



Dietary Adjustability of Grizzly Bears and American Black Bears in Yellowstone National Park

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ABSTRACT Grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) are sympatric in much of Yellowstone National Park. Three primary bear foods, cutthroat trout (*Oncorhynchus clarki*), whitebark pine (*Pinus albicaulis*) nuts, and elk (*Cervus elaphus*), have declined in recent years. Because park managers and the public are concerned about the impact created by reductions in these foods, we quantified bear diets to determine how bears living near Yellowstone Lake are adjusting. We estimated diets using: 1) stable isotope and mercury analyses of hair samples collected from captured bears and from hair collection sites established along cutthroat trout spawning streams and 2) visits to recent locations occupied by bears wearing Global Positioning System collars to identify signs of feeding behavior and to collect scats for macroscopic identification of residues. Approximately $45 \pm 22\%$ ($\bar{x} \pm \text{SD}$) of the assimilated nitrogen consumed by male grizzly bears, $38 \pm 20\%$ by female grizzly bears, and $23 \pm 7\%$ by male and female black bears came from animal matter. These assimilated dietary proportions for female grizzly bears were the same as 10 years earlier in the Lake area and 30 years earlier in the Greater Yellowstone Ecosystem. However, the proportion of meat in the assimilated diet of male grizzly bears decreased over both time frames. The estimated biomass of cutthroat trout consumed by grizzly bears and black bears declined 70% and 95%, respectively, in the decade between 1997–2000 and 2007–2009. Grizzly bears killed an elk calf every 4.3 ± 2.7 days and black bears every 8.0 ± 4.0 days during June. Elk accounted for 84% of all ungulates consumed by both bear species. Whitebark pine nuts continue to be a primary food source for both grizzly bears and black bears when abundant, but are replaced by false-truffles (*Rhizopogon* spp.) in the diets of female grizzly bears and black bears when nut crops are minimal. Thus, both grizzly bears and black bears continue to adjust to changing resources, with larger grizzly bears continuing to occupy a more carnivorous niche than the smaller, more herbivorous black bear. © 2012 The Wildlife Society.

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Grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*) coexisted historically over much of western North America (Herrero 1972). Although the current range of grizzly bears is greatly reduced, they continue to coexist with American black bears in several western wildernesses, including Yellowstone National Park (YNP). The coexistence of these 2 species in a relatively intact wilderness

provided an opportunity to understand their competition for dietary and spatial resources. Competition between the 2 species may evolve in response to ecosystem changes. Three primary bear foods have declined in the Yellowstone ecosystem in recent years.

Whitebark pine, a mast seeding species that has been associated with grizzly bear productivity (Mattson et al. 1992, Schwartz et al. 2006), has been attacked by white pine blister rust (*Cronartium ribicola*) and mountain pine beetles (*Dendroctonus ponderosae*). White pine blister rust, an exotic fungus, infected approximately 25% of the trees and

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mountain pine beetles 16% of the trees by 2005 in the Greater Yellowstone Ecosystem (GYE; Greater Yellowstone Whitebark Pine Monitoring Working Group 2006, Gibson 2007). Sixty-nine percent of tagged, live whitebark pine trees used to index cone production in 2002 were dead by 2009 (Haroldson and Podrutzny 2010).

The population of cutthroat trout in Yellowstone Lake and spawning streams has crashed to <10% of pre-1990 numbers because of the introduction of whirling disease (*Myxobolus cerebralis*) and nonnative lake trout (*Salvelinus namaycush*), and a persistent drought that reduced stream flows (Koel et al. 2003, 2005; Cook et al. 2004). During the 1990s, approximately 12–18% of the GYE grizzly bear population visited the 68 tributary streams feeding Yellowstone Lake in which cutthroat trout spawned (Jones et al. 1987, Gresswell et al. 1997, Haroldson et al. 2005).

Ungulates, mainly elk (*Cervus elaphus*) and bison (*Bison bison*) are primary food resources for Yellowstone grizzly bears throughout the year. Bears consume ungulates as carrion, kill members of all age groups, and usurp or scavenge kills of gray wolves (*Canis lupus*) and human hunters (Schleyer 1983, Gunther and Renkin 1990, Green et al. 1997, Podrutzny and Gunther 2006, Barber-Meyer et al. 2008). The bison population in the park has fluctuated largely because of a removal program directed at brucellosis (*Brucella abortus*) management (Cross et al. 2010b). Several large-scale removals occurred in 1996, 2006, and 2008 (Cross et al. 2010b). Approximately 40% of the park's bison population was lethally removed in 2008 (Cross et al. 2010a).

Elk counts on the northern range of YNP declined from around 17,000 in 1995 to fewer than 6,700 by 2007, in part because of wolf, bear, and human predation (Eberhardt et al. 2007, Barber-Meyer et al. 2008). Elk in the Madison-Firehole and Gallatin Canyon also declined, but elk counts from several herds in Wyoming on the east side of the park either decreased, remained constant, or increased (Garrott et al. 2009, Cross et al. 2010a, Middleton et al. 2012). Competition by predators for the ungulate resource has increased over time because of a 3-fold increase in grizzly bear numbers since the 1970s and the successful reintroduction of gray wolves in 1995 (Schwartz et al. 2006, Barber-Meyer et al. 2008, Middleton et al. 2012). Wolf populations grew from 31 reintroduced individuals in 1995–1996 to more than 376 individuals in 31 packs by 2006 (Sime and Bangs 2006).

Because of the recent changes in abundance and distribution of these major foods, bear advocacy groups have sued the United States Fish and Wildlife Service to prevent removal of GYE grizzly bears from Threatened Species status. Park managers are mandated with protecting all native species and are concerned with the impact created by the reduction in primary bear foods. To provide a scientific basis for understanding this dynamic, the objectives of our study were to determine 1) the diets of grizzly bears and black bears in the core of YNP and 2) how those diets have changed with shifts in the availability of the major food resources. We predicted that 1) grizzly bears would feed more heavily on ungulates, including calves, than would black bears; 2) male grizzly

bears, because of their larger size and higher energetic requirements, would a) feed more heavily on adult elk than would either female grizzly bears or black bears and b) be the first to experience the consequences of declining meat resources; 3) black bears and smaller grizzly bears would feed more heavily on plant matter and smaller, more dispersed animals, including insects and small mammals than would larger male grizzly bears; 4) cutthroat trout would no longer be a primary food resource for any of the bears and elk calves would replace trout as a major food resource for both sexes of grizzly bears during the spring and early summer; and 5) whitebark pine nuts would continue to comprise a large portion of the diets of both bear species during autumn in years of abundance because they are a preferred food, widely dispersed across the landscape, and therefore non-defendable (Kendall 1983; Blanchard 1990; Mattson et al. 1991; Felicetti et al. 2003, 2004).

