

AN INTEGRATED SATELLITE TECHNIQUE TO EVALUATE GRIZZLY BEAR HABITAT USE

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Abstract: I present a method that combines 2 previously described remote-sensing techniques: Landsat-derived vegetation types (Craighead et al. 1986, 1988) and National Oceanic and Atmospheric Administration (NOAA) Tiros satellite-derived locations of grizzly bears (*Ursus arctos horribilis*). This research was completed on a 5,931-km² study area north of the Squirrel River, a tributary of the Kobuk River, in northwestern Alaska. Six satellite radiocollared grizzly bears were located a total of 1,624 times from 1986 to 1988. Habitat use was quantified and statistically evaluated by superimposing bear locations and home ranges on a map of vegetation cover types. I acknowledge the variability of the remote measurements and describe a technique to estimate the central tendency of a sample set of vegetation complexes about bear occurrences. The inference of selection or avoidance was made from the juxtaposition of bear and habitat. The analyses showed that individual bears clearly selected for specific habitat types, but as a group the bears were quite diverse in habitat use. This indicates that habitat needs of the studied grizzly bears were very broad and that their area requirements were expansive.

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Key words: Alaska, grizzly bear, habitat selection, home range, satellite telemetry, *Ursus arctos horribilis*, vegetation mapping.

Conservation of large mammals requires precise knowledge of their habitat requirements. Other workers have evaluated grizzly bear habitat selection in arctic Alaska using field sightings, ground or aerial telemetry, or both, and conventional habitat analysis techniques (Reynolds 1974, 1979, 1980; Reynolds and Hechtel 1980, 1984; Gebhard 1982; Garner et al. 1985; Hechtel 1985; Phillips 1987). In remote areas, however, detailed information is costly to obtain by conventional techniques. Craighead and Craighead (1987) demonstrated the feasibility and practicality of tracking free-roaming caribou (*Rangifer tarandus*) in the vast arctic environment by satellite, and Craighead et al. (1988) demonstrated that, through satellite imagery, land cover types could be spectrally classified and accurately mapped. In 1986, I initiated a project to develop and field test a technique to quantify and describe grizzly bear habitat use in a study area in northwest Alaska by integrating remotely sensed data transmitted from 2 satellite systems: vegetation data from Landsat-II and grizzly bear location data from NOAA's Tiros-N.

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STUDY AREA

Fieldwork was conducted on a 5,931-km² study area in northwestern Alaska bounded by 67°09'N–67°38'N and 159°44'W–161°45'W (Fig. 1). The study area was bordered on the south by the Kiana Hills, on the north by the Baird Mountains, on the east by the Kallarichuk Hills, and on the west by the Maiyumerak Mountains. The central geographic feature was the Squirrel River, a tributary



Fig. 1. Alaska study area, 1986–88.

of the Kobuk River. The study area was defined by a polygon that encompassed all 6 bear home ranges.

Vegetation in this area was representative of the forest-tundra ecotone at the northern extension of the subarctic boreal forest (Hustich 1953). Treeline occurred at about 380 m above sea level, and the northern limit of tree growth was about 70 km north of the study area. Elevation ranged from sea level to 1,174 m in the Baird Mountains. The study area was geomorphically complex and supported a diverse flora and fauna (Melchior 1976), exhibiting many small, highly interspersed patches of habitat types. The mean patch size for all vegetation complexes was 4.6 ha, the range of the means of the 12 vegetation complexes was 1–8 ha, and the range for individual patches was 0.47–1,000 ha.

Habitat types, plant communities, and distribution of plant species varied latitudinally, longitudinally, and with elevation. River floodplains included such physical features as cutbanks, oxbow lakes, gravel bars, sloughs, lakes in various stages of eutrophication, and striated river bends. Above the floodplains were river terraces which extended gradually or abruptly to the mountain slopes. For detailed descriptions of the vegetation characterizing the study area, see Craighead et al. (1988).

Weather records reveal the area is characterized by cool, short summers and cold, long winters with a mean summer temperature (Jul–Sep) of 9.4 C and mean winter temperature (Oct–Jun) of -11.5 C (NOAA Ann. Climatological Summaries Kotzebue, Alas., unpubl. data). Mean annual precipitation is 22.8 cm (winter, 3.2 cm; spring, 2.7 cm; summer, 9.6 cm; and fall, 7.4 cm; Natl. Weather Serv., Kotzebue, Alas., unpubl. data).

METHODS

Field Methods

Vegetation Map and Classification.—From 1983 to 1986, vegetation of a 33,768 km² area in northwestern Alaska was mapped, botanically described, and classified using Landsat multispectral scanning system (MSS) satellite imagery; 880 vegetation relevé-type sample plots provided a detailed description of each vegetation complex down to species (Craighead et al. 1982, 1988). The bear study area, a subunit of the vegetation study area, encompassed 12 vegetation complexes and 4 land classes—gravel bars and ocean beaches, bare rock, water, and burns. The burned areas were in various stages of revegetation, and the other land classes were unvegetated. For purposes of analyzing habitat use, the land classes were pooled under a general heading. Water

occupied only 2.3% of the study area. Most bodies of water were small: nearly 90% were <5 ha and 45% were <0.5 ha. I considered the bodies of water to indicate the presence of a unique riparian or shoreline habitat. For detailed summary statistics of the vegetation complexes and plant communities in this area, see Craighead et al. (1988).

Physiognomic Vegetation Zones.—I classified vegetation complexes of the study area into 4 zones—rock-tundra, shrub-forest, shrub-tussock, and mesic complex—based on distinct climactic communities and a structural-physiognomic classification scheme (Fosberg 1961). The rock-tundra zone, composed of the bare rock land class and vegetated rock and alpine tundra vegetation complexes, accounted for 41.5% of the study area and was characterized by bare rock and decumbent and matted vegetation. The most distinctive communities were those of *Dryas* spp. The shrub-forest zone comprised the alpine shrubland, upland mixed spruce (*Picea* spp.), and upland white spruce (*P. glauca*) vegetation complexes; it accounted for 27.5% of the study area and was characterized by erect shrubs and trees with a low shrub and herb understory. The shrub-tussock zone was 21.1% of the study area, comprised the shrub tundra and tussock tundra vegetation complexes, and was characterized by tussock-forming *Carex* species. The mesic complex zone accounted for only 6.2% of the study area, but comprised the largest number of vegetation complexes—tall willow (*Salix* spp.), riparian spruce, riparian mosaic, and semi-vegetated rock. It was associated with streams and riverbanks and lake shores, and complexes characterizing the zone extended from sea level to 519 m. The tidal flat vegetation complex and the gravel bars and ocean beaches, burns, and water land classes were grouped in a category called other: they comprised 3.7% of the study area.

