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USE OF LODGEPOLE PINE COVER TYPES BY YELLOWSTONE GRIZZLY BEARS

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Abstract: Lodgepole pine (*Pinus contorta*) forests are a large and dynamic part of grizzly bear (*Ursus arctos*) habitat in the Yellowstone ecosystem. Research in other areas suggests that grizzly bears select for young open forest stands, especially for grazing and feeding on berries. Management guidelines accordingly recommend timber harvest as a technique for improving habitat in areas potentially dominated by lodgepole pine. In this paper I examine grizzly bear use of lodgepole pine forests in the Yellowstone area, and test several hypotheses with relevance to a new generation of management guidelines. Differences in grizzly bear selection of lodgepole pine cover types (defined on the basis of stand age and structure) were not pronounced. Selection furthermore varied among years, areas, and individuals. Positive selection for any lodgepole pine type was uncommon. Estimates of selection took 5–11 years or 4–12 adult females to stabilize, depending upon the cover type. The variances of selection estimates tended to stabilize after 3–5 sample years, and were more-or-less stable to slightly increasing with progressively increased sample area. There was no conclusive evidence that Yellowstone's grizzlies favored young (<40 yr) stands in general or for their infrequent use of berries. On the other hand, these results corroborated previous observations that grizzlies favored open and/or young stands on wet and fertile sites for grazing. These results also supported the proposition that temporally and spatially robust inferences require extensive, long-duration studies, especially for wide-ranging vertebrates like grizzly bears.

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Lodgepole pine is the most common overstory tree in the Yellowstone ecosystem. About 67% of forests in Yellowstone National Park (Despain 1990) and 48% of forests on adjacent public lands (Greater Yellowstone Coord. Comm. [GYCC] 1987) are dominated by this species. The structure and age of lodgepole pine forests have been influenced in recent years primarily by stand replacement fires, mountain pine beetle (*Dendroctonus ponderosae*) epidemics, timber harvest, and increasing dominance of more shade tolerant species (Cole and Amman 1980, Lotan and Perry 1983, McGregor and Cole 1985). Major mountain pine beetle epidemics swept through the western-half of the ecosystem from the 1960s

through the mid-1980s (McGregor and Cole 1985, Despain 1990). Timber harvest was increased on national forests to salvage merchantable beetle-killed timber, reduce fire hazard, and support local timber industries (Cole and Amman 1980, Cole 1985). About 68,000 ha of lodgepole pine forests on public lands were harvested during this period, typically by clear-cutting (Cole 1985, GYCC 1987). An additional ca. 562,000 ha of the ecosystem were partially or completely burned by wildfires during 1988, including substantial areas that had been occupied by mature lodgepole pine forests (Romme and Despain 1989, Schullery 1989).

Because Yellowstone's lodgepole pine forests are extensive, I anticipated that changes in their

Table 1. Descriptions (Despain 1990) and estimated ages at 1.4 m aboveground of lodgepole pine cover types in the Yellowstone ecosystem.

Cover type acronym	Cover type description	Estimated ages (yr) ^a			Age range (Despain 1990)
		\bar{x}	SD	Range	
LP0	Mix of grasses, forbs, shrubs, and seedling-sapling lodgepole pine			1–13	0–40
LP1	Typically dense pole-sized stand of lodgepole pine	91	39	51–186	50–150
LP2	Mature lodgepole pine, with little mortality or replacement by spruce-fir	133 (176) ^b	51 (19)	58–256 (136–206)	150–300
LP3	Old lodgepole pine, with substantial mortality and replacement by spruce-fir	166 (188)	38 (28)	98–232 (157–298)	300+
LP	Old lodgepole pine, with substantial mortality and replacement by lodgepole pine				300+
LP/NF	Mosaic of lodgepole pine and non-forest				

^a Ages are based on a sample ($n = 63$ stands) of grizzly bear relocations during 1992.^b Ages in parentheses are based on inventories ($n = 57$ stands) of 2 study areas in the whitebark pine zone (Mattson and Reinhart 1990).

structure would affect grizzly bear movements and feeding behavior. This expectation was further supported by research from study areas in northwestern Montana and southern Alberta that found greater amounts of high quality bear foods on forest sites that had been burned or harvested within the previous 10–70 years, especially compared to closed-canopy stands (Mealey et al. 1977, Servheen 1983, Zager et al. 1983, Hamer and Herrero 1987). Foods were more abundant on natural burns or on untreated or broadcast-burned harvest units, primarily due to increased berry and forb production (Mealey et al. 1977, Zager et al. 1983, Bratkovich 1986, Hillis 1986, Kasworm and Thier 1991).

Because of this research, the Interagency Grizzly Bear Committee (1986) has emphasized the potential for improving grizzly bear habitat by harvesting or burning forest stands on sites that can produce appreciable volumes of grazable foliage or edible berries, especially those of buffaloberry (*Shepherdia canadensis*), globe huckleberry (*Vaccinium globulare*), and whortleberry (*V. scoparium*). This recommended practice is especially relevant to management in the Yellowstone ecosystem because whortleberry or globe-huckleberry are potentially abundant on many sites occupied by lodgepole pine forests (Despain 1990).

Given this background, I posed the following null hypotheses:

H_{n1} : Grizzly bears do not use selectively young lodgepole pine stands (i.e., LP0 and LP1 cover types; Table 1) more than older lodgepole pine stands (i.e., LP2, LP3, and LP cover types);

H_{n2} : Grizzly bears consume berries in young lodgepole pine stands that occur on whortleberry/huckleberry sites (i.e., the VASC habitat type; Table 2) proportionally equal to or less often than expected by the availability of this stand and site combination at all sites known to be used by bears;

H_{n3} : Grizzly bears graze in young lodgepole pine stands on moist to wet sites (i.e., MESIC and WET habitat types; Table 2) proportionally equal to or less often than expected by availability of this stand and site combination at all sites known to be used by bears.

H_{n4} : Grizzly bears do not use different-aged and structured lodgepole pine stands (i.e., cover types) differently from that expected by their proportional area;

H_{n5} : Within forests dominated by lodgepole pine, grizzly bear activities (e.g., bedding or types of feeding) do not differ with the site (i.e., habitat type) or structure of the stand (i.e., cover type).

Hypotheses H_{n2} and H_{n4} are partly redundant except that H_{n2} focuses on selective use of young stands by grizzly bears, which is not specifically implied by H_{n4} . I test these 5 hypotheses in this paper and further describe how grizzly bears use lodgepole pine forests in the Yellowstone ecosystem. I also describe how the mean and variance of estimated grizzly bear selection for different cover types changes with increasing numbers of sampled years, bears, and areas. More fundamentally, I evaluate existing assumptions and provide information that managers and re-

Table 2. Descriptions of habitat types used to analyze variation in grizzly bear activities within lodgepole pine-dominated forests in the Yellowstone ecosystem.

Habitat type group	Description	Included habitat types ^a (acronyms)
DRY	Dry sites typified by <i>Carex rossii</i> , <i>C. geyeri</i> , or <i>Purshia tridentata</i> .	ABLA-PICO/CAGE, ABLA-PICO/CARO, PICO/PUTR, PICO/FEID, ABLA/ARCO, ABLA/ARLA, and ABLA-PICO/JUCO
VASC	Cold sites characterized by high coverage of <i>Vaccinium scoparium</i> , with or without <i>V. globulare</i> .	ABLA-PICO/VASC and ABLA/VAGL-VASC
CARU	Dry-moist sites, typically at low to mid-elevations, characterized by high coverage of <i>Calamagrostis rubescens</i> or <i>Spirea betulifolia</i> .	ABLA-PICO/CARU, ABLA/VASC-CARU, PSME/CARU, PSME/SPBE, ABLA/SPBE, ABLA/BERE, PSME/BERE
MESIC	Moist, typically mid-elevation sites characterized by relatively lush and species-rich understories.	ABLA/THOC, ABLA/SYAL, ABLA/LIBO, ABLA/VAGL-VAGL, and ABLA/OSCH
WET	Seasonally or perennially wet sites typified by <i>Calamagrostis canadensis</i> and <i>Equisetum arvense</i> .	ABLA/CACA, PIEN/EQAR, and PIEN/GATR

^a Acronyms are defined by Steele et al. (1983).

searchers can use to refine their working hypotheses (Murphy and Noon 1991).

