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HABITATS SELECTED BY GRIZZLY BEARS IN A MULTIPLE USE LANDSCAPE

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Abstract: The effects of sex, ageclass, and season on habitats and elevations selected by 56 radiocollared grizzly between 1979 and 1995 in the Flathead River drainage of southeastern British Columbia and the adjacent portion of Montana were evaluated using compositional analyses. Two habitat selection strategies were apparent in the population: mountain resident bears selected avalanche chutes at higher elevations during spring, while elevational migrating bears moved to low elevations and selected riparian habitats. During summer, both groups of bears showed selection for areas that had been burned by wildfire 50–70 yr previously. In autumn, riparian was the highest ranked habitat followed by forest and open forest. Regenerating cut-blocks and rock outcrops consistently ranked lowest. Results of this southern grizzly bear study differ from others in that bears were free to select habitats in both mountains and the wide valley and they showed strong selection for some low elevation habitats.

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Key words: British Columbia, forestry, grizzly bears, habitat selection, Montana, *Ursus arctos*.

Humans have had a tremendous effect on the distribution and abundance of grizzly bears in southern Canada and the United States. Within a century, the southern and eastern distribution of these bears contracted to rugged mountains and high plateaus where few people settled (McLellan 1998). Today, maintaining grizzly bears in southern areas is a major conservation challenge (Servheen 1990, Banci et al. 1994).

The remaining grizzly bears in Alberta and the lower 48 states of the United States are largely confined to parks and designated wilderness areas plus adjacent multiple-use lands of the interior mountain ranges. In contrast, only about 10% of the grizzly bears in British Columbia are confined to protected areas; the vast majority live on multiple-use lands (McCrory et. al. 1990, Herrero 1994). Yet, because most grizzly bears in the interior mountains live in British Columbia and it is through this province that bears in the United States and Alberta are connected to larger populations in the North, conservation efforts on British Columbia multiple-use lands are critical to all southern grizzly bears.

In an attempt to address conservation issues including the maintenance of grizzly bear populations, British Columbia has developed a grizzly bear conservation strategy, a series of land-use planning processes, and the Forest Practic-

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es Code Act (McLellan 1998). These initiatives are in an early, developmental stage and information on habitat preferences of grizzly bears in multiple-use landscapes is in demand.

The population of grizzly bears in the Flathead River drainage of southeastern British Columbia and adjacent Montana has been studied since 1979. This area provided a unique opportunity to investigate the ecology of southern grizzly bears where they were not restricted to mountainous terrain by severe habitat alteration and excessive mortality at lower elevations. The freedom for bears to select habitats in both mountains and the wide valley is unlike other study areas that had a history of disproportionate habitat change and bear removal from lower elevations due to agriculture, settlement, hydroelectric reservoirs, and timber harvesting (Servheen 1983, Zager et al. 1983, Wielgus and Bunnell 1994, Waller and Mace 1997).

Our primary objective was to rank habitats by their relative preference by grizzly bears to provide information needed by managers developing land-use plans and forest management guidelines. A secondary objective was to evaluate effects of sex, ageclass, and season on habitat selection of grizzly bears in a multiple-use landscape. The effects of sex and ageclass were chosen because other studies have reported different habitat selection patterns among these groups (Pearson 1975; Mattson et al. 1987; Wielgus and Bunnell 1994, 1995). The effect of season was selected because we suspected that changes in the diet of grizzly bears over the year (Mattson et al. 1991, McLellan and Hovey 1995) would strongly influence habitat selection.

STUDY AREA

The study was conducted in a 2000-km^2 area centered along the North Fork of the Flathead River drainage (NF Flathead) in southeastern British Columbia, Canada, and the adjacent portion of Montana, United States (49° N, 114° 30′ W). The river flows southward through the 4–10-km-wide valley at elevations from 1,550 to 1,025 m, crossing the Canada–United States border at 1,200 m. Surrounding topography consists of floodplains and rolling hills bordered by sub-ranges of the Rocky Mountains that rise to >2,900 m. The area's climate is characterized by short, cool summers and long, cold winters with heavy snowfall.

During the first half of the last century, most of the study area was burned by wildfires. More recently, bark beetle infestations (*Dendroctonus ponderosae* and *D. obsesus*) killed many trees that have since been harvested using clear-cutting. Although half of the cut-blocks were <22 ha in area, salvage logging resulted in most of the total harvested area to be in cut-blocks >1,000 ha. Lower elevations in the study area were in the Montane Spruce biogeoclimatic zone (Hope et al. 1991) and consisted of a mosaic of nonmerchantable lodgepole pine (*Pinus contorta*), immature larch (*Larix occidentalis*), and spruce (*Picea engelmannii* × *glauca*); low gradient riparian areas; marshes and dry meadows; and regenerating cut-blocks and roads. Forests in mountainous areas were in the Engelmann Spruce—Subalpine Fir zone (Coupé et al. 1991) and contained mixtures of spruce, subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and subalpine larch (*L. lyallii*). Early successional burns, avalanche paths, alpine meadows, regenerating cut-blocks, roads, and rock outcrops were also common in the mountains.

