CONSUMPTION OF FUNGAL SPOROCARPS BY YELLOWSTONE GRIZZLY BEARS

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Abstract: Sign of grizzly bears (*Ursus arctos horribilis*) consuming fungal sporocarps (mushrooms and truffles) was observed on 68 occasions during a study of radiomarked bears in the Yellowstone region, 1977–96. Sporocarps also were detected in 96 grizzly bear feces. Most fungi consumed by Yellowstone's grizzly bears were members of the Boletaceae (*Suillus* spp.), Russulaceae (*Russula* spp. and *Lactarius* sp.), Morchellaceae (*Morchella elata*), and Rhizopogonaceae. Consumption of false truffles (*Rhizopogon* spp.) was indicated by excavations that were deeper, on average (1.1 dm), than excavations for mushrooms (0.6 dm). Consumption of sporocarps was most frequent during September (7% of all activity), although median numbers of sporocarps excavated at feeding sites peaked during both August and September (22–23 excavations/site). Almost all consumption (75%) occurred on edaphically harsh sites typically dominated by lodgepole pine (*Pinus contorta*). At broad scales, consumption of sporocarps was most likely where these types of lodgepole pine-dominated sites were extensive or where high-elevation sites supporting mature whitebark pine (*P. albicaulis*) were rare. The number of sporocarps excavated at a feeding site was greatest when cone crops of whitebark pine were small and in stands with abundant lodgepole pine. At fine scales, consumption of fungi was positively associated with lodgepole pine basal area and negatively associated with total ground vegetation cover. Because of the strong association of sporocarp consumption with lodgepole pine and its disassociation at broad scales with availability of whitebark pine seeds, consumption of mushrooms and truffles by grizzly bears will likely increase in the Yellowstone ecosystem with global warming. Lodgepole pine is predicted to increase and whitebark pine to decline with global warming.

Hypogeous and epigeous sporocarps are often referred to as truffles and mushrooms, respectively, and are common reproductive structures of mycorrhizal fungi in temperate and boreal forests. These spore-producing structures are eaten and efficiently digested by omnivores such as humans and feral swine (*Sus scrofa*; Groot Bruinderink et al. 1994). Moreover, fungal sporocarps are present in the diets of numerous otherwise herbivorous or frugivorous mammals including wapiti (*Cervus elaphus*; Nelson and Leege 1982, Collins and Urness 1983) and tree squirrels (*Sciurus* spp., *Tamiasciurus* spp., and *Glaucomys* spp.; Hall 1981, Carey 1995, Steele 1998).

Consumption of fungi by animals is consistent with the abundance and nutritional characteristics of mushrooms and truffles. Conifer forests of interior North America can produce 10–17 kg of mushrooms per ha, dry weight, comprised of 15–35% crude protein (Mealey 1975, Fogel and Trappe 1978). This relatively high concentration of protein is complemented by a similarly high concentration of energy (4–6 kcal/g, dry weight), comparable to that of most hard and soft fruits (Fogel and Trappe 1978). Some edible mushrooms contain as little as 13–18% total dietary fiber (Cheung 1997), which equates to about 76–83% dry matter digestibility for grizzly and North American black bears (*U. americanus*; Pritchard and Robbins 1990).

The few records of ursids consuming truffles or mushrooms are limited to either entries in tables summarizing fecal contents or to short anecdotes. Most observations come from Eurasia, including the Alps (Couturier 1954), European Russia (Ognev 1931, Novikov et al. 1969), Pa-

kistan (Roberts 1977), and Hokkaido (Odachi and Aoi 1987). In North America, heavy consumption of fungi was observed among black bears in coastal Washington state (Poelker and Hartwell 1973). Among grizzly bears, more than incidental consumption has been recorded only in the Yellowstone region (Mealey 1975, Mattson et al. 1991, Mattson 1997*a*).

Grizzly bears in the Yellowstone region obtain most of their energy from seeds of whitebark pine (Mattson et al. 2001) or tissue of bison (*Bison bison*) and wapiti (Mattson 1997*b*), although there are marked differences in consumption of pine seeds and ungulate tissue among bears of different age and gender (Mattson 2000). Yellowstone grizzly bears consume most pine seeds during fall, primarily by digging whitebark pine cones from ground-level caches made by red squirrels (*Tamiasciurus hudsonicus*; Mattson et al. 2001). Tissue is obtained from ungulates primarily during spring by scavenging winter-killed animals (Mattson 1997*b*). When pine seeds or carrion are scarce, Yellowstone's grizzly bears eat diverse other foods, including fungal sporocarps (Mattson et al. 1991). Based on field observations of radiomarked grizzly bears, we speculated that consumption of sporocarps was concentrated in the fall and closely associated with pine trees in forest stands with sparse ground cover.

In this paper we describe features associated with consumption of fungal sporocarps by Yellowstone grizzly bears. Because virtually nothing is known about exploitation of mushrooms and truffles by bears, the analysis reported here is exploratory. We evaluated the effects of forest stand structure, date, type of bear, and availability

of known high-quality foods (i.e., pine seeds and ungulate carrion) using data collected during a study of radiomarked animals, 1977–96.

