

FORAGING STRATEGIES OF COASTAL GRIZZLY BEARS IN THE KIMSQUIT RIVER VALLEY, BRITISH COLUMBIA

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Abstract: An approach for relating fitness to foraging activity is described for 2 adult female grizzly bears (*Ursus arctos*) in coastal British Columbia. During berry season both bears roamed widely (seasonal home ranges of 3932 and 3565 ha) using at least 10 different species of berries in widely divergent habitats. Bears spent 62%–69% of their time in habitat types used for feeding. Habitat use by the bear with the smaller home range was correlated with food quantity and quality ($r_s = 0.79, P < 0.05$); that of the more widely ranging bear was not ($r_s = 0.11, P > 0.1$). During the berry season, both bears relied heavily on berries, but their diets differed. During the 3-year study, reproductive success of the more efficient bear (smaller home range, feeding activity correlated with food quality) was greater than that for the less efficient bear (3 vs. 2 cubs). These observations are discussed in terms of foraging theory. We conclude that 1 bear appears to be optimizing, but both bears could be satisficing.

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Several researchers have investigated the foraging strategies of grizzly bears and have performed proximate analysis on selected food items (Lloyd 1979, Mealey 1980, Sizemore 1980, Craighead et al. 1982, Hamer and Herrero 1983, Hamer 1985). Despite these efforts, relatively little information is available on the relationship between food quantity or quality (energy or protein content and apparent digestibility) and seasonal movements by bears. Defining food quality using simple indices of total digestible energy or protein is potentially misleading because some foods may be chosen on the basis of vitamin or mineral content or other criteria (Hamer and Herrero 1983). Similarly, some foods may be avoided because of the presence of protective or defensive agents (Robbins 1983). Despite these limitations, by regularly monitoring acid detergent fiber, crude protein, and gross energy levels of known grizzly bear foods at permanent plots and by seeking correlations between timing of use and levels of these nutrients, we may be able to explain why bears shift from 1 food to another (Hamer and Herrero 1983). By noting where these foods occur, it may also be possible to correlate habitat shifts with changes in food availability. A seasonal model of habitat use can assist both population and habitat management.

In British Columbia many grizzly bears inhabit mainland valleys of the Coast Mountains. These valleys are productive sites for grizzly bears and timber. They support some of the densest grizzly bear populations in North America and commonly yield 3–4 times more timber than other sites (Ainscough 1979). The annual economic value of the timber harvested in this area is \$1–2 billion (Archibald 1983). Some evidence suggests that grizzly bear abundance declines with logging, but it is unclear whether the declines are due to habitat change, excessive killing during and after logging, or other unidentified factors.

Research to provide information necessary to manage coastal grizzly bears effectively in areas being logged or scheduled for logging began in April 1982. A primary objective was to determine seasonal habitat requirements of coastal grizzly bears. A 3-part strategy of habitat classification, mapping, and evaluation was developed to meet this objective (Hamilton and Archibald 1986). The study area, a salmon-producing watershed in a mountainous area of mid-coastal British Columbia, offered a good opportunity to test hypotheses regarding the role of forage in habitat selection. Grizzly bear home ranges in this area are relatively small, allowing good access to feeding areas. For most of the active season, bears confine their activities to the river floodplain, where telemetry accuracy is high and where evidence of bears is easily found.

The key null hypothesis is that movements between habitat types by coastal grizzly bears are not associated with food availability (quantity and timing) or quality; that is, there are no correlations among forage nutrient levels, available biomass, and apparent use of habitat or food resources. The alternative hypothesis is that coastal grizzly bears concentrate their activities in habitat types with abundant, available, highly digestible foods of high nutrient value, including salmon (*Oncorhynchus* spp.). More specifically, except when consuming salmon, coastal grizzly bears concentrate use in those habitat types where plant phenology ensures higher quality food than in other available habitats.

This paper summarizes 1 component of the habitat evaluation procedure and discusses selected results of testing specific hypotheses relating grizzly bear use of habitats to abundance and quality of forage. The project is funded and administered cooperatively by the B. C. Min. of Environ. and For. Additional funding has been provided by the Univ. of B. C.; U.S.

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STUDY AREA

The study area is the Kimsquit River valley, located 500 km northwest of Vancouver in midcoastal B.C. (Fig. 1). Situated at the head of a long fjord-like inlet, the valley is about 80 km inland from the open Pacific coast. The lower 18 km of the valley exemplify a coastal-interior transition. Topography is rugged and steep, with elevations ranging from sea level to over 2000 m. Landforms and soils are generally representative of the Coast Mountains (Jungen and Lewis 1978). The historical influence of glaciation on surficial geology is evident, and most of the terrain has been modified by fluvial and colluvial processes and by accumulation of surface organic matter. The lower valley has a humid, suboceanic climate. Annual precipitation at the nearest, long-term climate station, Kemano, located 90 km northwest, averages 1,867 mm, of which 11% is snow. Annual mean temperature at Kemano is 6.5 C (Banner et al. 1986).