STUDY AREA

We conducted our study from May to October 2007–2009 in the area surrounding Yellowstone Lake, which is part of the GYE (Fig. 1). The GYE contains the headwaters of 3 major continental-scale river systems: the Missouri and Mississippi, Snake and Columbia, and Green and Colorado. Both bear species use habitats that range in elevation from 1,500 m to 3,600 m (Schwartz et al. 2003). The 10-year (1998–2008) mean high and low temperatures were -5.4°C and -17.0°C , respectively, in January, and 23.3°C and 4.6°C , respectively, in July at Yellowstone Lake

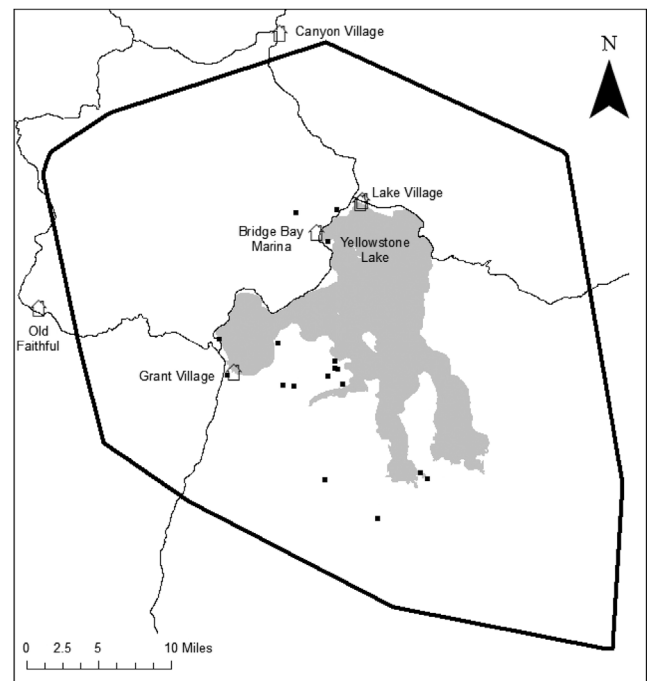


Figure 1. Map of the study area showing the outer limits of where we conducted site visits (heavy black line), developed areas (houses), and the locations of elk calves (black squares) killed by grizzly bears that we trapped and collared in the area immediately surrounding Yellowstone Lake in 2006–2009.

(Western Regional Climate Center 2010). Approximately 80% of annual precipitation falls as snow.

Patterns of precipitation and temperature produce predictable vegetation patterns (Marston and Anderson 1991). Low elevations (<1,900 m) support foothill grasslands or shrub-steppe communities. With increasing moisture, open stands of Rocky Mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), and Douglas-fir (*Pseudotsuga menziesii*) occur. Lodgepole pine (*Pinus contorta*) dominates mid-elevations with poor soils formed from rhyolite. With increasing elevation, spruce-fir or subalpine forests dominate. Engelmann spruce (*Picea engelmannii*) and whitebark pine form the upper tree line. Alpine tundra occurs at the highest reaches of all major mountain ranges (Patten 1963, Waddington and Wright 1974, Despain 1990).

Yellowstone Lake is a high-elevation (2,358 m) oligotrophic lake that covers 35,391 ha, has a mean depth of 42 m, and has a basin capacity of $14 \times 10^9 \text{ m}^3$ (Benson 1961). The lake is usually frozen from December until May or June (Reinhart and Mattson 1990). The Yellowstone Lake watershed covers 261,590 ha. The west and north drainages of the Yellowstone Lake basin contain small streams draining from low relief plateaus with lodgepole pine forests and alluvial meadows. The east and southeast drainages are characterized by higher relief mountain topography, closed canopy mixed forests, and subalpine slopes (Reinhart and Mattson 1990). The Lake supports native cutthroat trout and nonnative lake trout.

The Yellowstone Lake area supports a diversity of fauna. Large ungulates include elk, bison, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and moose (*Alces alces*). Elk and bison are the most abundant (Knight and Eberhardt 1985). Elk migrate into the Yellowstone Lake area from several wintering areas, including from the northern Yellowstone, North Fork Shoshone, Carter Mountain, and Jackson Hole ranges (White et al. 2010; P. J. White, Yellowstone National Park, personal communication). Small mammals include red squirrels (*Tamiasciurus hudsonicus*), pocket gophers (*Thomomys talpoides*), ground squirrels (*Spermophilus citellus*), and voles (*Microtus* spp.; Reinhart 1990). Other carnivores include gray wolves and coyotes (*Canis latrans*). The ranges of 4 gray wolf packs (Yellowstone Delta, Mollie's, Hayden Valley, and Nez Perce) overlap the study area (Smith 2005).

METHODS

We estimated diets using: 1) stable isotope and mercury analyses of hair samples collected from captured bears and from hair collection sites established along streams flowing into Yellowstone Lake and 2) visits to recent locations occupied by bears that were captured in the Yellowstone Lake area and fitted with Global Positioning System (GPS) collars to identify signs of feeding behavior and to collect scats for macroscopic identification of residues. We also used feeding trials with captive bears to develop a relationship between mercury intake and hair mercury concentrations to estimate cutthroat trout intake. Cutthroat trout have a rela-

tively high, naturally occurring mercury concentration that is virtually absent in all other foods (Felicetti et al. 2004).

Trapping and Handling Bears

Grizzly bears and black bears living around Yellowstone Lake were trapped using culvert traps between fall 2006 and summer 2009. Trapping was performed by members of the Interagency Grizzly Bear Study Team under procedures approved by the Animal Care and Use Committee of the United States Geological Survey, Biological Resources Division and conformed to the Animal Welfare Act and United States Government principles for use and care of vertebrate animals used in testing, research, and training. Trapping and handling procedures also conformed to Washington State University's Institutional Animal Care and Use Committee guidelines (permit #3480). The team weighed and sexed each trapped bear and collected blood and hair for stable isotope and mercury analysis and DNA fingerprinting.

We put Telonics GPS Spread Spectrum (SS) collars (Telonics, Inc., Mesa, AZ) on all bears, except dependent young. The units were programmed to attempt a GPS fix every 30, 60, or 120 minutes (Schwartz et al. 2008). We excluded collars that malfunctioned because of antenna fatigue when we calculated fix success. We programmed units to shut off during the expected denning season (15 Nov–14 Apr for grizzly bears and 31 Oct–14 Apr for black bears). We equipped collars with remote drop off devices programmed to release 1 October of the first or second year. In case of remote drop off failure, collars were also equipped with biodegradable cotton canvas spacers. Collars were equipped with a very high frequency (VHF) beacon to operate independently of the GPS device. We conducted telemetry flights weekly from late April through mid-October, weather permitting, and downloaded GPS data from the previous week.

Site Visits

We conducted field surveys of GPS bear locations from mid-May through mid-October during 2007–2009 to measure habitat and food use and to collect bear hair and scat. Although we trapped the bears in the immediate area of Yellowstone Lake, they foraged throughout much of the wider core of Yellowstone National Park (Fig. 1). We first randomly prioritized the order of all individuals (both sexes of grizzly bears and black bears) and randomly selected a date from the previous week's GPS locations for each bear. For bears with fix intervals <1 hour, we visited 1 fix for each hour. For bears with fix intervals ≥ 1 hour, we visited every fix. Field surveys occurred within 10 days of the fix to maximize identification of sign and to ascertain the type of bear use at each site. All field crews carried handheld GPS units and a VHF receiver and antenna. If a VHF signal indicated a collared bear was still present at a GPS location, we delayed our revisit until the bear left the area. In a few cases, we excluded a GPS site to avoid disturbing the bear.