STUDY AREA

The approximately 23,000 km² study area, from 43°30" to 45°15"N latitude and 109°30" to 111°30"W longitude, corresponded to the known range of Yellowstone's grizzly bear population. Most of the area occupied by grizzly bears was >2100 m elevation and consisted of remote mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Annual temperatures averaged about 0°C. Monthly averages ranged from −2°C to 13°C during April through October. Temperatures rarely exceeded 27°C in most areas. Precipitation varied in amount and timing with elevation and region and fell mostly as snow that reached accumulations of 20–260 cm, depending on location, before melting during March–June (Dirks and Martner 1982).

About 75% of the study area was forested. Lodgepole pine was the most common dominant tree species, although whitebark pine was abundant above 2,500 m elevation (Despain 1990). Forest structure varied considerably during the study primarily owing to mortality of trees caused by fire and by epidemic populations of mountain pine beetle (*Dendroctonus ponderosae*; Despain 1990). The largest fire occurred in 1988 and burned approximately 560,000 ha. Craighead et al. (1995) provide additional details about the study area.

METHODS

Grizzly bears were trapped, marked, and radiolocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). A subset of radiolocations was visited and described according to methods in Mattson (1997a, 2000). Field crews also described sites where grizzly bear feeding or bedding signs were encountered en route to and from telemetry locations. At each location, field crews located a variable-radius forest inventory plot at the center of grizzly bear activity. Trees were tallied, identified as live or dead, and the diameter of each was measured at 1.4 m above ground. Percent ground cover also was ocularly estimated for all graminoids, forbs, and shrubs within about 10 m of plot center. Each site was described in terms of habitat types described by Mattson et al. (1999). There were 10 forest habitat types, including 2 that characterized recently burned or harvested sites (Table 1).

Field crews described all feeding signs and collected all feces (scats) encountered during 1977–96. During 1986–96 descriptions of feeding activity included counts and measurements of excavations. For excavations of fungal sporocarps, length, width, and depth (all in dm) were measured and multiplied to estimate excavated volume. Excavations of sporocarps by bears were identified by several criteria including the presence of sporocarps, the absence of other potential foods, the presence of feces containing sporocarp remains, the presence of other grizzly bear signs, and excavation dimensions. Compared to excavations for sporocarps by other animals such as squirrels and wapiti, those by grizzly bears were the largest, averaging about 1.6 dm in width and 2.0 dm in length. Sporocarps judged to be the same type as those consumed by the bear were described and identified using a field key synthesized from Smith (1975) and Miller (1980). In some instances, sporocarps were collected and keyed in the lab. The field key emphasized visible features such as color, pattern, shape, size, structures of the cap or stipe, site type, and whether the sporocarp was epi- or hypogeous.

The concurrent collection of scats and information on feeding activity maximized comparability of data from these 2 sources at broad scales. We did not ascribe scat contents to specific feeding sites because foods found in scats were often not consumed at the site of collection given the 7–13 hr transit time of digesta (Pritchard and Robbins 1990). Thus, we compared data from scats and feeding sites at the scale of months but not specific feeding sites.

Scats were collected, dried, and analyzed for percent

Table 1. Forest habitat types used to map grizzly bear habitat and describe grizzly bear activity sites in the Yellowstone region.

Acronym	Habitat type description
DOPEN	Dry sites recently deforested by timber harvest or fire
HABLA	High-elevation subalpine fir (*Abies lasiocarpa*) climax sites; typified by *Arnica* spp. and *Juniperus communis*
HPIAL	High-elevation forested sites with mature whitebark pine
HPSME	High-elevation Douglas-fir (*Pseudotsuga menziesii*) climax sites; typified by *Arnica cordifolia, Berberis repens, Juniperus communis*, and *Symphoricarpos oreophilus*
HVASC	High-elevation sites, ground layer dominated by grouse whortleberry (*Vaccinium scoparium*)
LPICO	Low-elevation lodgepole pine-dominated sites; typified by *Carex geyeri, C. rossii, Calamagrostis rubescens*, and *Purshia tridentata*
MOPEN	Mesic–wet sites recently deforested by timber harvest or fire
LPIEN	Low-elevation Engelmann spruce (*Picea engelmannii*)-dominated sites; typified by *Calamagrostis canadensis, Equisetum arvense*, and *Galium triflorum*
MABLA	Mesic–wet subalpine fir climax sites; typified by *Thalictrum occidentale* and *Osmorhiza chilensis*
MPSME	Mesic Douglas-fir climax sites; typified by *Symphoricarpos albus, Spiraea betulifolia*, and *Calamagrostis rubescens*

content according to methods described by Mattson et al. (1991). When collecting scats we tried to minimize contamination with extraneous soil and debris. However, this was often impossible when collecting liquid feces typical of those containing mushroom remains. Scats were air-dried and later rehydrated before washing through 2 screens. Coarse material was retained by the large (0.806 cm²) mesh screen and fine material by the small (0.212 cm²) mesh screen. Diet items were identified to the finest taxonomic resolution possible and the percent volume of each was visually estimated. Remains of fungal sporocarps were typically identifiable as such, to the extent that stipes could sometimes be distinguished from caps, but almost never to the extent that genera or even families could be identified. Visual estimates of percent volume were routinely verified by liquid displacement in beakers. Results were reported by month and year as total frequency of occurrence in scats, percent of total fecal volume, and mean percent for scats in which the item occurred.