Vegetation in the area has been described in detail by Clement (1984a, 1984b), Banner (1985), and Banner et al. (1986). Habitat mapping was completed at a scale of 1:20,000 using the biogeoclimatic system developed by Krajina (1965). The habitat classification uses an ecological classification based on potential climax vegetation (Yole et al. 1982) modified to accommodate the extensive seral vegetation that develops after geomorphic and logging disturbances. The biogeoclimatic hierarchy of classification, i.e., zone, subzone, and variant (Fig. 2), is used by the B. C. Min. of For. and the forest industry in their planning. The additional ecosystematic categories within the system enable practical field observation, description, and classification of existing vegetation. Three categories were used to classify and map climax and seral vegetation: the ecosystem association, successional stage, and variation (Banner et al. 1986). When combined, these categories describe the vegetation of any land unit in terms of its potential climax con-

dition, present structure, and species composition. These units are hereafter called habitat types.

The following description of the vegetative cover of the study area (Yole et al. 1982) is arranged by physiognomic classes. Plant nomenclature follows Taylor and MacBryde (1977). Coniferous forests cover the largest proportion of the vegetated area; western hemlock (*Tsuga heterophylla*) is the dominant climatic climax species. Depending on local microclimate and edaphic features, western hemlock may be accompanied by a variety of other conifers that may dominate edaphic climax. For example, Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) are found on the rapidly drained, side slopes of the lower valley. Western red cedar (*Thuja plicata*) prefers wetter sites, as do sitka spruce (*Picea sitchensis*) and yellow cedar (*Chamaecyparis nootkatensis*). Amabilis fir (*Abies amabilis*) is found throughout the upper valley and on some moister, shadier sites in the lower Kimsquit. At higher elevations with heavy snow accumulations, mountain hemlock (*Tsuga mertensiana*) is common.

Deciduous forest covers considerable areas of the watershed, primarily in the lower valley. Two tree species dominate: red alder (*Alnus rubra*) is a fast-growing pioneer that rapidly colonizes disturbed sites; black cottonwood (*Populus balsamifera* var. *trichocarpa*) has high flood resistance and dominates the alluvial seral areas of the lower Kimsquit. The deciduous forests have relatively open canopies and a productive understory.

Five major shrub-dominated areas have been identified in the study area: avalanche chutes, riparian areas, fringes of bogs, subalpine shrub areas, and recent clearcuts. Numerous shrubs occur in the seral riparian areas, many of which are important bear foods such as salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*), and red elderberry (*Sambucus racemosa*).

Three significant areas of the Kimsquit are dominated by graminoids; tidal flats, estuary, and a large bog in the upper valley. The estuary and beach fringes have been classified in detail (Clement 1984a) and mapped at 1:2,500 because of their importance as grizzly bear feeding areas. Herb-dominated meadows are commonly found on avalanche chutes throughout the valley.

The Kimsquit River is 1 of the most important fishery systems of the central coast; it has major runs of all species of Pacific salmon. The timber value of the Kimsquit drainage is also high. The lower 6 km