Bear Capture and Radiocollaring.—Eight satellite radio transmitter collars (Telonics, Inc., Mesa, Ariz.) were fitted to 6 grizzly bears during the study. The collar weighed 2.1 kg and transmitted a 0.06-second, 1-W signal at 401.650 megahertz every minute throughout the life of the transmitter. One collar each was attached on 24 June and 2 July 1986; 5 in 1987 from 22–25 May; and 1 on 20 June 1988. One bear instrumented during 1986 was reinstrumented in 1987, and another instrumented in 1987 was reinstrumented in 1988. Data sets for these 2 bears were discriminated by year (2a, 2b; and 5a, 5b). The 2 data sets for each bear were combined for analysis of their home ranges and habitat selection. Bears were located from the air soon after emergence from dens. They were approached by helicopter and a projectile dart

(PaxArms, Ltd., Timaru, New Zealand) injected a solution of Telazol® (1:1 tiletamine and zolazepam [A.H. Robins Co., Richmond, Va.], Taylor et al. 1989). The condition of each bear was assessed, its body measurements taken, numbered ear tags attached, and identifying numbers tattooed on the inner lip and in the left axilla. Each was fitted with a radiocollar programmed to transmit to 2 concurrently operational NOAA Tiros-N satellites. This data was retransmitted to earth receiving stations where it was processed by Service Argos of the French Centre National d'Études Spatiales and provided to users as coordinate locations.

Integrating the Satellite Data

I used several computer programs to combine Argos bear location data with the Landsat-derived vegetation database and to determine what vegetation complexes the bears occupied. The computer program TELEBASE (J.M. Glassy, developed under contract) was used to reformat and summarize the raw bear location data into records that were managed in a PC-based database. Several biologically impossible outlier locations were eliminated from the data set. NOAA Tiros satellites orbited earth once every 101–103 minutes and provided a sampling of bear locations at a set interval throughout the study period, with the following exceptions. Because each overpass did not necessarily generate a usable location there was some variability in the sampling regiment, but because the absence or unusability of a location was a random event it did not introduce any bias into the sample set. Occasionally the overpasses of the 2 NOAA Tiros satellites coincided, and 2 locations were generated for approximately the same time. To avoid sampling bias, locations were filtered to eliminate locations that were separated in time by <1 hour. Because of satellite orbital mechanics, there was a period from approximately 2300 to 0200 hours (Alaska Standard Time) each day with fewer satellite overpasses and, therefore, fewer locations. Fortunately, this coincided with the period when bears were least active, a pattern also observed by Hechtel (1985).

I summarized the pixel values corresponding to vegetation complexes contained within circles having a radius of 40 m (single pixel) and 250 m (47 pixels) centered on each bear radio location within a digitized Landsat scene using the program RADIUS (R.V. Ringleb and E.J. Shubert, developed under contract). A measure of central tendency, or mean, was then computed for the sampling of vegetation complexes and compared to the expected values for the study area. A chi-square (χ^2) test was used to test for the goodness-of-fit of used vegetation complexes to available vegetation com-

plexes (Alldredge and Ratti 1986, White and Garrott 1990).

Porter and Church (1987) reported that the scale at which the vegetation is sampled can affect the type of pattern (regular, clumped, or random) that is observed and, thereby, determine the outcome (or interpretation) of a habitat selection–avoidance analysis. Thus, a measure was made of the relationship between the single-pixel and the 47-pixel samples. A harmonic moment estimator of home range, HM_PACK (Neft 1966, Dixon and Chapman 1980), and an average of 3 locations/day obtained on each bear throughout the study period were used to construct isoclines so that the largest density of a bear's locations was contained in the inner-most contour with successively smaller densities contained in outer contours. Grid resolution was set at 250 m, which was the variance of the most precise bear locations (Argos Class 3) in the accuracy test set. The program Hrange (R.V. Ringleb and E.J. Shubert, developed under contract) was used to summarize vegetation complexes within the 100% isocline (potential home range) and the 50% isocline (the intensive use area, or core home range) (Kaufmann 1962, Anderson 1982, Samuel et al. 1985, White and Garrott 1990).

Accuracy Assessment and Error Analysis

To quantify location error under field conditions, I placed 2 satellite transmitters at a specific location near Kotzebue just outside the study area. A mean error of location was calculated for this reference data set. Argos evaluated the accuracy of locations (Clark 1988, Service Argos 1988) and assigned each location to 1 of 4 classes. One standard deviation for Class 3 was 150 m; for Class 2, 350 m; and for Class 1, 1 km. Class 0 locations were unreliable (Service Argos 1988) and were not used in this study.

Spatial Registration of MSS Scene.—Using the image analysis computer program ERDAS (ERDAS, Inc. 1991), I further geo-referenced the bear study sub-scene of the Landsat vegetation map and Defense Mapping Agency elevational data to 20 recognizable geographical points on a 1:250,000-scale U.S. Geological Survey map.

Registration of Coordinate Systems.—To make the Argos bear locations compatible with the geo-referenced Landsat scene, I converted the Argos geographic locations from NAD (North American datum) 83 to NAD 27 using NADCON (Dewhurst 1990) and then to NAD 27 universal transverse mercator (UTM) coordinates using TELEBASE. The transformation resulted in a mean shift of bear locations 140 m to the northeast (69 m of latitude, -123 m of longitude). Argos required an assumed

transmitter elevation to derive locations. This vertical adjustment was applied to all locations, regardless of their actual elevation. The elevation adjustment used in this study was sea level.

Habitat Selection by Bears

In this study, I examined habitat use at various scales. Four methods are described.

Method 1.—The percent cover of vegetative complexes in the study area was computed and compared with the relative frequency of individual bear locations occurring within those complexes, and the percent cover and frequency of occurrence of bear food species in each vegetation complex was summarized and analyzed in relation to the percent of bear locations in each vegetation complex. Selection ratios (Manly et al. 1993:40) were calculated by dividing the percent bear locations in each vegetation complex by the percent of the study area within that complex. Food plants of bears were identified through direct observation of feeding bears, at digging sites, and by analysis of scats. Plants were classified as trace species when they occurred at <1% of cover in all plots within each complex (Appendix). Several plant species without direct evidence of use were included as “trace” in the list of food plants because these species were documented as bear foods in a study area approximately 60 km north of the current study area (Gebhard 1982, Hechtel 1985) or elsewhere (Sumner and Craighead 1973, Craighead et al. 1982, Pulliainen 1986).

Cottongrasses (*Eriophorum vaginatum*, and *E. angustifolium*) were recorded as preferred food plants because field observations indicated that bears preferentially grazed them. Grasses, most sedges, and *Equisetum* spp., however, were excluded from the preferred list. These ubiquitous species represented a large biomass of potentially available energy, but field observation indicated that they were consumed only concomitantly with preferred species. Two similar species of bearberry, *Arctostaphylos rubra* and *A. alpina*, were not always distinguished with certainty in the field and were treated together here.

Method 2.—The percent cover of vegetative complexes within each bear’s potential home range (100% isocline) and core home range (50% isocline) was compared with the relative frequencies of each bear’s locations. In this approach, vegetation complexes were combined, when necessary, to maintain a minimum of 1 expected location in each complex or combination of complexes.

Method 3.—The percent cover of vegetative complexes for the study area was compared with percent coverage in each bear’s core home range.