We used logistic regression analysis (Demaris 1992) to specify the effects of explanatory variables on the log odds that a bear had excavated fungal sporocarps at a given location. Radiotelemetry locations or feeding sites were units of analysis. We specified 2 types of models: one using only data from telemetry locations, including sites where no feeding signs had been found, and the other using only data from sites with feeding signs of all types, but including plots not at telemetry locations. We gave priority to the first type of model and used the second to confirm patterns. Given that excavation of sporocarps had occurred, we used multiple linear regression (Weisberg 1985) to specify the effects of explanatory variables on the total number of excavations. We used maximum likelihood methods for parameter estimation and the sample size-adjusted version of Akaike's Information Criterion (AIC$_c$; Burnham and Anderson 1998) for model selection. We used change-in-AIC$_c$ (Δ), obtained by deleting each variable in turn while holding the rest of the model constant, to quantify the relative effect of each variable in a given model (Burnham and Anderson 1998). Because the value of AIC$_c$ is affected by sample size, it is comparable within but not among models. We de-emphasized statistical hypothesis testing (Johnson 1999) and present P-values solely as confirmatory information.

We considered both proximal and distal effects in the analysis (Mattson 2000). Distal effects were those operational at broad temporal and spatial scales; proximal effects were operational at the scale of the immediate site. Proximal effects were represented by measures taken at telemetry locations or other sites of grizzly bear activity. Distal effects were enumerated from other sources. Numbers of cones on whitebark pine trees were taken from counts at fixed transects (Mattson 2000). Numbers of

bison in the ecosystem were taken from U.S. National Park Service (1997). Monthly temperatures (°C) and precipitation (cm) were taken from regional summaries published by the U.S. National Oceanic and Atmospheric Administration (1977–92). Grizzly bear activity sites were also associated with the spatial extent of habitat types in surrounding life-range-size areas on the basis of the Bear Management Units (BMUs) where they occurred (there are 18 BMUs in the Yellowstone ecosystem, each about the size of a female life range). Mattson (2000) provides a more detailed description of these distal factors and their sources.
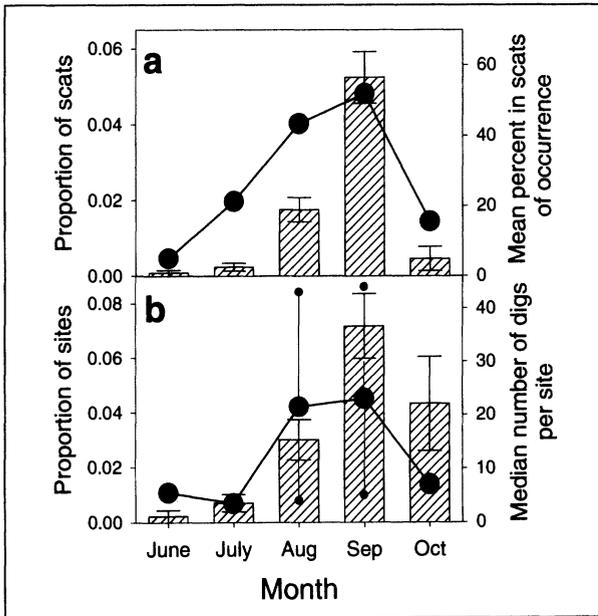
RESULTS

During 1977–96, 7,459 scats were collected and 2,134 telemetry locations from 175 radiomarked bears were investigated to determine activity of the associated animal. Feeding sign was found at 3,101 sites, including 1,940 sites not associated with a telemetry location. Remains of fungal sporocarps were found in 96 scats, whereas sign of foraging for sporocarps was found at 68 sites, 48 of which were associated with telemetry locations of 28 different radiomarked bears. Feeding sign took the form of shallow scrapes to more substantial paw-sized digs in forest litter and soil. Scats containing sporocarps were typically grayish in color and very liquid.

Of the scats containing fungal sporocarps, 80% contained additional items. Of these mixed-composition scats, 81% contained dirt and debris that accounted for an average 30% of total scat volume. Remains of grasses and sedges were next (32%) and accounted for an average 15% of total scat volume. All other items occurred in <15% of mixed-composition scats and comprised <5% of average scat volume.

Field crews commented on the type of sporocarp most likely eaten by bears at 48 of the sites where it was concluded that grizzly bears ate sporocarps. A likely hypogeous food ("truffles") was described at 5 sites. Based on 1 positive identification, these below-ground sporocarps were most likely false truffles of the genus Rhizopogon. Epigeous sporocarps (i.e., "mushrooms") were described at 35 sites, including 9 sites with gilled mushrooms, 7 sites with boletes (Boletaceae), 4 sites with morels (Morchella elata), and 1 site with puffballs (Calvatia sp.). Three of the probable instances where morels had been consumed occurred during 1989 in recently burned forests, 1 year after the extensive wildfires of 1988. The boletes were most likely of the genus Suillus, either S. brevipes or S. tomentosus. The gilled mushrooms were in 5 instances most likely of the genus Russula, in 2 instances of the genus Tricholoma, and in 1 instance of the genus Lactarius.