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STUDY AREA

The 23,000 km² study area corresponded to the known range of Yellowstone's grizzly bear population and included parts of Wyoming, Montana, and Idaho. The entire study area was drawn upon for analyzing variation in bear activities, such as bedding and different types of feeding, within lodgepole pine forests. Only Yellowstone National Park (8,694 km²) was used for analyzing landscape-level cover type selection because digital data necessary for these analyses were not available from the rest of the study area. Study area characteristics are described in greater detail by Knight and Eberhardt (1985), Blanchard and Knight (1991), and Mattson et al. (1991).

METHODS

Field Methods and Stratification

Grizzly bears were trapped, marked, and radio-relocated according to methods described by Blanchard (1985), Knight and Eberhardt (1985) and Blanchard and Knight (1991). In common with other studies of this nature, efforts were made to trap representatively (by area and less so by sex and age), but differences among animals in susceptibility to capture combined with administrative and logistical constraints on access precluded a truly random sample. All radio-relocations used in this analysis were made from fixed-wing aircraft and recorded by their universal transverse mercator (UTM) coordinates. A subsample of these relocations was visited and described on the ground. Again, this subsampling was not truly random, primarily because of logistical constraints. Most of the study area was without roads, and use of helicopters was either prohibited or expensive. Ground sampling consequently emphasized equal representation of different bears and different regions (i.e., bear manage. units), as well as visits to as many relocations as possible.

Each visited relocation was described according to protocols more fully reported by Blanchard (1985) and Mattson (1991). Field crews located variable-radius forest inventory plots at the center of grizzly bear activity, or in the absence of bear sign, at a randomly selected distance (≤ 10 m) and direction from the recorded radiotelemetry location. We identified all trees in the plot by species, whether dead or alive, and we measured the diameter of each at 1.4

m aboveground (Mattson 1991:3). During 1992 field crews cored dominant trees that had originated with the last stand-replacement fire and used the ages of these trees to estimate stand age (Barrett and Arno 1988).

We recorded additional information on vegetation structure within about 10 m of plot center in a 314-m² area (Mattson 1991:1–3). This information included 4 descriptors of coarse woody debris (amt [1–7, sparse to heavy], size [1–7, small to large], decomposition [1–6, solid to well-decomposed], and % cover), Fischer's (1981) classification of the size and volume of woody debris, and estimated percent cover of forbs, graminoids, shrubs, and overstory trees (>1.4 m tall). I worked with all field personnel who used these subjective descriptors from 1984 to 1992, and was able to standardize their application (i.e., we achieved consistent convergence in our estimates) through regular field exercises. Estimates of the current-year's standing crop of graminoids were based on double-sampling. Aggregate dimensions (average ht in cm and estimated % cover) were measured prior to clipping, oven-drying, and weighing graminoids from 10 to 15 systematically-placed 10-dm² microplots (Mattson 1991:1–2, Merrill et al. 1993).

Field crews described all grizzly bear sign found at ground-sampled relocations. We included sign that was spatially contiguous, often part of what appeared to be a single foraging bout, in these descriptions and ascribed it to a specific aerial relocation if the sign was within about 200 m of the specified UTM coordinates. Specific protocols were followed for measurement of each type of sign. Where roots were dug, we censused or estimated individual digs from systematically placed plots (Mattson 1991:6–8). We measured excavations in logs and hills for ants (Formicidae), including average diameter of the log where it was torn by the bear, total tear length, and average tear width as a percent of total log circumference (Mattson 1991:9–10). Total excavated volume was estimated from these dimensions and from similar dimensions of excavated ant hills as the product of length \times percent circumference \times cross-sectional area. Excavations in red squirrel (*Tamiasciurus hudsonicus*) middens for white-bark pine (*Pinus albicaulis*) seeds were also measured, and the total number of observable excavated cones were counted (Mattson 1991:9). I used standardized tables of edible dry weight for species, sex, and age-classes of un-

gulate (Mattson 1997a) to estimate the total biomass available to bears from carcasses found at radio-relocations. I calculated ingested biomass as the product of edible carcass biomass and the proportion of each carcass that was estimated to have been eaten by bears (Mattson 1997a).

I rated grazing activity as light, moderate, or heavy based upon direct evidence of grazing (cropping of the appropriate age, associated with bear tracks), the number of individual tracks and beds at a site, and the number and content (i.e., foliage comparable to that present at the site) of associated feces (Mattson 1991:10–11). Since grazing by bears is more difficult to detect than virtually any other feeding activity, I recognized a higher probability of overlooking grazing compared to other feeding activities if I used the same standards of evidence. My standards were thus more liberal (not requiring evidence typical of other activities, such as claw marks) when judging that grazing had occurred. Regardless, because these inferences relied upon evidence that was not related explicitly to forest stand structure, I assumed that judgements regarding grazing were not biased relative to hypothesis H_{n3}.

Forest cover types have been described for the Yellowstone ecosystem with criteria that reflect both stand structure and age (Despain 1990). Cover types are denoted by dominant species (e.g., LP = lodgepole pine dominant) and sequential numbers that roughly correlate with stand age (e.g., LP0 = recent disturbance and LP2 = maturity; Table 1). The Yellowstone ecosystem has also been described in terms of ecological landscape units called habitat types. Each habitat type is denoted by specific epithets of indicator plant species or, more commonly, by acronyms (Steele et al. 1983). Because of sample size constraints, I used shared indicator species and similarities of bear use to aggregate habitat types into 5 broad categories (Table 2) for analyzing variation in grizzly bear activity within lodgepole pine-dominated forests.

We keyed all ground-sampled relocations to habitat type and cover type in the field so as to describe site potential and existing stand structure. In addition, I classified the entire radio-relocation data set according to cover and habitat type using computer-generated intersections with preexisting digital maps for Yellowstone National Park (Despain 1990). I used these same digital maps to calculate the proportional use of cover types that would be expected if grizzly bears were not selective.

Bear relocations were also classified according to the bear management unit (BMU) within which they occurred. The Yellowstone ecosystem is divided for management purposes into 19 BMUs, 12 of which fall partly or entirely within Yellowstone National Park. A BMU is roughly the size of a female grizzly bear's life range (ca. 880 km²; Blanchard and Knight 1991), and was delineated to reflect both clustering of grizzly bear radio-relocations and major geomorphic features such as large lakes, mountain range crests, or major rivers (Weaver et al. 1986). Stratification by BMU allowed for analysis at a scale that most individual Yellowstone grizzlies lived, with sensitivity to major habitat differences within Yellowstone Park. For purposes of analysis, I aggregated the 12 Yellowstone Park BMUs into 6 larger units ("analysis areas" in this paper) with similar vegetation and geomorphology, and excluded one BMU (the Plateau unit) that received little use by radiomarked bears (Fig. 1).

Analysis Methods

I tested for differences in means or, for categorical variables, differences in frequency distributions of vegetation measurements among the lodgepole pine cover types. I used the *G*-test or Fisher's Exact test, as appropriate, for categorical variables and nonparametric analysis-of-variance (ANOVA) for the remainder. If I rejected the null hypothesis (no differences among cover types, at $\alpha = 0.1$), I then identified individual cover types that differed, for categorical variables, by a multiple-comparisons procedure using angular transformations of proportions (Zar 1984:401) or, for ordinal variables, by the Tukey-Kramer method (Day and Quinn 1989). Deadfall size and amount and graminoid crop dimensions were transformed to volume and dry weight, based upon statistical relations between double-sampled measurements of these variables. I estimated relations by least squares linear regression, using natural log-transformed values.

