

Consumption of voles and vole food caches by Yellowstone grizzly bears: exploratory analyses

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Abstract: Previously published observations of bears consuming murid rodents have been limited to short anecdotes. Only 2 studies reported bears consuming rodent food caches. I investigated the consumption of voles (*Microtus* spp.) and vole food caches by grizzly bears (*Ursus arctos*) in the Yellowstone region, 1977–92, using data collected during a study of 140 radiomarked bears. Study bears excavated vole nests, burrows, or food caches at 45 different sites. Excavations of nests ($n = 37$) were more common than excavations of food caches ($n = 15$). The remains of voles were found in 62 bear feces. Occurrences of voles in bear feces and excavations by bears for vole nests or food caches were essentially uncorrelated over time, suggesting that total consumption of voles and pursuit of voles or vole food caches by excavation were affected by different factors. Excavations by bears were largest in size and peaked in number during the driest months of the study period and were most likely to occur on gently sloping sites with abundant grasses, especially of the genus *Phleum*, and sedges (*Carex*). Bear excavations were more common during drought, probably because voles increased their burrowing in response to drying of wet soils, decreased above-ground security, and decreased abundance of above-ground foods. Food caching by voles has been documented in Canada and at high latitudes in the U.S., but prior to this study, only once in the U.S. Rocky Mountains. Bears consumed vole food caches primarily during September and were most successful finding caches at sites where yampah (*Perideridia gairdneri*) was abundant. Study bears excavated vole nests most often during spring and fall. Although voles were not a major source of energy for Yellowstone's grizzly bears, some individuals frequently foraged for voles during certain years.

Key words: food caching, food habits, foraging, grizzly bears, *Microtus*, *Ursus arctos*, voles, Yellowstone

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Numerous studies from throughout the Northern Hemisphere mention consumption of murid rodents (Rodentia: Muridae) by brown bears (*Ursus arctos*). Two studies, both from the same region of Alaska, noted consumption of food caches made by murid rodents—tundra and taiga voles (*Microtus oeconomus* and *M. xanthognathus*; Hechtel 1985, Shideler and Hechtel 2000). However, these references are short and anecdotal. Grizzly bears (*U. a. horribilis*) in the Yellowstone region of western North America are known to consume mice, primarily voles (*Microtus* spp.; Mattson et al. 1991, Craighead et al. 1995). This paper reports and explains aspects of that use.

Because little is known about consumption of mice by bears, this analysis is largely exploratory with respect to

bear behavior. By contrast, considerable is known about voles. I used information on voles to derive expectations about their demography and behavior and, from that, related responses by foraging bears. In particular:

1. Vole populations typically increase during the growing season from an annual nadir in spring (Johnson and Johnson 1982, Rodd and Boonstra 1984). All else equal, I expected that frequency of consumption by bears would increase from spring to fall.
2. Breeding among voles in environments like those of the Yellowstone region begins in late April to early June and lasts through September (Hodgson 1970, Negus et al. 1977, Krebs and Wingate 1985, Streubel 1989). Neonates are localized around nests that are often subterranean. I expected that bears would focus on exploiting vulnerable young in or near nests.

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3. Voles are more vulnerable to predation where and when herbaceous vegetation is sparse, whether because of drought, grazing, or site conditions (Beacham 1980, Negus et al. 1986, Peles and Barrett 1996). All else equal, I expected that consumption of voles by bears would be greatest during droughts.
4. Meadow and montane voles (*M. pennsylvanicus* and *M. montanus*, respectively) are the most common of their genus in the Yellowstone region (Brown 1967, Findley 1951, Hodgson 1970, Clark 1973, Streubel 1989). They are most numerous in mesic or wet meadows with abundant grasses and forbs. I expected that most sign of grizzly bears consuming voles would be in such sites.
5. Beginning in August and September, voles of high latitudes are known to accumulate large food caches consisting mainly of roots (Criddle 1926, Formozov 1966, Gates and Gates 1980, Wolff and Lidicker 1981, Johnson and Johnson 1982, Wolff 1984). I speculated that voles in Yellowstone's cold climate (about 0°C average annual temperature) also cached roots during fall. Given that Yellowstone's grizzly bears commonly consume root caches of northern pocket gophers (*Thomomys talpoides*; Mattson 2004), I expected that bears would also exploit root caches of voles.
6. Finally, because voles are active both above and below ground (Johnson and Johnson 1982), and given that the relative vulnerability of voles in burrows versus above ground might be dictated by different factors, I expected that sign of excavation for voles by bears would be weakly correlated, temporally, with remains of voles in bear feces.