Method 4.—The percent of bear locations was examined in terms of the number of bear food plants in the physiognomic vegetation zones and also on the basis of elevation, slope, and aspect and by season of year—spring, summer, or autumn.

Habitat selection (preference or avoidance) was concluded to have occurred when the proportion of bear locations in a given vegetation complex, or the proportion of a home range consisting of a given vegetation complex, was substantially greater or less than expected, respectively, in comparison to the total availability of that complex throughout the study area. The expected frequency of use for each vegetation complex was calculated by multiplying the total number of satellite bear locations by the proportion of the total area occupied by that vegetation complex in the study area or home range (Williams and Marshall 1938, Hess and Rainwater 1939, Hess and Swartz 1940, McLellan 1986).

A chi-square (χ^2) test was used to test for the goodness-of-fit of used habitat to available habitat complexes (Allredge and Ratti 1986, White and Garrott 1990). The χ^2 contribution of each vegetation complex was used as a measure of dissimilarity between expected and observed use in situations where use significantly differed from availability.

Adapting the approach of Stoms et al. (1992), I organized results in tables with the measure of association summarized by 1 of 3 levels of selection–avoidance: positive, negative, or no selection. A positive association indicated that bears preferentially occupied that vegetation complex; a negative association showed avoidance. No selection occurred when the proportion of bear locations in a vegetation complex was close to the proportion of the study area (or home range) attributable to the complex.

RESULTS

Argos Locations

For the test set of 487 locations, mean error for Class 3 locations was 228 m (range = 0–1,032 m; $n = 164$); 685 m (range = 0–4,349 m; $n = 202$) for Class 2; 880 m (range = 44–8,915 m; $n = 121$) for Class 1; and 580 m for all locations ($n = 487$). Of the 1,624 bear locations, 66% were categorized by Argos as Class 3 accuracy, 29% as

Class 2, and 5% as Class 1. Mean distances between locations for the 6 bears were 6.7, 5.6, 2.2, 2.1, 2.8, and 2.3 km, and the mean intervals between their locations were 46.1, 14.5, 5.1, 6.5, 8.5, and 4.6 hours respectively. The average point-to-point minimum speed for all bears was 350 m/hour.

Habitat Selection by Bears

Analysis of Individual Locations Relative to Entire Study Area (Method 1).—The null hypothesis of no preference or avoidance of vegetation complexes was rejected for all 6 bears (χ^2 test: $0.05 < P < 0.10$ for bear 1, and $P < 0.001$ for bears 2–6). Use by over half of the bears was greater than expected for alpine tundra, alpine shrubland, and upland mixed spruce. Bare rock was avoided by all 6 bears, water by 5, and riparian mosaic, semi-vegetated area and riparian spruce were avoided by 4 (Table 1). Overall, patterns of habitat use varied considerably from bear to bear (Fig. 2).

Analysis of Plant Food Species Relative to Vegetation Complexes (Method 1).—All vegetation complexes included at least some of the 55 plant species identified as bear food plants (Tables 2 and 3, Appendix). Ten plant species identified as bear food plants and comprising >1% of cover were categorized as preferred bear food plants based on use and scat analysis; 13 were classified as non-preferred. Thirty-two occurred at <1% of cover in all plots within each complex and were classified as trace food plants. There was no correlation between the percent of bear locations in a vegetation

complex and the percent cover and number of preferred and non-preferred bear food plants. When trace species of bear food plants were included, however, there was a correlation between bear locations and the number of bear food plant species occurring in a given vegetation complex. Three vegetation complexes—alpine tundra, upland mixed spruce, and alpine shrubland—showed a higher percent of bear locations (use rate) than expected (Table 4) and ranked second and tied for fourth, respectively, in total number of bear food species (Table 3). Only 1 preferred bear food plant, *Vaccinium uliginosum*, and 2 non-preferred species, *Carex bigelowii* and *Equisetum arvense*, occurred in all 3 preferred vegetation complexes.

Analysis of Individual Locations Relative to Individual Home Ranges (Method 2).—Percent cover of vegetative complexes within each bear's core area and 100% potential home range differed from the proportions of each bear's locations in those complexes (core areas: $P < 0.001$ for all bears, except bears 2 and 3 for which $P < 0.005$; 100% potential home range, $P < 0.001$ for all bears; Table 5). Alpine tundra, upland mixed spruce, and alpine shrubland again were preferred by most bears. There was little difference in patterns of use when comparing core areas with the 100% potential home ranges, although the core area polygons were ¼ the size and encompassed 82% of all bear locations. When results of Method 1 were compared with those of Method 2, however, approximately half the vegetation complexes differed in their selection designations. This variation

Table 1. Use of vegetation complexes by 6 bears relative to the availability of the complexes in the study area in northwestern Alaska, 1986–88.

Vegetation complex	Bear ^a						Frequency ^a		
	1	2	3	4	5	6	+	=	-
Vegetated rock	-	+	=	-	=	=	1	3	2
Alpine tundra	=	+	+	-	+	+	4	1	1
Alpine shrubland	+	+	+	-	=	+	4	1	1
Shrub tundra	=	-	-	+	=	-	1	2	3
Upland mixed spruce	=	=	+	+	+	+	4	2	0
Tussock tundra	=	-	-	+	=	-	1	2	3
Bare rock	-	-	-	-	-	-	0	0	6
Upland white spruce	=	-	-	=	+	=	1	3	2
Riparian mosaic	=	-	-	=	-	-	0	2	4
Water	-	-	-	=	-	-	0	1	5
Semi-vegetated areas	=	-	-	+	-	-	1	1	4
Burns and others	=	-	-	-	-	-	0	1	5
Riparian spruce	=	-	-	=	-	-	0	2	4

^a Selected +, Avoided -, Expected =.