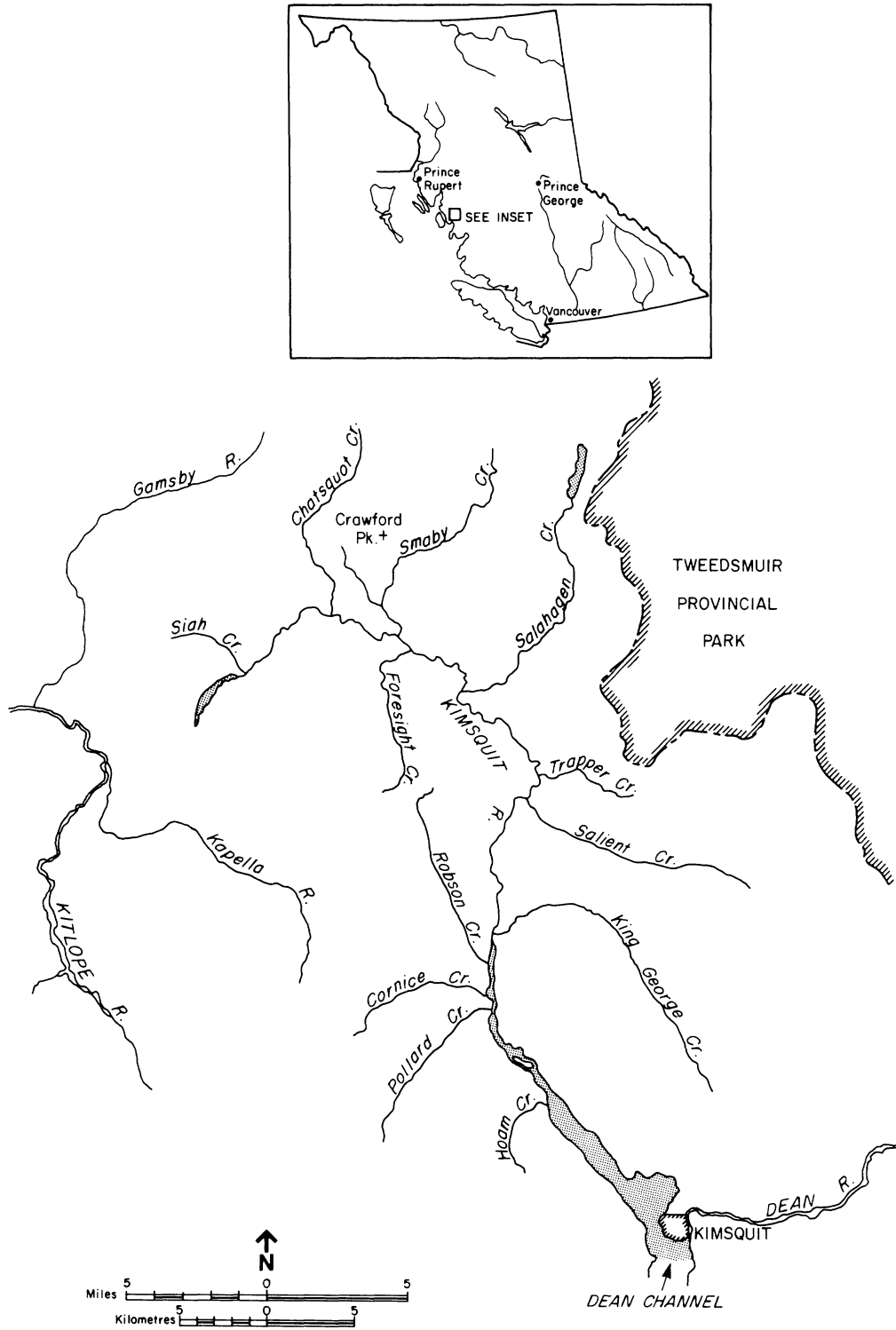


Fig. 1. Kimsquit River valley grizzly bear habitat study area.

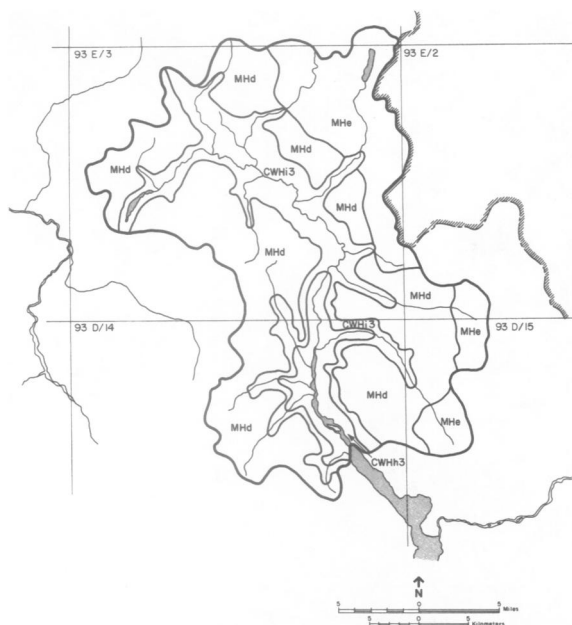


Fig. 2. Kimsquit River valley forested biogeoclimatic zones. Abbreviations: CWH, coastal western hemlock zone; CWHh, mid-coast drier transitional subzone; CWHl, wetter maritime subzone; MH, mountain hemlock zone; MHD, coastal subzone; MHe, transitional subzone.

was logged using a railway system in 1917 and 1918 to provide airplane-grade spruce; current harvesting began in 1979 and has removed approximately 400,000 m³ to date. Historical and current logging allowed evaluation of timber harvest practices on grizzly bears and their habitat. The effects of logging activity on collared grizzly bear movement are discussed by Archibald et al. (this volume).