I used these expectations to structure an analysis that was designed to elucidate and provisionally explain basic patterns of grizzly bear behavior associated with consumption of voles. I used data collected during a study of radiomarked grizzly bears in the Yellowstone region, 1977–92.

Study area

The approximate 23,000-km² study area corresponded to the known range of Yellowstone's grizzly bear population, extending south–north from 43°30' to 45°15' latitude and east–west from 109°30' to 111°30' longitude. Yellowstone National Park (YNP) comprised the core 8,700 km². Most of the area occupied by grizzly bears was >2,760 m elevation and consisted of remote mountains and plateaus surrounded by valleys and

plains more intensively settled or used by humans. December–February temperatures averaged about –10°C, and June–August temperatures averaged about 11°C. Precipitation varied in amount and timing with elevation and geographic location and fell mostly as snow that reached accumulations of 20–260 cm before melting during March–June (Dirks and Martner 1982).

About 75% of the study area was forested, and most of this forest was dominated by lodgepole pine (*Pinus contorta*; Despain 1990). Non-forest areas occurred as isolated mesic or wet meadows at mid-elevations of the extensive plateaus of YNP; to the north, as extensive lower-elevation grasslands, often co-dominated by sagebrush (*Artemisia* spp.); and, especially in the mountainous eastern parts of the study area, as alpine tundra and rock. Craighead et al. (1995) describe the study area in detail.

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 characterized according to methods described by Mattson (1997a, 2000). Field crews also described sites where grizzly bear feeding or bedding sign was encountered en route to and from telemetry locations. The measures taken at each location included ocular estimates of total graminoid, forb, and shrub cover (%), and lists of all plant species present within 10 m of plot center. Each species was ascribed an estimate of abundance (1 = rare, 2 = scattered, 3 = common, 4 = abundant, and 5 = dominant). Site measures included aspect, slope, and elevation.

Field crews described all feeding sign by grizzly bears at telemetry locations and elsewhere. During 1986–1992, this included measurements of excavations. For small mammals such as pocket gophers and voles, the length (*A*), width (*B*), and depth (*C*; all in dm) of all excavations were measured (Mattson 2004). Excavated volume (dm³) was estimated as the product of $A \times B \times C$ for each dig. Total volume for a feeding site was simply the sum of volumes from all individual digs.

Measures also were obtained from feeding sites that pertained to the total energy expended and gained by the involved bear. For vole excavations, this included the number of nests and caches exploited by bears for each dig and summed for the entire feeding site. Tallies of exploited nests and caches were probably a minimum given the chance that some were overlooked because they were covered with excavated debris or completely

consumed. One vole food cache was opportunistically collected and oven dried, weighed (g), and analyzed for percent crude protein, crude fiber, starch, and ash content (Mattson 1997b). Based on the relation between a double sample of crude fiber (*CF*) and total dietary fiber (*TDF*; $\text{logit } CF = -1.36 + 0.97 \text{ logit } TDF$, $r^2 = 0.84$; Mattson 2000), the equation from Pritchard and Robbins (1990) was used to estimate percent dry matter digestibility from estimated *TDF*.

As with feeding sites, all feces (scats) thought or known to be from grizzly bears were collected by field crews at and en route to and from telemetry locations, 1977–92. This concurrent collection allowed for comparability of information from scats and feeding sites at broad temporal and spatial scales. Scats were dried and analyzed for percent content according to methods described by Mattson et al. (1991). 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.