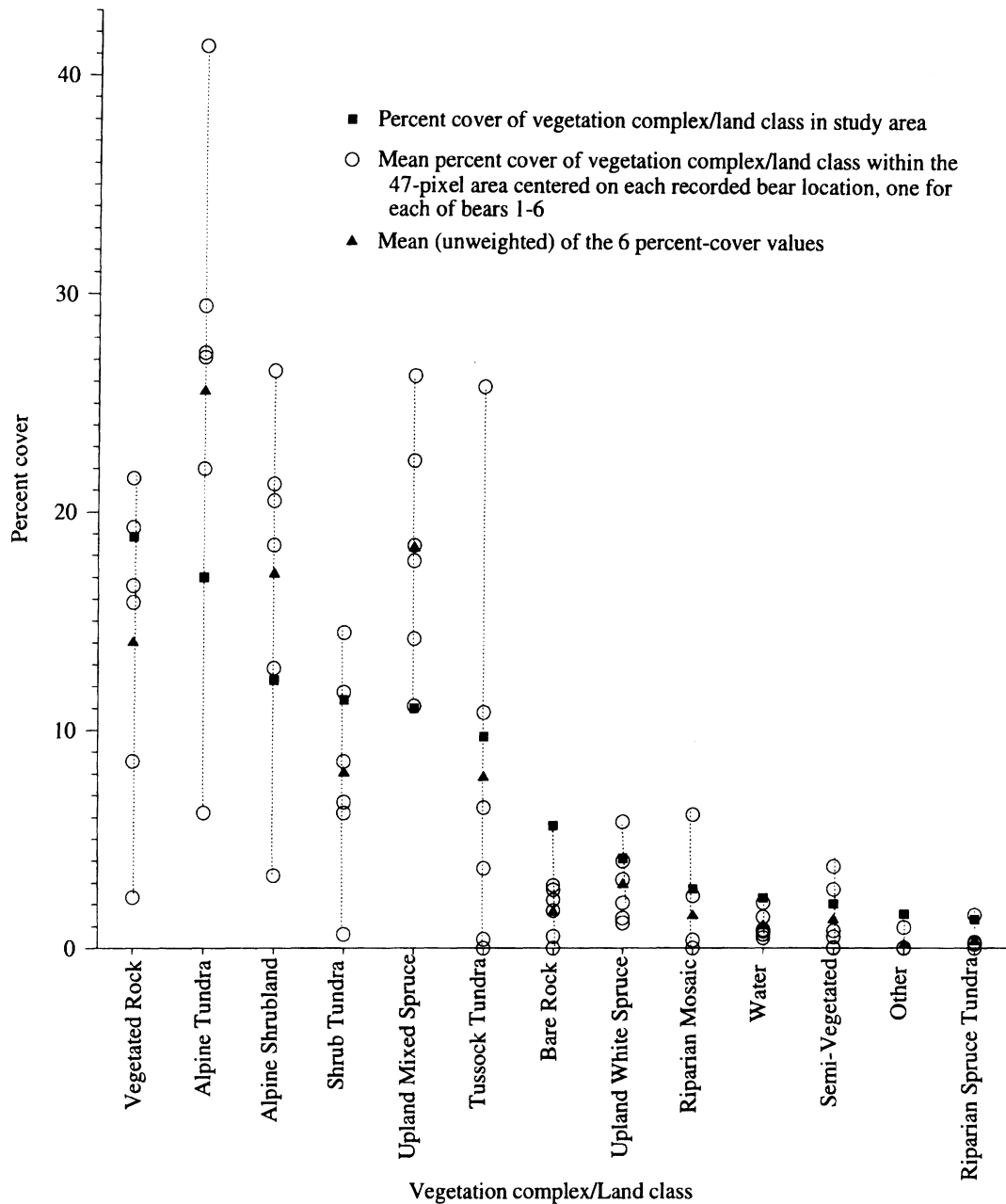


Fig. 2. Use (selection and avoidance) by 6 bears of available vegetation complexes in northwestern Alaska, 1986–88.

was due to the fact that bears selected home ranges with different vegetative composition from that of the study area as a whole.

Analysis of Core Home Ranges Relative to Study Area (Method 3).—Percent cover of vegetative complexes within the study area differed from their coverage in each bear’s core home range (Table 6). Although 4 of the 6 bears preferred upland mixed spruce, avoidance

or under-use was more obvious. All 6 bears avoided a grouping of burns, semi-vegetated rock, tall willow, and gravel bar types, 5 avoided bare rock, and 4 avoided tussock tundra, riparian mosaic, shrub tundra, and riparian spruce. Even more striking, though, were the differences between the bears in their selections. Each bear used a unique combination of vegetation complexes, and complexes preferred by some were avoided

Table 2. Percent cover of bear food plants (BFP) by vegetation complex of the study area in northwestern Alaska, 1986–88.

Bear food plants	Vegetation complex ^a											Mean % cover	No. of vegetation complexes
	AT	VR	AS	UWS	UMS	RS	TT	ST	TW	RM	S-V		
Non-preferred													
<i>Carex aquatilis</i>									2.0	8.4		0.2	2
<i>Carex bigelowii</i>	6.9		18.2		4.5		14.3	9.4		3.2		6.5	6
<i>Carex</i> other spp.	21.6	1.3	6.8	9.4	2.4	12.8	7.9	3.2		13.0	34.0	7.8	10
<i>Equisetum arvense</i>	10.1		2.6	32.1	6.5	14.1		7.9	39.6	6.7		5.4	8
<i>Equisetum fluviatile</i>									4.5	14.3		0.4	2
<i>Equisetum scirpoides</i>										3.0		0.1	1
<i>Equisetum variegatum</i>										2.5		0.1	1
<i>Equisetum</i> other spp.					4.7					1.9	1.2	0.6	3
Grasses	2.9		22.6	5.8	6.6	5.9		8.9	5.2	5.3	3.9	5.6	9
<i>Petasites frigidus</i>			1.7	5.2	1.9			3.4				1.0	4
Preferred													
<i>Arctostaphylos rubra/alpina</i>	1.3			3.1		4.6				2.2		0.5	4
<i>Empetrum nigrum</i>				9.0	7.4	3.4	2.3	2.3		1.3		1.8	6
<i>Eriophorum angustifolium</i>										1.6		0.0	1
<i>Eriophorum vaginatum</i>	3.0						43.4	11.8				6.1	3
<i>Hedysarum alpinum</i>						2.4						0.0	1
<i>Rubus arcticus</i>					1.0				5.5	1.8		0.2	3
<i>Rubus chamaemorus</i>			1.1	3.3	11.6		2.4	4.4				2.3	5
<i>Vaccinium uliginosum</i>	6.7		8.0	4.6	19.4	10.8	4.8	7.7		4.7		6.1	8
<i>Vaccinium vitis-idaea</i>				1.1	2.1	1.9	2.8	4.8		1.6		1.2	6
Percent BFP's by complex													
Preferred and non-preferred	52.5	1.3	61.0	73.6	68.1	55.9	77.9	63.8	56.8	71.5	39.1	45.9	
Preferred only	11.0	0.0	9.1	21.1	41.5	23.1	55.7	31.0	5.5	13.2	0.0	18.2	
No. of non-preferred species													
No. of non-preferred species	4	1	5	4	6	3	2	5	4	9	3		
No. of preferred species													
No. of preferred species	3	0	2	5	5	5	5	5	1	6	0		
Number of trace species													
Number of trace species	16	8	12	11	8	12	3	6	4	11	7		
Total species													
Total species	23	9	19	20	19	20	10	16	9	26	10		

^a AT = alpine tundra, VR = vegetated rock, AS = alpine shrubland, UWS = upland white spruce, UMS = upland mixed spruce, RS = riparian spruce, TT = tussuck tundra, ST = shrub tundra, TW = tall willow, RM = riparian mosaic, S-V = semi-vegetated.

by or of neutral value to others. The home ranges of the 2 male bears were 2–7 times larger than the female home ranges. Bear 5, a male, had 2 core areas approximately 10 km apart. Bears 1, 2, and 5 had 1 or more outlier locations within the 100% home range but isolated from the primary 100% isocline. All 6 home ranges in this study overlapped at least 1 other home range. Four home ranges shared a common area (Fig. 3), and the core areas within these shared the same common area (Fig. 4).