I analyzed grizzly bear selection of cover types with respect to total landscape availability (H_{n1} and H_{n4}) only for data collected before July 1988. After this date much of the vegetation cover in Yellowstone National Park was altered by wildfires during July–September of the same year (Schullery 1989). I assumed that this reconfiguration would affect grizzly bear habitat selection and so chose not to confound the analysis with an additional factor. In contrast, I

used all of the ground-sampled radio-relocations that had been visited 1977–92 to analyze differences in bear activity among habitat and cover types within lodgepole pine-dominated forests (H_{n2} , H_{n3} , and H_{n5}). I assumed that habitat and cover type were predictive of feeding and bedding opportunities (Mattson and Knight 1989), and that these inherent features would not change as long as the combined habitat and cover type did not change. By implication, a given habitat and cover type combination would exhibit the same vegetation structure and foraging opportunities, regardless of whether it was sampled before or after the 1988 fires. To check this assumption, I tested for independence (*G*-test) between grizzly bear activities, by type, and pre- and post-fire periods.

I used a selection index and ANOVA to describe and test landscape-level differences in grizzly bear selection of lodgepole pine cover types (H_{n1} and H_{n4}). I used the Vanderploeg and Scavia (1979) electivity index (*E*; Lechowicz 1982) to enumerate selection. In common with Manly's *B*, this index is desirable because it reflects the probability of a given type being used if all types are equally available (Manly et al. 1993). I estimated electivity by month, as well as for individual adult females, years, and analysis areas (Fig. 1). Although desirable in theory, I could not test for differences in mean electivity by multiple stratifications (i.e., simultaneously controlling for the effects of individual, area, year, and month) because of insufficient sample sizes. As a point of comparison, in each case I also tested for goodness-of-fit (*G*-test) between proportional use of cover types expected by random selection and proportional use exhibited by the sampled bears. If I rejected the null hypothesis, I then used Bonferroni confidence intervals (CIs) to identify types selected in proportions significantly greater than or less than those expected at random (Neu et al. 1974, Byers et al. 1984).

Because *E* has unknown statistical properties, I used the equivalent of nonparametric ANOVA to test for mean differences among lodgepole pine cover types, using months, years, areas, and individuals as sample units. I used normalized ranks and standard parametric models for both global tests and multiple comparisons (Conover and Iman 1981). Where overall differences were evident, I planned to use the Tukey-Kramer and Ryan-Einot-Gabriel-Welsch tests to identify individual types that differed,

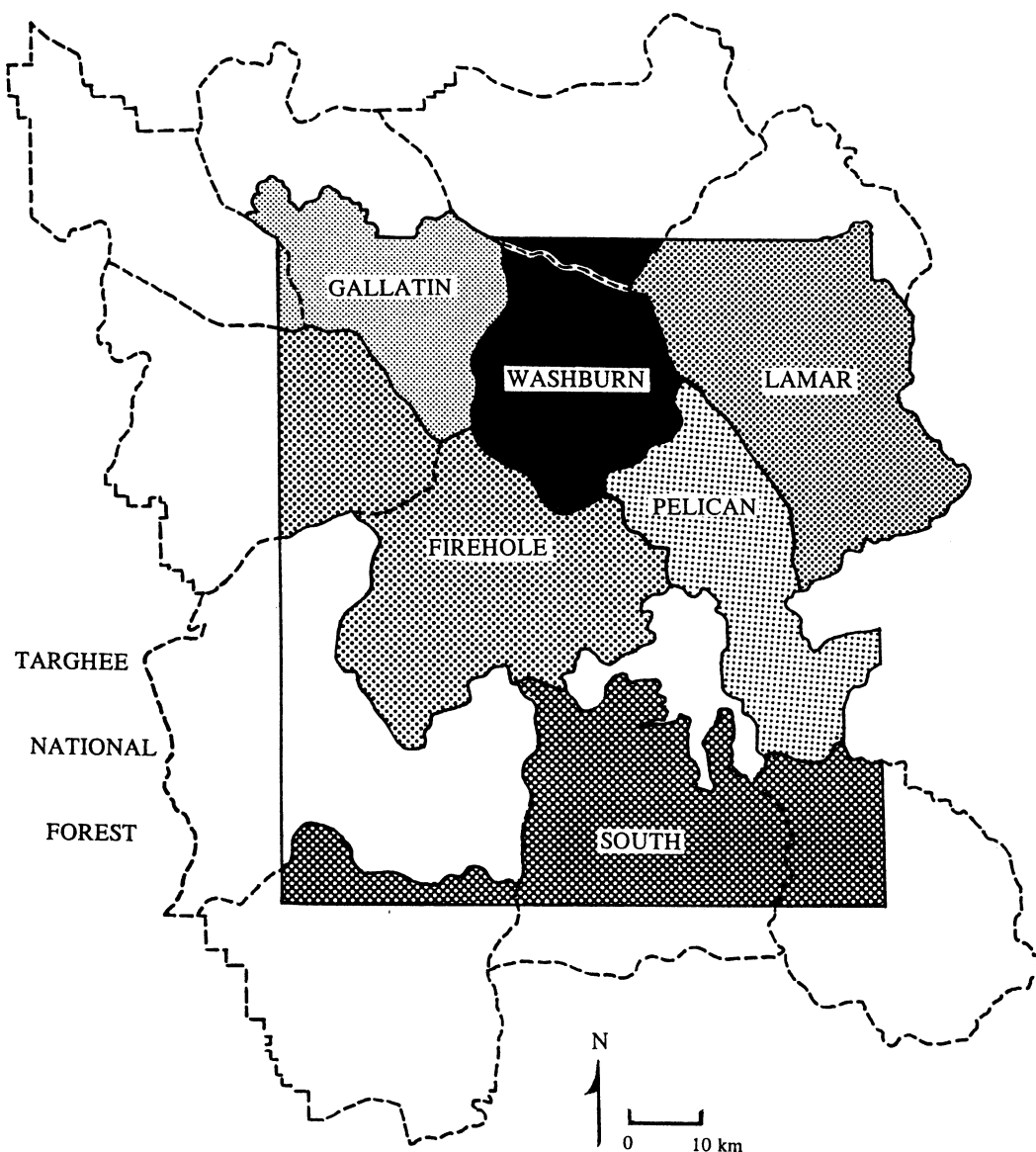


Fig. 1. The Yellowstone ecosystem study area, showing the 6 analysis areas composed of 12 bear management units (BMUs) that are contained wholly or partly within Yellowstone National Park. The shaded regions were used for stratification of the analysis. The remaining areas (e.g., the Plateau BMU within the park) were excluded from analysis of cover type selection because few grizzly bear locations were obtained there or because digital habitat data were missing. Dashed lines are BMU boundaries.

for unbalanced and balanced “designs” (Day and Quinn 1989).

I calculated E and analyzed cover type selection individually for 14 adult female grizzly bears that had radiotelemetry sample sizes >25 , although 13 of the 14 had sample sizes >50 (Aldredge and Ratti 1986). Cover type availability for these 14 bears was determined by intersecting 95% minimum convex polygons that estimated their home ranges with the digital cover type map.

I used all cover types, including those not dominated by lodgepole pine (i.e., Douglas-fir [*Pseudotsuga menziesii*], spruce-fir [*Picea engelmannii*-*Abies lasiocarpa*], whitebark pine, and nonforest types) when calculating E or testing for differences between observed and expected frequencies of bear use. However, I only report results that pertain to lodgepole pine. This approach was required to maintain a total landscape perspective on grizzly bear selection of lodgepole pine cover types. I also pooled the

LP0 and LP/NF types for analyses that involved months, years, areas, and individual bears because sample sizes for these 2 types were small and stand structures were similarly open.