I used logistic regression analysis (Hosmer and Lemeshow 2000) to specify the effects of explanatory variables on the likelihood that a bear had versus had not excavated vole nests or food caches at a given location or that a nest or cache had been exploited in an individual dig. Depending on the model, units of analysis were radiotelemetry locations, feeding sites, or individual digs. I specified two models for grizzly bear activity sites: one using only data from telemetry locations, including sites where no feeding sign had been found; and the other using only data from sites with feeding sign of all types, but including plots not at telemetry locations. I gave priority to the first type of model and used the second to confirm patterns. Given that use of voles had occurred, I used linear regression (Weisberg 1985) to specify the effects of total volume of excavated material on total number of excavated nests or food caches. I 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. I used area under the receiver operator characteristic (ROC) curve (Hosmer and Lemeshow 2000) and R^2_L (Menard 2002) to judge model performance, and judged the relative importance of explanatory variables by the change in AIC_c ($\Delta\Delta$ with piece-wise deletion of each variable, in turn, from a model). I de-emphasized statistical hypothesis testing (Johnson 1999) and present *P*-values solely as confirmatory information.

I considered both proximal and distal effects in the analysis (Mattson 2000, 2001). Distal effects were those

operating at broad temporal and spatial scales, whereas proximal effects were operational at the scale of the immediate site. I represented proximal effects by measures taken at telemetry locations or other sites of grizzly bear activity. I represented distal effects with temperature and precipitation data. I obtained mean monthly temperatures ($^{\circ}\text{C}$) and precipitation (ppt, in cm) from regional summaries published by the U.S. National Oceanic and Atmospheric Administration (NOAA). For May–October I calculated cumulative growing season ppt as the total of the prior and current month and, for April, as the total of winter and current month ppt. Mattson (2000) provides a more detailed description of distal factors and their sources.

Results

Field crews collected 6,662 scats and investigated 1,853 telemetry locations of radiomarked bears to determine activity of the located animal. Feeding sign was found at 2,769 sites, including 1,744 sites not associated with telemetry locations. Remains of voles were found in 62 scats, and 262 excavations for voles were found at 49 sites. Sixteen of these sites were attributable to telemetry locations of 10 different marked bears (6 adult females, 1 subadult–adult female, 3 subadult males, and no adult males).

Annual and seasonal patterns

Monthly frequencies of voles in grizzly bear feces and monthly frequencies of excavations for voles at feeding sites were relatively constant with the exception of a September peak at feeding sites (Fig. 1a) and an April peak in feces (Fig. 1b). The late peak in excavations was associated with the only month (Sep) when exploitation of vole food caches was common (Fig. 1c). The early peak in feces preceded a May peak in probability of finding an exploited nest in an individual dig, although mean numbers of nests exploited at a feeding site remained relatively constant among months (Fig. 1b). Total volume of material excavated in pursuit of voles at a feeding site tended to increase from spring to fall, peaking in July–September. Percent frequency of voles in grizzly bear feces and percent frequency of excavations for voles at feeding sites were weakly correlated annually and monthly. Annually, $r = 0.07$ ($n = 16$, $P = 0.81$), whereas monthly, $r = -0.24$ ($n = 8$, $P = 0.56$).

Consumption of voles reached substantial levels during certain months of certain years. Peak relative frequencies in feces occurred during April 1983 (22.2%), August 1984 (5.8%), and September 1988 (3.3%). Peak relative

