EXPLOITATION OF POCKET GOPHERS AND THEIR FOOD CACHES BY GRIZZLY BEARS

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I investigated the exploitation of pocket gophers (*Thomomys talpoides*) by grizzly bears (*Ursus arctos horribilis*) in the Yellowstone region of the United States with the use of data collected during a study of radiomarked bears in 1977–1992. My analysis focused on the importance of pocket gophers as a source of energy and nutrients, effects of weather and site features, and importance of pocket gophers to grizzly bears in the western contiguous United States prior to historical extirpations. Pocket gophers and their food caches were infrequent in grizzly bear feces, although foraging for pocket gophers accounted for about 20–25% of all grizzly bear feeding activity during April and May. Compared with roots individually excavated by bears, pocket gopher food caches were less digestible but more easily dug out. Exploitation of gopher food caches by grizzly bears was highly sensitive to site and weather conditions and peaked during and shortly after snowmelt. This peak coincided with maximum success by bears in finding pocket gopher food caches. Exploitation was most frequent and extensive on gently sloping nonforested sites with abundant spring beauty (*Claytonia lanceolata*) and yampah (*Perdieridia gairdneri*). Pocket gophers are rare in forests, and spring beauty and yampah roots are known to be important foods of both grizzly bears and burrowing rodents. Although grizzly bears commonly exploit pocket gophers only in the Yellowstone region, this behavior was probably widespread in mountainous areas of the western contiguous United States prior to extirpations of grizzly bears within the last 150 years.

Key words: excavation, grizzly bears, pocket gophers, *Thomomys talpoides*, *Ursus arctos*, Yellowstone

Grizzly bears (*Ursus arctos horribilis*) consume burrowing rodents throughout the bears' current North American range. Arctic ground squirrels (*Spermophilus parryii*) in the state of Alaska and in the Yukon and Northwest Territories of Canada have been the most commonly observed prey of rodent-hunting grizzly bears (Murie 1981; Pearson 1975; Phillips 1987; Reid et al. 1997; Stelmock and Dean 1986), although consumption of other ground squirrel species has been recorded along the eastern slopes of the Rocky Mountains as far south as Montana (Hamer et al. 1991).

South of Canada, it is known that grizzly bears commonly pursue burrowing rodents only in the Yellowstone region of Wyoming, Montana, and Idaho, where northern pocket gophers (*Thomomys talpoides*) rather than ground squirrels are the bears' primary underground prey (Craighead et al. 1995; Mattson et al. 1991), despite the common occurrence of 2 species of ground squirrels in the region (Streubel 1989). Although exploitation of pocket gophers by grizzly bears is currently restricted to the Yellowstone region, Brown (1985) and Storer and Tevis (1996) suggest that, prior to their extirpation, grizzly bears once consumed pocket gophers in California and the southwestern United States.

Whatever the prey species, virtually all records of grizzly bears consuming burrowing rodents have been based on anecdotes or occurrences of rodent remains in bear feces. Murie (1981) made the most detailed description, but his account lacked explanation or analysis that allows for generalization. With the exception of 1 instance involving tundra voles (*Microtus xanthognathus*—Shideler and Hechtel 2000), there has been no record of bears consuming food caches of subterranean rodents. All records involving ground squirrels state that squirrels, rather than food stores, were consumed.

In this paper, I describe and explain exploitation of northern pocket gophers by grizzly bears in the Yellowstone region. I analyzed data collected during a study of radiomarked bears in 1977–1992 to address the following questions: How important were pocket gophers as a source of energy and nutrients for grizzly bears in this region? How was exploitation of pocket gophers affected by weather and site and vegetation features? How important were pocket gophers as a source of energy and nutrients to grizzly bears, continent-wide, prior to extirpations within the last 150 years?

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I used field observations and the ecological literature on pocket gophers to develop the following research hypotheses that focused my analysis and provided context for interpreting results. (1) Grizzly bears focused on consuming pocket gopher food caches rather than the gophers themselves. (2) Grizzly bears consumed pocket gophers and their food caches most often during snowmelt because the gophers were restricted to shallow soil depths (Ingles 1952; Turner et al. 1973; Youmans 1979). (3) Grizzly bears had greatest success finding food caches soon after snowmelt at high elevations of the study area because, under those conditions, pocket gophers subsisted on root caches stored at shallow depths (Barnes et al. 1980; Stuebe and Anderson 1985). (4) Assuming that neonatal pocket gophers were more vulnerable than adults, grizzly bears had greatest success finding nests in May and June, during and shortly after peak parturition time of gophers (Tryon 1947; Turner et al. 1973). (5) Excavations by bears deepened during the growing season and were deepest, on average, where they had exploited a nest because pocket gophers locate their nests deeper than their food caches and at increasing depths through the growing season (Barnes et al. 1980; Moore and Reid 1951; Teipner et al. 1983; Turner et al. 1973). (6) Grizzly bears were less successful exploiting pocket gophers after winters with exceptionally deep snowpacks because pocket gopher populations tend to decrease after harsh winters (Anderson and MacMahon 1981; Hansen and Ward 1966). (7) Finally, sites where grizzly bears exploited pocket gophers were distinguished by abundant plant species (*Elymus*, *Bromus*, and *Polygonum bistortoides*) that increase with pocket gopher activity (Ellison and Aldous 1952; Laycock and Richardson 1975; McDonough 1974; Moore and Reid 1951; Turner et al. 1973) or that are preferred gopher foods (yampah [*Perideridia gairdneri*], false dandelion [*Agoseris glauca*], common dandelion [*Taraxacum*], spring beauty [*Claytonia lanceolata*], and oniongrass [*Melica*]—Aldous 1945; Barnes et al. 1980; Miller 1964; Moore and Reid 1951; Stuebe and Anderson 1985; Teipner et al. 1983; Tryon 1947; Turner et al. 1973; Vaughan 1974; Ward and Keith 1962; Youmans 1979).

MATERIALS AND METHODS

The study area was about 23,000 km^2 in size and corresponded to the known range of Yellowstone's grizzly bear population. This range extended south–north from 43°30′S to 45°15′N and east–west from 109°30′E to 111°30′W. Yellowstone National Park (YNP) comprised the core 8,700 km^2. Most of the area occupied by grizzly bears was >2,000 m elevation and consisted of remote mountains and plateaus surrounded by valleys and plains that were settled or otherwise used by humans. Annual temperatures averaged ~0°C. Precipitation varied in amount, and timing varied with elevation and geographic location. At high elevations, it fell mostly as snow, which reached accumulations of 100–260 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). Whitebark pine (*Pinus albicaulis*) was abundant above about 2,560 m elevation. Nonforest areas occurred as isolated mesic or wet meadows at midelevations of the extensive plateaus of YNP or, farther north, as extensive lower elevation grasslands, often codominated by sagebrush

(*Artemisia*). Alpine tundra and rock were extensive, especially in the mountainous eastern parts of the study area. Elk (*Cervus elaphus*) were abundant throughout the study area, whereas bison (*Bos bison*) were abundant only in northern and central YNP. Both ungulate species substantially increased in numbers during 1977–1988. Craighead et al. (1995) describes the study area in detail.