Excavations for false truffles and mushrooms differed. At the 11 sites where depths of excavations were measured, those for false truffles ($\bar{x} = 1.1$ dm, SE = 0.2, $n = 4$) were deeper than those for the bases of mushroom stipes (often described as "scrapes", $\bar{x} = 0.6$ dm, SE = 0.1, $n = 7$; $F = 16.0$, 1,9 df, $P = 0.003$). Even so, volumes of individual excavations for truffles and mushrooms, averaged by feeding site, did not differ substantially ($n = 10$, $F = 1.8$, 1,8 df, $P = 0.22$).

Consumption of fungal sporocarps by grizzly bears was not equally distributed among months. Frequency of sign in scats and at feeding sites peaked during September and was relatively common during August (Fig. 1). Median number of digs per feeding site and mean percent of individual scats comprised of sporocarp remains, considering only scats where such remains were found, also peaked in August and September, suggesting that meal sizes were larger and foraging bouts longer during these months. Evidence of sporocarp consumption from scats and feeding sites differed only in that sign from sites indicated comparatively common consumption during October whereas sign from scats did not. With the exception of 2 scats collected during May 1994, there was no evidence
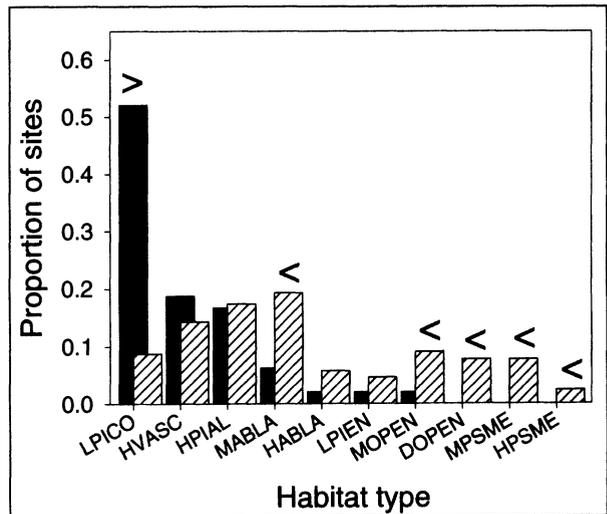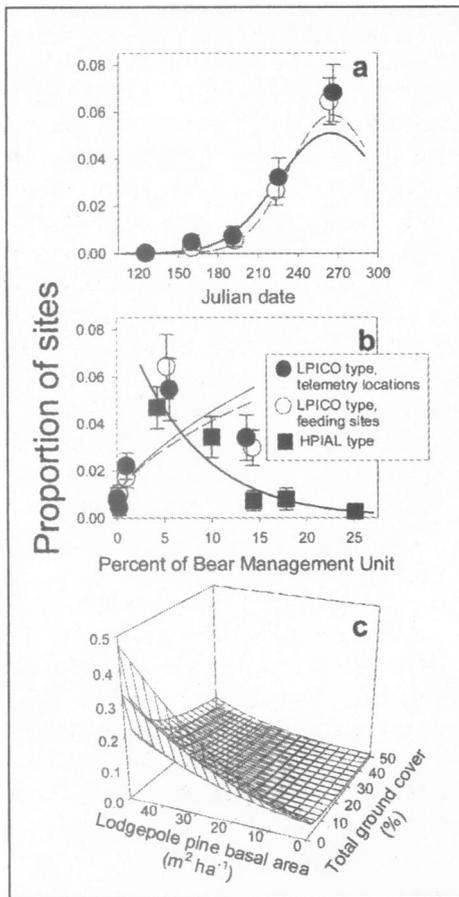
that grizzly bears consumed sporocarps prior to June.

Consumption of sporocarps was not evenly distributed among habitat types. Most consumption (89%) was observed in just 3 forest types (the LPICO [55%], HVASC [20%], and HPIAL [14%; Table 1]), whereas none was observed in non-forest types. Considering only forested or potentially forested habitat types, sporocarp consumption was distributed differently from all other grizzly bear feeding or bedding sign ($n = 1,742$, 9 df, homogeneity $G^2 = 121.2$, $P < 0.0001$). Consumption was concentrated more than expected in the LPICO type and less than expected in HABLA, MOPEN, DOPEN, MPSME, and HPSME (Fig. 2; based on Bonferroni simultaneous confidence intervals for differences between observed and expected proportions with $\alpha = 0.05$). Frequencies of sporocarp consumption in the HVASC, HPIAL, HABLA, and LPIEN types were consistent with what would be expected by frequencies of other feeding activities by bears in these habitat types.

Considering only distal factors, consumption of sporocarps was related to a polynomial of Julian date for both telemetry locations and feeding sites (Tables 2 and 3; Fig. 3a). The first derivatives of these polynomials (univariate) suggested that probability of use peaked at about 0.05–0.06 during Julian dates 264 and 266 (about 21 and 23 September) for telemetry locations and feeding sites, respectively. Otherwise, analysis of telemetry locations suggested that probability of consumption was positively

Fig. 1. Monthly occurrence of sporocarp consumption by Yellowstone grizzly bears, 1977–96, as indicated by (a) scats and (b) feeding sites. In (a) bars (± 1 SE) indicate the proportion of scats that contained remains of sporocarps (left scale) and solid dots indicate the mean percent of individual scats comprised of sporocarp remains, considering only scats where such remains were found (right scale). In (b) bars indicate the proportion of feedings sites where evidence of sporocarp consumption was found (left scale) and large solid dots the median number of excavations for sporocarps at feeding sites (right scale). The small dots above and below the median for August and September denote the 75% and 25% quartiles, respectively.

