

SELECTION OF MICROSITES BY GRIZZLY BEARS TO EXCAVATE BISCUITROOTS

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Roots of the biscuitroot (*Lomatium cous*) are a common food of grizzly bears (*Ursus arctos horribilis*) in drier parts of their southern range. I used random sampling and locations of radiomarked bears in the Yellowstone ecosystem to investigate the importance of mass and starch content of roots, digability of the site, and density of plants relative to selection of sites by grizzly bears to dig biscuitroots. Where biscuitroots were present, most differences between dug and undug sites were related to digability of the site and mass and starch content of roots. Grizzly bears more often dug in sites where average milligrams of starch per kilogram of pull per root (\approx energy gain) was high. Density of biscuitroots was not related to selection of sites by grizzly bears. Mass of biscuitroot stems also provided relatively little information about mass of roots. Distribution of biscuitroots was associated with increased cover of rocks and exposure to wind, and with decreased slopes and cover of forbs. Digs by grizzly bears were associated with the presence of biscuitroots, proximity to edge of forest, and increased cover of rocks. Results were consistent with previously observed tendencies of grizzly bears to concentrate their feeding within 50-100 m of cover.

Key words: *Ursus arctos*, grizzly bears, biscuitroots, habitat selection, optimal foraging, Yellowstone National Park

Grizzly bears (*Ursus arctos horribilis*) can be distinguished from black bears (*U. americanus*) by their ability to excavate roots and other subterranean foods (Herrero, 1978). Mass of the suprascapular muscle and long claws that characterize grizzly bears are considered adaptations to digging (Craighead and Mitchell, 1982; Herrero, 1978). This contention is supported by studies at high latitudes ($>49^{\circ}\text{N}$) in North America where grizzlies rely on roots of hedysarum (*Hedysarum*) seasonally, during the entire active season, or during years when berries are scarce (Hamer and Herrero, 1987; Hamer et al., 1991; Murie, 1981; Pearson, 1975).

Hedysarum is rare south of the United States-Canada border where grizzly bears commonly excavate the biscuitroot (*Lomatium cous*), particularly in arid regions east of the Continental Divide where the biscuitroot often is abundant (Craighead et al., 1982; Mace and Jonkel, 1986; Mattson et

al., 1991). Biscuitroots and yampahs (*Perideridia gairdneri*) are the most common roots used by grizzly bears in the Yellowstone ecosystem of Wyoming, Montana, and Idaho, but unlike yampahs, biscuitroots can comprise most of the diet of grizzly bears during the hyperphagic period of July through October (Mattson et al., 1991).

Excavation of biscuitroots by aboriginal North Americans started just before or during full flower and probably was contingent on the size and starch content of roots (Hart and Moore, 1976; Hunn and French, 1981). My observations from the Yellowstone ecosystem suggested that this also was true for grizzly bears. Starch content of biscuitroots can exceed 30% (Mealey, 1975) and comprises a highly digestible (ca. 78%—Mealey, 1975; Pritchard and Robbins, 1990) part of this food. Phenology of biscuitroots and presumably the volume of digestible nutrients (Hamer and Herrero, 1987) are retarded by increased elevation and northerly as-

pects; peak bloom occurs in mid-May at the lowest elevations occupied by grizzly bears (Mueggler, 1983) and as late as July and August in alpine areas.

Excavation of roots by grizzly bears probably depends on the net balance between digested and expended energy. Optimal-foraging theory (Stephens and Krebs, 1986) predicts that grizzly bears will select patches and microsites within them that have the highest densities of the largest and most digestible roots in soils that are easiest to dig. If bears cannot detect such information about features of sites and availability of roots, or are constrained by other factors, such as security from humans and other bears, these predictions may not be confirmed by behavior of grizzly bears. Excavations of roots of yellow hedsarum (*Hedysarum sulphurescens*) by grizzly bears (Edge et al., 1990; Holcroft and Herrero, 1984) suggested that they excavate plants with large roots, select soils that are easily dug, or use dense patches of hedsarum. However, these studies did not consider simultaneously all of the factors likely to affect selection by bears (e.g., size, density, nutrient content of roots, and digability of the soil), or relate patterns of use by bears to those expected at random.

This study was designed to determine factors that were associated with microsites where grizzly bears chose to dig biscuitroots in contrast to those where they did not, and distribution of biscuitroots and features of roots that seemed to promote use by grizzly bears. I tested the null hypothesis: grizzly bears dig biscuitroots at sites where size, density, and starch content of roots and digability of the soil did not differ from randomly sampled sites that contained biscuitroots. I also developed a model that could be used to assess sites for potential excavation of biscuitroots by grizzly bears.