I also analyzed the effect that number of sample years and bears had on the stability of estimated selection for individual types, and the effect of increasing the number of sample years and areas on the variance of these estimates. I judged stability in terms of the degree to which estimates for individual cover types differed from full sample means as years or bears were added to the calculation, up to the full sample. I standardized differences between partial and full sample estimates across types, dividing each by the full-sample among-years or among-individuals standard deviation (SD) observed for all types. I judged an uninterrupted series of these standardized differences that were <0.1 to indicate a "highly stable" estimate. I also recalculated SD for each type with the sequential addition of another year or analysis area to the sample. Because area, unlike time, does not have a theoretically finite starting point, I averaged results starting and progressively expanding from 3 different peripheral areas—the Gallatin, Lamar, and South (Fig. 1).

I used log-linear analysis to address H_{n2} , H_{n3} , and H_{n5} . I tested whether each identified grizzly bear activity (e.g., berry use or grazing) varied independently of cover or habitat type within lodgepole pine forests, treating all other activities in aggregate as a single group. A collectively large number of bears, but small individual-bear sample sizes did not allow me to do this on a by-bear basis. I modeled cumulative logits (activity_i = 1, all other activities = 0), estimated response functions by weighted-least-squares, and tested goodness-of-fit by the Wald χ^2 statistic (Kritzer 1979). I added 0.5 to response populations when there was no observed bear use (Demaris 1992, Aebischer et al. 1993).

As a classification tool, log-linear analysis probably under-assesses true differences between "used" and "unused" sites. Given 3 possible categories—(1) capable of being used and documented, (2) capable of being used and undocumented, and (3) not capable of being used—(2) and (3) are subsumed as "unused" (Johnson 1981). However, bear use was likely observed at sites with inherently the greatest odds of being occupied by bears for the given analyzed purpose, resulting in a tendency to emphasize the most "favorable" sites in analysis results. I therefore assumed that this issue was

of little practical consequence to interpreting the analyses presented here.

RESULTS

Relations Between Measures of Vegetation Structure

I was able to relate several indices used to describe vegetation structure in this study to some more commonly measured parameters. Double-sampled graminoid dimensions (average graminoid ht [*HGT*] and % graminoid ground cover [*GCVR*]) and oven-dried standing crop (*GBMASS*, in kg/m²) were related ($F = 899.6$; 1, 15 df; $r^2 = 0.984$; $P < 0.001$) as follows:

$$\ln GBMASS = 1.042 \ln(HGT \times GCVR).$$

I was able to relate the ordinal descriptors of deadfall amount (*DDFAMT*) and size (*DDFSZ*) to total coarse woody debris volume (*DDFVL*, in kg/m²; derived from site classifications according to Fischer 1981) ($F = 163.2$; 1, 56 df; $r^2 = 0.745$; $P < 0.001$):

$$\ln DDFVL = -0.0008 + 0.7638 \ln(DDFAMT \times DDFSZ).$$

Estimates of percent forest overstory cover (*PFOR*) from this study were consistently less than canopy closure (*CC*) estimates used by the U.S. Forest Service. However these 2 measures could be associated through common relations to overstory basal area (*BA*). I relied upon Dealey (1985) for the relation of *CC* to *BA*, and developed the relation of *PFOR* to *BA* from this study's data ($F = 185.9$; 1, 413 df; $r^2 = 0.31$; $P < 0.001$):

$$CC = -20.29 + 41.80 (\log_{10} [(BA + 1)])$$

and

$$PFOR = -25.80 + 26.18 (\log_{10} [(BA + 1)]).$$

Thus, by solution:

$$CC = 20.90 + 1.597 PFOR.$$

I used these results to convert the dimensionless or otherwise less meaningfully expressed measures from this study into dimensions with greater relevance to management or to comparison with other research.

Sample Sizes and Independence

Ninety-three different autonomous bears were relocated 3,392 times in Yellowstone National Park, April–October, from 1975 through

Table 3. Estimated means for measures of vegetation structure, by lodgepole pine cover type, at ground-sampled relocations of radiomarked grizzly bears, the Yellowstone ecosystem, 1977–92 ($n = 734$). Results are also given for global tests (ANOVA) of differences among types for each measure.

Parameters	ANOVA		Lodgepole pine cover type ^a					
	χ^2	<i>P</i>	LP/NF	LP0	LP1	LP2	LP3	LP
Overstory								
% forest cover	214.5	<0.001	13.1c	6.5c	27.8ab	28.5a	30.2a	21.2b
Total basal area (m ² /ha)	59.4	<0.001	12.4c	21.3b	24.8ab	28.1a	29.6a	22.7ab
Live basal area (m ² /ha)	213.5	<0.001	9.8c	0.9d	20.2ab	23.3a	24.7a	15.8bc
Large diam. basal area (≥25.4 cm at 1.4 m)	80.4	<0.001	10.8cd	14.9bc	6.5d	17.8b	21.9a	13.3bc
Understory								
Graminoid biomass (kg/ha)	33.1	<0.001	564a	398b	397b	458b	423b	492ab
% graminoid cover	55.3	<0.001	27.4a	8.2c	11.5bc	25.6bc	11.9bc	17.5b
% forb cover	39.0	<0.001	20.1a	12.3b	7.4c	10.5bc	9.3bc	9.0bc
% shrub cover	97.8	<0.001	3.3cd	2.1d	8.1bcd	10.6abc	14.2a	9.4ab
% deadfall cover	22.3	<0.001	3.7b	6.1b	5.5b	6.5b	9.0a	10.7a
Deadfall biomass (kg/m ²)	69.9	<0.001	1.06b	1.44b	1.02b	1.36b	1.80a	1.95a
Deadfall decomposition (% in classes ≥5)	64.9 ^b	<0.001	35.8bc	10.2e	20.6d	30.6c	41.8b	52.9a

^a All means followed by the same letter in rows are not statistically different.

^b Log-likelihood test for independence (G-test); all other test results are for Kruskal-Wallis ANOVA.

June 1988; and 1,893 of these locations were in lodgepole pine-dominated forest stands. An average of 20.8 (range 11–35) bears were monitored each year in the Park at some time during the active season, with each bear monitored an average of 2.8 (range 1–8) years. Field crews also visited and ground-sampled 741 radio-relocations of 105 different bears that had occurred in lodgepole pine cover types, 1977–92. My assumption that types of bear activity did not differ among habitat-cover type combinations, depending upon whether the period was before or after the fires of 1988, was supported by a test that demonstrated independence between grizzly bear feeding and bedding activity, by type, and pre- and post-fire time periods ($G = 13.6$, 11 df, $P = 0.257$).

Relocation data used in this analysis satisfied the assumption that observations were independent, using the standards of Swihart and Slade (1985) (Blanchard and Knight 1991). Even so, relocations are not likely to be independent if relatively few individuals account for most locations, or if individuals are highly related or socially interactive. However, in the case of locations sampled during this study to document bear activity, relatively few points were sampled from numerous bears, often widely separated both in time and space. Although independence may never be achieved in theory, this circumstance supports the judicious use of individual points in log-linear analysis.