Grizzly bears were trapped, marked, and radiolocated according to methods described by Blanchard and Knight (1991) and Knight and Eberhardt (1985). A subset of radiolocations was visited and characterized according to methods described by Mattson (1997a, 2000). Field crews also described sites where, en route to and from telemetry locations, they encountered grizzly bear feeding or signs of bedding. At each site, field crews located a variable-radius forest inventory plot (Avery 1975) at the center of grizzly bear activity. Trees were tallied and identified as live or dead, and the diameter of each was measured at 1.4 m aboveground. Within 10 m of plot center, field crews visually estimated and recorded total graminoid, forb, shrub, and woody debris cover (as percentage of total cover). They listed all plant species present and recorded indices of coarse woody debris amount (1–7, none to heavy), size (1–7, small to large), and decomposition (1–6, solid to well decomposed). Each plant species was ascribed an estimate of abundance (1–5, rare to dominant). Site measures included aspect (compass direction in degrees), slope (degrees from the horizontal), and elevation (m).

Field crews described grizzly bear feeding signs at telemetry locations and wherever encountered elsewhere. After 1985, crews measured the average length (*A*), width (*B*), and depth (*C*, dm) of individual excavations by bears for small mammals, including pocket gophers, and individual roots, including those of yampah and biscuitroot (*Lomatium cous*). Approximate excavated volume (dm^3) was calculated as the product of $A \times B \times C$ for each digging. Total volume for a feeding site was the sum of estimated volumes from all individual diggings.

Field crews also obtained measures related to total energy gained and expended by foraging bears. For pocket gopher excavations, crews recorded numbers of nests and caches exploited by bears by individual dig and summed them for the entire feeding site. Remains of 10 pocket gopher root caches exploited by bears were collected, oven dried, and weighed (g). Individual roots of yampah and biscuitroot also were collected from 60 and 76 sites, respectively, where they had been consumed by bears. Samples were analyzed for percentage crude protein, crude fiber, starch, and ash content. For a subsample, we also analyzed percentage total dietary fiber (Mattson 1997b). On the basis of the relation between paired measures of crude fiber and total dietary fiber (logit Crude Fiber $= -1.36 + 0.97$[logit Total Dietary Fiber], $r^2 = 0.84$—Mattson 2000), I estimated percentage dry matter digestibility from measured or estimated total dietary fiber (Pritchard and Robbins 1990). To simulate energy expended to obtain roots or exploit pocket gophers, I measured the maximum force required to dig up the soil using a 5-tined potato fork that was modified in the laboratory to approximate the front paw and claws of a bear (and which we refer to as a clawometer—Holcroft and Herrero 1984; Mattson 1997b). We inserted the tines into the ground at a 45° angle at sites where pocket gophers or roots had been excavated and measured the force (in kg) necessary to lift the soil.

All feces (scats) thought or known to be from grizzly bears were collected by field crews at and en route to and from bear telemetry locations in 1977–1992. This concurrent collection allowed for comparison of information from scats and feeding sites at broad temporal and spatial scales. Scats were dried and analyzed as described by Mattson et al. (1991). Results were reported for individual diet items by month and year as total frequency of occurrence in scats, percentage
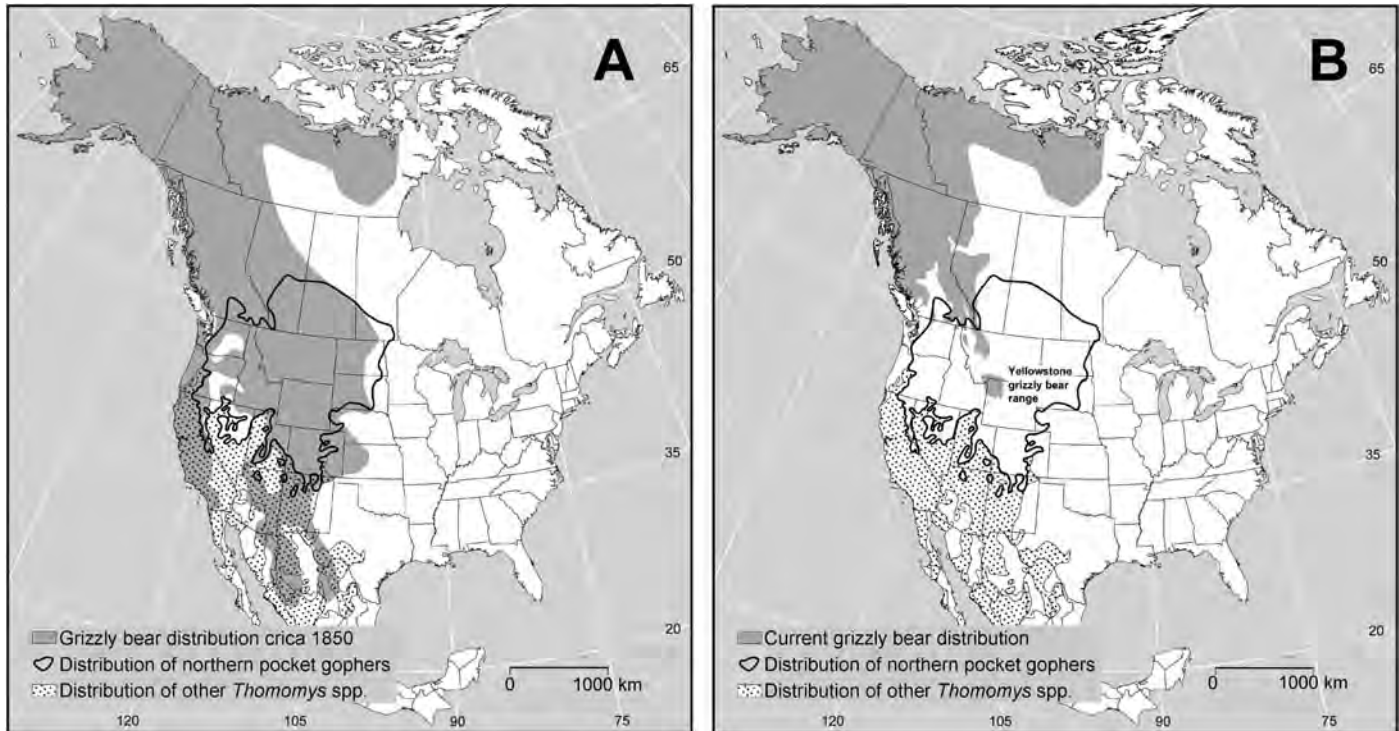
FIG. 1.—Distributions of pocket gophers (*Thomomys*—Hall 1979) and grizzly bears (Mattson and Merrill 2002) in North America A) in about 1850 and B) currently. Grizzly bear range is dark gray, the range of northern pocket gophers is circumscribed by a solid line, and ranges of other pocket gophers in the genus *Thomomys*, exclusive of northern pocket gophers, are stippled.