MATERIALS AND METHODS

Study area.—I delineated five sampling areas in or near Yellowstone National Park, Wyoming (44°29'–44°58'N; 109°58'–110°30'W), in areas

with a history of continuous occupancy by grizzly bears. Over a period of 13 years, 42% of 33 radiomarked grizzly bears that excavated biscuitroots did so in these sampling areas and accounted for 47% of all instances where biscuitroots were excavated at a radiotelemetry location. The study area spanned the range of elevations (2,127–3,048 m) and diversity of sites known to be used by grizzly bears for digging biscuitroots. Because biscuitroots and excavations by grizzly bears occurred almost exclusively in non-forested parts of the convex ridge systems that characterized my sampling areas (Craighead et al., 1982; Mattson et al., 1991), I restricted sampling to these conditions.

Non-forested ridges within the study area supported a mosaic of grasses, forbs, and sagebrush (*Artemisia tridentata*) vegetation that reflected variation in depth, rockiness, and moisture of soil from variation in slope, exposure, and redistribution of snow by winds (Despain, 1990). Prevailing winds from the southwest (202–248°; Dirks and Martner, 1982) often swept southwest-facing slopes free of snow during winter and created harsh xeric conditions, especially near ridgecrests, that were exacerbated by the relatively dry (<35–60 cm precipitation/year) climate. The most common herbaceous species at the sampling areas were *Festuca idahoensis*, *Agropyron caninum*, *Poa alpina*, *P. scabrella*, *Agoseris glauca*, *Phlox multiflora*, *Besseyia wyomingensis*, *Delphinium bicolor*, *Potentilla glandulosa*, *Polygonum bistortoides*, *Sedum lanceolatum*, *Balsamorhiza sagittata*, *Allium*, and the biscuitroot.

Sampling.—Non-forested parts of the sampling areas were delineated on United States Geological Survey, 1:24,000 scale, maps, and sample points ($n = 180$ total; 20, 30, 47, 49, and 34 in the five sampling areas) were selected randomly within these bounds. Sampling occurred in 1990 (with the exception of 30 high-elevation points sampled in 1991) and followed the seasonal progression of flowering of biscuitroots from low elevations in mid-May to the highest elevations in mid-July. Macroplots (10-m² radius) were located as close as possible by map interpretation and were placed 10 m from that location at a random compass bearing.

Elevation (m), slope (°), aspect (°), landform (ridge, upslope, midslope, bench, or low slope), percentage of cover of shrubs and trees (by ocular estimate), mean height of shrubs (dm), and

ratings of the extent (classes 0–3, none exposed to very rocky) and size (classes 1–7, gravel to large boulders) of exposed rock were estimated in macroplots. A double sample at 30 plots allowed me to relate the extent of exposed rock (X) to estimated percentage cover of rock (\hat{Y}): $\hat{Y} = (e^{0.118+1.26X}) - 1$ ($r^2 = 0.95$). Size of macroplots was 314 m² because it approximated the maximum size of areas of contiguous feeding activity of grizzly bears and was close to the median area that had been excavated by grizzly bears for biscuitroots during this study (319 m²).

Ten 2-by 5-dm microplots also were sampled, systematically arrayed in two lines of five, with the long-axis of this 10-by 2.5-m array oriented across the slope. Mean height and percentage cover of forbs and graminoids were estimated visually in microplots and macroplots. The number of biscuitroot plants in each microplot also was recorded. Because biscuitroots were often not detected by this approach when densities were $\leq 1/\text{m}^2$, biscuitroots were counted in two 0.5-by 10-m belt transects that overlapped the microplots when none had been otherwise detected. Based on previous observations, I postulated that the presence of biscuitroots, more than their density, determined use by grizzly bears. I therefore wanted to insure that the presence of biscuitroots were recorded, which was done in terms (i.e., numbers/m²) commensurate with other plots where biscuitroots were more abundant.

Roots were excavated from 10 to 24 plants that were typical of what grizzly bears dug in macroplots. These were dried at 40°C to a constant weight. Roots were collected from microsites that had not been affected by any detectable digging by grizzly bears during the previous year. When whole plants were collected ($n = 15$ sites), roots were separated from stems and weighed to the nearest 0.1 mg. Roots were pooled by site and analyzed for starch content by a calorimetric method developed by K. Goering (pers. comm.). Mass of roots by site was calculated as the mean of collected samples.

Digability of roots at each site where it was present was estimated with a clawometer (Holcroft and Herrero, 1984). This consisted of a five-tine potato rake with a span of ca. 16 cm and tines that were shaped and shortened to ca. 8 cm to approximate the front paw and claws of grizzly bears. A box spring with a sliding gauge to record maximum spring extension (i.e., kilo-

grams of pull) was attached to the shortened handle of this rake. Tines of the rake were pushed into the ground at the base of biscuitroot plants to ca. 50% of their depth at a 45° angle with the ground and pulled until the tines disengaged. Maximum kg of pull was recorded from 10 excavations and averaged to characterize each site.