Analysis of Physiognomic Zones Relative to Bear Foods (Method 4).—The rock–tundra, shrub–forest, shrub–tussock, and mesic complex zones accounted for 42.7%, 37.5%, 14.9%, and 2.2% of the bear locations, respectively. The rock–tundra zone was neither selected nor avoided, the shrub–forest zone

was preferred, and the shrub–tussock and mesic complex zones were avoided. The plant composition of the rock–tundra, shrub–forest, shrub–tussock, and mesic complex zones included 7, 12, 10, and 16 species of preferred and non-preferred bear food plants, respectively (Table 7). Of all bear locations, 80% were in the rock–tundra and shrub–forest zones, yet these zones contained 32% fewer species of bear food plants.

The mean elevation of the study area was 287 m (range = 0–1, 174 m), and the mean slope was 7.5° (range = 0–51°). The median elevation for all bear locations was 305 m (range = 15–809 m), and the mean slope was 9° (range = 0–51°). No preference for any particular slope, aspect, or elevation was noted, regardless of season. Seasonal distribution of

Table 3. Frequency of occurrence of bear food plants (BFP) by vegetation complex of the study area in northwestern Alaska, 1986–88.

Bear food plants	Vegetation complex ^a											Mean freq.	No. of vegetation complexes	
	AT	VR	AS	UWS	UMS	RS	TT	ST	TW	RM	S-V			
Non-preferred														
<i>Carex aquatilis</i>									20.0	24.2		0.7	2	
<i>Carex bigelowii</i>	17.9		57.1		42.6		79.1	55.1		12.9		29.1	6	
<i>Carex</i> other spp.	82.1	66.7	26.5	64.5	21.3	68.5	31.3	14.3		41.1	93.8	43.4	10	
<i>Equisetum arvense</i>	44.6		10.2	100.0	31.3	66.7		21.4	82.9	34.7		20.8	8	
<i>Equisetum fluviatile</i>									14.3	33.9		0.9	2	
<i>Equisetum scirpoides</i>										8.9		0.2	1	
<i>Equisetum variegatum</i>										9.7		0.3	1	
<i>Equisetum</i> other spp.					24.6					8.1	31.1	3.6	3	
Grasses	55.4		85.7	61.3	63.9	77.8		52.0	54.3	54.0	25.0	38.5	9	
<i>Petasites frigidus</i>			32.7	48.4	52.5			39.8				16.4	4	
Preferred														
<i>Arctostaphylos rubra/alpina</i>	32.1			54.8		75.9				20.2		9.3	4	
<i>Empetrum nigrum</i>				77.4	77.0	53.7	64.2	24.5		18.6		21.9	6	
<i>Eriophorum angustifolium</i>										9.7		0.3	1	
<i>Eriophorum vaginatum</i>	16.1						94.0	55.1				18.2	3	
<i>Hedysarum alpinum</i>						29.6						0.4	1	
<i>Rubus arcticus</i>					23.0				37.1	26.6		3.3	3	
<i>Rubus chamaemorus</i>			22.4	29.0	67.2		61.2	51.0				23.1	5	
<i>Vaccinium uliginosum</i>	64.3		51.0	64.5	83.6	83.3	98.5	79.6		31.5		49.7	8	
<i>Vaccinium vitis-idaea</i>				32.3	54.1	31.5	61.2	65.3		19.4		21.7	6	
No. of non-preferred species	4	1	5	4	6	3	2	5	4	9	3			
No. of preferred species	3	0	2	5	5	5	5	5	1	6	0			
Number of trace species	16	8	12	11	8	12	3	6	4	11	7			
Total species	23	9	19	20	19	20	10	16	9	26	10			

^a AT = alpine tundra, VR = vegetated rock, AS = alpine shrubland, UWS = upland white spruce, UMS = upland mixed spruce, RS = riparian spruce, TT = tussuck tundra, ST = shrub tundra, TW = tall willow, RM = riparian mosaic, S-V = semi-vegetated.

bear locations did not vary, indicating that food resources were uniformly abundant.

DISCUSSION

The Technique

This study was designed to quantify bear locations within vegetation complexes. The inference of selection-avoidance was made from the juxtaposition of bear and habitat. No effort was made to measure or quantify bear activities such as feeding bouts. There was much variability in the remote measurements, precluding alignment of an Argos-generated bear location precisely with the correct Landsat pixel; however, the averaging of a large set of vegetation pixels about bear locations reliably estimated the true measure of bear use.

The vegetation was classified into vegetation complexes to facilitate discussion and analysis, but it is, in fact, a

continuum. From the plant species database, vegetation can be classified to plant associations, plant communities, vegetation complexes, forest types, and with the aid of remote imagery, eco-spectral classes. Information is lost at each successive clumping, but the database can be consulted at any time and the original detail regained.

In a strict sense, the current technique only quantifies bear use of vegetation complexes, not preference for or avoidance of them. Because a bear can be in only 1 place at a given time, this method measures use of a specific vegetation complex to the exclusion of all others. To properly express preference, the bear must have equal access to all vegetation complexes at any moment of observation, a physical impossibility in this field study. It is reasonable to hypothesize, however, that a bear carries a long-term awareness or memory of the resources available in its environment, and hence, that it will with some consistency, select for or against locales. I used the terms selection and avoidance in that context. The

Table 4. Relative abundance of bear food plants by vegetation complex and their use by 6 bears in northwestern Alaska, 1986–88.

Vegetation complex	Study area		Bear food plants				% of bear locations in vegetation complex (n = 1,624)	% use rate ^a
			Preferred and non-preferred		Preferred			
	ha	%	% cover	No. of species or groups	% cover	No. of species or groups		
Vegetated rock	95,021	18.8	1.3	1	0.0	0	16.7	88.6
Alpine tundra	85,715	17.0	52.5	7	11.0	3	26.0	152.9
Alpine shrubland	62,009	12.3	61.0	7	9.1	2	16.5	134.2
Shrub tundra	57,498	11.4	63.8	10	31.0	5	7.9	69.3
Upland mixed spruce	55,633	11.0	68.1	11	41.5	5	18.3	165.8
Tussock tundra	49,100	9.7	77.9	7	55.7	5	7.0	71.9
Upland white spruce	20,805	4.1	73.6	9	21.1	5	2.7	65.4
Riparian mosaic	13,775	2.7	71.5	15	13.2	6	0.9	32.9
Semi-vegetated	10,216	2.0	39.1	3	0.0	0	1.2	59.2
Riparian spruce	6,575	1.3	55.9	8	23.1	5	0.1	7.7
Tall willow	554	0.1	56.8	5	5.5	1	0.0	0.0
Other	47,261	9.4	—	—	—	—	2.7	28.7
Total	504,160	100.0					100.0	

^a % use rate = (% of bear locations in complex) ÷ (% of study area in complex) × 100. If bear locations occur at random locations, the expected value of each of these is 100% (1 pixel/location).

Table 5. Use of vegetation complexes by 6 bears relative to the availability of vegetation complexes within each bear's core and potential home range in northwestern Alaska, 1986–88.