METHODS

Capture and Monitoring

We captured bears with Aldrich foot snares using methods similar to those described by Flowers (1977) and commonly reported elsewhere (e.g., Lloyd 1979, Russell et al. 1979). Cubbies were baited with 10–20 kg of meat scraps suspended in a burlap sack at the anchor tree. Trail sets were frequently set along spawning channels and near the baited cubbies. We attached transmitter beacons to each snare to permit monitoring of the trapline from a distance (Nolan et al. 1984). Captured bears were immobilized with M-99 (etorphine hydrochloride, Cyanamid Canada Ltd.) administered with a jabstick or immobilization rifle (Dist-inject, Biosonics, Edmonton, Alberta). Mature grizzly bears were equipped with radiocollars (Te-

lonics, Inc., Mesa, Ariz.); 3 yearling bears were equipped with ear tag transmitters (Servheen et al. 1981). A premolar tooth was removed from each bear to determine bear age using cementum annuli; standard body measurements were also taken (Russell et al. 1979).

Transmitter-equipped bears were monitored from the air and the ground. Upon receiving an aerial signal, the bear was located as accurately as possible; its position and associated uncertainty area were plotted on a 1:50,000 topographic map. Unless the bear was observed, the uncertainty area was considered to be at least 100 m in diameter. Habitat types were assigned to aerial locations by plotting the site on type-labeled 1:24,000 color aerial photographs. If the uncertainty area overlapped more than 1 habitat type, the dominant type near the center point of the uncertainty area was chosen.

We developed a ground monitoring system that allowed rapid data collection, precise field determination of bear locations, protected the equipment from heavy rain, and was easy to use after dark (Hamilton and Archibald 1986). Output from this system included the best estimate of the bear's location, based on the intersection of several bearings, in Universal Transverse Mercator (U.T.M.) coordinates.

Site and Forage Investigations

Radiolocations guided site investigations, which were conducted in areas of recent grizzly bear activity to identify and evaluate habitat characteristics potentially important in determining movements between, and use of, specific habitat types. Locations having an uncertainty area of less than 1 ha were investigated after the bear left the vicinity. Activity information was recorded if the exact site and date of use could be confirmed and if the bear responsible was definitely a grizzly bear. Track characteristics (Lloyd 1979) and hair color, thickness, and length were used to confirm species identification. When possible, activities were assigned to known bears. Direct visual observations, periodic checks in areas of traditional grizzly bear use, and chance encounters with grizzly bear sign also provided records of activity.

We investigated sites from 1983 to 1985. Information collected included security cover value and distance to an opening; soil type and canopy cover of trees, shrubs, and herbs; and age of sign and bed measurements (Hamilton and Archibald 1986). Ac-

tivities were classified as feeding, bedding, tree marking, trail marking, traveling, and other. Typically, more than 1 activity was recorded at each site.

Seasons of grizzly bear activity, like those defined by Lloyd (1979), were adapted to the Kimsquit study area. Eight seasons were identified (Table 1) based on plant phenology and the availability of preferred foods. Dates are only approximations because of between-year variation in seasons.

In 1983 and 1984, we completed plant species lists at verified grizzly bear feeding, bedding, and marking sites. Percent ground cover, height class, distribution, and vigor were recorded for each species in a 20 by 20 m plot. Prominence values of food species at these sites ($N = 309$) formed the basis for food quantity rankings. Prominence values are the average percent ground cover of a species multiplied by the square root of its percent frequency of occurrence across all sample plots within a particular habitat type (Banner et al. 1986). These values were used as indices of plant biomass. Food availability was estimated at 89 reference plots. Prominence values from these plots were compared with corresponding values from bear activity sites to help determine if bear habitat use was correlated with food availability.

Where feeding activity was verified, we listed food species in order of estimated volume consumed and classified them by phenological stage (Dierschke 1972). For fruit-producing shrubs, we estimated berry abundance from the percentage of fruit-bearing stems and the average abundance (high, medium, or low) of berries per stem. In 1984, we collected 3 types of food samples for nutrient analyses: remains of what the bear had consumed, a mimic of what the bear had selected, and a 2nd mimic collected up to 1 month later at the same site.

We established permanent plots in 18 different habitat types to sample food species. Plots were visited

once in each of seasons 2–7 (Table 1) to monitor phenology, estimate food abundance, and collect samples of all known food plant parts for nutrient analyses. Food samples collected for nutrient content determination were frozen in 750 ml plastic bags and submitted to the Agric. Can. Res. Branch Lab. for analysis. Laboratory techniques followed accepted standards of proximate analysis (AOAC 1980) for determining crude protein (6.25 by Kjeldahl nitrogen) and gross energy content. We used acid detergent fiber (ADF) content (Waldern 1971) to indicate relative forage digestibility (Bunnell and Hamilton 1983).