Sites where grizzly bears fed also were sampled when study crews visited aerial telemetry relocations of radiomarked animals. Where grizzly bears had excavated biscuitroots, sites were sampled in the same way as at random points, except the plot was oriented with the long-axis of the observed feeding sign. Information was obtained from 111 such sites, 1987–1992, in areas that also were sampled randomly. Digability was estimated at feeding sites of grizzly bears only from 1990 through 1992 ($n = 35$ of 111). Methods for radiomarking and aerial tracking of bears during this study were provided by Blanchard and Knight (1991), and general methods for ground sampling of aerial telemetry locations were provided by Mattson (in press).

Data analysis.—Multivariate hypothesis were tested by the likelihood-ratio test using Wilks' Λ ($\alpha = 0.1$). The relative contributions of variables to multivariate differences were estimated by standardized canonical coefficients (Johnson and Wichern, 1992). I had no basis for assuming that variables were multivariately normal, so I used rank transformations of the data in parametric statistical procedures (Conover and Iman, 1981). I used an F -test to determine whether the ratio of two standardized variances was different from one (Zar, 1983).

I integrated several variables into a single measure of net energetic benefit (NET) and explored how frequency of excavation varied with this indicator of energy gain. This measure had units of milligrams of starch per kilogram of pull and was a direct function of mass of roots (MASS in milligrams), starch content (STARCH, as a proportion of the mass of roots), and digability of soil (DIG in kilograms): $\text{NET} = (\text{MASS} \times \text{STARCH})/\text{DIG}$. Because I did not collect all three measures at all random points or at all sites excavated by grizzly bears, $n = 65$ for NET.

I tested my primary hypothesis on two levels: contrasting random points, including those where excavations for biscuitroots were found ($n = 10$ of 180), with feeding sites for biscuitroots observed during sampling with radiotelemetry,

TABLE 1.—Features of sites associated with the presence and absence of biscuitroots at random points in the Yellowstone ecosystem, 1990–1991. Standardized canonical coefficients from multivariate analysis of variance and results of the Wald χ^2 test are given ($n = 180$). Natural-log transformations were used for all independent variables in logistic regression analysis, but $\bar{X} \pm SE$ is given in nontransformed units.

Variable	With biscuitroots	Without biscuitroots	Canonical coefficient	Wald test	
	$\bar{X} \pm SE$	$\bar{X} \pm SE$		χ^2	P
Intercept				2.3	0.130
Percentage cover of rocks (ROCK)	23 \pm 2.0	11 \pm 1.4	0.708	17.3	<0.001
Relative duration of winds >8 kph (WIND)	12 \pm 1.1	9 \pm 0.9	0.299	5.8	0.016
Slope (SLOPE) ($^\circ$)	13 \pm 1.1	14 \pm 0.8	-0.264	3.0	0.083
Percentage cover of forbs (FORB)	5 \pm 0.4	8 \pm 0.5	-0.729	21.8	<0.001

and contrasting excavations by grizzly bears at random points and radiotelemetry locations with only those random points where no excavations were found. In both, only sites where biscuitroots were present were evaluated.

I used other approaches to investigate features of sites associated with presence of biscuitroots and excavations by grizzly bears. In the case of excavations, I used the full sample, including sites without biscuitroots, stratified by whether a bear had or had not excavated biscuitroots, and I related the probability of excavation to density of biscuitroots, cover of rocks, cover of other vegetation, and distance from edge of forest. Because there was management interest in the relationship of bears foraging in open areas to distance from edge of forest (cover; United States Forest Service, 1990), I also analyzed this univariate relationship for use of biscuitroots by grizzly bears. For presence of biscuitroots, I used only random points, stratified by those with and without biscuitroots, and related the probability of the presence of biscuitroots to cover of rocks and vegetation and the duration of high-velocity winds. Because aspect typically served as a surrogate for more direct ecological effects and because I hypothesized a dominant effect of wind, I construed aspect as the relative duration of exposure to winds ≤ 8 km/h (Dirks and Martner, 1982; elevations $\leq 2,425$ m).