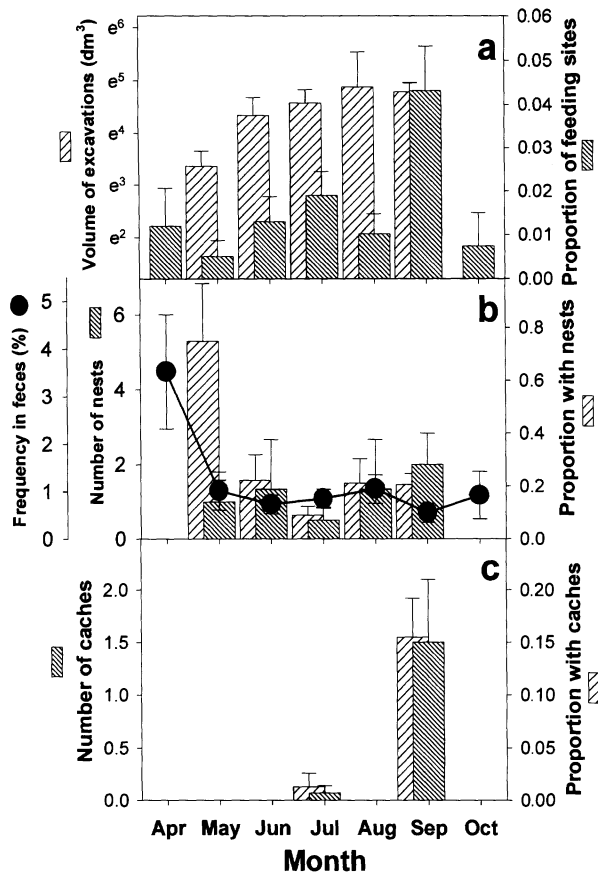


Fig. 1. Monthly values related to consumption of voles or their food caches by Yellowstone grizzly bears: (a) proportion of all feeding sites where excavation of voles by bears was detected, 1977–92, and mean total volume of those excavations, 1986–92; (b) proportion of individual digs with an exploited food cache and mean number of total caches exploited per feeding site, 1986–92; and (c) proportion of individual digs with an exploited vole nest, mean total number of nests exploited per feeding site, 1986–92, and percent frequency of voles in grizzly bear feces collected 1977–92. Error bars correspond to +1 SE.

frequencies of excavations at feeding sites occurred during June, July, and September of 1988 (5.0, 6.5, and 29.6%, respectively), and during July and October of 1992 (4.9 and 4.8%, respectively). During September 1988, 56% of feeding sites where vole burrow systems had been excavated yielded caches and 67% yielded nests.

Probability that voles were excavated at a feeding site

The probability that a radiomarked bear had excavated vole burrow systems versus any other type of

activity was related to 4 factors considered in this analysis, 3 of which were proximal (Table 1). By this model, grizzly bears were most likely to excavate for voles or vole food caches during the cumulatively driest months of the study on gently sloping south-facing slopes with abundant timothy grass (*Phleum* spp.) (Fig. 2). With the exception of aspect, these effects were confirmed by the model for sites with feeding sign from both marked and unmarked animals (Table 1). This model additionally suggested that grizzly bears were most likely to excavate voles or vole food caches on sites with few forbs, extensive graminoid cover, and abundant wheatgrass (*Elymus* spp.).

Size and profitability of excavations

Total volumes excavated by grizzly bears at a feeding site in pursuit of voles or their food caches (Vol , where $Vol' = \ln[Vol + 1]$) were greatest during the driest months of the study and were more strongly positively related to numbers of excavated nests than to numbers of excavated caches. The model was:

$$Vol' = 6.5 - 0.33Ppt + 0.27Nest;$$

with $n = 32$; $R^2 = 0.54$; $F = 17.2$; 2, 29 df; and $P < 0.0001$; where Ppt is current month ppt and $Nest$ is number of excavated nests. Volumes were more or less equally affected by Ppt ($\Delta = 3.0$) and number of excavated nests ($Nest$; $\Delta = 3.9$).

The number of nests exploited by grizzly bears at a feeding site ($Nest$, where $Nest' = \sqrt{Nest}$) increased with increasing total volume of excavations and amounts of onion grass (*Melica spectabilis*) present at the site and decreased with increasing amounts of water sedge (*Carex aquatilis*). The model was:

$$Nest' = 0.76 + 0.0047Vol + 0.91 \ln(Mesp + 1) - 0.22 \ln(Cxaq + 1);$$

with $n = 31$; $R^2 = 0.71$; $F = 22$; 3, 27 df; and $P < 0.0001$; where $Mesp$ is indexed abundance of onion grass and $Cxaq$ is indexed abundance of water sedge. The relative effects of Vol , $Mesp$, and $Cxaq$ (i.e., Δ) were 13.4, 4.6, and 0.1, respectively.

The logit-transformed probability that an individual dig yielded a nest was greatest where digs were widest and deepest, during months when ambient temperatures were the coolest, and at mid-elevations (Table 2). The probability that an individual dig yielded a food cache was greatest where digs were the widest and where yampah and hairgrass (*Deschampsia cespitosa*) were most abundant (Table 2). Compared to nests (i.e., the probability that the dig yielded a cache versus a nest),

Table 1. Logistic regression models for relations between the logit-transformed probability that voles had been excavated at a site and distal and proximal factors, for Yellowstone grizzly bears, 1977–92. β is a parameter estimate and Δ is change in AIC_c with deletion of that variable from the model. Statistics for logistic regression models are for goodness-of-fit tests.