The British Columbia portion of the study area is one of the largest unsettled drainages in southern Canada. There, a limited number of grizzly bear hunting permits was issued using a lottery system for residents and a quota for outfitters for use by their nonresident clients. The United States portion contained national forest lands, private land with about 100 permanent and seasonal residents, and the relatively remote northwest corner of Glacier National Park.

METHODS

Bears were captured in foot snares or culvert traps. Because of more prevalent snow and a less connected road network in the mountains, trapping was more efficient in the valley. To reduce the potential of capturing a disproportionate number of grizzly bears in the valley, an effort was made to capture most, if not all resident grizzly bears in the study area (McLellan 1989*a*). Once captured, bears were immobilized to allow handling and then ear-tagged and tattooed for permanent identification. To determine the age of grizzly bears older than 1 year, a premolar was removed and sectioned (Stoneberg and Jonkel 1966). Grizzly bears were classified as cubs (0–1 yr), yearlings (1–2 yr), subadults (2–5 yr), and adults (≥6 yr) and then fitted with radiocollars designed to drop off within

Table 1. Characteristics and description of the habitat units in the Flathead River study area.

Habitat unit	Percentage of area	Polygon size (ha)[a]		Elevation (m)[a]		Slope (%)[a]		Road density (km/km^2)[a,b]		
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
Forest	32.7	216	726	1,513	239	27.7	20.0	0.48	0.79	Forest with >30% canopy cover and trees >10 m tall.
Open forest	16.4	64	205	1,747	280	39.8	23.7	0.23	0.54	Forest with 5–30% canopy cover and trees primarily >10 m tall.
Open forest burn	5.2	41	89	1,807	214	44.7	19.6	0.13	0.42	Conifers <10 m in height and 5–30% canopy cover due to early succession after a wildfire.
Open burn	7.4	116	231	1,878	187	49.9	19.2	0.07	0.19	Conifers <10 m in height and <5% canopy cover due to early succession after a wildfire.
Regenerating cut-block	13.2	160	500	1,497	198	22.9	14.6	1.36	1.19	Less than 40-yr-old planted or naturally regenerating conifers after timber harvest.
Riparian	4.2	72	310	1,310	129	8.6	10.7	0.68	0.85	Unlogged ecosystems adjacent to streams, lakes, or wetlands that are influenced by high and persistent moisture content.
Rock-talus	17.3	158	542	2,061	253	65.8	30.9	0.08	0.34	Scree, talus, or bedrock with plant communities intermixed.
Avalanche chute	3.5	18	22	1,619	234	48.8	24.1	0.18	0.39	Steep, open areas where periodic avalanches limit vegetation to forbs, graminoids, shrubs and narrow groups of trees.

[a] Canadian portion of study area only.
[b] Road Density estimated using 1 km^2 moving circular window.

3–5 years for adult females and 1–2 years for younger females and all males.

Each year during grizzly bears' active seasons (Apr–Nov), the location of all radiocollared individuals was determined from fixed-wing aircraft at about 1-week intervals. For each location, the habitat unit being used was recorded visually from the aircraft and the elevation was recorded from a topographic map. Accuracy of locations from aircraft was estimated to be <7 ha, which is similar to the accuracy determined by Waller and Mace (1997), but less accurate than estimated by Wielgus and Bunnell (1994). The study area's high road density (≈44 km/100 km^2) provided widespread access that enabled most bears to be located from the ground every 1–10 days. Locations from the ground were usually obtained by recording a compass bearing from ≥3 positions. Only locations with error polygons of <15 ha were used. All telemetry locations of individuals were obtained on separate days.

To permit comparisons among studies and facilitate communication with managers, we partitioned the study area into 8 habitat units (Table 1) similar to those described by Servheen (1983), Zager et al. (1983), Waller and Mace (1997). These units were distinct enough to be identified from aircraft or color aerial photographs, yet of sufficient size to encompass most telemetry location errors (90% of the study area in was composed of habitat polygons >29 ha). In Canada, habitat units were delineated on 1: 20,000 digital map sheets of forest inventory planning files (Resources Inventory Branch 1995) using the forest inventory and 1:15,000 color aerial photographs. Availability was defined as the proportion of the 95% adaptive kernal (Program Home Ranger, F. W. Hovey) composite range of all radiocollared bears that was in each habitat or elevation category. Elevation was divided into 5 categories of equal availability determined with a GIS (PAMAP GIS, 5.2, Victoria, British Columbia, Canada). Habitat units were censused in the Canadian portion of the study area using a GIS but, because habitat maps were not available in the United States, habitat coverage there was estimated using random-point locations (Marcum and Loftsgaarden 1980). Season dates were based on changes in grizzly bear diet (McLellan and Hovey 1995); spring was from den emergence to 31 July, summer was 1 August to 20 September, and autumn was 21 September to when the grizzly bears began hibernating.