To account for GPS collar error, we searched a 20-m radius around each GPS location for bear sign. Crews thoroughly searched for scat, hair, beds, signs of foraging, and carcasses.

We collected all recent bear scats and assumed they came from the collared bear. Previous tests of this assumption in the GYE using mtDNA analysis of scats correctly verified species of collared bear 97.9% of the time (S. Podrutzny, U.S. Geological Survey, Bozeman, unpublished data). We froze scats at -20°C until we screened them for identifiable fragments. We collected hair during site visits from daybeds and rub trees. We identified and recorded all potential foods and those showing signs of use.

If we detected evidence of feeding during GPS site visits, we collected representative plant and animal foods for reference samples and stable isotope and mercury analyses. Signs of feeding included disturbance and excavation of red squirrel middens for whitebark pine cones; claw marks and broken branches on whitebark pine trees; residues of yellow jackets (*Dolichovespula maculata*) and their hives; remains of ungulate carcasses including bones, hair, blood, or hooves; demolished decaying logs with residual ants (*Camponotus* and *Formica* spp.); small scrapings in duff next to lodgepole pine trees where false-truffles (*Rhizopogon* spp.) grew; excavations of roots and the accompanying vegetative residues; residual pedicels on fruiting shrubs where berries had been harvested; and clipped stems or leaves of forbs and grasses. Because bears often fed heavily on specific foods when seasonally available and bedded near feeding sites, fecal residues characteristic of foods being consumed were often present. We collected spawning cutthroat trout from 7 spawning streams. We stored all foods at -20°C until the end of the field season (<6 months) and then freeze-dried and ground them in a Wiley mill for stable isotope and mercury analyses.

Because we were interested in understanding the influence of bears as predators on elk calves, we invested considerable effort to visiting as many sites as possible in late May, June, and early July when calves were most vulnerable (Gunther and Renkin 1990, Barber-Meyer et al. 2008). We counted individual ungulate carcasses or kill sites, whether adults or calves, only once irrespective of the number of collared bears or number of visits by individual bears that occurred. We assigned site visits where an elk calf had been killed to the first bear that occurred at that site. We cannot exclude the possibility that uncollared bears or wolves killed a calf, and that subsequently a collared bear visited that site during a GPS fix. Such an occurrence would lead to an overestimate of the calf kill rate and, therefore, the number of calves being killed by the bear population. However, that potential overestimate may be offset by kills that could have occurred between GPS fixes. If a GPS fix did not occur at the kill site such that we would have identified the remains during a later site visit, the kill rate would be underestimated. We used a ratio-type estimator to compute the number (± 1 SD) of elk calves killed by bears (Cochran 1977).

Fecal Screening and Food Habit Estimates

We floated defrosted scat in 1 L of water, rinsed the residues through a 2-mm screen, poured the residues into a shallow tray, and visually estimated percentage volume of each food. We summed volumes to estimate percentage content. We

applied correction factors to account for differential disappearance of food items during consumption and passage in an effort to crudely estimate food habits (Hewitt and Robbins 1996). We used correction factors of 3 for ungulates, 4 for rodents, 1.1 for insects and false-truffles, 0.16 for horsetail (*Equisetum* spp.), 0.24 for graminoids, 0.26 for forbs, 1 for roots, 1.2 for fleshy fruits, and 1.5 for pine nuts (Hewitt and Robbins 1996).

Hair Collection Sites and Stream Surveys

During 2007–2009, we placed 48 hair collection sites on 35 streams that were tributaries of Yellowstone Lake and previously supported spawning cutthroat trout. Longer streams received 2 hair collection sites 800 m apart. Each hair collection site consisted of a single strand of barbed wire about 17 m long strung around 3–5 trees at 50 cm above the ground. We hung a cattle blood lure in the center of the site higher than what a large bear could reach (Haroldson and Anderson 1997). We visited each site biweekly from mid-May to mid-August to collect hair. To avoid pooling hair samples from successive years, we stopped hair collections in mid-August when newly grown hair began appearing on the barbs. We collected all hair in paper envelopes, labeled them as to date and location, and returned them to the lab for later individual and sex identification and population estimation (Teisberg 2012). We pooled multiple hair samples that were grown during the same year and collected from the same bear identified by DNA analyses. In conjunction with checking hair collection sites, we surveyed streams for spawning cutthroat trout and bear sign (scat, hair, feeding and bedding activity).

Stable Isotope and Assimilated Diet Estimates

We prepared and analyzed all hair and food samples as in Felicetti et al. (2003). We ground a 15-mg representative portion of each sample using a wig-l-bug, which uses a metal capsule and ball combined with shaking to grind each sample. We analyzed all samples for isotopic nitrogen content at the Washington State University Stable Isotope Core Laboratory. 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). We reported isotopic compositions ($\delta^{15}\text{N}$) as parts per thousand (‰) relative to N_{air} using the internationally distributed standards USGS (U.S. Geological Survey) 32, 25, and 26. Based on known standard samples run with our samples, we estimated our analytical error at $\pm 0.1\text{‰}$. We estimated the proportion of plant and animal matter in the assimilated diets using the $\delta^{15}\text{N}$ of hair for each unique bear identified by DNA analyses during each year of the study. Although we determined $\delta^{13}\text{C}$, we did not use those values to estimate assimilated diets because of the absence of C_4 plants and marine-derived foods. Cutthroat trout have the same $\delta^{13}\text{C}$ value as ungulates (Felicetti et al. 2003).

We analyzed nitrogen isotope values of foods for statistical differences between food types (PROC GLM, SAS Institute, Inc. 1998) and clustered them into plant

($-1.0 \pm 2.5\%$) and ungulates ($4.1 \pm 0.7\%$) before entering them into the mixing model (Table 1). We used a weighted mean for ungulates based on the estimated percentage intake from Mealey (1975): 90% elk, 6% mule deer, and 4% bison. We chose MixSIR, a Bayesian based software program, for our mixing model because it accounts for variation among source isotopic compositions and fractionations (Semmens and Moore 2008). We performed statistical analyses on nitrogen isotope values testing for differences among species, sexes, and years prior to running MixSIR (PROC GLM, SAS Institute, Inc. 1998). We excluded false-truffles ($\delta^{15}\text{N}$, $11.3 \pm 2.7\%$) and insects ($\delta^{15}\text{N}$, $2.7 \pm 1.7\%$) from inclusion in mixing models because of the unknown nature and digestibility of nitrogen isotopes found in non-protein chitin as compared to the actual protein (Cork and Kenagy 1989, Claridge and Cork 1994, Noyce et al. 1997, Claridge et al. 1999, Swenson et al. 1999). Use of the insect isotope value rather than the ungulate value would not have changed the assimilated diet estimates as they did not differ ($F_{1,8} = 0.73$, $P = 0.42$). Cutthroat trout ($\delta^{15}\text{N}$, $7.2 \pm 0.5\%$) were not included in the mixing model as mercury analyses indicated they were no longer a primary food source. Discrimination values used were $4.5 \pm 0.5\%$ for plants and $4.0 \pm 0.1\%$ for meat (Robbins et al. 2005, Florin et al. 2011).