of total fecal volume, and mean percentage for scats in which the item occurred. I assumed that all roots detected in bear feces collected during April and May, excluding those of biscuitroot, represented the remains of pocket gopher food caches. During spring, the only individually excavated roots that bears consumed were those of biscuitroot, and only at sites that were distinct from those where they exploited pocket gophers (Mattson 1997b; Mattson et al. 1991); otherwise, their only known source of roots during spring was pocket gopher food caches.

I adopted the principles of statistical explanation (Salmon 1984) and conditional independence (Dawid 1979; Kyburg 1969) as a basis for most inferences in this analysis. These principles invoke model building that considers a broad range of biologically plausible explanatory factors as a means of correcting for bias introduced by uncontrolled field conditions (Mattson 2000). I did not base conclusions on statistical hypothesis testing (Johnson 1999) and present *P* values solely as confirmatory information. I used logistic regression analysis (Hosmer and Lemeshow 2000) to specify the effects of explanatory variables on the log odds that a bear either had excavated pocket gopher nests or food caches at a given activity site or had found and exploited a nest or cache in an individual dig. Radiotelemetry locations, feeding sites, and individual digs were units of analysis for different models. I specified 2 models for grizzly bear activity sites: one with only data from telemetry locations, including sites where no signs of feeding or bedding had been found, and the other with only data from sites with signs of feeding or bedding, but including plots not at telemetry locations. I gave priority to the 1st type of model and used the 2nd for confirmation. Given that exploitation of pocket gophers had occurred, I used multiple linear regression (Weisberg 1985) to specify the effects of explanatory variables on total excavated volumes and total numbers of excavated nests or food caches. I used maximum likelihood methods for parameter estimation and the sample size–adjusted version of Akaike's in-

formation criterion (AIC$_c$—Burnham and Anderson 1998) for model selection.

I considered proximal and distal effects in the analysis. Distal effects were those operational at broad temporal and spatial scales, whereas 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. I enumerated distal effects, primarily related to weather, from other sources. I obtained monthly temperatures (°C) and precipitation (cm) from regional summaries published by the United States National Oceanic and Atmospheric Administration (NOAA; http://www1.ncdc.nodc.noaa.gov/pub/orders). I calculated cumulative 2-month precipitation rates for May–October as the sum of precipitation for the previous and current month. For April, I calculated this value as the sum of the current month and total winter precipitation. I calculated total winter precipitation as the sum of precipitation for November–March. I used snow depths and date of snow melt (1st spring day with 0 cm of snow recorded on the ground) from records for Yellowstone Lake weather station—the station nearest most of the pocket gopher feeding observed during this study. Mattson (2000) provides a more detailed description of these distal factors and their sources.

RESULTS

Distributions of grizzly bears and Thomomys pocket gophers.—Overlap between the North American ranges of grizzly bears and pocket gophers during the mid-1850s amounted to 2,297,200 km^2 or 26% and 89% of grizzly bear and gopher ranges, respectively (Fig. 1A). Current North American ranges of grizzly bear and northern pocket gopher

TABLE 1.—Parameter estimates related to energetics of Yellowstone grizzly bears consuming pocket gopher root caches and individual roots of biscuitroot and yampah, 1986–1992. Sample sizes (*n*) and *SE*s are given for mean values of variables obtained from field samples, but not for values derived by calculation. A clawometer is a 5-tined potato fork modified to approximate the front paw and claws of a bear.

	Parameter estimate ($\bar{X} \pm SE$)					
Food	Mass of cache remains or excavated root (g)	Estimated dry matter digestibility of cache or root (proportion)	(D) Volume excavated per individuated dig (dm^3)	(E) Proportion of rewards that were caches vs. nests	(F = D × E) Volume excavated per cache (dm^3)	(G = F/3.9) Number of paw-sized digs per cache or root, using biscuitroot as the standard	Resistance to extraction of clawometer (kg/dig)
Pocket gopher caches							
April			104.2 ± 24.0 (*n* = 14)	0.53 ± 0.04 (*n* = 21)	55.3	14.1	
	37.8 ± 9.4 (*n* = 10)	0.48 ± 0.06 (*n* = 10)					3.3 ± 0.6 (*n* = 17)
May			85.6 ± 12.8 (*n* = 57)	0.59 ± 0.02 (*n* = 75)	50.7	12.9	
Biscuitroot roots	0.90 ± 0.04 (*n* = 102)	0.62 ± 0.02 (*n* = 76)	3.9 ± 1.2 (*n* = 30)			1.0	6.0 ± 0.5 (*n* = 50)
Yampah roots	0.78 ± 0.04 (*n* = 76)	0.72 ± 0.01 (*n* = 60)	4.7 ± 2.7 (*n* = 21)			1.2	8.6 ± 0.6 (*n* = 32)

overlap very little (103,250 km^2, or 5% of current grizzly bear range; Fig. 1B). Yellowstone's grizzly bears occupy the core of northern pocket gopher distribution.

Sample sizes.—Activity of Yellowstone grizzly bears was investigated at 1,853 telemetry locations attributable to 140 radiomarked bears. The median number of sites per bear was 8, and the upper limits of the 1st and 3rd quartiles were 3 and 19 locations, respectively. There were 2,769 sites with documented signs of feeding or bedding, including 1,744 sites not associated with telemetry locations. Grizzly bears excavated pocket gopher nests or food caches at 275 of these sites. Remains of pocket gophers were detected in 51 of the total 6,662 feces collected and analyzed. Models were specified with somewhat fewer observations than given here (see *n* values in Tables 1–4) because data were missing for some explanatory variables in many of the observations.