Home Range and Habitat Use

We analyzed grizzly bear home ranges using the minimum convex polygon method (Harestad 1981). Verified ground and aerial telemetry locations for all seasons were used to construct 100% minimum convex polygons. Repeat locations of bears in dens were not included in home range analysis. Two 1:20,000 habitat type maps covering the intensive study area were digitized for the Computer-aided Planning Assessment and Map Production (CAPAMP) system used by the B. C. Min. of the Environ. A FORTRAN computer program summarized areas by habitat type within selected home ranges. Program input consisted of a sequential list of map polygon numbers inside the home range outline. Area summaries in the output were arranged hierarchically, from the highest to the lowest levels of the habitat type classification.

Continuous monitoring of collared bears was not possible because telemetry was limited by the rugged topography and thick vegetation in the area. Bears were monitored on a 24-h basis when they were within ground telemetry range, and habitat units subject to the higher accuracy and precision of ground telemetry are overrepresented in the location fre-

Table 1. "Seasons" of grizzly bear activity in the Kimsquit River Valley, B.C.

Season no.	Start	Definition
1	Early Apr	Emergence to valley floor leaf flush
2	Mid-Apr	Leaf flush to avalanche chute green-up
3	Late May	Avalanche chute green-up to berries
4	Late-Jun	Berry production, no salmon
5	Late Jul	Berries and salmon
6	Late Aug	Salmon, no berries
7	Mid-Oct	Post salmon
8	Early Nov	Denning

quency sample. Because of this bias and problems of autocorrelation (Swihart and Slade 1985), time spent in a habitat unit (bear days) was used as an index of selection and value derived from the unit. The number of days spent in a particular unit was calculated as the total of half the number of days since the previous location plus half the number of days to the subsequent location. Comparison of bear day totals on a percentage basis was used to develop a seasonal rank of grizzly bear use for each habitat type.

The activity (e.g., feeding) frequency data are also potentially misleading. The usefulness of such data is a function of sample independence (Hulbert 1984). To keep sample sizes at a useable level, frequency of feeding behavior was used without removing non-independent sample points. Rank testing removed some of the potential bias, because absolute comparisons were avoided.

Statistical Analysis

We coded and keypunched data from telemetry, site investigation, vegetation, scat, and nutrient content and used SAS (SAS Institute Inc.) for most statistical analyses. Summary statistics were calculated for continuous variables. Nonparametric techniques were also used because categorical variables in frequency summaries were not normally distributed. The Friedman single-factor analysis of variance by ranks was used to test for significant differences between bears in habitats used for feeding, and food species consumed.

We conducted use/availability analyses (Neu et al. 1974) on a seasonal basis to facilitate evaluation of habitat types using methods of area and observed use proportions summarized previously. Frequency and summary statistics were used to rank habitat types and grizzly bear foods for observed use and potential

“value.” Use and value rankings were compared using Spearman’s rank correlation coefficients.

RESULTS

To limit the length of data presentation, detailed tests relating bear movement to forage quality and quantity are presented only for Season 4. This season occurs from mid-June to late July, before the salmon run; most berries are available at that time (Table 1).

Capture

Most of the habitat use information was collected from 2 resident, adult female grizzly bears. Bear 08 was first captured as a 13-year-old on 17 May 1982. She was accompanied by 2 male yearlings; by 30 June 1983 she was alone. Bear 08 did not breed or produce cubs in 1984 or 1985, but when recaptured on 21 April 1985, she was in excellent condition. Bear 25 was first captured as a 16-year-old on 8 July 1982. She was accompanied by 1 female and 1 male yearling. She did not produce cubs in 1984 but emerged from her den in May 1985 with 1 cub-of-the-year. The relative merits and difficulties associated with monitoring so few bears have been discussed by Hamer and Herrero (1983).

Monitoring and Home Range

Bear 08’s home range is based on 236 locations. Of these, 142 were obtained from ground telemetry and confirmed by evidence (sign) seen during site investigations; the remaining 94 locations were obtained from aerial surveys, direct visual observations, and capture. Bear 25’s home range is based on 241 locations; 165 ground telemetry locations supported by site investigations and 76 locations from aerial surveys, direct visual observations, and capture. Obvious differences in seasonal home range sizes were recorded (Table 2). For seasons 5 and 6, when salmon

Table 2. Home range summary for 2 adult female grizzly bears in the Kimsquit River Valley, B.C., 1982–85.