Vegetation complex	Core home range ^a						Potential home range ^a																	
	Bear						Frequency						Bear						Frequency					
	1	2	3	4	5	6	+	=	-	1	2	3	4	5	6	+	=	-						
Vegetated rock	=	=	-	+	-	=	1	3	2	=	=	-	+	=	=	1	4	1						
Alpine tundra	+	+	+	+	+	-	5	0	1	+	+	+	=	+	-	4	1	1						
Alpine shrubland	+	+	=	+	=	+	4	2	0	+	+	=	+	+	=	4	2	0						
Shrub tundra	-	-	-	-	+	+	2	0	4	-	-	-	=	=	=	0	3	3						
Upland mixed spruce	=	-	+	+	+	+	4	1	1	=	-	+	+	+	+	4	1	1						
Tussock tundra	-	-	=	-	+	+	2	1	3	-	-	=	-	-	+	1	1	4						
Upland white spruce	=	-	-	=	+	-	1	2	3	=	-	-	=	+	=	1	3	2						
Riparian complexes	=	-	=	-	-	-	0	2	4	=	=	=	-	-	-	0	3	3						
Land classes	=	-	=	=	-	-	0	3	3	=	-	=	=	-	-	0	3	3						

^a Selected +, Avoided -, Expected =.

manifestation of selection, however, does not automatically imply that the selected vegetation complex is critical or even important to the fitness or long-term survival of the bear.

A basic assumption when evaluating habitat selection in terms of individual bear locations is that bears have the opportunity to choose freely from the entire study area. There are several reasons why this assumption was war-

ranted in this study. The study area was minimized to encompass the 6 bear home ranges so that, if a bear chose, it could have traversed the study area in a short time. There were no major physical barriers within the study area to impede travel. The substantial overlap of 5 of the 6 home ranges indicates that the bears did not exclude one another from parts of the study area (Figs. 3, 4). In fact, grizzly bears are social, gregarious animals, forming so-

Table 6. Availability of vegetation complexes in each bear's core home range relative to availability of vegetation complexes in the study area in northwestern Alaska, 1986–88.

Vegetation complex	Bear ^a						Frequency ^a		
	1	2	3	4	5	6	+	=	-
Vegetated rock	-	=	+	-	+	=	2	2	2
Alpine tundra	-	+	+	-	=	+	3	1	2
Alpine shrubland	=	+	+	-	=	=	2	3	1
Shrub tundra	+	-	-	+	-	-	2	0	4
Upland mixed spruce	-	+	+	+	=	+	4	1	1
Tussock tundra	+	-	-	+	-	-	2	0	4
Bare rock	-	-	-	-	+	-	1	0	5
Upland white spruce	-	-	-	+	-	=	1	1	4
Riparian mosaic	+	-	-	-	-	-	2	0	4
Water	+	-	-	-	=	=	1	2	3
Semi-vegetated areas	-	-	-	+	=	=	1	2	3
Burns and others	-	-	-	-	-	-	0	0	6
Riparian spruce	=	-	-	=	-	-	0	2	4

^a Selected +, Avoided -, Expected =.

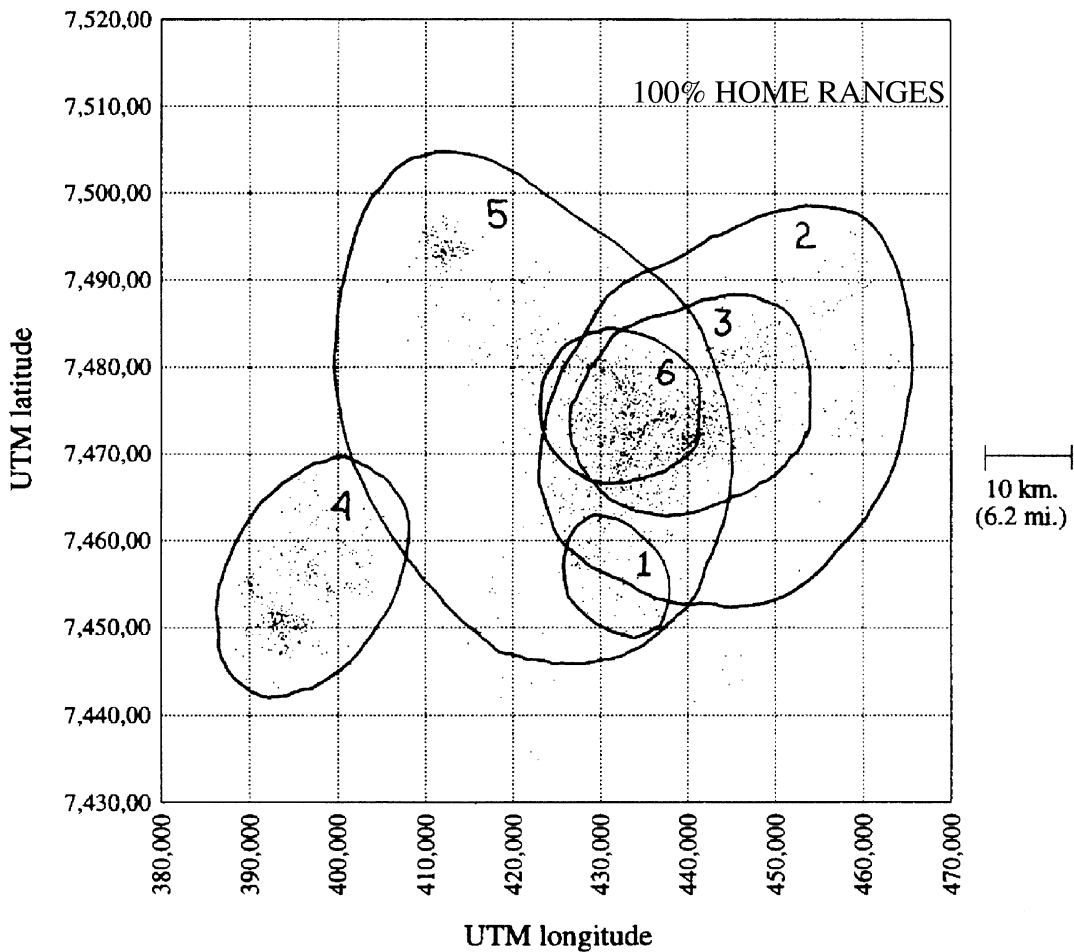


Fig. 3. Locations and estimated home ranges of 6 grizzly bears in northwestern Alaska, 1986–88. (Sizes of estimated home ranges: 44 km² for bear 1; 944 km² for bear 2; 396 km² for bear 3; 320 km² for bear 4; 1,410 km² for bear 5; 202 km² for bear 6.)

cial hierarchies when drawn together by a food source (Craighead and Mitchell 1982, Craighead et al. 1995).