Independent variables	Probability of excavation: Telemetry locations only			Probability of excavation: Feeding sites only		
	β	SE	Δ	β	SE	Δ
Constant	-0.5	1.2		-4.0	1.3	
Distal factors						
Cumulative precipitation (cm) ^a	-2.4	0.54	18.7	-2.4	0.49	17.2
Cumulative precipitation (cm) ^b				0.0066	0.0025	2.1
Proximal factors						
Abundance of <i>Phleum</i> spp. (index) ^b	0.25	0.046	23.5	0.21	0.036	30.7
Abundance of <i>Elymus</i> spp. (index) ^b				0.11	0.032	10.3
Slope ^a	-1.2	0.41	9.2			
Slope				-0.18	0.068	9.4
Degrees from N aspect	0.016	0.0058	7.6			
Distance to forest edge (m) ^a				0.35	0.13	6.0
Total cover of graminoids (%) ^a				1.0	0.25	16.2
Total cover of forbs (%)				-0.53	0.014	21.0
Statistics						
G^2 (df)	102 (2×10^3)			204 (2×10^3)		
P	1.00			1.00		
R_L^2	0.96			0.93		
Area under the ROC curve	0.92			0.92		
n	1786			1990		

^aCoefficient was estimated for data transformed by $\ln(x + 1)$.

^bCoefficient was estimated for data transformed by x^2 .

caches were more likely to be found in individual digs at sites where yampah was abundant:

$$\text{Logit}(p_{\text{cache}}) = -2.5 + 2.3 \ln(\text{Yampah} + 1);$$

with $n = 51$, $r_L^2 = 0.29$, area under ROC curve = 0.76; $G^2 = 4.0$, 1 df, and $P = 0.046$.

The single collected vole food cache consisted almost entirely of onion grass corms. Crude protein, crude fiber, ash, and starch were 5.1%, 5.2%, 4.9%, and 8.3%, respectively. Estimated digestibility was 57.2%.

Excavations for voles versus pocket gophers

Individual digs for voles were distinguished from individual digs for pocket gophers ($\text{Logit}[p_{\text{vole_dig}}]$) by being shallower and wider and by less often containing a food cache:

$$\begin{aligned} \text{Logit}(p_{\text{vole_dig}}) = & 0.23 - 3.8 \ln(\text{Depth} + 1) \\ & + 0.88 \ln(\text{Width} + 1) - 1.6 \text{Cache}; \end{aligned}$$

with $n = 1483$, $R_L^2 = 0.49$, area under ROC curve = 0.76; $G^2 = 657$, 772 df, and $P = 1.00$. *Cache* indicates presence (1) or absence (0) of a food cache. The relative strength of *Depth*, *Cache*, and *Width* effects (i.e., Δ)

were 128.5, 39.9, and 11.9, respectively. Average dimensions of an individual dig for voles or their caches ($n = 260$) were 4.8 dm (SE = 0.2), 2.7 dm (SE = 0.1), and 0.9 dm (SE = 0.03) for length, width, and depth, respectively. The same figures for digs made by bears in pursuit of pocket gophers ($n = 1194$) were 8.9 dm (SE = 0.3), 2.9 dm (SE = 0.06), and 1.4 dm (SE = 0.02). The proportion of excavations for voles that contained a food cache was 0.07 (SE = 0.018) versus 0.28 (SE = 0.013) for pocket gophers.