Mercury and Cutthroat Trout Intake Estimates

We used 6 captive grizzly bears (3 M and 3 F) in a year-long feeding trial to determine relationships between consumption rates of mercury-contaminated trout and bioaccumulation of mercury in hair. The bears were at the Washington State University Bear Research, Education, and Conservation Facility in Pullman, Washington. The study was approved by the Washington State University Institutional Animal Care and Use Committee (protocol ASAF # 3181).

In the summer of 2004, we collected almost 400 kg of cutthroat trout from Yellowstone Lake. These fish were accidentally gill-netted as part of the park's annual effort

to control lake trout. We froze freshly netted fish in waxed cardboard boxes and shipped them to Washington State University where they were stored (-20°C) until fed. We started our feeding trials on 30 May, and fed bears fish for 33 days to simulate the normal time course of cutthroat trout consumption in Yellowstone (Felicetti et al. 2004). We varied the amount of fish in the diet from zero to 25% of ad libitum in increments of 6.25% based on observations from Felicetti et al. (2004) indicating that cutthroat trout were a small portion of each bear's intake. Before and after the 33-day trial, we fed bears a low-mercury (<10 ppb) commercial bear chow (21% crude protein; Command Chunk, Land O' Lakes Feeds, Seattle, WA) and apples and allowed them to graze low-mercury white clover (*Trifolium repens*) and grasses growing in their enclosure.

We collected hair samples from captive bears in late October just prior to hibernation. We collected hair along the middle of the back, the area where hair would most likely be sampled when wild bears moved under a barbed-wire hair snare. We used linear least-squares regression (PROC REG; SAS Institute, Inc. 1998) to model the relationships between mercury intake and hair mercury content. We used analysis of variance (ANOVA) and least squares means to test for differences between the mercury content of male and female grizzly bears (PROC GLM and LS Means; SAS Institute, Inc. 1998).

All hair and food samples were analyzed for mercury content at the University of Idaho Analytical Sciences Laboratory. We digested samples with trace metal grade nitric acid and hydrochloric acid and analyzed them for total mercury using cold vapor atomic fluorescence spectrometry (CVAFS) with a HYDRA AF Automated Mercury Analyzer (Teledyne Leeman Labs, Hudson, NH). The reference material we used was NRC TORT-2 Lobster Hepatopancreas (National Research Council Canada, Institute National Measurements Standards, Ottawa, Ontario, Canada). Our reporting limits varied by sample, depending on sample size (range of 10–200 mg sample size and limit of 5–5,000 $\mu\text{g/kg}$).

We compared the mercury content of the hair samples from Yellowstone bears between species, sexes, and decade (1997–2000 and 2007–2009) for statistical differences (PROC GLM, SAS Institute, Inc. 1998). Although the grizzly bear hair samples from the 1997 to 2000 had been analyzed previously (Felicetti et al. 2004), black bear hair samples from that study had not. We were able to determine the mercury content of hair samples from 10 male and 8 female black bears that were collected during the 1997–2000 study (Haroldson et al. 2005).

We estimated cutthroat trout intake (kg) by Yellowstone grizzly bears based on each bear's hair mercury content by 1) estimating the mercury intake ($\mu\text{g/kg}$ bear/year) that would have been required to produce that level of hair mercury (ppb) based on feeding trials with captive bears, 2) multiplying that estimated mercury intake by either the mass of bears that were captured or the average body masses for male (191.3 kg) or female (122.6 kg) grizzly bears in Yellowstone if their hair was collected remotely at hair

Table 1. Stable isotope values (mean \pm SD) for major food groups consumed by grizzly bears and black bears in Yellowstone National Park in 2007–2009. Ungulates included bison, elk, and mule deer; insects included ants and yellow jackets; grasses included bluegrass (*Poa* spp.), oniongrass (*Melica* spp.), timothy (*Phleum* spp.), wheatgrass (*Agropyron* spp.), and wild-rye (*Elymus* spp.); forbs included Angelica (*Angelica* spp.), clover, cow parsnip (*Heracleum maximum*), dandelion, elk thistle (*Cirsium scariosum*), fern-leaved lovage, fireweed (*Epilobium* spp.), and lousewort (*Pedicularis* spp.); roots included biscuitroot, bistort (*Polygonum* spp.), glacier lily (*Erythronium grandiflorum*), licorice root, and yampa; and berries included buffaloberry (*Shepherdia canadensis*), dwarf huckleberry (*Vaccinium caespitosum*), elderberry (*Sambucus racemosa*), globe huckleberry, gooseberry (*Ribes* spp.), grouse whortleberry, raspberry (*Rubus* spp.), and strawberry (*Fragaria* spp.).

Food	$\delta^{15}\text{N}$ (‰)
Ungulates	4.1 ± 0.7
Insects	2.7 ± 1.7
Grasses, sedges, and <i>Equisetum</i>	0.4 ± 2.4
Forbs	-0.8 ± 1.1
Roots	-0.8 ± 3.7
Berries	-3.8 ± 1.4
Whitebark pine nuts	-1.6 ± 0.8

collection sites to estimate mercury intake per bear, and 3) divided that mercury intake by the mercury content of fresh Yellowstone Lake cutthroat trout (183 ± 30 ppb). We estimated cutthroat trout intake by black bears as above but 1) assumed the relationship between mercury intake and hair mercury content in black bears was the same as measured in grizzly bears because no black bear-specific regression exists and 2) used the average body masses for male (101.8 kg) and female (71.4 kg) black bears in Yellowstone if their hair was collected remotely at hair collection sites to estimate mercury intake per bear. We estimated the number of trout consumed by dividing the total mass of trout consumed by their average mass ($1,039 \pm 569$ g).

RESULTS

We deployed 34 collars on 27 individual bears that consisted of 8 female and 13 male grizzly bears and 6 male black bears. Two subadult male grizzly bears left YNP during portions of the study and were not followed outside park boundaries. Our GPS collars successfully obtained 85.0% of the 105,999 fix attempts for all bears. We visited over 2,000 locations (1,926 grizzly bear and 512 black bear) during our 3-year study and found bear sign (i.e., feeding, daybed, scat, or hair) at 1,385 sites. We observed signs of feeding at 987 (787 grizzly bear and 200 black bear) sites and collected 996 scat samples (778 grizzly bear and 218 black bear). We collected 1,535 hair samples at hair collection sites and identified a minimum of 63 grizzly bears (42 M, 21 F) and 27 black bears (17 M, 10 F). We estimated that 35 male and 17 female (i.e., 52 ± 7) adult or subadult grizzly bears annually visited streams from 2007 to 2009 (Teisberg 2012). Although we were not able to estimate the number of black bears visiting cutthroat trout streams, we identified a minimum of 15 ± 2 adult or subadult black bears each year as having visited hair collection sites (Teisberg 2012).