Season*	Area (ha) of seasonal home ranges			
	Bear 08	N	Bear 25	N
2	3,041	19	2,189	28
3	4,116	28	1,625	25
4	3,932	50	3,565	67
5	511	72	655	58
6	669	51	511	55
7	616	7	328	8
All locations	8,546	236	5,964	241

* Seasons as presented in Table 1.

were available, home range size decreased dramatically.

Data for season 4 showed clear differences between overall habitat use and habitat availability. Rank testing showed poor correlation between habitat use and availability; $r_s = 0.27$ for bear 08 ($N = 76$) and $r_s = 0.39$ for bear 25 ($N = 87$). Differences were statistically significant ($P < 0.05$) when comparing observed with expected: $X^2 = 1023$ for bear 08 ($df = 75$) and $X^2 = 794$ for bear 25 ($df = 86$). During season 4 many habitat types in the bears' seasonal home ranges were not used. For bear 08, use was recorded in 23 of 76 (30%) habitat types available within her home range. Similarly, bear 25 used 23 of 87 (26%) of the types within her season 4 home range.

Site Investigation and Diet

Usually more than 1 activity type was recorded at each site investigation. The data base consisted of 253 activities at 142 sites for bear 08 and 289 activities at 165 sites for bear 25. For season 4, data consisted of 62 activity records at 31 sites, and 83 activity records at 49 sites for bears 08 and 25, respectively. Differences between bears were found when the frequencies and ranks of season 4 feeding activity by habitat type were compared. Feeding was recorded in 18 habitat types; only 8 of which were used by both bears. The ranks of feeding frequency within these 8 habitats were not significantly different between bears ($P > 0.1$). The sums of bear days for habitats in which feeding activity was recorded account for 62% and 69% of the total bear days recorded in season 4 for bears 08 and 25, respectively.

To date, 30 grizzly bear foods have been identified in the Kimsquit study area (Table 3). In season 4 the animals relied heavily on berries (Table 4), although there were a few occurrences of digging licorice root (*Osmorhiza chilensis*) roots and grazing on lady-fern (*Athyrium filix-femina*) and sedges (*Scirpus microcarpus*, *Carex sitchensis*). Differences in food species selection in season 4 were observed between bears; 10 of 15 species were used by both. Analysis of variance by ranks of these 10 food species showed no significant difference ($P > 0.1$).

Food Quality, Quantity, and Availability

We combined food species prominence values and phenological records by habitat type from grizzly bear activity sites and vegetation mapping plots. To simplify comparison of the nutrient levels within a

species across forage sample types, we derived an index of overall nutritional value by dividing the average ADF by the sum of the average protein and energy values. When no significant differences among types were found, data were combined. The inverse of these indices was multiplied by the prominence value for that species in a specific habitat type to give a combined quality/quantity or "importance" value. We obtained a total food value for the habitats used for feeding in season 4 by summing the species importance values within each type. Their usefulness is as relative values that can be compared to grizzly bear use information after ranking. Total food values and rank for the 18 habitat types used by bears 08 and 25 in season 4 are shown in Table 5 with the area of each habitat type within the season 4 home ranges. Frequency of use and rank over habitat types are also shown. Spearman's rank correlation coefficients between the ranks of use and total food availability were significant for bear 25 ($r_s = 0.79$) but not for bear 08 ($r_s = 0.11$).

DISCUSSION

Numerous studies reveal dramatic seasonal shifts in the diet of grizzly bears. Such shifts are thought to result from attempts to maximize the net rate of energy intake by selecting highly digestible forage (Bunnell and Hamilton 1983). Although they have retained the ability to digest meat efficiently, grizzly bears have apparently evolved only limited capability to digest coarse forage. This constrained digestive efficiency, together with the need for rapid weight gain imposed by denning, has caused several authors to speculate that grizzly bear habitat selection is related to the quantity and quality of available forage (Lloyd 1979, Mealey 1980, Sizemore 1980, Stelmock 1981, Craighead et al. 1982, Hamer and Herrero 1983, Hamer 1985).

The 2 bears discussed here show broad similarities and striking differences. Both bears roamed widely during berry season compared to other seasons, covering 46%–60% of their overall range (Table 2). Berry-producing shrubs comprised the top 4 food plants in the diet of each bear (Table 4), but the total diet of the bears differed significantly. Switching to a berry-dominated diet from one dominated by the succulent forbs of avalanche chutes appeared to depend on the snowpack of the previous winter and temperature and rainfall during early spring. When snowpack at higher elevations was slow to melt be-

Table 3. Verified grizzly bear foods in the Kimsquit valley, B.C., 1982-85.