I used logistic regression analysis (Demaris, 1992) to develop a model that investigators could use to identify habitats where digging by grizzly bears was likely to occur. This analysis was distinct from those related to testing my primary hypothesis because all sites, with and without biscuitroots, were considered and fea-

tures less intimately associated with roots were used as variables. I also used logistic regression analysis to characterize differences between random sites with and without biscuitroots and relationships between the probability of excavation and NET and the probability of excavation and distance from forest cover. Logits of probabilities (\hat{Y}) were modelled, but probability of occurrence (\hat{P}) of either biscuitroots or digging by bears was obtained by back-transformation: $\hat{P} = e^{\hat{Y}} / (1 + e^{\hat{Y}})$. I judged model performance in terms of goodness-of-fit to saturated models by the likelihood-ratio statistic (G), statistical significance of coefficients (Wald χ^2 statistic), and the percentage of correct classification of observations using a jackknife procedure (SAS Institute, Inc., 1989). Fit of models was adequate when observed and expected frequencies were not different; i.e., when P -values exceeded α .

I used logistic regression rather than discriminant analysis for development of models because dispersion matrices of groups were unequal (Williams, 1983) and the alternate quadratic form was highly sensitive to non-normal distributions (Remme et al., 1980). However, because the conceptualization of response in logistic regression (probability of an event) was not strictly in accord with my design for analyzing excavations by grizzly bears, outputs of models should be used to indicate the likelihood that grizzly bears will excavate a site rather than literal predictions of the probability of use.

Analysis of variance was used to test if sizes of stems and roots of individual biscuitroot plants were related and if grizzly bears could thereby assess mass of roots by mass of stems prior to digging. I used natural log-transformed

TABLE 2.—Characteristics of roots and digability of soil where grizzly bears did and did not dig biscuitroots in the Yellowstone ecosystem. Analyses were stratified by sites with and without digging by bears and by whether they were random points or radiotelemetry locations. Standardized canonical coefficients are from multivariate analysis of variance ($n = 65$). The telemetry sample is from 1987 through 1992 and the random sample is from 1990 and 1991.

Variable	Stratification by presence versus absence of digging		Stratification by telemetry versus random sample	
	With digging $\bar{X} \pm SE$	Without digging $\bar{X} \pm SE$	Telemetry sample $\bar{X} \pm SE$	Random sample $\bar{X} \pm SE$
Dry weight of roots (MASS) (g)	0.95 \pm 0.050	0.70 \pm 0.044	0.96 \pm 0.050	0.74 \pm 0.054
Percentage starch content of roots (STARCH)	32.1 \pm 1.2	25.4 \pm 2.2	32.0 \pm 1.3	26.9 \pm 1.9
Density of biscuitroots (DENSITY) (n/m^2)	12.5 \pm 1.1	3.7 \pm 0.6	12.3 \pm 1.1	4.3 \pm 0.6
Digability ^a	13.6 \pm 0.9	24.5 \pm 1.4	14.1 \pm 1.4	22.7 \pm 1.4
			Canonical coefficient	Canonical coefficient
			0.399 ^b /0.436 ^c	0.708/0.767
			0.469/0.415	0.548/0.385
			0.073	-0.063
			-0.763/-0.793	-0.325/-0.419

^a Maximum registered pull (kg) to disengage times of clawometer (Holcroft and Herrero, 1984).

^b Including DENSITY in the analysis.

^c Excluding DENSITY from the analysis.

masses (g) of 181 individual plants from 15 different sites and controlled for effects of site by introducing site as a covariate. I also used least-squares multiple regression (Weisberg, 1985) to test if NET was related to features of sites and, thus, detectable to grizzly bears prior to excavation.

Results

Distribution of biscuitroots.—Biscuitroots were not randomly distributed in my study area. I rejected the hypothesis that the multivariate means of percentage cover of rocks, exposure to strong winds, slope, and percentage cover of forbs were not different between sites where biscuitroots were and were not present (Wilks' $\Lambda = 0.696$, $F = 18.7$, $df. = 4,171$, $P < 0.001$). Cover of rocks and exposure to strong winds were greater, slopes were steeper, and cover of forbs was less at sites where biscuitroots were present compared to sites where they were absent (Table 1). The associated logistic regression model ($\hat{Y} = 1.39 + 0.64ROCK + 0.50WIND - 0.47SLOPE - 1.66FORB$) provided an adequate statistical fit to the data ($G = 176.8$, $df. = 171$, $P = 0.364$; $n = 176$ rather than 180 because of missing values) and correctly classified 77% of the observations (20% error for sites without biscuitroots and 26% error for sites with).