Seasonal patterns of exploitation.—Exploitation of pocket gophers by grizzly bears, whether reckoned as frequency or size of excavations, peaked during April and May when this activity composed about 20–25% of all observed grizzly bears activity (Fig. 2A). Although total volumes of excavations declined (Fig. 2A), average depths of excavations tended to increase with date (Fig. 2A): DEP^2 = −5.6 + 1.6 ln(JD + 1), where DEP is depth of excavation and JD is Julian date (r^2 = 0.04; *d.f.* = 1, 156; *F* = 6.1; *P* = 0.015). Average number of exploited food caches and probabilities of finding caches in individual digs also peaked during April–May (Fig. 2B). Frequency of pocket gopher in grizzly bear feces and average number of exploited nests peaked in April and declined through July. By contrast, proportion of individual digs containing exploited nests peaked during July after an increase that started with advent of parturition among pocket gophers in May (Fig. 2C). Moreover, the ratio of feces containing pocket gopher remains to total number of exploited nests increased through the growing season (Fig. 2C), suggesting that number of

gophers captured by bears per nest was lowest during spring and highest during late summer into fall.

Fortnightly, there was a strong relation between snowmelt and grizzly bear exploitation of pocket gophers (Fig. 3). Virtually no consumption of pocket gophers or their food caches occurred prior to the advent of significant melt in mid-April (Fig. 3A). After early May, the frequency of pocket gopher exploitation by bears declined as snow depths also lessened. Volume of excavation peaked in late May (Fig. 3A), however, coincident with the culmination of snowmelt and peaks in average numbers of exploited nests and food caches and proportion of caches in individual digs (Figs. 3A–C). Exploitation of caches dropped dramatically during June after snow cover had disappeared. During April–June, proportion of digs containing exploited nests increased, whereas average number of exploited nests per feeding site generally declined (Fig. 3C).

Comparative energetics of consuming pocket gopher food caches.—The remains of what were probably pocket gopher food caches occurred in 90 of 724 scats collected during April and May 1977–1992. Food caches comprised 5.3% ± 0.9% ($\bar{X} \pm SE$) of fecal volumes pooled for the 2 months averaged over all years. By individual month, the putative remains of caches comprised 8.8% ± 1.4% and 3.7% ± 1.0% of fecal volume during April and May, respectively. Annually, volume ranged from 0% to 16% during April and 0% to 15% during May, with peak volume pooled for both months occurring in 1980 (11%) and 1988 (11%). The bulbaceous roots of oniongrass comprised 66% and 52% of total putative cache residue in bear feces during April and May, respectively.

The rewards and costs of exploiting pocket gopher food caches differed from those of exploiting individual roots (i.e., biscuitroot and yampah roots; Table 1). The mean volume of caches exploited by grizzly bears (Table 1) differed little from mean volume of unexploited caches collected by other

TABLE 2.—Logistic regression models relating explanatory factors to the log odds that pocket gophers or pocket gopher food caches were consumed by Yellowstone grizzly bears at a site, 1977–1992; for telemetry locations only, with or without signs of feeding and for sites with signs of feeding only, including sites from unmarked bears. ß refers to an estimated parameter and Δ to change in AIC_c with deletion of the corresponding variable. Statistics are for goodness-of-fit tests.

Explanatory variable or statistic	Log odds					
	Telemetry locations only			Feeding sites only		
	ß	SE	Δ	ß	SE	Δ
Constant	−1.5	0.30		8.5	3.7	
Proximal factor						
Yampah abundance (index)	0.52[a]	0.26	1.8	0.72[a]	0.14	23.4
Spring beauty abundance (index)	0.75[a]	0.33	2.9	0.77[a]	0.21	11.1
Oniongrass abundance (index)	0.84[a]	0.33	4.1			
Poa spp. abundance (index)				−0.36[a]	0.14	4.9
Total graminoid cover (%)				0.000012[b]	5.0×10^{-6}	7.1
Total forest basal area (m²/ha)	−0.44[a]	0.18	4.5	−0.39[a]	0.12	10.8
Amount of deadfall (index)	−1.4[a]	0.48	10.4	−0.46	0.14	12.1
Slope (°)	−0.040	0.020	2.9	−0.0021[b]	0.00063	14.7
Distal factor						
Number of days after snowmelt	−0.012	0.0038	8.9	−0.053	0.0066	60.6
Number of days after snowmelt (squared)				0.00027[b]	0.000045	28.2
Statistics						
G^2 (d.f.)	368 (2×10^3)			841 (2×10^3)		
P	1.00			1.00		
R_L^2	0.84			0.71		
n	1,689			2,104		

[a] Coefficient is for data transformed by $\ln(x + 1)$.

[b] Coefficient is for data transformed by $(x)^2$.

researchers in Idaho and Utah (44.1 g dry weight—Barnes et al. 1980; Stuebe and Anderson 1985), suggesting that grizzly bears consumed a small part ($\sim 44 - 38 = 6$ g) of each cache. Even so, individually excavated roots were much smaller ($\sim$0.8–0.9 g; Table 1) than a reward of this size. On average, grizzly bears excavated roughly 13.5 times the volume of soil to obtain a cache compared with the volume they excavated to obtain an individual root (Table 1), although soils excavated to obtain individual roots were $\sim$2 times more resistant to the clawometer compared with soils excavated to obtain caches.

Effects on probability of exploitation.—On the basis of telemetry locations of marked bears, the odds that Yellowstone grizzly bears had exploited pocket gophers or their food caches at a site were strongly related to 7 factors considered in this analysis (Table 2). Grizzly bears most often exploited pocket gophers during or shortly after snowmelt on gently sloping sites with abundant yampah, spring beauty, and oniongrass. A typical site also had little or no forest overstory or coarse woody debris (deadfall; Fig. 4). Factors related to forest structure (deadfall and overstory basal area) had a greater effect ($\Delta = 66.0$) than factors related to abundance of potential herbaceous root foods (yampah, spring beauty, and oniongrass; $\Delta = 17.3$). Amount of deadfall, time since snowmelt, and forest basal area had the greatest individual effects.

Except for the effect of oniongrass, effects specified from telemetry locations were confirmed in the analysis of feeding sites only from both marked and unmarked bears (Table 2; Fig. 4). In addition, a positive effect of total graminoid cover and a negative effect of bluegrass (*Poa*) abundance were identified.

Time since snowmelt, abundance of yampah, site slope, and amount of deadfall had the greatest individual effects in this model.