Fig. 2. Proportional occurrence of feeding on fungal sporocarps by Yellowstone grizzly bears (black bars) versus all other feeding and bedding activity (hatched bars) in forested habitat types, 1977–96. Greater than sign (>) signifys habitat types where consumption of sporocarps was much more frequent than expected by the occurrence of all other grizzly bear activity (Bonferroni confidence intervals, $\alpha = 0.05$); less than signs (<) signify types where consumption was much less frequent than expected. Habitat types are described in Table 1.

Fig. 3. Univariate relations between the proportion of sites where Yellowstone grizzly bears consumed fungal sporocarps, 1977–96, and distal or proximal factors with the greatest apparent effects on this behavior: (a) Julian date, (b) extent of the LPICO (circles) and HPIAL (squares) habitat types in the surrounding bear management unit (BMU), and (c) lodgepole pine basal area and total ground cover. In (a) and (b) the symbols and SE bars are for proportions of quintiles of the data and illustrate goodness-of-fit (univariate). The gray mesh in (c) is the relation estimated from telemetry locations, the open mesh the relation estimated from feeding sites.

correlated with size of whitebark pine cone crops (Table 2), whereas analysis of feeding sites suggested that consumption was positively correlated with numbers of bison in the ecosystem (Table 3). Similarly, telemetry locations revealed a negative correlation between consumption of sporocarps and extent of whitebark forests (HPIAL) in the surrounding area, whereas feeding sites revealed a positive correlation with the extent of LPICO and HVASC habitat types (Fig. 3b).

Some of the discrepancies between results using telemetry locations and results using feeding sites were likely related to spatial correlations among habitat types and other landscape features, by bear management unit. The extent of HPIAL was negatively correlated with the extent of

LPICO and HVASC, considering both telemetry locations (–0.49 and –0.46, respectively) and feeding sites (–0.44 and –0.39, respectively). By contrast, based on feeding sites, the extent of bison winter range was positively correlated with the extent of LPICO and HVASC (0.56 and 0.63, respectively). Moreover, the log odds that grizzly bears had fed on bison during August and September (y) was positively associated with the extent of bison winter range (x) in the surrounding BMU:

$$y = -8.6 + 0.37x$$

with $n = 756$, $R^2_L = 0.94$, 7 df, $G^2 = 2.3$, $P = 0.94$.

Considering distal and proximal factors together, both telemetry locations and feeding sites showed that consumption of fungal sporocarps was more likely where there was sparse ground cover, abundant pines, gentle slopes, and extensive LPICO habitats in the surrounding area (Tables 2 and 3; Fig 3b). Of all effects, the positive one of lodgepole pine was the greatest, especially when combined with the negative effect of ground cover (Fig. 3c). The effect of Julian date also persisted. Analysis of feeding sites further suggested that the log odds of sporocarp consumption was negatively correlated with amounts of total forest basal area, live and dead, offset by a positive correlation with amounts of live basal area. In other words, greater total basal area had an inhibiting effect that was less pronounced if comprised of live trees rather than dead ones.

Not all types of grizzly bears appeared equally likely to consume fungal sporocarps. Considering only distal factors, subadult females (autonomous bears <5 years old and without cubs) were more likely than any other type of bear to consume sporocarps, especially in contrast to subadult males (Table 2). This effect persisted and was accentuated when considering proximal effects (Table 3). In other words, even at optimal times and when proximal features were most favorable, subadult females apparently were more likely than any other type of bear to consume sporocarps.

Numbers of excavations for sporocarps per feeding site (y'; where $y' = \ln [y + 1]$) tended to decline with increasing size of the current whitebark pine cone crop (cone; cones/tree):

$$y' = 3.1 - 0.00042cone^2$$

with $n = 48$, $r^2 = 0.11$, $F = 5.4$; 1, 46 df, $P = 0.024$.

Although this simple model minimized AIC_c (at 14.9), another model containing more parameters, but with a higher AIC_c value (15.4), was biologically interpretable and helped explain some otherwise obscure broader scale relations. This more complex model suggested that num-

Table 2. Parameters (β) of logistic regression models describing the log odds that mushrooms were consumed at a site versus any other type of activity for Yellowstone grizzly bears, 1977–96. Models are based on telemetry locations only, including sites where no feeding or bedding signs were found. Δ values are change in AIC$_c$ with piece-wise deletion of individual variables or groups of variables. Statistics (G^2 and P) are for goodness-of-fit tests; smaller G^2 values and larger P values indicate better fit.