Isotopes and Assimilated Diet Estimates

We analyzed 186 hair samples for $\delta^{15}\text{N}$, 136 from grizzly bears (85 M, 51 F from 54 M, 27 F individuals) and 50 from black bears (35 M, 15 F from 23 M, 10 F individuals). We detected a greater $\delta^{15}\text{N}$ value for grizzly bears ($\bar{x} \pm \text{SD}$: $5.1 \pm 1.6\text{‰}$) than black bears ($3.2 \pm 1.2\text{‰}$; $F_{1, 121} = 55.71$, $P < 0.001$), and male grizzly bears had a greater $\delta^{15}\text{N}$ ($5.5 \pm 1.4\text{‰}$) than female grizzly bears ($4.5 \pm 1.7\text{‰}$; $F_{1, 90} = 13.55$, $P < 0.001$). We found no difference between male ($3.4 \pm 1.2\text{‰}$) and female black bears ($3.0 \pm 1.2\text{‰}$; $F_{1, 29} = 1.14$, $P = 0.29$). We did not find a difference in $\delta^{15}\text{N}$ among years for grizzly bears (males: $F_{2, 83} = 0.89$, $P = 0.41$; females: $F_{2, 39} = 3.48$, $P = 0.40$), but we detected a difference between years for black bears ($F_{2, 30} = 20.20$, $P < 0.001$). Using MixSIR, we estimated that $45 \pm 22\%$ (95% CI = 39–51%) and $38 \pm 20\%$ (95% CI = 30–46%) of the assimilated nitrogen consumed by male and female grizzly bears, respectively, came from meat. The 2 estimates were not different ($F_{1, 68} = 1.46$, $P = 0.23$). For male and female black bears, approximately $23 \pm 7\%$ (95% CI = 20–26%, annual range

17–29%) of the assimilated nitrogen came from meat, which was less than for grizzly bears ($F_{1, 100} = 24.10$, $P < 0.001$).

Ungulates

Consumption of ungulates by grizzly bears occurred during June in the form of elk calves and during August and September when grizzly bears killed adult male elk or fed on elk carcasses of either sex that were killed by wolves (Figs. 2 and 3). The ungulate proportion of the estimated annual food habits based on applying correction factors to the fecal residues did not differ between male ($45 \pm 29\%$) and female ($27 \pm 19\%$) grizzly bears ($F_{1, 26} = 3.80$, $P = 0.062$), but ungulates composed a much smaller proportion of the estimated annual food habits of black bears ($5 \pm 7\%$) than for either male or female grizzly bears ($F_{1, 35} = 12.68$, $P \leq 0.001$). Elk accounted for 84% of all remains identified at site visits and were the dominant species eaten by both grizzly bears and black bears. Bison (9% of all ungulates) and mule deer (7%) remains occurred less frequently at site visits with bison primarily being scavenged from wolf-kills in the Hayden and Pelican Valleys. We estimated from site visits that each grizzly bear (either sex) killed an elk calf every 4.3 ± 2.7 days during June, and each black bear killed a calf every 8.0 ± 4.0 days. Seventy percent of the sites where elk calves were killed by grizzly bears were located at night-time

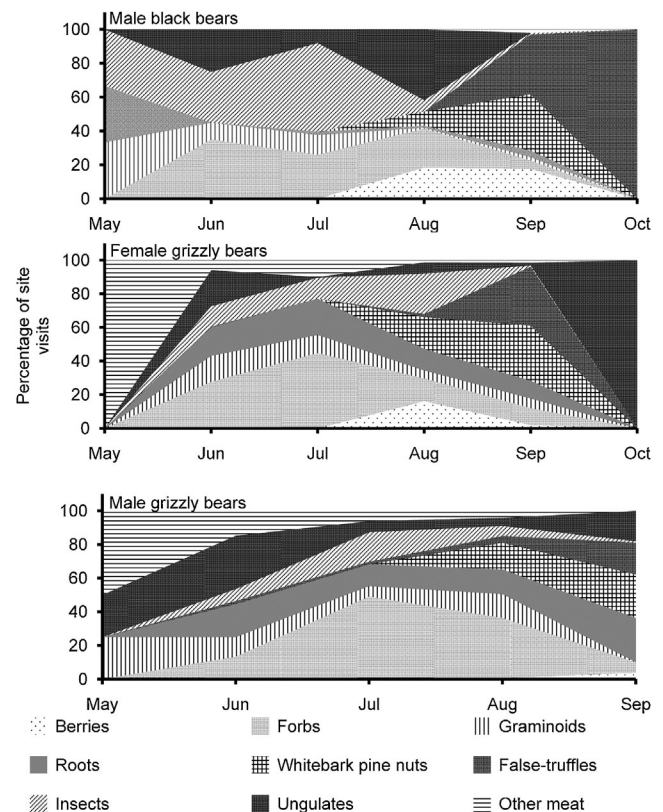


Figure 2. The relative annual distribution of foods used by male black bears, female grizzly bears, and male grizzly bears based on 987 site visits to locations used by Global Positioning System (GPS)-collared bears living in the vicinity of Yellowstone Lake, Yellowstone National Park, between 2007 and 2009. All male grizzly bears removed their collars in the fall as they fattened. Thus, we obtained no site visits for male grizzly bears in October.

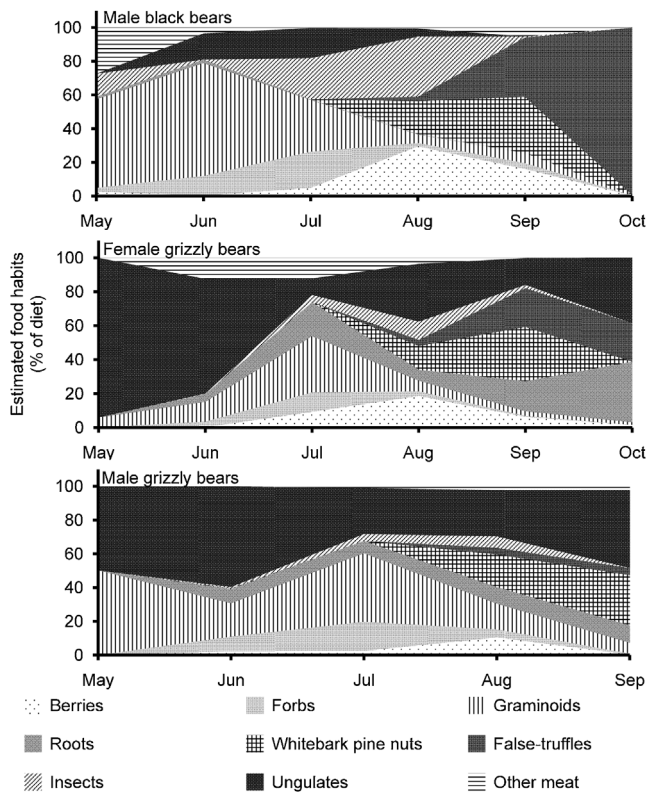


Figure 3. Estimated food habits of male black bears, female grizzly bears, and male grizzly bears living in the vicinity of Yellowstone Lake, Yellowstone National Park, between 2007 and 2009 based on the percentage of major food items found in feces when corrected for differential disappearance (Hewitt and Robbins 1996).