Effects on intensity of exploitation.—Average numbers of nests and food caches exploited by grizzly bears at feeding sites were related to 4 and 5 factors, respectively, considered in this analysis, including a polynomial of excavated volume (Table 3). Numbers of exploited nests and caches both increased with increasing total volumes of excavations and decreased with increasing mean depths. Exploited nests were most numerous at sites with abundant *Elymus*, whereas exploited food caches were most numerous during the wettest months at sites with abundant spring beauty. Total excavated volume was greatest on sites with gentle slopes and abundant spring beauty shortly after snowmelt (Table 3). Excavated volume otherwise tended to be smallest after wet winters and abundant precipitation during the current and previous month. Time since snowmelt and abundance of spring beauty had the greatest individual effects on excavated volumes.

Effects on probability of finding a nest or cache.—Volumes of individual digs differed depending on whether a reward was obtained and whether it was a nest or cache. Canonical analysis indicated that most differences were attributable to length and width of digs. The 1st canonical variate accounted for 91% of total variation (Wilks' $\lambda = 0.80$; d.f. = 9, 3074; $F = 32.4$; $P < 0.0001$), and standardized coefficients for length, width, and depth of excavations were 0.77, 0.59, and 0.07, respectively. Lengths and widths were both least where no reward had been obtained and greatest where both a nest and cache had been ex-

TABLE 3.—Multiple regression models relating explanatory factors associated with site features or weather to total volume of excavations and total number of pocket gopher food caches or nests exploited by Yellowstone grizzly bears at feeding sites, 1986–1992. ß refers to an estimated parameter and Δ to change in AIC_c with deletion of the corresponding variable. Models were specified for numbers of nests or caches (y) transformed by $(y + 0.5)^{0.5}$.

Explanatory variable or statistic	Total volume of excavations (dm^3)			Number of nests[a]			Number of food caches[a]		
	ß	SE	Δ	ß	SE	Δ	ß	SE	Δ
Constant	10.0	1.4		0.11	0.16		1.8	0.19	
Proximal factor									
Spring beauty abundance (index)	0.97[b]	0.24	4.7				0.37[b]	0.12	1.7
Elymus abundance (index)				0.023[a]	0.0079	1.6			
Slope (°)	0.0024[a]	0.00095	0.5						
Total volume of excavations (dm^3)				0.00029	0.000029	21.8	0.00026	0.000038	15.9
Total volume of excavations (dm^3; natural log)				0.26[b]	0.032	30.9	0.33[b]	0.046	17.5
Depth of excavations (dm)				−0.10[a]	0.022	6.9	−0.43	0.12	3.9
Distal factor									
Number of days after snowmelt	−0.59[b]	0.10	11.4						
Total winter precipitation (cm)	−1.2[b]	0.44	1.2						
Cumulative 2-month precipitation (cm)	−0.0044[a]	0.0017	0.7						
Current month precipitation (cm)							0.31[b]	0.13	0.6
Statistics									
F (d.f.)	15.1 (5, 140)			97.9 (4, 130)			63.8 (5, 130)		
P	<0.0001			<0.0001			<0.0001		
R^2	0.35			0.75			0.71		
n	146			135			136		

[a] Coefficient is for data transformed by $(x)^2$.
[b] Coefficient is for data transformed by $\ln(x + 1)$.

ploited. Otherwise, individual digs where a cache had been exploited were substantially wider than digs where a nest had been found (3.6 ± 0.15 dm versus 3.0 ± 0.12 dm, respectively). Mean depths of digs for nests (1.5 ± 0.04 dm) and caches (1.5 ± 0.03 dm) were nearly identical.

Consistent with the previous results, odds that bears found pocket gopher nests or food caches in individual digs were strongly related to excavated volumes (Table 4; Fig. 5). At any given volume, bears were more likely to have found and exploited a cache than a nest, although the probability of finding both declined relative to unit increases in sizes of excavations (Fig. 5A). Otherwise, the odds of finding a nest in a dig were greatest on sites with abundant *Deschampsia cespitosa* and *Elymus* and following dry winters (Fig. 5D). Caches were more likely to be found in wide digs at high elevations early in the year or during wet months that followed 2 dry months (Fig. 5). Precipitation during the current month, date, and volume of excavation had the greatest individual effects on odds of finding a cache.

DISCUSSION

Although grizzly bears have morphological features that facilitate efficient digging (e.g., long claws, large suprascapular muscles, and large postscapular fossa—Davis 1949; Herrero 1978), these features are not well developed compared with other species that specialize in scratch digging (Mattson 1998). Even so, excavated foods are a distinguishing feature of grizzly bear diets (Herrero 1985; Mattson 1998). Given that the energetic demands of digging are high (Hildebrand 1985) and

that grizzly bears lack well-developed physical adaptations, bears likely compensate behaviorally by digging at times and places when costs are low and benefits high. As elaborated in the following sections, this analysis showed that grizzly bears were highly selective when exploiting subterranean foods.

How important are pocket gophers to Yellowstone grizzly bears?—Yellowstone's grizzly bears frequently sought out and exploited pocket gophers during spring, consuming both gophers and vegetal foods that the gophers had cached. Consistent with hypothesis 1, food caches were a primary source of energy. This was partly reflected in the extent to which grizzly bear foraging was sensitive to the availability of caches. The frequency and size of excavations by bears declined after May, commensurate with a precipitous drop in their success finding caches. This decline in use occurred despite continued success finding nests, and even despite an increase in the apparent rate at which they consumed pocket gophers from or near exploited nests. This interpretation is consistent with the finding that pocket gopher remains in grizzly bear feces during spring were less frequent (1–4%) than putative food cache residues (3–9%). The only evidence for an effect of parturition on vulnerability of gophers was the greater success of bears in finding nests with progression of the growing season. Otherwise, in contradiction to hypothesis 4, grizzly bears did not increase their exploitation of nests during or shortly after peak parturition among gophers, nor was the apparent reward per nest greatest at that time.

Conditions profitable for exploiting pocket gophers were apparently widespread only during spring and were restricted to fewer favorable microsites thereafter. Most likely, this was

TABLE 4.—Logistic regression models relating explanatory factors to the log odds that pocket gopher nests or food caches were found by Yellowstone grizzly bears in an individual excavation, 1986–1992. ß refers to an estimated parameter and Δ to change in AIC_c with deletion of the corresponding variable. Statistics are for goodness-of-fit tests.

| | Log odds | | | | | |
| | Nest present | | | Food cache present | | |
Explanatory variable or statistic	ß	SE	Δ	ß	SE	Δ
Constant	19.2	6.6		−8.2	1.2	
Proximal factors						
Volume of individual excavation (dm^3)	0.54[a]	0.064	74.7	0.61[a]	0.082	55.7
Width of individual excavation (dm)				1.1[a]	0.26	16.6
Deschampsia cespitosa abundance (index)	0.041[b]	0.013	7.0			
Elymus abundance (index)	0.22	0.070	8.0			
Elevation (m)				6.5[a]	1.8	11.1
Distal factors						
Total winter precipitation (cm)	−1.3	0.50	6.1			
Current month precipitation (cm)				2.2[a]	0.28	85.4
Cumulative two-month precipitation (cm)				−0.095	0.033	6.4
Julian date				−5.6[a]	0.78	70.2
Statistics						
G^2 (d.f.)	1,159 (1×10^3)			1,182 (1×10^3)		
P	0.37			0.90		
R_L^2	0.29			0.33		
n	1,204			1,269		