Independent variables	Distal factors only			Distal and proximal factors		
	β	SE	Δ	β	SE	Δ
Intercept	−24.2	7.3		−29.1	8.2	
Distal factors						64.6
Number of whitebark pine cones/tree	0.00040[a]	0.00019	1.9			
Extent of LPICO (% of BMU)				0.61[b]	0.18	9.3
Extent of HPIAL (% of BMU)	−0.17	0.032	36.2			
Julian date	0.17	0.062	32.9	0.22	0.071	15.1
Julian date squared	−0.00032[a]	0.00013	17.2	−0.00045[a]	0.00015	10.9
Sex and age class[c]			1.9			2.7
Adult female	−0.18	0.24		−0.37	0.26	
Adult male	0.03	0.28		−0.33	0.31	
Subadult female	0.87	0.32		1.13	0.36	
Subadult male	−0.72[d]			−0.43[d]		
Proximal factors						38.3
Lodgepole pine basal area (m²/ha)				0.049	0.0097	23.6
Whitebark pine basal area (m²/ha)				0.00070[a]	0.00026	3.2
Total ground cover (%)				−0.64[b]	0.16	12.4
Slope (B)				−0.59[b]	0.20	6.7
Statistics						
G^2 (df)		310 (2 × 10³)			281 (2 × 10³)	
P		1.00			1.00	
R_L^2		0.88			0.88	
N		2088			1630	

[a] Coefficient was estimated for squared values of the independent variable.
[b] Coefficient was estimated for values of the independent variable (x) transformed as $\ln(1 + x)$.
[c] Class variable.
[d] Coefficient was calculated by subtraction.

Table 3. Parameters (β) of logistic regression models describing the log odds that mushrooms were consumed at a site versus any other type of feeding or bedding activity, for Yellowstone grizzly bears, 1977–96. Models are based only on sites where feeding signs were found, including sites not associated with telemetry locations. Δ values are change in AIC$_c$ with piece-wise deletion of individual variables or groups of variables. Statistics (G^2 and P) are for goodness-of-fit tests; smaller G^2 values and larger P values indicate better fit.

Independent variables	Distal factors only			Distal & proximal factors		
	β	SE	Δ	β	SE	Δ
Intercept	−54.8	10.5		−32.1	9.9	
Distal factors						56.5
Number of bison in study area	2.1[a]	0.59	13.4			
Extent of LPICO (% of BMU)	0.50[a]	0.17	5.8	0.78[a]	0.17	19.7
Extent of HVASC (% of BMU)	0.00069[b]	0.00017	15.6			
Julian date	0.26	0.078	18.0	0.24	0.084	13.8
Julian date squared	−0.00048[b]	0.00016	12.2	−0.00046[b]	0.00018	9.5
Proximal factors						71.8
Lodgepole pine basal area (m²/ha)				0.074	0.015	28.6
Whitebark pine basal area (m²/ha)				0.0013[b]	0.00036	7.4
Total basal area (m²/ha)				−0.0012[b]	0.00034	18.6
Total live basal area (m²/ha)				0.059	0.021	7.3
Total ground cover (%)				−0.63[a]	0.17	10.9
Slope (B)				−0.59[a]	0.21	5.8
Statistics						
G^2 (df)		394 (2 × 10³)			313 (2 × 10³)	
P		1.00			1.00	
R_L^2		0.89			0.90	
N		2911			2207	

[a] Coefficient was estimated for values of the independent variable (x) transformed as $\ln(1 + x)$.
[b] Coefficient was estimated for squared values of the independent variable.

bers of excavations (y') were related to a polynomial of cone crop size and otherwise increased with ambient temperature (*temp*), Julian date (*jd*), and lodgepole pine basal area (*lpp*):

$$y' = -7.8 + 0.14cone - 0.0031cone^2 + 1.9[\ln(temp + 1)] + 0.021jd + 0.00041lpp^2$$

with $n = 44$, $R^2 = 0.45$, $F = 6.2$, 5, 38 df, $P = 0.000$.

DISCUSSION

Consumption of fungal sporocarps by Yellowstone grizzly bears peaked in September and was rare prior to July. Julian date probably functioned in this analysis as a surrogate for seasonal availability of preferred fungal sporocarps in preferred habitats. By all indications, the epi- and hypogeous sporocarps consumed by grizzly bears during this study were most abundant during the fall, although there may have been a secondary spring peak in abundance for some species (Smith 1975, Thiers 1975, Fogel and Trappe 1978, Miller 1980, North et al. 1997, States and Gaud 1997). If the seasonal chronology of grizzly bear consumption tracked abundance of preferred sporocarps, then we predict that peak availability occurred, on average, about the third week of September.

Consumption of sporocarps may have been indirectly, positively, affected by number of bison in the ecosystem. The habitats where most sporocarp consumption occurred (the LPICO and HVASC types) were positively spatially correlated with bison winter range, which was positively associated with the year-round distribution of bison (Meagher 1973). Moreover, consumption of bison during peak sporocarp consumption (August and September; Mattson 1997b) took place near or in bison winter ranges. Even so, it is not clear how this might have led to increased consumption of sporocarps and whether such an effect, if any, might have been due to effects of bison on sporocarp production or effects of bison consumption on overall grizzly bear foraging strategies, including potential avoidance by subordinate bears of dominant bears on bison carcasses (Craighead et al. 1995).