Scientific name	Common name	Parts consumed
Plants		
<i>Angelica genuflexa</i>	White angelica	Roots, stem, leaves
<i>Athyrium filix-femina</i>	Ladyfern	Pinnae
<i>Carex sitchensis</i>	Sitka sedge	Blades
<i>Cicuta douglasii</i>	Water hemlock	Stems, leaves
<i>Cornus sericea</i>	Red-osier dogwood	Berries
<i>Equisetum</i> spp.	Horsetail	All?
<i>Heracleum sphondylium</i>	Cow parsnip	All
<i>Lonicera involucrata</i>	Black twinberry	Berries
<i>Lupinus nootkatensis</i>	Nootka lupine	Roots
<i>Lysichiton americanum</i>	Skunk cabbage	Roots, some leaves
<i>Oplopanax horridus</i>	Devil's club	Leaves, stems, berries
<i>Osmorhiza chilensis</i>	Licorice root	Roots
Poaceae	Grasses	Blades
<i>Ribes bracteosum</i>	Stink currant	Berries
<i>Rubus idaeus</i>	Red raspberry	Berries
<i>R. spectabilis</i>	Salmonberry	Shoots, leaves, berries
<i>Sambucus racemosa</i>	Red-elderberry	Berries
<i>Scirpus microcarpus</i>	Small-fruited bulrush	Blades
<i>Carex</i> spp.	Sedges	Blades
<i>Streptopus roseus</i>	Rosy twisted stalk	Berries
<i>Vaccinium</i> spp.	Huckleberries	Berries
<i>Veratrum viride</i>	False hellebore	Stems
<i>Viburnum edule</i>	Highbush cranberry	Berries
Insects		
<i>Cedoptera</i> spp.	Beetles	Larvae
<i>Bombus</i> spp.	Honeybees	Larvae
Fish		
<i>Oncorhynchus gorbuscha</i>	Pink salmon	All
<i>O. keta</i>	Chum salmon	All
<i>O. nerka</i>	Sockeye salmon	All
Mammals		
<i>Alces alces</i>	Moose	Flesh

cause of heavy snowfall the previous year or a cold spring, berry use was delayed and bears continued to use avalanche chutes until late June, as in 1984. In southeast Alaska, avalanche chutes remain important as summer progresses, and bears feed extensively on a number of berry species (Schoen and Beier 1985). In the Kimsquit, however, during the early part of the berry season, both bears made exploratory movements among avalanche chutes, floodplain, and estuary and were sometimes lost to ground telemetry. Gradually, they restricted their movements on the valley floor, making especially heavy use of floodplain seral forests as the salmonberry, twinberry (*Lonicera involucrata*), devil's club, and elderberry became available. Late in the berry season, they began to move from the floodplain to climax, hemlock-dominated sidehill forests to feed on the huckleberries (*Vaccinium* spp.) found there. The large home ranges during the berry season reflect this variable move-

ment pattern and the fact at least 10 species of berries from widely different habitats were eaten.

The most striking difference between bears is their frequency of feeding by habitat type (Table 5). Bear 08 roamed much more widely than bear 25, and her overall home range was 43% larger (her season 4 home range was 10% larger). By some criteria bear 25 appears to be more efficient, because her use of habitat types was significantly correlated with total food value in those types, whereas bear 08's feeding showed no correlation to food value. Observed differences between bears may be related to poor ground access to some of the habitat types during season 4. Verified sign was found at 31 sites (25 feeding) after 85 ground telemetry closures (37%) for bear 08 and 49 sites (34 feeding) after 84 ground closures (58%) for bear 25.

Fitness of bear 25 was also higher over the study period (3 vs. 2 cubs). It is tempting to suggest that

Table 4. Season 4 grizzly bear food species frequency and ranks from activity site investigations, Kimsquit River valley, B.C., 1983–85.

Food species	Use		Rank	
	Bear 08	Bear 25	Bear 08	Bear 25
Devil's club	15	20	1.0	1.0
Elderberry	8	15	2.0	2.0
Twinberry	1	5	10.5	3.0
Salmonberry	5	4	3.0	4.0
Cow parsnip	3	3	5.5	5.0
Small-fruited bulrush	1	2	10.5	6.5
Ladyfern	2	2	7.5	6.5
Huckleberry	4	1	4.0	10.5
Insects	1	1	10.5	10.5
Water hemlock	—	1	—	10.5
Licorice root	3	1	5.5	10.5
Sitka sedge	—	1	—	10.5
Grasses	—	1	—	10.5
Skunk cabbage	2	—	7.5	—
Red raspberry	1	—	10.5	—

this increased fitness and the apparent association of movements with food availability were related. Hirnstein (1970: 243), however, warned "The temptation to fall back on common sense and conclude that animals are adaptive, i.e., doing what profits them most, had best be resisted, for adaptation is at best a question, not an answer."