[a] Coefficient is for data transformed by $\ln(x + 1)$.
[b] Coefficient is for data transformed by $(x)^2$.

because, after May, number of food caches declined, difficulty of excavation increased, and burrowing by pocket gophers deepened (see below—Turner et al. 1973). Excavations by grizzly bears also tended to deepen during the growing season but, at their deepest, averaged only ~2 dm. Most caches were shallower than this (Barnes et al. 1980; Teipner et al. 1983). Conversely, most runways and nests were much deeper (3–15 dm), especially after soils thawed and dried (Barnes et al. 1980; Moore and Reid 1951; Teipner et al. 1983; Turner et al. 1973). Thus, in contradiction to aspects of hypothesis 5, bears dug no deeper for nests than for caches. These patterns suggest that grizzly bears exhausted available caches at the same time that gophers were reducing their caching activity and beginning to burrow deeper. This would have predictably resulted in major declines in the energetic rewards of pursuing pocket gophers and pocket gopher food caches.

Although pocket gophers and pocket gopher food caches generally were not a major source of energy and nutrients for Yellowstone's grizzly bears, they were a consistent food that composed a sometimes substantial part of bears' diets during April and May. In 1980 and 1988, putative food caches alone composed over a 10th of spring fecal contents. More significantly, exploitation of pocket gophers composed ~20–25% of all feeding activity by grizzly bears during spring. For this reason alone, the open habitats favored by bears for exploiting pocket gophers were important as a location of concentrated springtime grizzly bear activity. Managers desiring to minimize encounters between grizzly bears and humans should consider these habitats when designing conservation plans.

How does weather affect exploitation of pocket gophers?— Consistent with hypotheses 2 and 3, the dynamics of snowpack accumulation and melt apparently affected exploitation of pocket gophers by grizzly bears more than any other suite of factors. Snowpack in most areas where grizzly bears exploited pocket gophers reached depths of about 1 m in late March and early April, with exploitation of pocket gophers beginning as terminal melt started in late April. At that time, I observed bears digging through >5 dm of snow, precisely targeting nests and food caches on the ground below. Levels of exploitation and success at finding caches peaked for bears during snow-melt, dropping sharply as soon as snowmelt was complete. No doubt, this pattern reflected both peak availability of pocket gopher food caches and peak vulnerability of caches and gophers to grizzly bears (Ingles 1952; Turner et al. 1973; Youmans 1979). Moreover, soils saturated by snowmelt were much easier to excavate than soils any other time of year.

Consistent with hypothesis 6, grizzly bears were least successful in finding nests and made the smallest excavations after wet winters. Assuming that number of nests was positively correlated with number of pocket gophers, this result probably reflected declines in pocket gopher populations subjected to the stresses of a deep persistent snowpack. On the other hand, small excavations also could have been caused by pocket gophers remaining longer at shallow depths because of prolonged snowmelt and the resulting prolonged saturation of soils.

Residual to the effects of snowpack and snowmelt, grizzly bears exploited more caches or were more successful in finding caches in individual excavations during the wettest months of the growing season. This ancillary effect could be attributed to
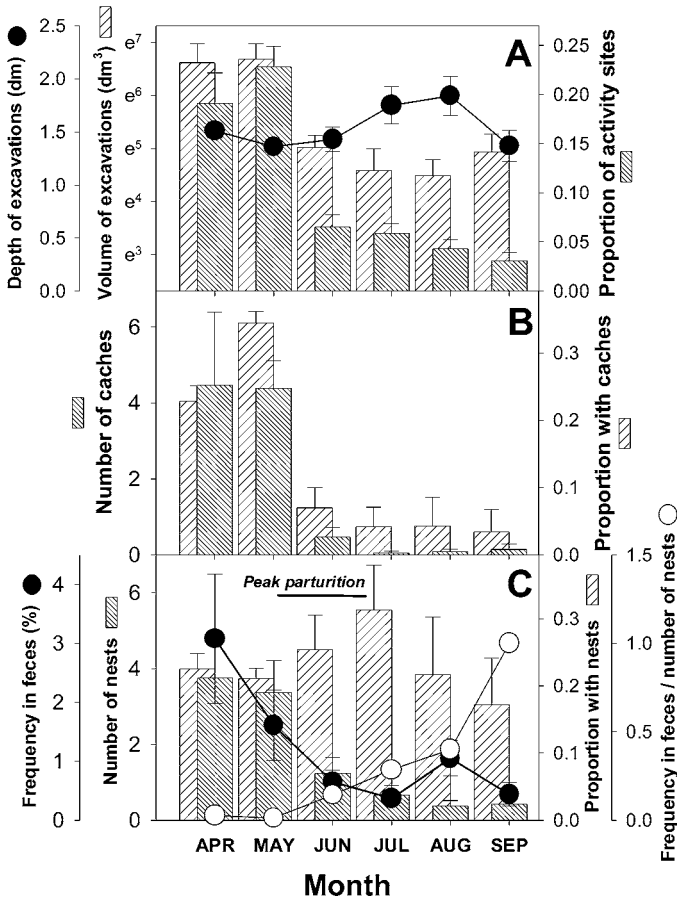
FIG. 2.—Monthly diet and activity related to consumption of pocket gophers or their food caches by Yellowstone grizzly bears: A) sites where signs of pocket gopher exploitation were observed as a proportion of all feeding sites, 1977–1992, and mean total volumes and depths of excavations, 1986–1992; B) mean number of caches exploited at a feeding site and proportion of individual diggings with signs of a food cache, 1986–1992; and C) relative frequency of pocket gophers in grizzly bear feces, 1977–1992, and mean number of nests exploited at a feeding site and proportion of individual diggings with signs of a nest, 1986–1992. The period of peak parturition is shown for pocket gophers. Error bars correspond to 1 *SE*.

both greater ease of digging by bears and greater rates of root caching by gophers. Root caching is positively related to rates of burrowing (Anderson and MacMahon 1981). Some studies have shown a positive relation between burrowing and soil moisture (Kuck 1969; Miller 1948), although this result has not been universal (Bandoli 1981; Miller and Bond 1960). Persistent wet soils could also force pocket gophers to store caches at shallower depths, where bears would be more successful at finding them.

