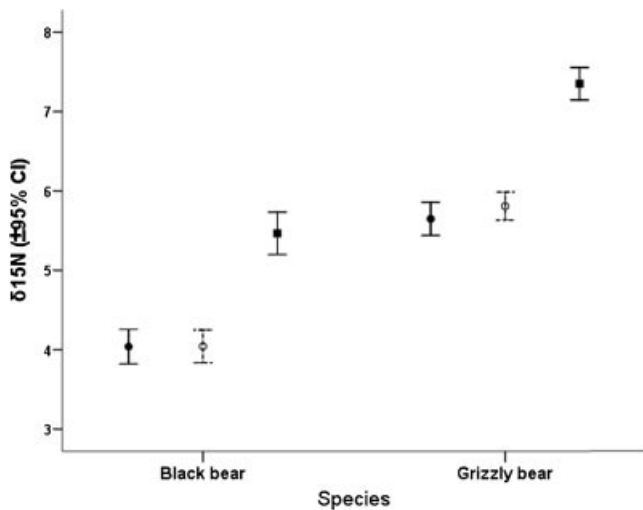
We found no difference in body mass and body fat levels in good versus poor whitebark pine seed years, which suggests that grizzly bears were able to find adequate alternative foods to compensate for annual variation in whitebark pine seed production. Indeed, we found greater levels of meat consumption, with  $\delta^{15}\text{N}$  in serum, in the autumn of years of poor seed production versus good. We did not find similar results with either  $\delta^{15}\text{N}$  in hair or blood clots. The  $\delta^{15}\text{N}$  value in hair and blood clots were similar, but serum levels were much higher (Fig. 7). Serum would be more responsive to short-term (i.e., days to weeks) changes in diets than would either hair or blood clots. Thus, we are not surprised that we did not detect a change in annual meat consumption

**Table 1.** Summary of relevant statistics contrasting body fat, body mass, and diet as determined with isotopic nitrogen in hair, blood clots, and serum from grizzly bears and black bears in the Greater Yellowstone Ecosystem, Montana, Idaho, and Wyoming, USA, 2000–2010.

Item	Fat		Mass		$\delta^{15}\text{N}$ hair		$\delta^{15}\text{N}$ blood clot		$\delta^{15}\text{N}$ serum	
	Black	Grizzly	Black	Grizzly	Black	Grizzly	Black	Grizzly	Black	Grizzly
Trend (annual)	None	Decrease (Ad F)	None	None	None	None	Decrease	Increase	None	None
Cohort	Ad > Sa	Ad > Sa	Ad > Sa	Ad > Sa	None	None	None	Ad > Sa	None	Ad > Sa
Whitebark pine		None		None		None		None		Poor > good
Species contrast	Gz > Bk		Gz > Bk		Gz > Bk		Gz > Bk		Gz > Bk	

Ad, adult; Sa, subadult; Gz, grizzly bear; Bk, black bear.





**Figure 7.** Concentrations of  $\delta^{15}\text{N}$  in hair (solid circle), blood clots (open circle), and serum (solid square), collected from black and grizzly bears in the Greater Yellowstone ecosystem, USA, 2000–2010.

relative to good and poor years of seed production when using hair and blood clots that require months to equilibrate with the diet (Hilderbrand et al. 1996). These findings indicate that grizzly bears were capable of substituting meat for pine seeds in poor seed years and obtaining fat levels in the alternate diet equal to those in good seed years.

The consumption of false truffles by grizzly bears during years of poor whitebark pine seed production has the potential to confound estimates of meat content of the assimilated diet. False truffles are a dominant, alternate food for female grizzly bears during years of poor pine nut production, although male grizzly bears made little use of them (Fortin et al. 2013). The  $\delta^{15}\text{N}$  value of false truffles ( $11.3 \pm 2.7\text{‰}$ ) is much greater than Yellowstone ungulates ( $4.1 \pm 0.7\text{‰}$ ) and pine nuts ( $-1.6 \pm 0.8\text{‰}$ ). Thus, if false truffles were confounding our estimates of the dietary component of meat, we would have expected to see 1) greater  $\delta^{15}\text{N}$  values in females during years of poor pine nut production when they are consuming false truffles than during good pine nut production years, and 2) greater  $\delta^{15}\text{N}$  values in females than males during poor pine nut production years when females would be consuming false truffles, whereas males would not. Neither of these occurred. Thus, we hypothesize that much of the elevated  $\delta^{15}\text{N}$  in false truffles is in chitin and not available to grizzly bears, and that our estimates of the use of meat by Yellowstone grizzly bears are correct.