Selection of biscuitroots.—Grizzly bears did not dig biscuitroots at random or without apparent regard to size and starch content of roots and digability of the soil. Whether I contrasted dug and undug sites, or random and telemetry-sample sites, I rejected my primary null hypothesis (Wilks' $\Lambda = 0.699$, $F = 8.62$, $df. = 3,61$, $P < 0.001$ and Wilks' $\Lambda = 0.818$, $F = 4.44$, $df. = 3,61$, $P = 0.007$, respectively). Density of biscuitroots explained little of the differences between multivariate means (Table 2). Including this variable, I rejected my null hypothesis stratified by dug and undug sites (Wilks' $\Lambda = 0.734$, $F = 4.98$, $df. = 4,56$, $P = 0.002$) but did not reject it when stratified by random and telemetry-sample

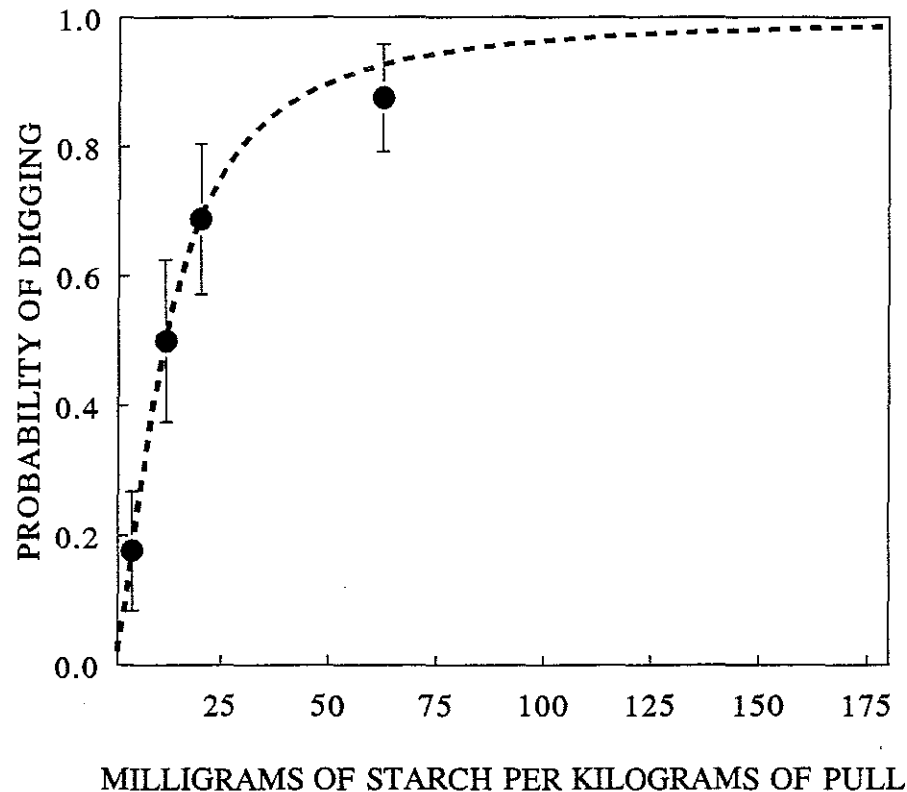


FIG. 1.—Relationship between the probability that biscuitroots were dug by grizzly bears at a site and net energy gain (NET; in mg of starch/kg of pull) in the Yellowstone ecosystem, 1990–1992. Values of NET ranged from one to 180; each point and associated error bar is the $\bar{X} \pm 1 SE$ probability calculated for quartiles of the sample; dashed line depicts the relationship estimated by logistic regression analysis.

sites (Wilks' $\Lambda = 0.873$, $F = 1.99$, $d.f. = 4, 56$, $P = 0.108$). This analysis only considered sites where biscuitroots were present ($n = 65$), given that some of these sites had missing values.

Grizzly bears apparently excavated sites with roots that were heavy, high in starch content, and embedded in easily dug soils and without much regard to density of biscuitroots (Table 2). Of these factors, digability contributed most to distinguishing between sites that were dug and undug, but mass of individual roots contributed most to distinguishing between use observed by radiotelemetry sampling and that expected at random. Given that among-site variation might explain differences in both the relative biological importance (Stephens and Charnov, 1982) and statistical performance of digability of soil and mass of roots, I

tested and rejected the hypothesis that coefficients of variation of average mass and digability were equal ($F = 2.17$, $d.f. = 69, 74$, $P = 0.001$); i.e., digability of soil varied more than the mass of individual roots among sites.