How do site features affect exploitation of pocket gophers?—Grizzly bears most often exploited pocket gophers in gently sloping, nonforested valleys. These conditions are consistent with what is known of the habitat distribution of northern pocket gophers, including their avoidance of conifer forests (e.g., Hansen and Beck 1968; Vaughan 1974) because of the scarcity of subterranean foods (Anderson and Mac-Mahon 1981).
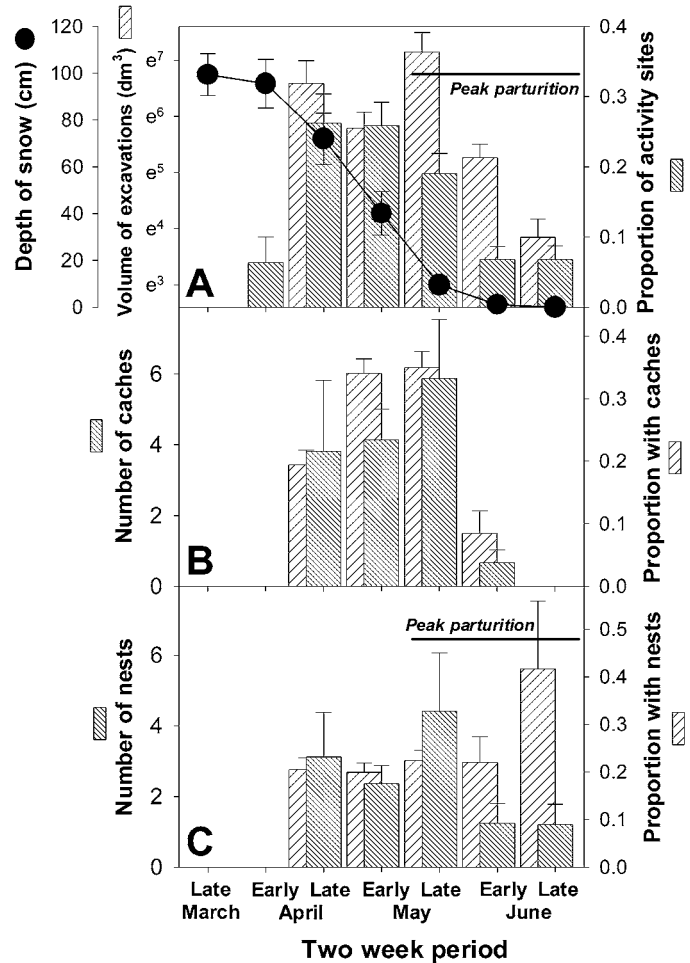
FIG. 3.—Factors related to consumption of pocket gophers or their food caches by Yellowstone grizzly bears, fortnightly, during spring and early summer: A) mean snow depth and sites where signs of pocket gopher exploitation were observed as a proportion of all sites with feeding activity, 1977–1992, and mean total volume of excavations, 1986–1992; B) mean number of caches exploited at a feeding site and proportion of individual diggings with signs of a food cache, 1986–1992; and C) mean number of nests exploited at a feeding site and proportion of individual digs with signs of a nest, 1986–1992. The period of peak parturition is shown for pocket gophers. Error bars correspond to 1 *SE*.

Consistent with hypothesis 7, exploitation of pocket gophers by Yellowstone grizzly bears was positively associated with on-site abundance of preferred root foods, especially spring beauty. Spring beauty is a substantial part of pocket gopher food caches wherever it occurs (Aldous 1945; Stuebe and Anderson 1985; Tryon 1947; Youmans 1979). Moreover, spring beauty's ephemeral stems desiccate and virtually disappear shortly after snowmelt. Spring beauty might have indicated not only sites but also times that favored grizzly bear foraging on gopher food caches. Yampah and oniongrass were also positively associated with sites where grizzly bear exploited pocket gophers. Like spring beauty, oniongrass and yampah are often important parts of pocket gopher food caches (Aldous 1945; Barnes et al. 1980; Moore and Reid 1951; Tryon 1947; Turner et al. 1973; Youmans 1979). Moreover, oniongrass was the most common
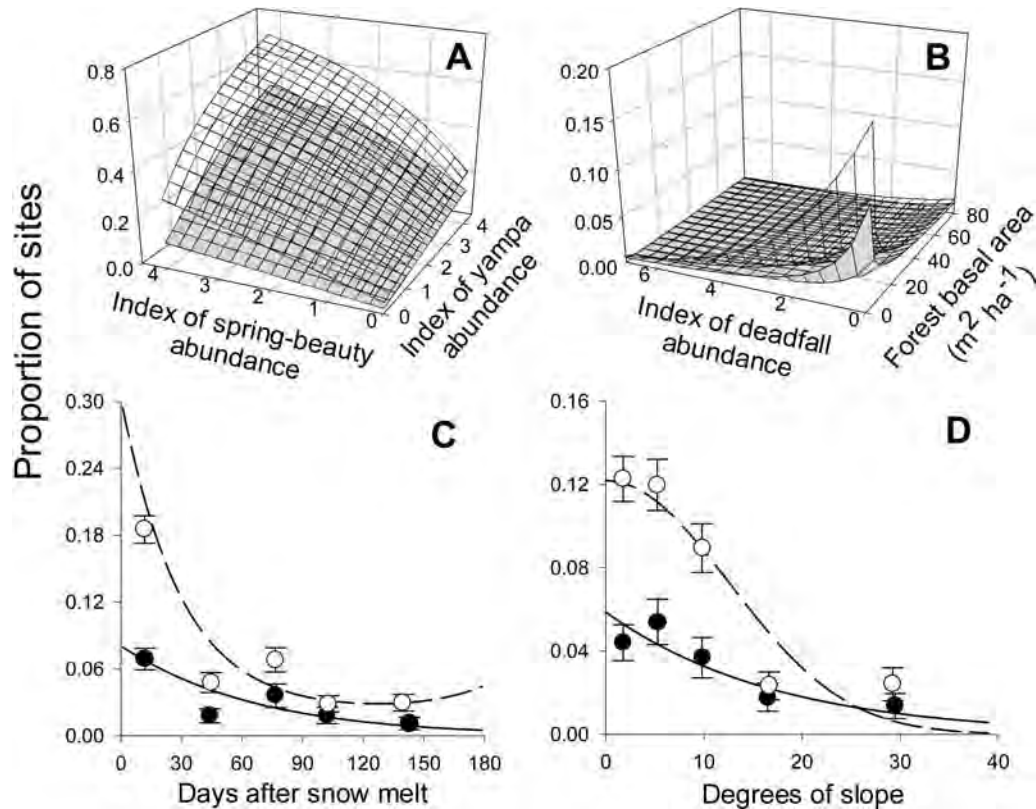
FIG. 4.—Univariate and bivariate relations between proportions of sites where Yellowstone grizzly bears excavated pocket gophers or their food caches, 1977–1992, and A) abundance of spring beauty and yampah at the site, B) forest overstory basal area and amount of coarse woody debris (deadfall), C) number of days after complete snow melt at Lake Yellowstone weather station, and D) site slope. Gray mesh surfaces show relations using only telemetry locations of radiomarked bears. Open mesh surfaces show relations using only sites with signs of feeding, including sites not associated with radiomarked bears. Circles and associated error bars denote proportions and *SE*s for quintiles and are shown to 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 signs of feeding or bedding from marked and unmarked bears.