An animal's use of available habitat may be the outcome of choices at different levels of the landscape, and different patterns of habitat selection may occur at each level (Nicholas and Robertson 1993). This study area exhibited a wide range of spatial heterogeneity-homogeneity among the vegetation complexes, and these varied considerably in their pattern of occurrence (regular, clumped, random), suggesting that the appropriate or optimum sampling area could be different for each vegetation complex. Meentemeyer (1989) reviews problems and questionable inferences that can result from sampling at different scales. Because the 250-m radius (47 pixel) sample closely approximated the error of location for Class 3 locations, I initially thought that this was the appropriate sample size to analyze individual bear locations. An

examination of a scatter plot (Fig. 5) comparing a single-pixel sample with a 47-pixel sample size indicated, however, that both techniques yielded similarly proportioned samples.

The Field Study

Selection-avoidance by bears was found in all 4 methods of analysis. Bears selected for 3 vegetation complexes within the study area and for the same 3 vegetation complexes within their home ranges. In selecting their core home ranges, bears preferred 1 of 4 physiognomic vegetation zones. Although individual bears selected strongly for specific habitat types, the population as a whole was not vegetation-specific in its habitat use and all vegetation complexes were used to some degree.

Percent cover and frequency of occurrence of bear food plants only partially explain a bear's selection of a home

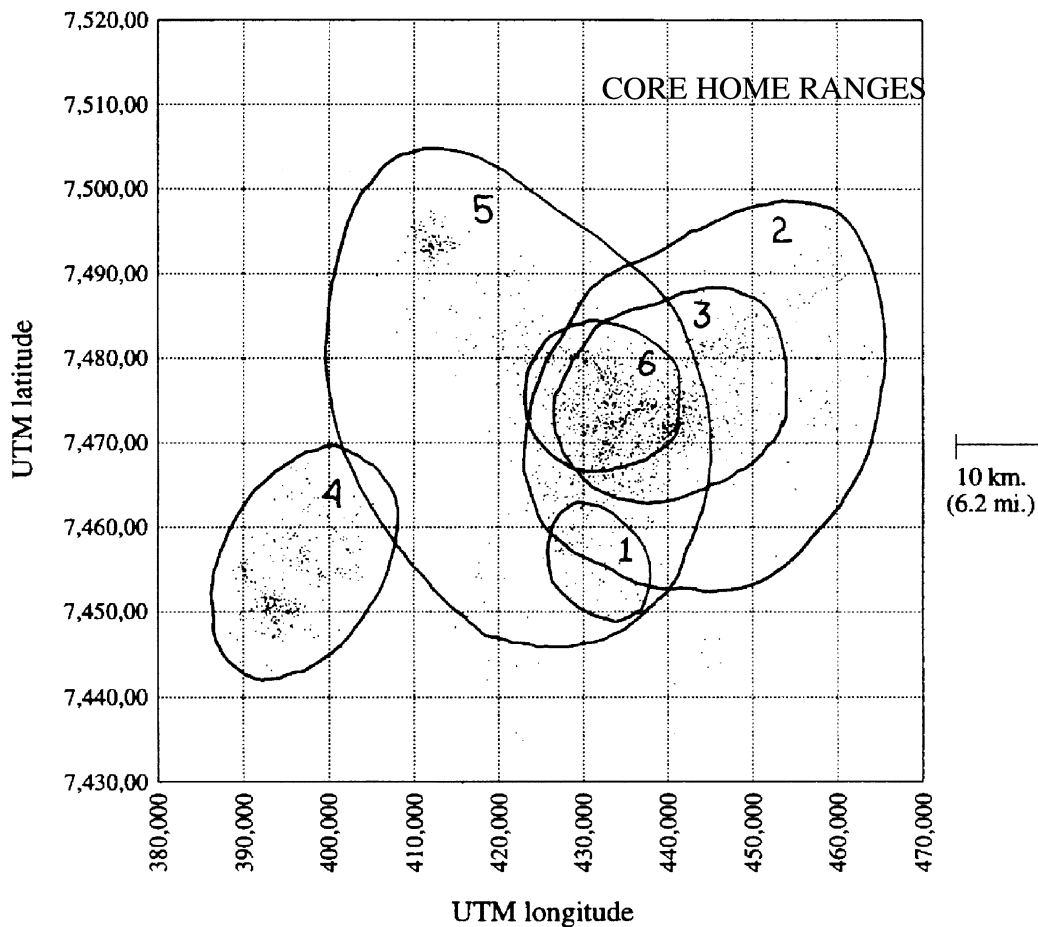


Fig. 4. Locations and estimated home range core areas of 6 grizzly bears in northwestern Alaska, 1986-88. (Sizes of estimated home range core areas: 16 km² for bear 1; 251 km² for bear 2; 58 km² for bear 3; 72 km² for bear 4; 328 km² for bear 5; 45 km² for bear 6.)

Table 7. Bear locations and food plants by physiognomic vegetation zones for study area in northwestern Alaska, 1986–88.

Zone	% of study area	% of bear locations	Number of species		
			Preferred	Non-preferred	Trace
Rock–tundra	41.5	42.7	3	4	20
Shrub–forest	27.5	37.5	6	6	18
Shrub–tussock	21.1	14.9	5	5	6
Mesic complex	6.2	2.2	7	9	20
Other	3.7	2.7	0	0	0

range and its use of the habitat within the range. Since grizzly bears are omnivorous, some of their feeding efforts should be directed at specific prey. Although the use of vegetation nomenclature is a convenient way of classifying bear habitat use, both plant and animal components are involved. However, “the grizzly is not a highly efficient predator and must utilize a wide range of plant foods . . . [and] is directly dependent on the plant base Therefore, an evaluation of the plant resource provides a reliable method for assessing the basic ecological value of the habitat” (Craighead et al. 1982:43). Temporal and spatial variations in food plant availability and abundance may influence what grizzly bears eat. The important plant variables are abundance, distribution,

phenology, and potential energy content. For example, grizzly bears in northwest Alaska are known to forage on *Boykinia richardsonii*. Hechtel (1985) ranked it as an important plant for the summer season based on scat analyses, site analyses, and field observations. In the current study, however, this species was found only in the alpine tundra, alpine shrubland, and upland mixed spruce complexes; in these, it measured <0.5% cover and was recorded only as a trace bear food plant. Thus, because of its limited abundance and distribution, *Boykinia richardsonii* was a limited resource, despite its value as an important food plant.