We used compositional analysis (Aitchison 1986) with MANOVA (Aebischer et al. 1993) to test our hypotheses. The MANOVA model treated sex, ageclass, and season as factors. Because aerial and ground telemetry may produce different results (McLellan and Shackleton 1988), we performed a preliminary analysis using a MANOVA model that also included the method of telemetry (aerial vs. ground) as a factor. Individual variation in the number of telemetry locations was accounted for by weighting the log-ratio differences by the squareroot of the total number of times each bear was located. Habitats were ranked by relative use using paired *t*-tests (Aebischer et al. 1993). Data from bears with <10 locations within a sex-age-season category were excluded from that category. Possible violations in multivariate normality were avoided by replacing standard tests with those based on data randomization (Manly 1991). For each MANOVA term and *t*-test, levels of probabilities were determined from 999 random permutations of the data. The significance of *t*-tests was determined with the experimentwise error rate adjusted for the number of comparisons using Bonferoni criteria. The level of rejection of a null hypothesis was set at 0.05.

RESULTS

From 1979 to 1995, we recorded 6,227 telemetry locations on 63 grizzly bears that met our accuracy criteria. Each of these bears had ≥15 telemetry locations. When grouped into ageclass-sex-season categories with sample sizes on individuals restricted to ≥10 locations/category, 5,502 locations were obtained from 56 grizzly bears (26 F and 30 M). Seven females and 3 males were monitored as both adults and subadults. Our preliminary analysis indicated that the method of telemetry (i.e., aerial or ground) was not a significant factor ($F_{7,140} = 1.42$, $P = 0.197$) as a main effect or in interactions ($0.131 < P < 0.924$) with other factors; therefore, we pooled telemetry data and repeated the analysis using a reduced model that excluded this term.

When bears were not hibernating, forest had the highest mean proportion of telemetry locations; however, it also was the most common habitat (Table 1). Grizzly bears used other habitats disproportionately more than the area they represented. Riparian and avalanche chutes, for example, composed only 4.2% and 3.5% of the study area respectively, but had relatively high mean use (24.2% and 7.0%, respectively).

Compositional analysis of these proportions using sex, ageclass, and season as factors showed that grizzly bears used habitats differentially, but season was the only factor we investigated that had a significant effect ($F_{7,232} = 8.541$, $P < 0.001$); sex, ageclass, and interactions were not significant ($0.077 < P < 0.897$). Paired *t*-tests performed within season groupings indicated that riparian habitats were selected over other habitats during spring (Table 2); 30 of 55 bears were located more frequently in riparian than in any other habitat (Fig. 1). Only 7 bears had <10% of their locations in riparian and 5 of these were found in avalanche chutes more frequently than any other habitat.

During summer, grizzly bears selected open-forest burns and open burns over other habitats (Table 2); 21 of the 32 grizzly bears were found most often in these habitats (Fig. 1). During autumn, riparian was selected over other habi-

Table 2. Seasonal habitat ranks determined by pairwise *t*-tests for grizzly bears from the Flathead River drainage of British Columbia and Montana, 1979–95. The habitats were F = forest, OF = open forest, OFB = open forest burn, OB = burn, RC = regenerating cut-block, RN = riparian, RK = rock-talus, and AC = avalanche chute.

Season	Habitat ranks
Spring	RN AC F OF OFB RC OB RK
Summer	OFB OB RN OF AC F RK RC
Autumn	RN F OF OFB AC OB RK RC