GPS fixes, indicating the kills occurred at dusk or during the night. The first calf whose remains were found was killed on 29 May, and none were found after 29 June. Although determining whether wolves or bears killed adult elk at some site visits was difficult or impossible, male grizzly bears fed on an adult elk carcass every 3.9 ± 4.4 days, female grizzly bears every 13.5 ± 13.6 days, and black bears every 66.0 ± 26.9 days.

Cutthroat Trout

We observed an increase in both the average number of spawning cutthroat trout/stream (0.8 ± 1.4 in 2007, 1.6 ± 3.1 in 2008, and 3.6 ± 5.6 in 2009; $F_{2, 104} = 5.22$, $P = 0.008$) and the number of streams with spawning fish (10 in 2007 to 21 in 2009). Mercury levels in cutthroat trout (620 ± 101 ppb, 100% dry matter basis) were much higher than all other Yellowstone foods (<25 ppb; $F_{1, 25} = 77.28$, $P < 0.001$). We did not detect a difference in the mercury content of hair between male (236 ± 181 ppb) and female (192 ± 190 ppb) grizzly bears ($F_{1, 108} = 1.48$, $P = 0.23$), nor did we detect a difference among years in the current study ($F_{2, 47} = 1.26$, $P = 0.26$). However, mercury levels in male grizzly bear hair decreased by 55% since 1997–2000 (526 ± 639 ppb; $F_{1, 96} = 10.30$, $P = 0.002$), but mercury levels in female hair had not changed (134 ± 282 ppb; $F_{1, 60} = 1.42$, $P = 0.24$; Felicetti et al. 2004).

Very few Yellowstone grizzly bears had mercury concentrations in their hair that suggested significant cutthroat trout consumption (Fig. 4). The mercury content of fully grown hair collected just prior to hibernation in captive grizzly bears increased as mercury intake increased ($F_{1, 5} = 7.32$, $P = 0.015$; Fig. 5). We did not detect a difference between male and female or small and large bears in this relationship for captive bears when expressed on a per kg basis. Male grizzly bears in Yellowstone from 2007 to 2009 consumed more cutthroat trout (7.3 ± 6.3 kg) than females (3.5 ± 3.9 kg; $F_{1, 108} = 11.87$, $P < 0.001$; Fig. 6). However, 90% of female grizzly bears and 56% of male grizzly bears consumed <5 kg of spawning cutthroat trout/year. The estimated population of grizzly bears that annually visited the streams (i.e., 35 M and 17 F) consumed 314 kg of cutthroat trout (255 kg by M and 59 kg by F), or 302 trout/year.

Mercury levels in black bear hair did not differ between sexes in 1997–2000 (M, 1096 ± 1290 ppb; F, 686 ± 407 ; $F_{1, 16} = 0.74$, $P = 0.40$) or 2007–2009 (M, 407 ± 224 ppb; F, 495 ± 334 ppb; $F_{1, 45} = 1.11$, $P = 0.30$), but mercury levels had decreased by 52% during the decade between the 2 studies (1997–2000, 914 ± 997 ; 2007–2009, 446 ± 305 ; $F_{1, 64} = 8.63$, $P = 0.005$). However, black bears (433 ± 261 ppb) had hair mercury concentrations during 2007–2009 that were approximately double that of grizzly bears (220 ± 185 ppb; $F_{1, 155} = 33.98$, $P < 0.001$). Estimated trout intake by individual black bears decreased by 69% from 20.4 ± 39.4 kg (M, 29.7 ± 51.8 kg; F, 8.8 ± 6.6 kg) in 1997–2000 to 6.4 ± 6.1 kg (M, 6.6 ± 6.5 kg; F, 5.9 ± 5.4 kg) in 2007–2009 ($F_{1, 64} = 5.80$, $P = 0.019$). Thus, the minimum of 15 black bears identified each year at hair collection sites along cutthroat trout streams in 2007–2009 consumed approximately 96 kg of cutthroat trout, or 92 trout. Consumption of trout by both male and female black bears (6.4 ± 6.1 kg) in 2007–2009 was similar to that of male grizzly bears (7.3 ± 6.3 kg; $F_{1, 126} = 0.01$, $P = 0.95$), but greater than that of female grizzly bears (3.5 ± 3.9 kg; $F_{1, 92} = 11.10$, $P \leq 0.001$).

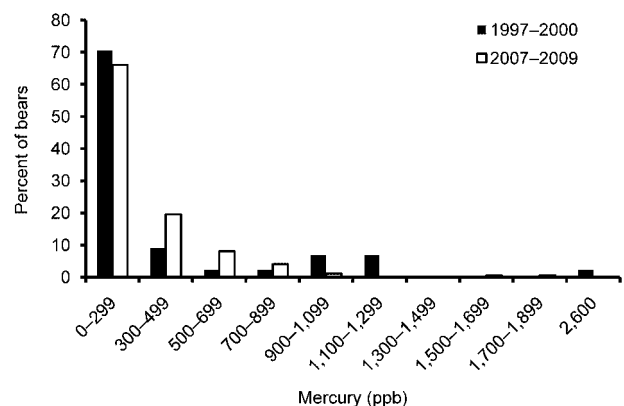


Figure 4. Comparison of levels of mercury in grizzly bear hair samples collected at hair collection sites on streams flowing into Yellowstone Lake, Yellowstone National Park, between 2007 and 2009 (current study) and a decade earlier (1997–2000; Felicetti et al. 2004).

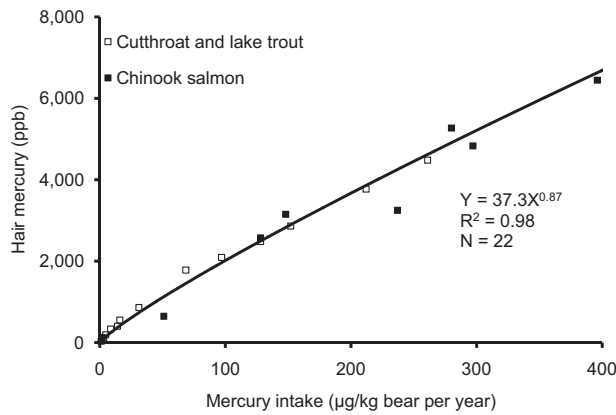


Figure 5. The relationship between mercury intake as fish, including cutthroat trout, lake trout and Chinook salmon (*Oncorhynchus tshawytscha*), and the mercury content of fully grown grizzly bear hair collected in late October during captive bear feeding studies (data from Felicetti et al. 2004; M. B. VanDaele and C. T. Robbins, Washington State University, unpublished data; and current study).

Whitebark Pine Nuts

When pine nuts were available, both grizzly bears and black bears raided squirrel middens or climbed trees (black bears only) to acquire the nuts. We did not detect a difference in pine nut use by grizzly bears and black bears when using either the annual percentage of site visits with signs of nut foraging (grizzly bears = $10 \pm 15\%$, 15% , black bears = $7 \pm 12\%$; $F_{1, 34} = 0.50$, $P = 0.48$) or the percentage in the estimated annual food habits (grizzly bears = $13 \pm 19\%$, black bears = $12 \pm 18\%$; $F_{1, 34} = 0.02$, $P = 0.89$). Similarly, we found no difference in use of pine nuts between male and female grizzly bears in either the annual percentage of site visits with signs of nut use ($F = 13 \pm 16\%$, $M = 8 \pm 13\%$; $F_{1, 25} = 1.00$, $P = 0.33$) or the proportion in the estimated annual food habits ($F = 17 \pm 22\%$, $M = 9 \pm 15\%$; $F_{1, 25} = 0.96$, $P = 0.34$).