Subadult females apparently were more likely than any other type of grizzly bear to consume fungal sporocarps, even where and when immediate site and vegetation conditions were otherwise conducive to consumption of sporocarps by other bears. However, there is no ready explanation for this behavior. It is suggestive that subadult females were probably energetically the least stressed of all bears (Mattson 1990), that they consumed the least tissue from ungulates (Mattson 1997b), and that, of all types of females, their overall patterns of habitat use were the most distinct from patterns of habitat use by males

(Mattson 2000). Even so, it is unclear if or to what extent consumption of sporocarps by subadult females was part of a risk-averse strategy and a consequence of their being able to afford consumption of a lower quality food (compared to ungulate tissue or whitebark pine seeds) in a habitat less often used by dominant bears such as adult males.

Consumption of fungal sporocarps by Yellowstone grizzly bears was positively associated with edaphically harsh sites dominated by lodgepole pine. This was manifest, distally, by an increased proclivity to consume sporocarps where the LPICO habitat type was most extensive and, proximally, by a positive association with mature lodgepole pine and sparse vegetation ground cover. The importance of LPICO sites is emphasized not only by the concentration of sporocarp consumption here, but also by the apparent self-reinforcing effects of this type at broad scales; i.e., bears were more likely to consume sporocarps, all else equal, when the LPICO type was more common in the surrounding BMU. By contrast, no consumption of fungal sporocarps was observed in non-forest habitat types or in forest types that had been recently harvested.

These patterns are consistent with what is known about production of edible sporocarps by mycorrhizal fungi in boreal or high-elevation conifer forests. For example, of the edible boletes and truffles or false truffles, most are strongly associated with pine-dominated forests (Thiers 1975; Molina and Trappe 1982, 1994; Danielson 1984; States 1990; States and Gaud 1997). Production and diversity of edible sporocarps of all types tends to peak in drier conifer forests (Fogel and Trappe 1978, Danielson 1984). Otherwise, sporocarps tend to be more abundant in thinned stands, but much less abundant in recently burned or clearcut forests of lodgepole pine and the ecologically similar jack pine (*P. banksiana*; Visser 1995, Kropp and Albee 1996).

Consumption of sporocarps appeared to be complexly related to availability of whitebark pine trees and cones. Interpreting these patterns depends on distinguishing between effects of cone crops and effects of the trees themselves. Some sporocarp consumption occurred in whitebark pine habitats near whitebark pine trees. Thus, to a limited extent, the odds that grizzly bears would consume mushrooms increased where whitebark pine was proximally more abundant, which occurred more often when cone crops were large because bears concentrated in whitebark pine stands to eat pine seeds (Mattson et al. 2001). On the other hand, BMUs with extensive whitebark pine habitats contained only limited habitats, especially of the LPICO type, where consumption of sporocarps was most concentrated. Thus, at broad scales, the extent of whitebark pine habitats was negatively associated with likelihood of sporocarp consumption. Finally, although grizzly bears consumed sporocarps where whitebark pine

was abundant, their foraging was less intense compared to when they were consuming sporocarps amongst abundant lodgepole pine. This tendency was probably accentuated because distributions of whitebark and lodgepole pines were negatively correlated, probably through direct competition between the 2 species (Mattson and Reinhart 1990).

Fungal sporocarps will likely become a more important food of Yellowstone grizzly bears with warming of the global climate, especially if warming leads to drier conditions. During this study consumption of sporocarps peaked, on average, in September at only 7% of all activity. Nonetheless, under optimal combinations of sparse ground cover and abundant lodgepole pine, probabilities of consumption reached about 30–50% (see Fig. 3c). Such conditions were most common on the types of sites that are projected to become substantially more widespread in the Yellowstone region with climate warming (Romme and Turner 1990, Bartlein et al. 1997). Under this scenario, whitebark pine is predicted to decline and perhaps virtually disappear. Thus, these results offer a preview of a food and a foraging behavior that may become more important to the management of Yellowstone's grizzly bear population.

ACKNOWLEDGMENTS

LITERATURE CITED

BARTLEIN, P.J., C. WHITLOCK, AND S. L. SHAFER. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11:782–792.

BLANCHARD, B.M., AND R.R. KNIGHT. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41–67.

BURNHAM, K.P., AND D.R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York, New York, USA.

CAREY, A.B. 1995. Sciurids in Pacific Northwest managed and old growth forests. Ecological Applications 5:648–661.

CHEUNG, P.C-K. 1997. Dietary fiber content and composition of some edible fungi determined by two methods of analysis. Journal of Science Food and Agriculture 73:255–260.

COLLINS, W.B., AND P.J. URNESS. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. Journal of Wildlife Management 47:646–663.

COUTURIER, M.A.J. 1954. L'ours brun *Ursus arctos* L. Grenoble, France. (In French.)

CRAIGHEAD, J.J., J.S. SUMNER, AND J.A. MITCHELL. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Washington, D.C., USA.

DANIELSON, R.M. 1984. Ectomycorrhizal associations in jack pine stands in northeastern Alberta. Canadian Journal of Botany 62:932–939.

DEMARIS, A. 1992. Logit modeling: practical applications. SAGE Publications, Newbury Park, California, USA.

DESPAIN, D.G. 1990. Yellowstone vegetation: the consequences of history and environment in a natural setting. Robert Rinehart, New York, New York, USA.

DIRKS, R.A., AND B.E. MARTNER. 1982. The climate of Yellowstone and Grand Teton National Parks. U.S. National Park Service Occasional Paper No. 6.

FOGEL, R., AND J.M. TRAPPE. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science 52:1–31.