Bunnell and Gillingham (1985) reviewed optimal foraging theory for large herbivores and concluded that it had 2 major limitations: observer difficulties

in establishing constraints for optimality, and animals not needing to be optimal. Our explicit assumptions were that use of an area represents selection and that time spent in an area was proportional to its value to an individual. Both assumptions may be incorrect. The dramatic differences between reproductively successful bears suggest that if the assumptions are broadly correct, they are not highly restrictive. The greatest value of positing an optimal solution may be its ability to act as a well-defined null hypothesis. In

Table 5. Season 4 frequency of grizzly bear feeding by habitat type (Banner et al. 1986), type rank, type area, and total food index, Kimsquit River valley, B.C., 1983–85.

Habitat type	Food total	Bear 08			Bear 25		
		Area (ha)	Use	Rank	Area (ha)	Use	Rank
Cottonwood-devil's club mature seral	363	31	2	5.5	31	6	1.0
Cottonwood-alder-salmonberry-devil's club mature seral	317	81	1	10.5	106	5	2.5
Floodplain spruce-devil's club old-growth	335	28	3	2.5	21	5	2.5
Cottonwood-spruce-salmonberry-devil's club mature seral	211	56	5	1.0	100	4	4.0
Floodplain-spruce-devil's club young climax	316	5	—	—	7	3	5.0
Devil's club-fern mature seral	181	28	2	5.5	21	2	7.0
Alder-salmonberry-elderberry mature seral	354	39	—	—	64	2	7.0
Avalanche chute shrub seedling pioneer seral	183	21	—	—	15	2	7.0
Devil's club-fern recently logged	189	25	1	10.5	23	1	11.0
Devil's club-fern pole sapling	92	3	1	10.5	3	1	11.0
Estuary	131	—	—	—	39	1	11.0
Alder-grass pole sapling	171	4	1	10.5	4	1	11.0
Cottonwood-alder-twinberry pole sapling	184	23	—	—	23	1	11.0
Devil's club-fern young climax	126	56	3	2.5	89	—	—
Devil's club-fern mature climax	154	149	2	5.5	43	—	—
Alder-salmonberry pole sapling	139	37	2	5.5	49	—	—
Moist oak fern-moss young climax	83	60	1	10.5	114	—	—
Skunk cabbage swamp mature climax	459	15	1	10.5	4	—	—

this case we reject the theory for bear 08 and accept it for bear 25. Examination of the annual pattern of habitat use, rather than a single active season, may lead to different conclusions. Regardless, it is also possible that although neither bear is optimizing, both may be "satisficing," or attempting to ensure survival.

Satisficing models investigate decision rules for which the animal's objective is not to maximize or minimize some quantity but to survive (Bunnell and Gillingham 1985). Satisficing while foraging is analogous to the existential game of Slobodkin (1964), in which fulfilling the goal means staying in the game. An animal adapting such an approach acts not to optimize its choice of feeding habitat or diet but to stay alive. It may be able to stay alive and reproduce without optimizing any single variable. Hamer (1985) noted a number of factors other than the availability of preferred foods that may influence a grizzly bear's movements and choice of habitat: learned family traditions, reproductive processes, defense or exploration of home range, use of cover, or resource partitioning between sex and age classes. Bunnell and Gillingham (1985) noted that the complexity of most wild herbivore environments makes it nearly impossible to select the variable to be optimized and that satisficing does not evade the problem. Some minimally satisfactory thresholds must still be set.

Among female grizzly bears, all components of the reproductive rate (litter size, breeding interval, age of puberty) appear under some nutritional control (Bunnell and Tait 1981), and some apparent optimality in foraging behavior is expected (Bunnell and Hamilton 1983). Grizzly bears are also long-lived, and the major influence on a female's life-time fitness will be her survivorship (Bunnell and Tait 1981); in un hunted populations survival rate may be 90% or more among females in their prime (Bunnell and Tait 1985). These conditions, and the fact that mean litter sizes are rarely less than 1.6 (Bunnell and Tait 1981), suggest the possibility of Slobodkin's (1964) existential game. The bears may be satisficing. Our data are based on observations of reproductively successful female bears during 4 years. We can conclude only that 1 female closely approximated the optimal foraging function we posited for the berry season, and 1 behaved differently but was also successful. The relative importance of survivorship to the fitness of a long-lived species reduces the likelihood of short-term optimization and optimization specifically for foraging.

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