Use of pine nuts by both bear species differed between years and reflected the large variation in availability (Haroldson and Podrutzny 2010). For example, the frequency of site visits

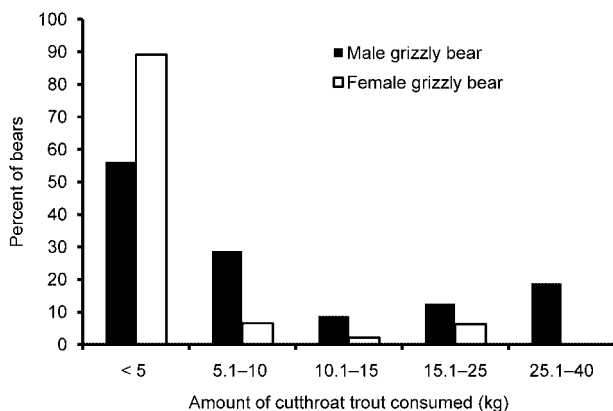


Figure 6. Estimated annual consumption (kg) of cutthroat trout by male and female grizzly bears living in the vicinity of Yellowstone Lake, Yellowstone National Park, between 2007 and 2009.

in which pine nuts were consumed by both bear species varied from 0.4 ± 1.0 in 2008 when the mean number of cones/tree was 9, but increased to 17 ± 17 in 2009 when the number of cones/tree increased to 46 ($F_{1, 33} = 7.05$, $P = 0.003$). The same trend was seen in the estimated annual food habits in that $0.4 \pm 1\%$ were pine nut in 2008, but increased to $25 \pm 22\%$ in 2009.

Other Food Items

Use of other foods, particularly plant matter, varied by season and was likely associated with availability and nutritional content (Figs. 2 and 3). Grass (*Elymus* spp., *Festuca* spp., and *Poa* spp.) use peaked in May and June whereas forb, primarily fern-leaved lovage (*Ligusticum filicinum*), dandelion (*Taraxacum* spp.), and clover (*Trifolium* spp.), use peaked in July in both bear species. False-truffles were a dominant food in September and October 2007 and 2008 for black bears and female grizzly bears when whitebark pine nut production was minimal. During those years, all black bears and all female grizzly bears used false-truffles, and neither the percent of annual site visits ($14 \pm 23\%$; $F_{1, 11} = 0.55$, $P = 0.48$) nor the percentage in the estimated annual food habits ($12 \pm 14\%$; $F_{1, 11} = 1.34$, $P = 0.27$) differed between the 2 groups. Male grizzly bears made little use of false-truffles ($1 \pm 3\%$ of all site visits and $2 \pm 1\%$ of the estimated annual food habits in 2007 and 2008). Only 17% of the male grizzly bears made use of false-truffles at site visits.

Berry consumption, mostly grouse whortleberry (*Vaccinium scoparium*) and globe huckleberry (*V. globulare*), was greatest in August and September 2008 when berries were abundant and whitebark pine nuts were uncommon. During that year, $23 \pm 19\%$ of all site visits for black bears indicated use of berries, as compared to $4 \pm 9\%$ of all site visits for male and female grizzly bears ($F_{1, 9} = 5.23$, $P = 0.048$). Berry crops were minimal in 2007 and 2009. Black bears used insects more than both male and female grizzly bears in all years (site visits, $F_{1, 34} = 9.29$, $P = 0.004$; estimated annual food habits, $F_{1, 35} = 24.51$, $P < 0.001$). Greatest use of insects occurred during the summer of 2008 when yellow jackets were abundant. During that year, $40 \pm 16\%$ of all site visits and $28 \pm 9\%$ of the estimated annual food habits for black bears indicated yellow jacket use, as compared to $17 \pm 15\%$ of all site visits and $9 \pm 10\%$ of the estimated annual food habits for grizzly bears (site visits: $F_{1, 9} = 5.08$, $P = 0.05$; fecal residues $F_{1, 10} = 10.09$, $P = 0.010$).

Grizzly bears used roots, such as yampa (*Perideridia gairdneri*), biscuit root (*Lomatium* spp.), and licorice root (*Osmorhiza* spp.), more than did black bears (grizzly bear site visits $13 \pm 9\%$, black bear site visits $4 \pm 5\%$; $F_{1, 34} = 9.07$, $P = 0.004$; grizzly bear estimated annual food habits $9 \pm 12\%$, black bear estimated annual food habits $0.5 \pm 0.8\%$, $F_{1, 35} = 4.59$, $P = 0.039$). We found no difference in the use of roots between male and female grizzly bears (site visits, $F_{1, 25} = 3.59$, $P = 0.07$; estimated annual food habits, $F_{1, 26} = 1.05$, $P = 0.31$). Root use occurred primarily from June through September (Figs. 2 and 3).

DISCUSSION

The diets of bears in YNP varied between species, among sexes of the same species, and among seasons and years within a species. The greater proportion of meat in the assimilated diet of male grizzly bears than female grizzly bears and grizzly bears than sympatric black bears is consistent with earlier studies in which larger bears seek more energy dense diets (Welch et al. 1997, Rode et al. 2001, Robbins et al. 2004). Historically, spawning cutthroat trout were one of the most calorically dense, concentrated foods available to Yellowstone bears (Mealey 1975, Pritchard and Robbins 1990, Mattson and Reinhart 1995). However, use of trout by bears has declined markedly during the past 30 years. The estimated number of spawning cutthroat trout consumed by grizzly bears dropped from 20,910/year in the late 1980s (Stapp and Hayward 2002), to 2,266/year in the late 1990s (Felicetti et al. 2004), to only 302/year in the late 2000s (current study).

Stapp and Hayward (2002) may have overestimated trout consumption by assuming that cutthroat trout composed 90% of the energy intake of any bear living within 500 m of a spawning stream. However, the methods and assumptions of Felicetti et al. (2004) were identical to ours, so results from 1997 to 2000 and 2007 to 2009 should be directly comparable. Although the mercury content of spawning cutthroat trout in this study (620 ± 101 ppb) was higher than in Felicetti et al. (2004; 508 ± 93 ppb), this should not have adversely affected the estimates of trout intake if both values were correct for the trout populations at that time. For example, the relationship between mercury intake and the mercury content of the hair of captive bears was independent of the source or concentration of mercury in the fish (e.g., 328 ± 36 ppb for Chinook salmon to 620 ± 101 ppb for cutthroat trout; Fig. 5).