Characteristics of Lodgepole Pine Cover Types

Estimates of stand age at ground-sampled grizzly bear relocations and from inventories of stands in 2 study areas in the whitebark pine zone (Mattson and Reinhart 1990) indicated that there was substantial age overlap between successional types that theoretically constituted a temporal sequence. Greatest overlap existed between the LP2 and LP3 types, with only 12–33 years difference between mean estimates of age (Table 1). Even so, overstory and understory vegetation structure varied substantially among types (Table 3). Taken together, these structural measures indicated that the greatest amounts of coarse woody debris occurred in the LP3 and LP types, and that the greatest biomass and cover of graminoids and forbs occurred in the ecotonal LP/NF type. Conversely, overstory basal area and percent forest cover were greatest in the LP2 and LP3 types. Among older-aged cover types, the LP2 type thus differed from the LP3 and LP types primarily by less coarse woody debris, and the LP2 and LP3 types differed from the LP type by greater overstory crown cover and basal area. The LP1 type was distinguished by relatively little decomposed deadfall, few large (≥25.4-cm at 1.4-m) trees and yet basal area comparable to that of the LP2 and LP3 types.

Other differences among types, although not

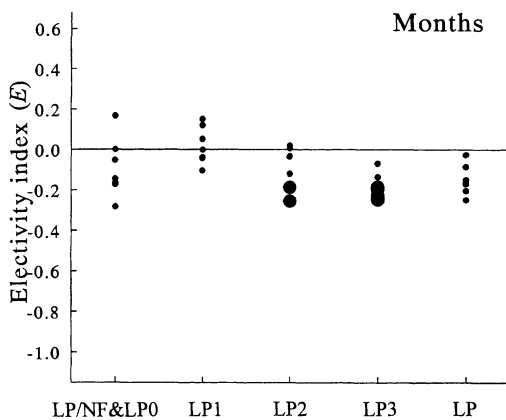


Fig. 2. Selection of lodgepole pine cover types by grizzly bears in Yellowstone National Park, calculated in terms of the Vanderploeg and Scavia (1979) electivity index (E). The spectrum of points for each type represent electivity for each month, April–October. Larger points indicate use less than or greater than expected by proportional availability (Neu et al. 1974, Byers et al. 1984).

directly measured, were implicit to these results. By definition, the LP3 cover type contained more subalpine fir in the understory than any other lodgepole pine cover type (Despain 1990). Also, even though we did not collect enough data to estimate directly mean age of the LP type, the large amounts of coarse woody debris in these stands coupled with relatively open overstories, suggested older age comparable to the LP3 type (Despain 1990).

Selection of Lodgepole Pine Cover Types

Variation Among Months.—With months as observations, mean selection (E) differed among lodgepole pine cover types ($F = 3.16$; 4, 30 df; $P = 0.028$), given that month did not account for significant variation in E ($P = 0.584$) when included in an initial model with overall $P = 0.141$. Of individual types, selection for the LP1 type differed from and was greater than selection for the LP and LP3 types. The LP3 type was furthermore used less than expected at random (by Bonferroni CIs) during all months except April and October, while the LP2 type was used greater than expected during July and October (Fig. 2). There was also a tendency towards greater than expected use of the LP1 type in both June and July.

Variation Among Years and Analysis Areas.—Mean selection did not differ among cover types with either years ($F = 1.51$; 4, 55 df; $P = 0.212$) or analysis areas ($F = 0.77$; 4, 25 df; $P = 0.552$) as observations, given that neither year ($P =$

0.568) nor area ($P = 0.870$) accounted for significant variation of E in initial models. Selection of individual cover types varied widely among years and areas, although significant negative selection was exhibited for all types during at least one of the 12 study years (Fig. 3a and 3b). At extremes, the LP1 type was used greater than expected during 1977 and in the South analysis area, while the LP3 type was used less than expected during 7 of the 12 study years.

Variation Among Individual Adult Females.—Mean selection also did not differ among cover types with individual adult females as sample units ($F = 1.95$; 4, 56 df; $P = 0.115$), given that differences among individuals did not account for significant variation in E ($P = 0.584$) in the initial model ($P = 0.372$). These results from the 14 adult females were even more varied than results that used year or area as sample units (Fig. 3c), with relatively fewer instances of statistically significant selection (using Bonferroni CIs) by this approach (16% compared to 29 and 40% for the other 2 approaches; Fisher's Exact test, $P = 0.037$). Fewer instances of significant selection were plausibly due partly to differences in per unit sample sizes.

The Effects of Study Duration and Study Area Size.—Depending upon the cover type, estimates of selection did not converge upon and remain close to the full sample mean (i.e., differences remain <0.1 of the max. SD observed for any cover type) until between 5–11 years or 4–12 adult females had been sampled (Fig. 4). The SD of selection estimates, by comparison, was relatively stable with increasing sample sizes of both years and analysis areas and did not change appreciably after 3–5 years (Fig. 5a) and either did not change or tended to slightly increase with progressively greater sample area (by accretion of adjacent analysis areas; Fig. 5b). Aside from the effects of sample size on parameter estimates, selection of lodgepole pine cover types also appeared to change over time. Most of the variation in 3-year running averages of E was erratic, with the exception of an apparent trend toward increasing selection for the LP2 type (Fig. 6).

Bear Activity Within Lodgepole Pine Cover Types

Description of Activities.—Grizzly bears engaged in varied activities within lodgepole pine-dominated forests. Excavation and consumption of invertebrates was the most common feeding

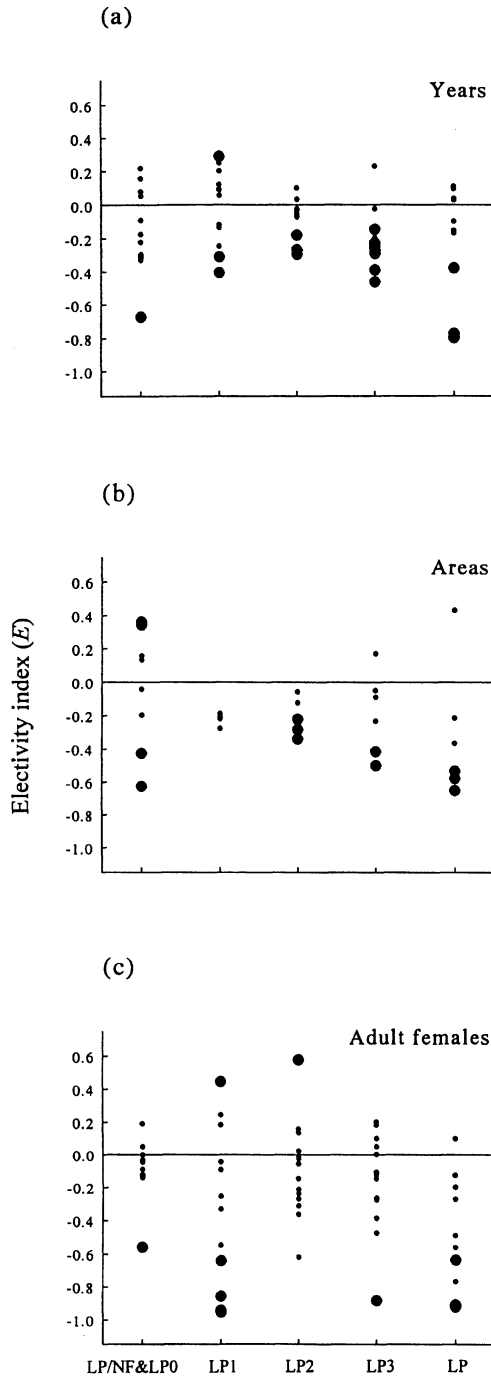


Fig. 3. Selection of lodgepole pine cover types by grizzly bears in Yellowstone National Park, calculated in terms of the Vanderploeg and Scavia (1979) electivity index (E). The spectrum of points for each type represent electivity for (a) individual years, 1976–87, (b) individual analysis areas, and (c) individual adult females. Larger points indicate use less than or greater than expected by proportional availability (Neu et al. 1974, Byers et al. 1984) (a) for all of Yellowstone National Park, (b) by each analysis area, and (c) by each individual female's home range.