The NET (milligrams of starch per kilogram of pull) differed between sites that were dug ($n = 36$) and undug ($n = 29$) (Wilcoxon test, Z -approximation = -4.30 , $P < 0.001$) and on average was $2.9\times$ greater where bears had dug compared to where they had not ($\bar{X} = 34$ and 12 , respectively). The probability that grizzly bears would excavate biscuitroots also was related to natural log-transformed values of NET ($G = 66.4$, $d.f. = 63$, $P = 0.360$) and surpassed 0.8 , rapidly approaching an asymptote of 1.0 , at comparatively low values of NET (Fig. 1). The NET, in turn, was positively

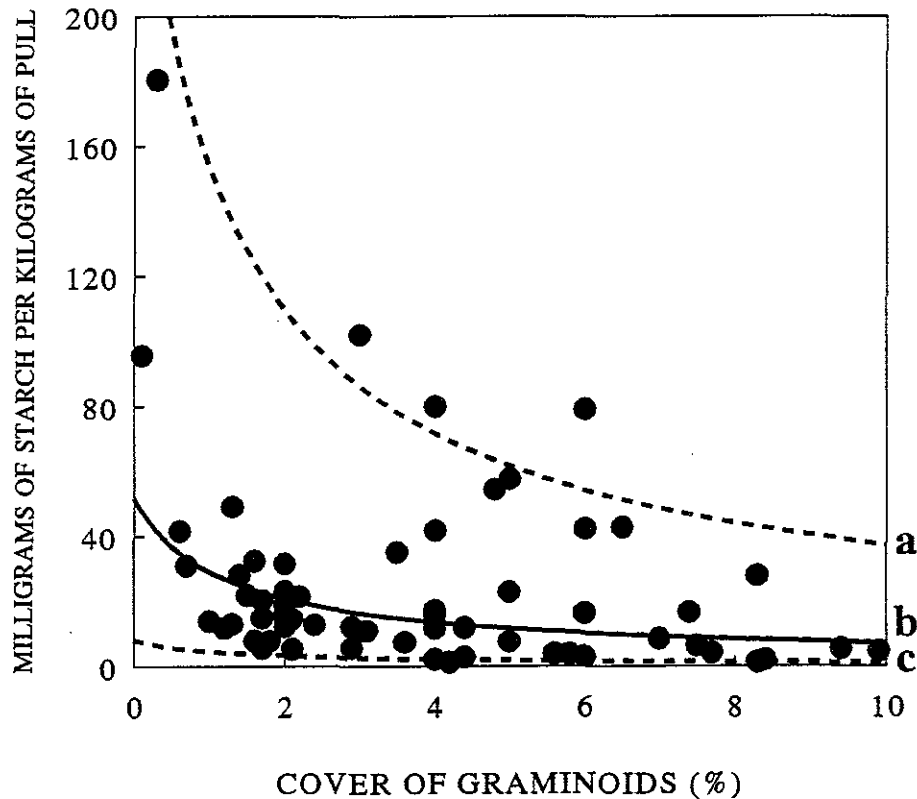


FIG. 2.—Relationship between net energy gain (NET; in mg of starch/kg of pull) for biscuitroots and percentage cover of graminoids at feeding sites of grizzly bears in the Yellowstone ecosystem, 1990–1992. Lines depict relationships estimated by multiple regression analysis (a) where other variables were set to extreme observed values that were positively associated with excavation of biscuitroots, (b) where other variables were set to their mean values, and (c) where other variables were set to extreme observed values that were negatively associated with excavation of biscuitroots.

related to percentage cover of forbs and negatively related to elevation, percentage cover of graminoids, and distance to edge of forest ($F = 7.61$, $d.f. = 4,60$, $P < 0.001$), with the strongest effect attributable to cover of graminoids (Fig. 2). The regression

model was: $\hat{Y} = 27.1 - 0.83\text{GRAM} + 0.59\text{FORB} - 2.98\text{ELEV} - 0.22\text{DIST}$ (Table 3), but the total R^2 of the model was only 0.34.

Grizzly bears might have used visible mass of stems to judge mass of roots and

TABLE 3.—Regression parameters for site features related to net energy gain (NET) in mg of starch/kg of pull of biscuitroots in the Yellowstone ecosystem, 1990–1992 ($n = 65$). Natural log-transformed values of independent variables were used for the analysis. The t -test was used to determine if each parameter value = 0 ($d.f. = 1$).

Variable	Standardized coefficient	t -test	
		t	P
Intercept		2.8	0.006
Percentage cover of graminoids (GRAM)	-0.430	-4.0	<0.001
Elevation (ELEV) (m)	-0.273	-2.4	0.020
Distance to nearest forest cover (DIST) (m)	-0.219	-2.0	0.047
Percentage cover of forbs (FORB)	-0.309	2.7	0.010

TABLE 4.—Features of sites associated with the presence and absence of diggings by grizzly bears for biscuitroots in the Yellowstone ecosystem, 1987–1992. Standardized canonical coefficients from multivariate analysis of variance and results of the Wald χ^2 test are given ($n = 289$). Natural-log transformations were used for independent variables in logistic regression analysis, but $\bar{X} \pm SE$ is given in nontransformed units.