What environmental and behavioral variables dispose a bear to use a particular habitat and to inhabit a particular environment remains an unanswered question. Knowledge of the extent to which a bear samples its environment and decides the best place to be is limited. Although we can measure the use of a particular area by a bear and the area’s biotic potential, we have no measure of the spatio-temporal availability of the environment in relation to the bear nor, finally, of the specific environmental needs to ensure fitness of the bear. The results of this study indicate that these individual bears could find and use quite different combinations of needed resources within their environment. The grizzly bear is omnivorous, opportunistic, mobile, and a generalist. Furthermore, bears have a long parental attachment, during which time the off-

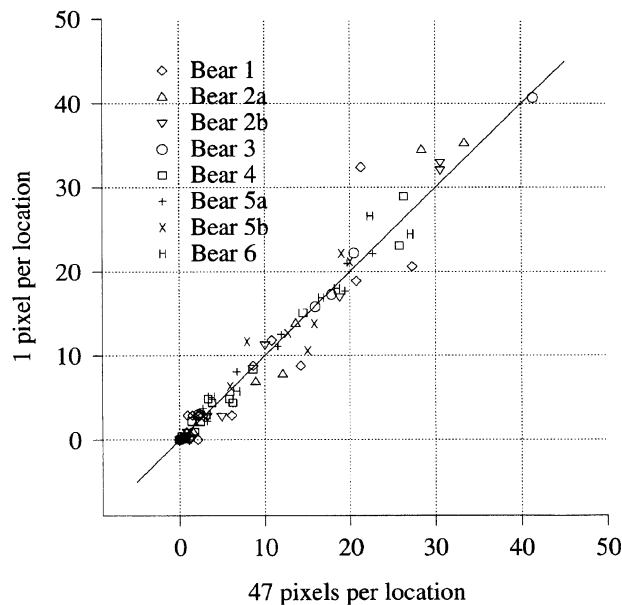


Fig. 5. Comparison of percent covers of each vegetation complex–land class using one pixel of habitat/recorded bear location (y) versus using 47 pixels of habitat/recorded bear location (x), northwestern Alaska, 1986–88. Symbols distinguish each of 8 bear-years.

spring learn foraging techniques and locations. Such filial learning could explain the strong habitat selection exhibited by individuals, who would continue to use the preferred sites until they were no longer productive, then search out alternative foraging areas. This strategy would depend on large, diverse areas of intact wilderness to ensure the bears' continued survival. Protection of specific enclaves of habitat selected on the basis of critical habitat criteria and classifying it into management situation categories (U.S. Fish and Wildl. Serv. 1993) is an approach that, in this study, might have helped a few individual bears over the short-term, but might not have provided the variety of resources and space necessary for population viability over the long-term.

When extrapolating habitat use by bears into larger but similar biogeographical areas, the notion of availability becomes of increasing concern. I believe analyses of larger areas are of interest, however, and are justified by field observations. Reynolds (1989), working north of this study, radiotracked a young female bear that traveled 100 km south and denned just north of this study area before returning to her maternal home range. She repeated this trip annually for 6 years, and presumably 1 of her offspring made the same peregrination (H.V. Reynolds, Alas. Fish and Game Dep., Fairbanks; pers. commun., 1995). In the same study, a marked adult male left its normal home range and traveled 280 km north before being shot. In a study of grizzly bears of Yellowstone, "some annual ranges approaching 1,000 km² and total home ranges in excess of 3,500 km²" were reported (Blanchard and Knight 1991:64). These movements suggest that the area available to some individual bears may be large enough to justify a broader analysis of habitat use. Although these movements may be the exception, they do suggest that the area available to some individual bears may be extremely large, which begs the question, what is an appropriate area of availability for analysis of habitat use? The great range of environs that grizzly bears inhabit throughout North America indicates that its environmental limits are broad and that it is proficient at locating and using essential components of a large and diverse wilderness landscape.

CONCLUSIONS

This research was a feasibility study. Its objective was to develop and field test a technique for integrating digitized location data from Argos with digital vegetation data from the Landsat MSS. This objective was met, allowing for a synoptic examination of bears' use of their habitat. Accuracy and precision of the Argos-generated bear

locations was poor in relation to the resolution of the Landsat vegetation map. With improved hardware and software, remote sensing measurements will improve, decreasing the variance about the measurements. Currently, global positioning systems (GPS) with approximate location error of 100 meters are being marketed for use in wildlife management and research. Within 10 years, location error will likely be in meters. The addition of a GPS system will greatly increase the types of situations in which habitat selection can be monitored remotely.

The application of satellite remote-sensing devices and computers allows an investigator to record animal locations in numbers impractical for most ground-based techniques. Data can be gathered day or night, during any season, anywhere in the world (Craighead and Craighead 1987).

Patterns of habitat use by the grizzly bears in this study were very broad, and the area used was expansive. Bears used a diversity of vegetation types, and this diversity may be necessary to ensure long-term survival of the species.

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APPENDIX

Bear food plants of study area in Northwestern Alaska, 1986–88.

Bear food plant species^a

<i>Allium schoenoprasum</i> (t)	<i>Linnaea borealis</i> (t)
<i>Arctagrostis latifolia</i> (n)	<i>Oxycoccus microcarpus</i> (t)
<i>Arctostaphylos alpina</i> (p)	<i>Oxyria digyna</i> (t)
<i>Arctostaphylos rubra</i> (p)	<i>Oxytropis campestris</i> (t)
<i>Astragalus umbellatus</i> (t)	<i>Oxytropis maydelliana</i> (t)
<i>Boschniakia rossica</i> (t)	<i>Oxytropis mertensiana</i> (t)
<i>Boykinia richardsonii</i> (t)	<i>Oxytropis nigrescens</i> (t)
<i>Calamagrostis canadensis</i> (n)	<i>Oxytropis viscida</i> (t)
<i>Carex aquatilis</i> (n)	<i>Pedicularis capitata</i> (t)
<i>Carex bigelowii</i> (n)	<i>Pedicularis groenlandica</i> (t)
<i>Carex saxatilis</i> (t)	<i>Petasites frigidus</i> (n)
<i>Carex scirpoidea</i> (t)	<i>Petasites hyperboreus</i> (t)
<i>Carex vaginata</i> (t)	<i>Poa alpigena</i> (n)
<i>Claytonia acutifolia</i> (t)	<i>Polemonium acutiflorum</i> (t)
<i>Claytonia sarmentosa</i> (t)	<i>Polygonum alaskanum</i> (t)
<i>Empetrum nigrum</i> (p)	<i>Polygonum bistorta</i> (t)
<i>Epilobium angustifolium</i> (t)	<i>Polygonum viviparum</i> (t)
<i>Equisetum arvense</i> (n)	<i>Ribes triste</i> (t)
<i>Equisetum fluviatile</i> (n)	<i>Rubus arcticus</i> (p)
<i>Equisetum pratense</i> (n)	<i>Rubus chamaemorus</i> (p)
<i>Equisetum scirpoides</i> (n)	<i>Rumex acetosa</i> (t)
<i>Equisetum silvaticum</i> (n)	<i>Rumex arcticus</i> (t)
<i>Equisetum variegatum</i> (n)	<i>Shepherdia canadensis</i> (t)
<i>Eriophorum angustifolium</i> (p)	<i>Taraxacum phymatocarpum</i> (t)
<i>Eriophorum vaginatum</i> (p)	<i>Trisetum spicatum</i> (n)
<i>Hedysarum alpinum</i> (p)	<i>Vaccinium uliginosum</i> (p)
<i>Hedysarum mackenzii</i> (t)	<i>Vaccinium vitis-idaea</i> (p)
<i>Heracleum lanatum</i> (t)	

^a p = preferred bear food plant, n = non-preferred bear food plant, t = trace species