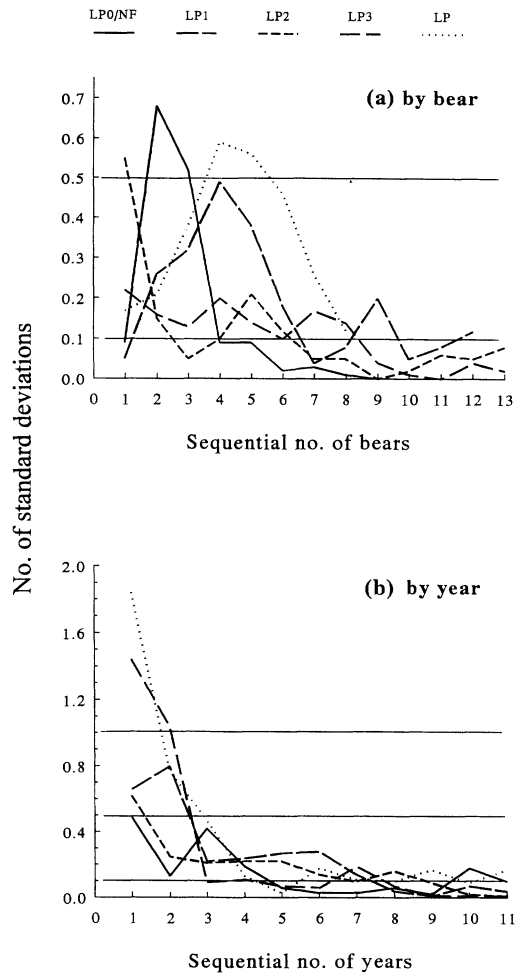


Fig. 4. Deviation of selection estimates (E) from total sample means for individual lodgepole pine cover types, with increasing numbers of (a) sampled adult female bears and (b) sampled years, for grizzly bears in Yellowstone National Park, 1976–87. Deviations were standardized to the largest SD observed for any individual type, for the (a) adult female and (b) annual sample.

activity (found at 18.4% of all sampled relocations), followed by grazing of graminoids and forbs (11.5%) and consumption of ungulates (7.2%; Fig. 7). Most (69.8%) invertebrate use involved the excavation of ants (Formicidae) out of semi-decomposed logs, and most excavated ants were either *Camponotus* spp. (64%) or *Formica* spp. (28%). Grizzly bears grazed about 25 species of plants, and among these dandelions (*Taraxacum* spp.; 38%) and fireweed (*Epilobium angustifolium*; 27%) were the most commonly grazed forbs and wheatgrass (*Agropyron caninum*; 22%) and bluegrasses (*Poa* spp.; 24%) were the most commonly grazed graminoids.

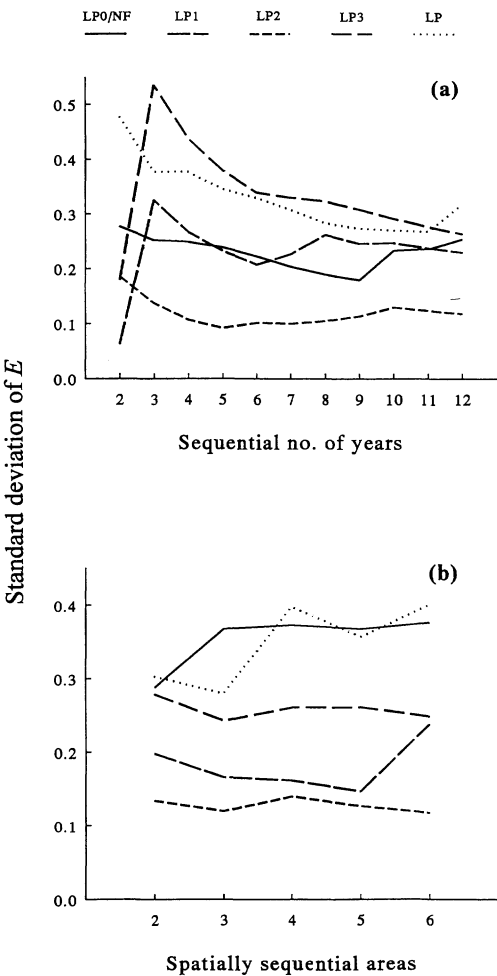


Fig. 5. The SD of selection estimates (E) for individual lodgepole pine cover types as a function of increased number of (a) sequential sample years, 1976–87, and (b) adjacent analysis areas, for grizzly bears in Yellowstone National Park.

The majority of ungulates used by grizzlies were either bison (*Bison bison*; 24%) or adult elk (*Cervus elaphus*; 36%). Grizzly bears also spent significant time in lodgepole pine forests excavating mushrooms (primarily Basidiomycetes; 4.3%), roots (4.3%), and whitebark pine seeds (3.5%). Most root excavations were either for sweetcicely (*Osmorhiza* spp.; 53%) or yampah (*Perideridia gairdneri*; 31%). Virtually all use of whitebark pine seeds (92%) involved the excavation of cones cached in middens by red squirrels.

Grizzly bear feeding in lodgepole pine forests changed with the season (Fig. 7). The bears frequently scavenged winter-killed ungulates during April–May, but consumed less food per carcass during this time compared to the less frequent instances of ungulate use during and af-

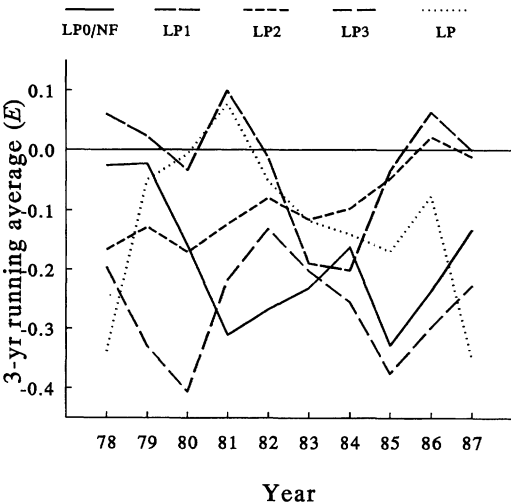


Fig. 6. The 3-year running average of selection estimates (E) for individual lodgepole pine cover types, for grizzly bears in Yellowstone National Park, 1976–87.

ter August. Grazing of forbs and graminoids was most common during May–June and declined in both frequency and intensity especially after August. Consumption of invertebrates was common from June on, and reached peak frequency during July–August. The size of excavations for invertebrates increased progressively from May through August, and then declined slightly. Root, mushroom, and whitebark pine seed excavations all peaked during fall or late summer, during hyperphagia (Mattson et al. 1991). Although use of these latter 3 items was relatively less common than grazing and ant excavations, bears sometimes consumed large quantities of these high quality foods during a given bout.

Evidence of bear feeding in lodgepole pine forests was least frequent April–July, especially during June (Fig. 8). This relative dearth of feeding coincided with a high frequency of bear relocations on or near major wildlife trails (May–Jun) and a low frequency of bedding during June (Fig. 7). Taken together, these results fit the expectations of high mobility during estrus (Jun) and heavy feeding during hyperphagia (Jul–Oct; Nelson et al. 1983, Mattson et al. 1991).