Variable	With digging	Without digging	Canonical coefficient	Wald test	
	$\bar{X} \pm SE$	$\bar{X} \pm SE$		χ^2	P
Intercept				17.8	<0.001
Density of biscuitroots (DENSITY) (n/m^2)	12 \pm 1.1	4 \pm 0.6	0.870	45.3	<0.001
Percentage cover of rocks (ROCK)	32 \pm 1.5	15 \pm 1.3	0.725	28.1	<0.001
Percentage cover of graminoids, forbs, and shrubs (TCOVER)	14 \pm 1.0	14 \pm 0.7	0.310	10.4	0.001
Distance to nearest forest cover (DIST) (m)	77 \pm 9.6	126 \pm 11.3	-0.394	15.2	<0.001

the related profitability of digging if mass of stems provided information about what was below ground. I found that there was a relationship between masses of roots and stems, controlling for differences among sample sites ($F = 7.69$, $d.f. = 15,165$, $P < 0.001$). Even so, mass of stems explained only 20% of the variation in mass of roots; site explained the remainder of the total R^2 of the model (0.41).

Distribution of excavation sites.—Excavations were not distributed randomly with respect to features of site and landscape, considering all sites with and without biscuitroots. The multivariate mean density of biscuitroots, percentage cover of rocks, combined percentage cover of forbs, graminoids, and shrubs, and distance to the nearest edge of forest differed between sites where grizzly bears had dug biscuitroots and sites where they had not (Wilks' $\Lambda = 0.516$, $F = 61.3$, $d.f. = 4,262$, $P < 0.001$). Not surprisingly, grizzly bears were most likely to dig biscuitroots at sites where their presence had been recorded. In addition, they selectively dug biscuitroots close to edges of forest, where there was considerable exposed rock, and yet average vegetation cover (Table 4). A logistic regression model from these variables ($\hat{Y} = -7.39 + 1.21DENSITY + 1.69ROCK + 1.14TCOVER - 0.73DIST$) correctly classified 81% of the observations and provided a good fit

($G = 185.3$, $d.f. = 261$, $P = 1.000$). Univariate logistic-regression analysis confirmed that excavations by grizzly bears were not independent of distance to cover ($\hat{Y} = 1.41 - 0.42DIST$; $G = 56.8$, $d.f. = 45$, $P = 0.112$) and suggested that the probability of excavation was exponentially greater within 100 m of edge of forest (Fig. 3).

DISCUSSION

Optimal foraging.—These results support my initial hypothesis that grizzly bears in the Yellowstone ecosystem were selective in their use of sites to excavate biscuitroots. If biscuitroots were present, grizzly bears selected sites to dig primarily on the basis of mass and starch content of individual roots and ease of excavation. This selectivity apparently waned at an exponential rate as the NET from use of roots increased, which was predicted by optimal-foraging theory (Pyke, 1984; Stephens and Krebs, 1986). Grizzly bears favored consumption of large, starchy roots in soils that were easily dug, and when some minimum criteria were satisfied, they would almost always stay and dig rather than move on to a better site (Collier and Rovee-Collier, 1981; Pyke, 1984).

In common with use of hedysarum by grizzly bears (Edge et al., 1990; Holcroft and Herrero, 1984), digability of soil distin-