Discussion

There was little correlation between when voles occurred in grizzly bear feces and when grizzly bears excavated vole burrow systems. This lack of correlation is consistent with expectation 6 (weak correlation between signs of excavation and remains of voles in feces) and with expected lags or other asynchronies in vole numbers, their burrowing, their accumulation of food caches, and factors affecting their relative vulnerabilities to grizzly bear predation when above and below ground. Inconsistent with expectation 1 (frequency of

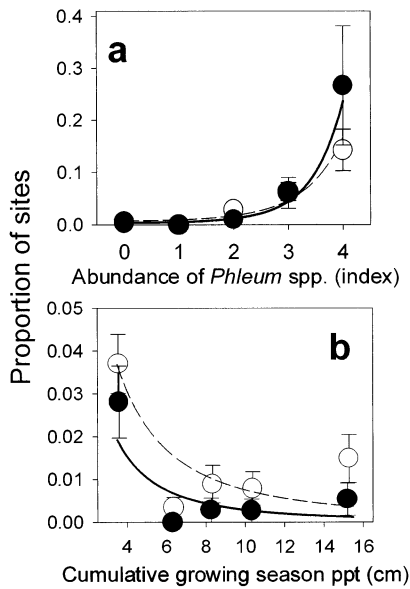


Fig. 2. Univariate relations between proportions of sites with excavations for voles by Yellowstone grizzly bears, 1977–92, and (a) abundance of *Phleum* spp. at the site, and (b) precipitation (ppt) during the current and prior months (cumulative ppt). Circles and associated error bars denote proportions and SEs for quintiles and illustrate goodness-of-fit. Filled circles and solid lines are for relations using all activity sites of radiomarked bears. Open circles and dashed lines are for relations using only sites with feeding or bedding sign, from marked and unmarked animals.

consumption of voles by bears would increase from spring to fall), there was little or no evidence that consumption of voles by Yellowstone grizzly bears increased during the growing season in response to putative increases in vole populations. Numbers and vulnerabilities of voles both probably played a role in determining how many voles were eaten by Yellowstone grizzly bears.

Consistent with expectation 3 (voles are more vulnerable to predation where and when herbaceous vegetation is sparse), excavations were most common during dry years. Drought probably made voles easier to capture above ground, and plausibly created incentives for both voles and bears to dig. Drought could have allowed meadow voles to more often dig and use burrows in the wet-site habitats preferred by them—sites that otherwise would be too saturated (Streubel 1989). Drought would have also predictably reduced the biomass of graminoids and forbs in meadows favored by both montane and meadow voles, as was probably

the case during the drought year of 1988 when excavations for voles by bears peaked.

Sparse ground cover could benefit bears in two ways. First, voles are known to be more vulnerable to predation without cover provided by dense herbaceous vegetation (Beacham 1980, Garsd and Howard 1982, Negus et al. 1986, Peles and Barrett 1996). Second, deprivation of green above-ground forage could stimulate food caching among voles. Bergeron and Jodoin (1994, 1995) found that voles with access to abundant nutritious herbage did not face nutritional constraints during winter. However, removal of green herbage during fall precipitated consumption of low quality foods, which led to rapid population declines. Such conditions might stimulate consumption and caching of below-ground foods by voles where this was an option.

To my knowledge, caching of roots by *Microtus* spp. during the fall has not been documented in the Rocky Mountains in the U.S. except by Benedict and Benedict (2001). Because voles and other vole sign (e.g. feces) were abundant at or near most of the caches ascribed to them during this study and consistent with expectation 5 (bears will exploit root caches of voles), I am confident that voles were caching roots beginning as early as July, and most intensively during September. From these data it is unclear whether both montane and meadow voles made caches or whether caching occurred every year. Commencing in fall, some voles of boreal climates in Canada and Alaska apparently make large communal food caches (Criddle 1926, Wolff and Lidicker 1981, Wolff 1984). It is not surprising that voles at higher elevations of the Yellowstone region engaged in similar behavior in a similarly harsh climate. The positive association between yampah abundance and grizzly bear success at finding vole food caches was probably because both grizzly bears (Mattson et al. 1991) and burrowing rodents (Mattson 2004) heavily exploit this root food in the Yellowstone region.