GROOT BRUINDERINK, G.W.T.A., E. HAZEBOEK, AND H. VAN DER VOOT. 1994. Diet and condition of wild boar, *Sus scrofa scrofa*, without supplementary feeding. Journal of Zoology (London) 233:631–648.

HALL, J.G. 1981. A field study of the Kaibab squirrel in Grand Canyon National Park. Wildlife Monograph 75.

JOHNSON, D.H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

KNIGHT, R.R., AND L.L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

KROPP, B.R., AND S. ALBEE. 1996. The effects of silvicultural treatments on occurrence of mycorrhizal sporocarps in a *Pinus contorta* forest: a preliminary study. Biological Conservation 78:313–318.

MATTSON, D.J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:33–56.

———. 1997a. Use of lodgepole pine cover types by Yellowstone grizzly bears. Journal of Wildlife Management 61:480–496.

———. 1997b. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation 81:161–177.

———. 2000. Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Ph.D. Dissertation, University of Idaho, Moscow, Idaho, USA.

———, K. BARBER, R. MAW, AND R. RENKIN. 1999. Coefficients of productivity for Yellowstone's grizzly bear habitat. USGS

Forest and Rangeland Ecosystem Science Center, Colorado Plateau Field Station, Flagstaff, Arizona, USA.

————, B.M. BLANCHARD, AND R.R. KNIGHT. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. Canadian Journal of Zoology 69:1619–1629.

————, K.C. KENDALL, AND D.P. REINHART. 2001. Whitebark pine, grizzly bears, and red squirrels. Pages 121–136 *in* D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

————, AND D.P. REINHART. 1990. Whitebark pine on the Mount Washburn massif, Yellowstone National Park. Pages 106–116 *in* W.C. Schmidt and K.J. McDonald, compilers. Proceedings–Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. Forest Service General Technical Report INT-270.

MEAGHER, M.M. 1973. The bison of Yellowstone National Park. U.S. National Park Service, Scientific Monograph Series No. 1.

MEALEY, S.P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973–1974. M.S. Thesis, Montana State University, Bozeman, Montana, USA.

MILLER, O.K. 1980. Mushrooms of North America. E.P. Dutton, New York, New York, USA.

MOLINA, R., AND J.M. TRAPPE. 1982. Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. Forest Science 28:423–456.

————, AND ————. 1994. Biology of the ectomycorrhizal genus, *Rhizopogon*. I. Host associations, host-specificity and pure culture synthesis. New Phytologist 126:653–675.

NELSON, J.R., AND T.A. LEEGE. 1982. Nutritional requirements and food habits. Pages 323–367 *in* J.W. Thomas and D.E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

NORTH, M., J. TRAPPE, AND J. FRANKLIN. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78:1543–1554.

NOVIKOV, G.A., A.E. AIRAPET'YANTS, YU.B. PUKINSKY, E.K. TIMOFEEVA, AND I.M. FOKIN. 1969. Some peculiarities of the brown bear population in the province of Leningrad. Zoological Journal 68:885–900. (Translated from Russian, Canadian Department of Secretary of State, Translation Bureau, Foreign Languages Division, Ottawa, Ontario, Canada, 1970).

ODACHI, S., AND T. AOI. 1987. Food habits of brown bear in Hokkaido, Japan. International Conference on Bear Research and Management 7:215–220.

OGNEV, S.I. 1931. Mammals of eastern Europe and northern Asia. Volume II. Carnivora (Fissipedia). Glavnauka - Gosudarstvennoe Izdatel'stvo, Moskva. (Translated from Russian, Israel Program for Scientific Translation, Jerusalem, Israel, 1962.)

POELKER, R.J., AND H.D. HARTWELL. 1973. Black bear of Washington. Washington State Game Department, Biological Bulletin 14.

PRITCHARD, G.T., AND C.T. ROBBINS. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

ROBERTS, T.J. 1977. The mammals of Pakistan. Ernest Benn, London, U.K.

ROMME, W.H., AND M.G. TURNER. 1991. Implications of global climate change for biogeographic patterns in the greater Yellowstone ecosystem. Conservation Biology 5:373–386.

SMITH, A.H. 1975. A field guide to western mushrooms. University of Michigan Press, Ann Arbor, Michigan, USA.

STATES, J.S. 1990. Mushrooms and truffles of the Southwest. University of Arizona Press, Tucson, Arizona, USA.

————, AND W.S. GAUD. 1997. Ecology of hypogeous fungi associated with ponderosa pine. I. Patterns of distribution and sporocarp production in some Arizona forests. Mycologia 89:712–721.

STEELE, M.A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species 586:1–9.

THIERS, H.D. 1975. California mushrooms: a field guide to the boletes. Hafner Press, New York, New York, USA.

U.S. NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1977–92. Climatological data. Annual summary. Wyoming. U.S. Department of Commerce, Washington, D.C., USA.

U.S. NATIONAL PARK SERVICE. 1997. Yellowstone's Northern Range: complexity and change in a wildland ecosystem. U.S. National Park Service, Yellowstone National Park, Wyoming, USA.

VISSER, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytologist 129:389–401.

WEISBERG, S. 1985. Applied linear regression. Second edition. John Wiley and Sons, New York, New York, USA.