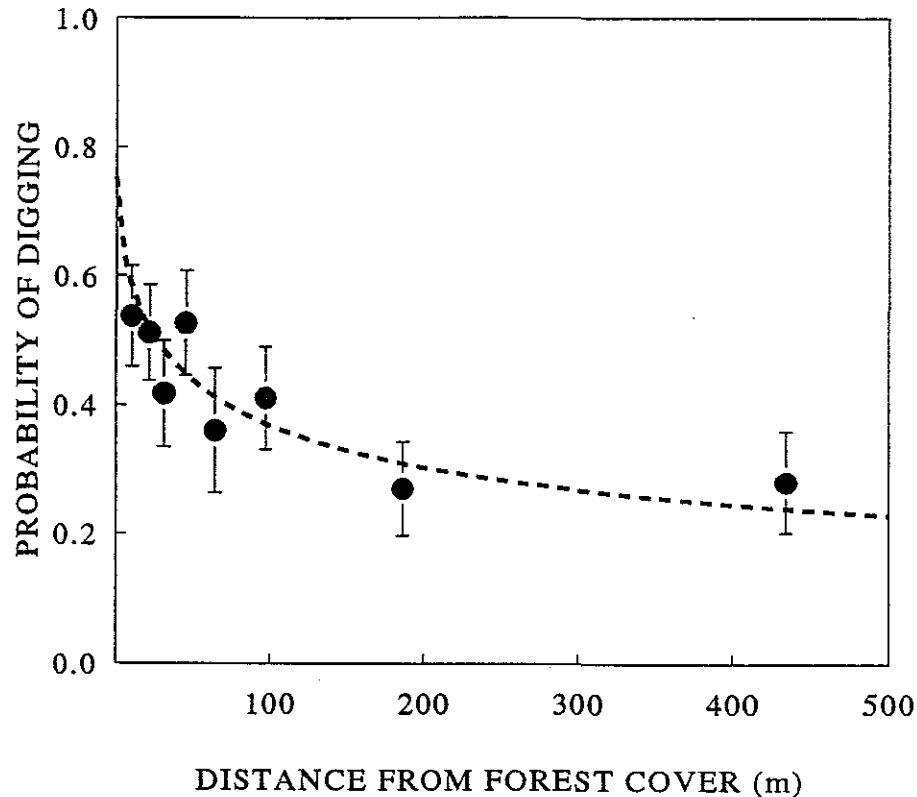


FIG. 3.—Relationship between the probability that biscuitroots were dug by grizzly bears at a site and distance from forest cover (m) in the Yellowstone ecosystem, 1987–1992. Each point and associated error bar is the $\bar{X} \pm 1 SE$ probability calculated for eight equal percentiles of the sample; dashed line depicts the relationship estimated by logistic regression analysis.

guished sites that were dug from those that were not. Digability, as much as any other factor, limited where grizzly bears could excavate biscuitroots. Foraging theory predicts that a more variable habitat feature, such as digability, will be more constraining than one that is consistent (Stephens and Krebs, 1986). Digging can be costly, and in species that specialize in digging, it is typically associated with major adaptations of musculature and skeleton (Hildebrand, 1985). Despite a degree of adaptation to digging (Davis, 1949), grizzly bears do not exhibit the extreme morphological traits common to specialized diggers (Hildebrand, 1985; Taylor, 1989). Although grizzly bears frequently dig for food, they must be selective in their choice of sites as a means of compensating for the limitations of their more generalized anatomy.

Abundance of biscuitroots had less influ-

ence on whether bears excavated a site than might be expected. This was consistent with selection of sites by grizzly bears to excavate roots of yellow *Hedysarum* (Holcroft and Herrero, 1984; Skinner, 1986) and constraints of size of bite (i.e., mass of individual roots in this case) on rates of intake of some herbivores (Gross et al., 1993). It was contrary to the emphasis placed on within-patch abundance of foods by optimal-foraging theory (Stephens and Krebs, 1986). In contrast to constraints imposed by high handling costs, search time, and movements within a patch were probably a relatively small part of the energetic budget of grizzly bears when consuming biscuitroots. Given that bears seem to distinguish colors (Bacon and Burghardt, 1976), it may be that use of the yellow-flowered biscuitroot during anthesis facilitated foraging within a given patch.

Features of sites offered limited information about the energetic benefits of using available roots, and the mass of stems offered even less immediate information about mass of roots (i.e., size of bite). This situation could lead to continual sampling and learning within a patch (Hainsworth and Wolf, 1979; McNamara and Houston, 1985). Conversely, as evident by the degree of documented selection of sites grizzly bears may have been using olfactory cues and past experiences and were better informed about their foraging opportunities than my analysis would indicate (Orians, 1981).

Distribution of biscuitroots and excavations by bears.—Similar to yellow *Hedysarum* on the east front of the Canadian Rocky Mountains (Hamer and Herrero, 1987; Holcroft and Herrero, 1984), biscuitroots and associated excavations by grizzly bears were concentrated on rocky wind-exposed slopes, where cover of other vegetation was not dense. It is possible that both biscuitroots and excavations by grizzly bears were favored by less vegetation cover. If so, both species may benefit from the excavations; grizzly bears directly by acquisition of food from an easily dug matrix and biscuitroots indirectly by reduced competition. Edge et al. (1990) speculated that a similar mutualistic relationship existed between grizzly bears and *Hedysarum*. Although I did not explicitly record sequences of use during this study, a number of sites were repeatedly excavated in same or different years. Under these conditions, it is possible that disturbance caused by grizzly bears was enough to substantially affect composition and cover of vegetation.

Grizzly bears excavated more biscuitroots within ca. 100 m of forest cover than at sites that were more distant. Blanchard (1983), Graham (1978), and Green (1994) documented a similar concentration of activity by grizzly bears in the Yellowstone ecosystem within ca. 50–100 m of trees. These results support conservation of ecotones and other habitat near forest edges

with an emphasis on open areas <150 m from forests that currently is used in suitability models of habitat of grizzly bears (United States Forest Service, 1990).

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