Consistent with expectation 4 (most sign of grizzly bears consuming voles would be in mesic or wet meadows with abundant grasses and forbs), the types of sites selected by grizzly bears for excavation of voles or vole food caches fit the habitat distributions of voles common to the Yellowstone region. Meadow voles tend to be densest in wet meadows typified by *Carex aquatilis*, *C. microptera*, and *Deschampsia cespitosa*, sometimes to the exclusion of montane voles. Montane voles tend to be most abundant on sites typified by the graminoid species that were most strongly associated with successful grizzly bear excavations—onion grass, timothy grass, and wheatgrass (Findley 1951, Koplin

Table 2. Regression models for relations between the logit-transformed probability that a nest or cache had been exploited at an individual dig and distal and proximal factors, for Yellowstone grizzly bears, 1986–92. β is a parameter estimate and Δ is change in AIC_c with deletion of the corresponding variable from the model. Statistics are for goodness-of-fit tests.

Independent variables	Probability of a nest exploited at a single dig			Probability of a food cache exploited at a single dig		
	β	SE	Δ	β	SE	Δ
Constant	-1575	811		-14.8	3.1	
Distal factor						
Current month's temperature ($^{\circ}\text{C}$) ^a	-0.011	0.0032	11.0			
Elevation (m) ^b	-220	112	1.5			
Elevation (m) ^a	0.000023	0.000011	2.3			
Proximal factors						
Total volume of excavations (dm^3)						
Depth of excavation (dm) ^b	2.8	0.90	8.0			
Width of excavation (dm) ^b	1.8	0.67	5.6	4.4	1.2	13.8
Abundance of <i>Perideridia gairdneri</i> (index) ^b				3.4	0.80	28.6
Abundance of <i>Deschampsia cespitosa</i> (index) ^a				0.29	0.10	13.9
Statistics						
G^2		162 (204)			47 (102)	
P		0.99			1.00	
R_L^2		0.46			0.78	
Area under the ROC curve		0.80			0.91	
n		214			214	

^aCoefficient was estimated for data transformed by x^2 .

^bCoefficient was estimated for data transformed by $\ln(x + 1)$.

and Hoffman 1968, Hodgson 1970, Clark 1973)—suggesting that montane voles, rather than meadow voles, were more often the target of digging grizzly bears.

The dimensions of excavations by grizzly bears for voles were consistent with what is known of vole burrows. Where burrows have been measured, average lengths and depths ranged from 9 to 10 dm and from 0.8 to 2.1 dm, respectively, with nests located at lower average depths within the burrow system, probably to escape predators (Reynolds and Wakkinen 1987, Davis and Kalisz 1992, Laundré and Reynolds 1993). The dimensions of grizzly bear excavations suggest that bears selected for shallower portions of burrows (bear digs averaged 0.9 dm deep), and that they exploited only about $\frac{1}{2}$ the length (i.e., 4.8 dm) of a typical burrow. The greater average depth of excavations yielding nests also fit the tendency for nests to be located deeper within burrow systems.

Although Yellowstone grizzly bears undoubtedly benefited from food caches made by voles, nests were the primary putative source of below-ground reward for bears during most of this study. This contrasted with exploitation of pocket gophers, where food caches probably comprised most of the consumed biomass

(Mattson 2004). Even so, it is unclear to what extent nests produced a reward, to what extent that reward consisted of neonate versus adult voles, and how the fractions of each changed over time, if at all. As a consequence, this analysis is inconclusive regarding the extent to which grizzly bears focused on capture of neonates (expectation 2). In any case, vole root caches probably provided a net reward comparable to that of pocket gopher food caches. The single sampled vole food cache was of comparable quality to pocket gopher root caches (Mattson 2004), and excavations for vole food caches were smaller (Mattson 2004).

In general, voles and vole food caches were not a major source of energy for Yellowstone's grizzly bears. Even so, these small rodents were frequently exploited by bears during certain months of the study, especially during 1988. It is not clear how much energy grizzly bears derived, *per capita*, from the capture of voles. However, even though voles averaged substantially smaller than pocket gophers (20–45 g versus 50–140 g; Hansen and Bear 1964, Clark 1973, Vaughan 1974, Barnes et al. 1980, Reich 1981, Krebs and Wingate 1985), grizzly bears did not dig as deep nor as far when exploiting voles compared to when exploiting gophers. As a potential topic of future study, I speculate

that consumption of voles or vole food caches by Yellowstone grizzly bears was limited primarily by the agility and small size of voles, by their infrequent accumulation of sizable underground food caches, and by the availability of alternate foods.

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