Frequency of Activities by Habitat and Cover Type.—There was good basis for rejecting H_{n5} (Table 4). Except for ungulate and berry consumption, major grizzly bear activities were related to the habitat or cover type of sites dominated by lodgepole pine. Graminoid and forb grazing were both positively associated with LP/NF and LP0 cover types and with MESIC and WET habitat types, and negatively associ-

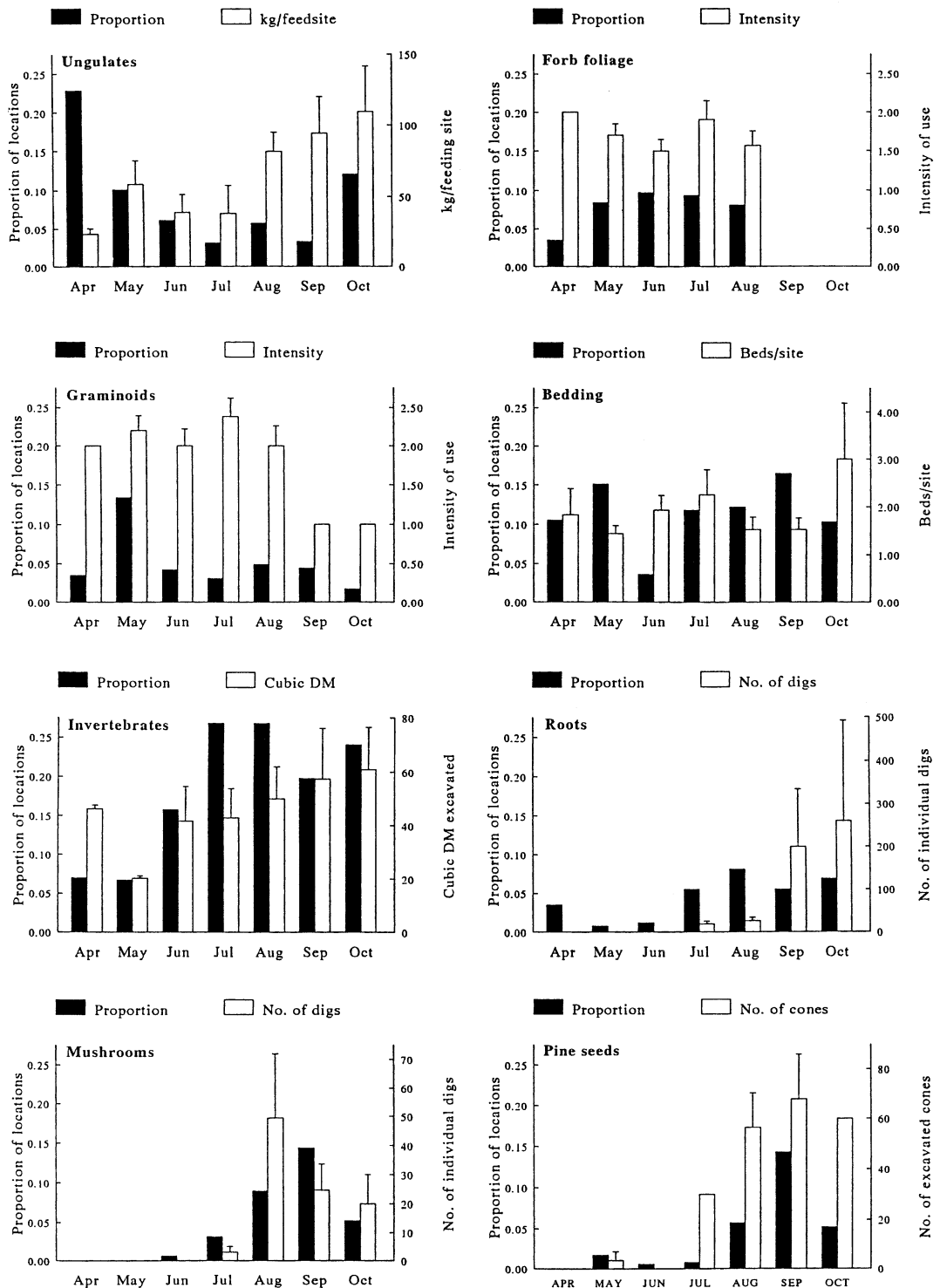


Fig. 7. The intensity and relative frequency of bedding and major grizzly bear feeding activities in lodgepole pine cover types of the Yellowstone ecosystem, by month, 1977–92. Intensity is construed, for example, as excavated or consumed volumes, number of digs, or as an index, and expressed as the mean and its standard error among sites.

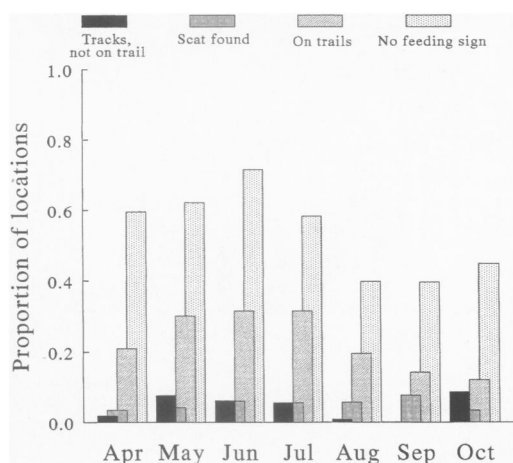


Fig. 8. The proportion of grizzly bear locations in lodgepole pine cover types at which neither feeding nor bedding sign was found, including total proportions of these locations that coincided with major wildlife or human recreational trails or were associated with feces, for the Yellowstone ecosystem, by month, 1977–92. Categories are not mutually exclusive.

ated with LP3 and DRY types. By contrast, mushroom excavations were positively associated with mid- to late-successional LP1, LP2, and LP cover types and drier DRY and VASC sites, and negatively associated with LP/NF and MESIC types.

Invertebrate excavations and bedding varied independent of habitat type but not cover type, while sweet-cicely and whitebark pine seed excavations varied only with habitat type. Interestingly, use of invertebrates was positively associated with the ecotonal LP/NF type and negatively associated with the similarly open LP0 type. Bedding was also relatively least frequent in the LP0 type, and positively associated with both relatively dense LP1 and more open LP stands. Excavation of sweet-cicely roots was relatively most frequent in CARU and MESIC habitat types and least common in the VASC type, while, to the contrary, whitebark pine seed excavations and the VASC type were highly positively associated.

Berry Use in Lodgepole Pine Forests.—Grizzly bears made infrequent use of berries in Yellowstone's lodgepole pine forests. Berry consumption occurred at 2.0% of investigated sites, year-round, and most commonly involved whortleberry (7 of 15 instances), although we also recorded use of globe huckleberry (3 instances), buffaloberry (3 instances), and strawberry (*Fragaria* spp.; 2 instances). Bear use of whortleberries and globe huckleberries on VASC sites alone varied independently of

cover type (Fisher's Exact test, $P = 0.953$), and accorded with results of the log-linear analysis.

DISCUSSION

Grizzly Bear Habitat Selection

Grizzly bear selection did not differ unequivocally among lodgepole pine cover types. Differences in selection with years, analysis areas, and individual bears as sample units were not statistically significant. In aggregate, lodgepole pine forests were under-used or, at most, used as available wherever they occurred. More importantly, grizzly bear use of any given cover type was quite variable. All of the types were used less than expected by their proportional area during some year or in some area, while the LP0, LP/NF, LP1, and LP2 types were subject to both substantial positive and negative selection. This variation in grizzly bear use of lodgepole pine forests is consistent with previous observations of variability in both diets and the use of other habitats by grizzly bears in the Yellowstone area (Mattson et al. 1991, 1992, 1994; Mattson 1997a). Given these vagaries, I could not confidently reject either H_{n1} or H_{n4} .

Even so, grizzly bears in this study tended to use the LP1 cover type with greater relative frequency, especially compared to the LP3 type; most clearly in the analysis where months were used as sample units. Although grizzlies are often thought to ignore physical barriers, some researchers have observed that bears avoided impediments such as thick slash left from logging operations (Smith 1978, Zager and Jonkel 1983). Based on my field observations and results of this analysis, I hypothesize that grizzlies more consistently avoided the LP3 type primarily because of the impediment posed to travel by the thick undergrowth and large volumes of coarse woody debris associated with these older, more diverse, stands.