part of putative cache residues found in grizzly bear feces during this study, and abundances of both species are positively correlated with density of pocket gopher mounds (Youmans 1979).

Other plants, although not important pocket gopher or bear foods, are known to be affected by gophers or were positively associated with foraging on pocket gophers by bears during this study. In particular, biomass of mesic-site species of *Elymus* increases with persistent high densities of gophers (Ellison and Aldous 1952; Laycock and Richardson 1975; Turner et al. 1973). Thus, it is not surprising that high biomass of *Elymus* was associated with greatest number of exploited nests and greatest odds of finding nests in individual excavations. Odds of finding nests were also high at sites where hairgrass was abundant. This is consistent with a positive association between hairgrass and pocket gophers in alpine meadows in Colorado (Thorn 1982). The explanation for this relation is not obvious, except that hairgrass is abundant only on open sites and, in contrast to species such as *Carex aquatilis*, indicates seasonally dry rather than persistently wet soil moisture in meadows typical of the Yellowstone ecosystem (Mattson 1984).

How important were pocket gophers to grizzly bears in 1850?—Grizzly bear and pocket gopher ranges once over-

lapped much more extensively than they do now, suggesting that relations between grizzly bears and pocket gophers in the Yellowstone region are a relict of a condition that was once widespread. Exploitation of pocket gophers by grizzly bears was probably commonplace in the western contiguous United States 150 years ago (Brown 1985; Storer and Tevis 1996). If so, then the widespread extirpation of grizzly bears nearly led to the loss of unique behaviors associated with unique relations between gophers and bears.

It is likely that grizzly bears would have exploited pocket gophers only where seasonally frozen or saturated soils occurred because vulnerabilities of pocket gophers and their food caches are tied to snowmelt. If so, exploitation of gophers would have been restricted either to high latitudes with cold winters or high elevations with abundant snow. Such conditions are common within the ranges of northern pocket gophers, Sierra pocket gophers (*Thomomys monticola*), and northern or high-elevation populations of pygmy pocket gophers (*T. umbrinus*). Conditions most like those associated with heavy exploitation of pocket gophers by Yellowstone grizzly bears occur throughout the mountains of Colorado, Utah, and Wyoming. If restoration of grizzly bears is contemplated in these regions, pocket gophers should be
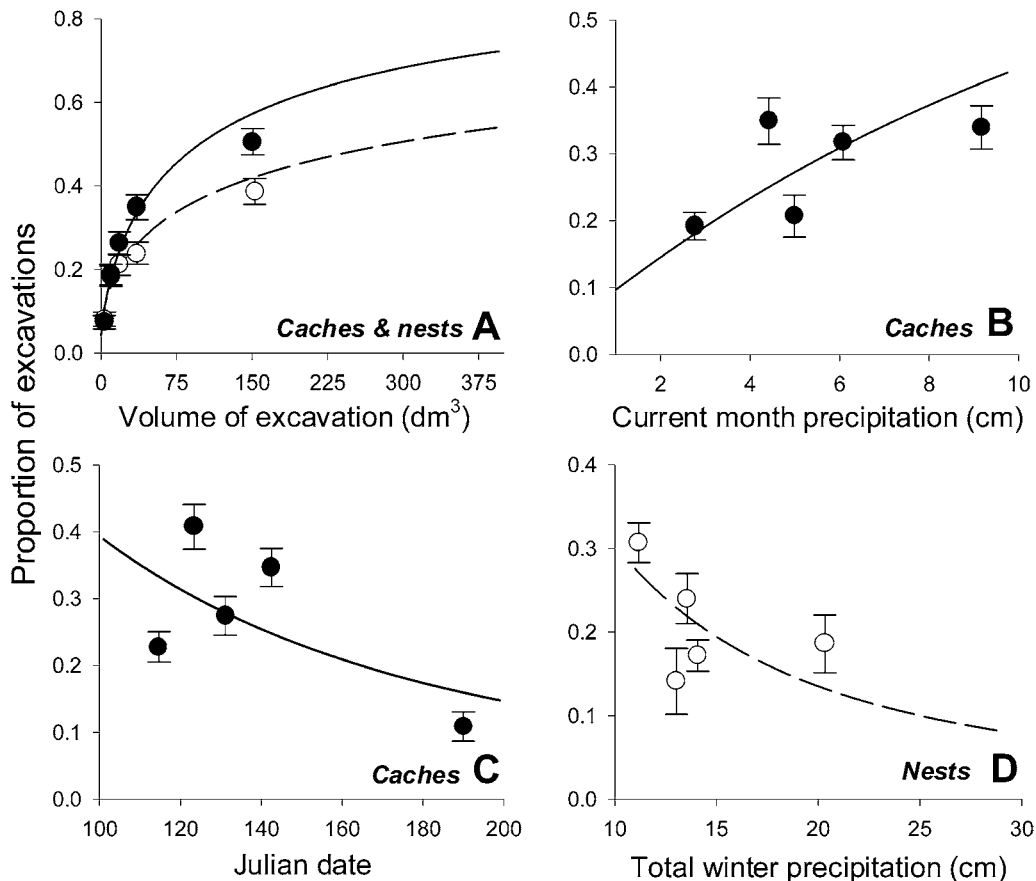
FIG. 5.—Univariate relations between proportion of individual grizzly bear excavations containing exploited pocket gopher food caches or nests, 1986–1992, and A) volume of the excavation, B) precipitation during the current month, C) Julian date, and D) total winter precipitation. Circles and associated error bars denote proportions and *SE*s for quintiles and are shown to illustrate goodness of fit. Filled circles and solid lines are for relations involving pocket gopher food caches, and open circles and dashed lines are for relations involving nests.

considered a likely source of food for the bears and included in habitat evaluations.

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