Seed production of whitebark pines not only varied annually but yields likely decreased over our study period because of substantial tree mortality from mountain pine beetle and white pine blister rust. Consequently, when we examined if body and diet composition showed trends over time, we found mixed results regarding changes in autumn fat levels. We observed no year, sex, nor year  $\times$  sex effects in our general linear model, suggesting body fat levels did not change over the study period. When we analyzed male and female data separately, however, we found a decline in female

body fat over time, primarily because of lesser body fat measurements during 2007–2010. That finding, however, may be confounded because data are restricted to adult females during September–October, primarily from Yellowstone National Park, resulting in small sample sizes (mean  $n = 2.6$  bears/yr). An increase in percent body fat for 2011 further indicates trends should be interpreted with caution ( $\bar{x} = 24.5\%$ ,  $n = 5$ ). Clearly, additional research is required to ascertain if this downward trend is in fact real or an artifact of small sample sizes. Robbins et al. (2012) suggested that female grizzly bears with  $<20\%$  body fat do not reproduce even when bred, so a useful test would be to determine if fecundity has declined. Recent analyses of demographic rates (IGBST 2012) do not indicate a biological difference in fecundity for 1983–2001 ( $\bar{x} = 0.32$ , 95% CI = 0.28–0.36) compared with 2002–2011 ( $\bar{x} = 0.29$ , 95% CI = 0.23–0.35).

During the fall hyperphagia period, grizzly bears have sufficient dietary plasticity to switch between 2 primary food sources: when whitebark pine seed production is poor, grizzly bears readily consume more meat. Although we could not measure assimilation of whitebark pine into bear diets ( $\delta^{34}\text{S}$  isotope has provided confounding results; C. Schwartz, U.S. Geological Survey [Emeritus], unpublished data), our analyses indicate support for the diet switching hypothesis, primarily as a function of annually varying yields of whitebark pine seed. Our results indicate this plasticity was consistent over the course of our study. Although no accurate predictions exist regarding future patterns of whitebark pine mortality in the GYE, mortality of cone-producing trees was substantial (approx. 73%) by the end of our study period. The net effect of that mortality presumably was reduced availability of seeds over time, in both good and poor years. Percent body fat of adult males did not change during 2000–2010, indicating bears compensated not only for annual variation in seed crops but also for declining yields over time. For adult females the latter was less evident; although based on small sample sizes, we observed a decrease in percent body fat after 2006. However, the relative dietary content of meat in both hair and serum remained constant during our study period. In fact, meat intake likely has remained constant for females for several decades. Fortin et al. (2013) documented no change in meat intake among females for 1977–1996 ( $43 \pm 29\%$  of assimilated diet; ecosystem-wide estimate) compared with 2007–2009 ( $38 \pm 20\%$ ; Yellowstone Lake area). In contrast, Fortin et al. (2013) showed that male grizzly bears experienced a decline in meat intake from estimates of  $68 \pm 26\%$  of assimilated diets in 1977–1996 (ecosystem-wide estimate) to  $45 \pm 22\%$  in 2007–2009 (Yellowstone Lake area; Fortin et al. 2013). Our results using hair as the tissue sample agree with these findings, but our results with blood clots do not, which actually indicated an increase in meat consumption during the last decade. Considering the combined findings of our study, we found most support for our hypothesis that the grizzly bear population has not been affected by changes in food resources during our study period. Body mass, percent body fat, and consumption of meat resources remained constant during a decade in which ungulate, fish, and

whitebark pine resources declined. These findings suggest that sufficient alternative food resources were available to grizzly bears during our study period. Indeed, based on a recent literature review of diet items consumed by grizzly bears, IGBST documented use of 234 different food species, of which 75 were consumed frequently (K. Gunther, National Park Service, unpublished data).

## MANAGEMENT IMPLICATIONS

The dietary plasticity we documented indicates that individual grizzly bears have been able to meet nutritional needs despite substantial dynamics in the distribution and productivity of food resources within the GYE. The lack of change in body and diet composition during our study period was consistent among cohorts, suggesting that the grizzly bear population was not affected by food and thus below K. The only exception was a decline in percent body fat among adult females in later years. Because that trend was based on small sample sizes from only a portion of the ecosystem, body fat measurements over the next few years should be used to test if this trend is real.

Bioimpedance and stable isotope analyses are effective techniques to track how grizzly bears respond to changing resources at the individual level. Continuation of this data collection is valuable to detect if changing resources affect body mass and percent body fat of bears in the GYE and to determine if diet patterns are changing. We recommend screening all 3 tissues (hair, blood clots, and serum) for  $\delta^{15}\text{N}$  because this combination of tissues provided more insight into diet composition and change than any single tissue type alone.

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