These results are pertinent to questions regarding the appropriate duration, geographic extent, and delineation of habitat selection studies. My results clearly reiterate those of Schooley (1994); i.e., annual variation in habitat selection by wide-ranging vertebrates such as grizzly bears will likely bias the results of short-term studies, especially when addressing hypotheses that pertain to long-term habitat use. In this case, results from a 2- or even 4-year study would have generated results that could easily mislead managers. Geographic variation in selection at the scale of female life ranges

similarly suggests that extrapolation of results beyond study area boundaries is risky without knowing the causes of that variation. This point is especially relevant, as in this case, where selection of most types included a wide range of both positive and negative values. These results support the argument for studies that are geographically extensive and of long-duration (Gaud et al. 1986).

The legitimacy of extrapolating results such as these in both time and space is contingent partly on the spatial and temporal homogeneity of habitat units (Manly et al. 1993:30). Yet these results suggest that grizzly bear use of lodgepole pine cover types varied considerably among months, years, and areas, presumably commensurate to variation in security, feeding opportunities, and the suite of nearby habitats. Individual lodgepole pine cover types almost certainly did not represent a uniform environment for bears. Given that this is so, further increases in knowledge will be contingent upon understanding the combined effects of weather, food availability, bear density, overall habitat composition, and nearness to humans on grizzly bear habitat selection.

Unit of Analysis

Several researchers have advocated the analysis of habitat use strictly on the basis of individual animals and their home ranges; i.e., Johnson's (1980) third-order selection (Thomas and Taylor 1990, Aebischer et al. 1993). These authors focused on the effects that sample unit definition, unequal individual sample sizes, and the arbitrary delineation of availability have on the results of use/availability analysis. Given this study was extensive and of long duration, and that data from individual bears were not contemporaneous, the individual-based analysis incorporated spatial, temporal, and individual variation. With individuals as sample units, it was thus difficult to assess habitat selection with any temporal or spatial specificity or control for intervening temporal and spatial factors. In studies of wide-ranging low-density animals, such as this one, it may be virtually impossible to collect enough information from enough animals to allow for an integrated statistical treatment of effects attributable to season, year, and area, much less other effects attributable to sex, age, and reproductive status, with individuals as sample units. These are important considerations, given that agencies rarely manage habitat for individual animals, and more commonly

Table 4. Coefficients of linear additive response functions and results of tests for independence of activity type and cover and habitat type, from log-linear analysis, for ground-sampled relocations of radiomarked grizzly bear that occurred in lodgepole pine forests, Yellowstone ecosystem, 1977–92. Coefficients marked with an * were statistically significant.

Activity type	Wald χ^2 test		Cover and habitat type coefficients										
	Cover type		Habitat type									CARU	VASC
	χ^2	P	χ^2	P	LP0	LP1	LP2	LP3	LP	DRY	MESIC		
No feeding or beds	22.8	<0.001	8.5	0.074	0.85*	-0.20	0.06	0.31	-0.11	0.12	0.09	0.37*	-0.42*
Graminoid grazing	22.9	<0.001	23.4	<0.001	0.79*	0.01	-0.30	-1.83*	-0.24	-0.85*	-1.20*	0.01	0.74*
Forb grazing	20.2	0.001	23.1	<0.001	1.04*	-0.15	-0.17	-2.00*	0.48	-0.98*	-0.53	-0.42	1.17*
Mushroom use	11.4	0.044	8.2	0.086	0.70	3.18*	2.13*	0.10	1.93*	2.70*	1.86*	0.96	-6.35*
Invertebrate use	11.3	0.046	7.4	0.117	-1.35*	0.11	0.11	0.27	0.22	0.11	0.22	0.66*	-0.82
Bedding	10.7	0.058	1.3	0.860	0.29	0.82*	0.25	0.19	0.66*	0.04	-7.30*	2.23*	4.25*
Digging sweet-cicely roots	2.4	0.790	16.6	0.002	-2.21*								
Digging whitebark pine seeds	0.6	0.998	18.8	0.001									
Ungulate use	3.6	0.613	7.3	0.121						-2.56	10.40*	-2.65	-2.50
Berry use	4.6	0.469	2.5	0.638									

manage specific areas with allowance for seasonal or annual variation in use. Making the critical assumption that sampling bias was spatially and temporally uniform, use of years and analysis areas as sample units allowed me to estimate variation in these explicit dimensions, and also provided estimates of selection that were specific to a given time or place.

Grizzly Bear Activity

By negative evidence (i.e., lack of feeding and bedding sign or coincidence with a trail), grizzly bears used the recently disturbed LP0 type primarily for travel. These relatively open sites presumably facilitated movement, although I question whether this result would be repeated with data collected 20 years after the 1988 fires, after most currently standing snags had fallen (Lyon 1984). As expected by studies elsewhere, grizzlies also made greatest use of the open LP0 and LP/NF types for grazing forbs and graminoids, especially on wetter, more fertile sites. Based on these results, I confidently rejected H_{n3} . On the other hand, and again as expected by open stand conditions, grizzlies strongly avoided the LP0 type for bedding. Together, these observations suggested that grizzly bears derived less net energy from their use of the LP0 type especially compared to their use of the LP1, LP, and LP/NF types.

With the exception of mushrooms, grizzly bear use of the highest quality foods in lodgepole pine forests was not associated with forest structure, and in the case of berries and ungulates, was not contingent upon habitat type. This result was partly a function of small sample sizes and low statistical power, especially in the case of berry and whitebark pine seed use. Only 15 instances of berry use were recorded at radiotelemetry locations in lodgepole pine forest during 16 years of data collection. This infrequent use of berries agrees with the infrequent presence of berries in grizzly bear feces from the Yellowstone area, especially in contrast to the feces of grizzlies in northwestern Montana and southern Canada (Mattson et al. 1991). Nonetheless, these 15 instances of berry use were not obviously related to successional stage, and are a tentative basis for not rejecting H_{n2} . In the case of whitebark pine, it is implausible, a priori, that use was not related to stand age. Whitebark pine does not produce seeds under typical stand conditions within 40 or even 100 years of stand replacement disturbance (Mattson and Reinhart 1994). However, forest struc-

ture probably had little effect on seed use after canopy closure.

MANAGEMENT IMPLICATIONS

These results do not support the premise that widespread conversion of lodgepole pine forests to early successional stages would benefit grizzly bears in the Yellowstone area. There is no rationale here for the systematic harvest of older stands to increase bear use of berries. Yellowstone's grizzlies consume few berries probably because of climatic constraints especially upon globe huckleberry production (Mattson et al. 1991, Mattson and Reinhart 1994). There is also evidence that in areas of Yellowstone where berry consumption is more common (as on the Targhee National Forest), globe huckleberry is substantially diminished by total overstory removal, especially on drier or more exposed sites (Martin 1983, Orme and Williams 1986). On the other hand, these results support the proposition that grazing opportunities for bears can be increased by logging on wetter sites, although it is highly improbable that grazing opportunities limit grizzly bear densities anywhere in the Yellowstone ecosystem (Bunnell and Hamilton 1983, Pritchard and Robbins 1990, Mattson 1997b).

Even so, these results suggest that Yellowstone's grizzlies would not respond strongly to any changes in lodgepole pine forest structure, per se, with the following 2 provisos. First, I cannot address the effects of changes in landscape-level structure of lodgepole pine forests beyond the range of what was analyzed here. This point holds for effects of the 1988 fires, especially given the attrition of snags expected during the next 2 decades (Lyon 1984) and the possible complications to movement posed by such an accumulation of large woody debris (Fancy and White 1985). Second, because whitebark pine seeds are a high quality food, and because seed production is limited to mature or near-mature trees, grizzlies will be affected adversely by the removal of lodgepole pine-dominated stands that contain productive whitebark pine (Mattson and Reinhart 1994).

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