Thus, our estimates suggest that grizzly bears consumed 70% less trout biomass (1,060 kg vs. 314 kg) and 87% fewer trout by 2007–2009 than a decade earlier, which likely reflects the simultaneous decline in the cutthroat trout population (Felicetti et al. 2004, Koel et al. 2005, current study). As trout numbers declined, the number of grizzly bears visiting cutthroat trout streams decreased by 31%, from 68 in 1997–2000 to 52 in 2007–2009 (Felicetti et al. 2004, Haroldson et al. 2005, Teisberg 2012). Whereas the mass of trout consumed by each male grizzly bear decreased by 72% (26 kg/bear to 7.3 ± 6.3 kg/bear), female intake did not change (4 kg/bear to 3.5 ± 3.9 kg/bear). The lack of a decline in trout consumption by female grizzly bears is not surprising as they ingested a relatively small amount of trout in both studies, which suggests that trout have not been a significant food resource for female grizzly bears for some time.

The reduction in the cutthroat trout population may have had an even greater effect on black bears. For example, when controlled for equal hair collection effort in the 1997–2000 (Haroldson et al. 2005) and 2007–2009 studies, Teisberg (2012) estimated that the number of black bears visiting cutthroat trout streams decreased by 84% over the decade.

When coupled with the 69% reduction in the estimated annual intake of cutthroat trout per bear between 1997–2000 (20.4 kg) and 2007–2009 (6.4 kg), annual trout consumption by black bears decreased by 95%. Thus, the use of cutthroat trout by the more subordinate black bear dating back to at least 1997–2000 suggests that grizzly bears may have already been seeking other meat resources to replace the declining cutthroat trout.

Assimilated diets estimated from isotopes suggest that male and female grizzly bears are being differentially affected by the loss of cutthroat trout and, perhaps, a declining elk population. For example, females living in the Yellowstone Lake area had the same relative proportion of meat in their assimilated diets in 1997–2000 ($49 \pm 18\%$) as they did in 2007–2009 ($38 \pm 20\%$), and those levels did not differ from the ecosystem-wide estimates from 1977 to 1996 ($43 \pm 29\%$) that occurred while the grizzly bear population was expanding and pre-dated wolf recovery ($F_{2, 56} = 1.86$, $P = 0.17$; Jacoby et al. 1999, Felicetti et al. 2003, current study). However, the proportions of meat in the assimilated diets of adult and subadult male grizzly bears have decreased over time. For example, males living in the Yellowstone Lake area had a lesser proportion of meat in their assimilated diets in 2007–2009 ($45 \pm 22\%$) than they did in 1997–2000 (54 ± 20 ; $F_{1, 94} = 4.80$, $P = 0.031$), and both of those levels were less than the ecosystem-wide estimates from 1977 to 1996 ($68 \pm 26\%$; 2007–2009; $F_{1, 63} = 13.43$, $P < 0.001$ and 1997–2000; $F_{1, 69} = 5.61$, $P = 0.020$; Jacoby et al. 1999, Felicetti et al. 2003, current study). These observations support our initial prediction that male grizzly bears would be the first to experience the consequences of declining meat resources.

The long-term loss of Yellowstone Lake cutthroat trout as a primary food source for both male and female grizzly bears may have put additional pressure on other meat resources. For example, the mass of 1 elk calf during June (15–38 kg; Robbins et al. 1981, Barber-Meyer et al. 2008) far exceeds the total mass of trout consumed by each male or female grizzly bear or black bear in 2007–2009. On the northern range of YNP from 2003 to 2006, 69% of the elk calves died within their first year, 86% of those deaths occurred during the first month, predators caused 94% of those deaths, and grizzly bears accounted for 38% and black bears 24% of the deaths due to predators (Barber-Meyer et al. 2008). Annual survival of elk calves decreased from 0.43 in 1987–1990 when the elk population averaged 15,042 to 0.22 in 2003–2005 when the elk population had declined to 9,032 (Barber-Meyer et al. 2008).

The observed predation rate per grizzly bear in this study of 1 elk calf killed every 4.3 ± 2.7 days during June is less than the estimated rate at which grizzly bears killed calves on the northern range (1 calf every 1.9 days; Barber-Meyer et al. 2008). However, the northern range provides both winter and summer habitat for elk, whereas much of the area used by grizzly bears during June in this study (e.g., Flat Mountain and Two Ocean Plateau) provides high elevation summer habitat for elk that is not available until significant snowmelt (Fig. 1; Houston 1982). Thus, elk calves are frequently older

and less vulnerable to bear predation by the time they move into this portion of the study area (Gunther and Renkin 1990). The 52 ± 7 grizzly bears that visited the cutthroat trout streams each year between 2007 and 2009 would have killed approximately 367 ± 130 elk calves during June following a light snowfall winter when elk were present during the entire month (e.g., 2007) to as few as 183 ± 65 calves following a heavy snowfall winter when elk were not in the area until mid-June (e.g., 2008). Each black bear killed a maximum of 4 calves during June (i.e., 1 calf every 8.0 days), or a maximum of 56 calves were killed by the 15 ± 2 black bears that visited cutthroat trout streams each year (Teisberg 2012). Variances for the number of elk calves killed by black bears could not be estimated because of the relatively low number of sites visited where black bears killed an elk calf. Thus, elk calves born in the Yellowstone Lake area may have benefited from abundant, spawning cutthroat trout populations in the past if grizzly bears and black bears stayed along stream corridors and fed on spawning trout during June when elk calves were being born across the wider landscape (Felicetti et al. 2003).

Although the successful restoration of wolves has increased elk predation and been a factor in reducing some elk populations (Barber-Meyer et al. 2008), both grizzly bears and black bears feed on wolf-killed ungulate carcasses (Smith et al. 2003). Almost half of the adult elk and all of the bison carcasses seen at site visits for grizzly bears during this study had wolf sign present. Grizzly bears generally prevailed in interactions with wolves, even when outnumbered by wolves (Ballard et al. 2003, Smith et al. 2003). Thus, during the active season, wolves may increase the availability of meat to adult grizzly bears, with the exception of females with cubs that are less likely to usurp wolf-killed ungulate carcasses (Servheen and Knight 1993, Ballard et al. 2003, Gunther and Smith 2004).

MANAGEMENT IMPLICATIONS

Grizzly bears and black bears continue to adjust to changing food resources in Yellowstone National Park. As spawning cutthroat trout have decreased, bears may compensate for this declining food resource by increasing consumption of neonatal elk calves (Barber-Meyer et al. 2008, current study). This change to increased dependence on elk calves may ultimately affect herd demographics, reduce the number of calves and adults available to predators, and reduce the number of adult elk available for sport-hunting outside the park (Schwartz et al. 2006, Barber-Meyer et al. 2008, Middleton et al. 2012). These changes may require all wildlife agencies responsible for managing elk populations that live in and around Yellowstone National Park to develop cooperative management programs that reflect the increased biological complexity of the ecosystem. If whitebark pine trees continue dying and reach levels where they no longer are a primary food resource for bears, female grizzly bears and black bears will likely depend more heavily on false-truffles as they currently do during years of poor seed production (Mattson et al. 2002, Haroldson and Podrutzny 2010). However, the ability of the bears to adjust to the loss of

higher value food resources is undoubtedly limited. Over time, the loss of more nutritious foods may have a disproportionate effect on the larger more carnivorous grizzly bear, particularly males, than the more herbivorous and smaller black bear (Welch et al. 1997, Rode et al. 2001, Robbins et al. 2004). Thus, managers must monitor food resources and population dynamics of Yellowstone bears as the ecosystem continues to change.

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