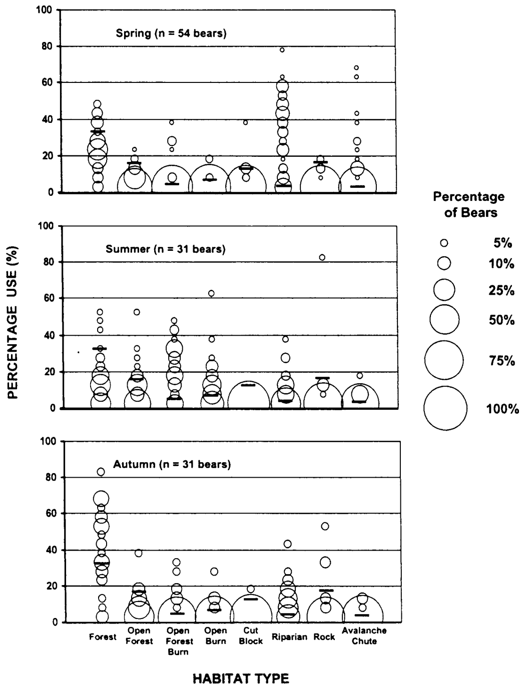

Fig 1. Bubble chart showing individual variation of habitat use during each season by grizzly bears with >10 locations/season in the Flathead River Valley, British Columbia and Montana, 1979–95. The proportion of each bear's locations that were in each habitat was categorized into 1 of 20, 5% categories ranging from 0% to 100%. The size (area) of the bubble is proportional to the number of individual bears in each of the 20 categories. The proportion of the study area covered by each habitat (availability) is marked with a dash.

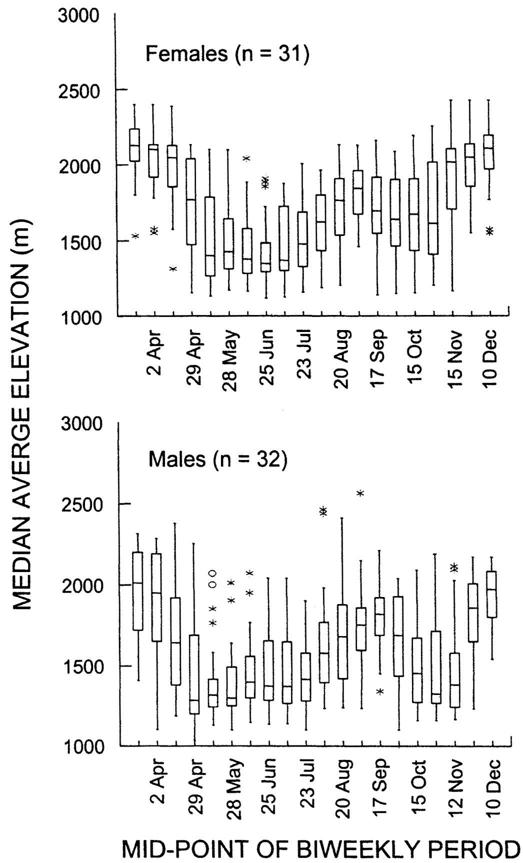

Fig. 2. Box and whisker plot (SYSTAT 1996:106) of average biweekly elevations of 31 female and 32 male grizzly bears in the Flathead River Valley, British Columbia and Montana, 1979–95. The box indicates the median, 25% and 75% quartiles. Whiskers are the smallest and largest values that are not outliers. Outliers (asterisk) and far outliers (circle) are at least 1.5 and 3.0 times the interquartile range beyond these quartiles, respectively.

tats followed by forest and open forest (Table 2). Regenerating cut-blocks and rock outcrops were consistently selected less than other habitats for all within-season comparisons.

Compositional analysis showed that grizzly bears used elevation categories unequally and season was again the only factor of those investigated that had an effect ($F_{8,242} = 2.900$, $P = 0.004$); sex, ageclass and interactions were insignificant ($0.171 < P < 0.951$). Use of elevations by grizzly bears reflected their use of habitats across seasons. Bears were at high elevations either in their dens or close to their den sites early in the spring (Fig. 2). The median average elevation declined after emerging from dens and it remained low for about 12 weeks as the grizzly bears primarily used riparian habitats. Some individuals, however, remained at high elevations at this time of year (Fig. 2). The median average elevation of bears increased in summer when open-forest burns and open burns were frequently used. Two male bears used talus at high elevations during summer. In autumn, the median average elevation declined again, but increased to high elevations where grizzly bears hibernated (Fig. 2).

DISCUSSION

Although grizzly bears are flexible in habitats they use (Waller and Mace 1997), general patterns were apparent in our study. Season was a significant factor influencing habitats and elevations selected by grizzly bears. Early in spring, before the flush of new vegetation, major foods were hedysarum roots (*Hedysarum sulphurescens*) and ungulates (McLellan and Hovey 1995). After flush, horsetails (*Equisetum arvense*), graminoids, and cow parsnip (*Heracleum lanatum*) in particular dominated the

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diet. All of these spring foods occurred in riparian habitats and some were largely limited to wet sites characteristic of riparian and some avalanche chutes (Hope et al. 1991, Coupé 1991).

Because the Flathead Valley is broad and there were productive spring habitats in both the valley and adjacent mountains, 2 general habitat selection patterns of grizzly bears were apparent (McLellan 1989*b*). Most bears were elevational migrators and shortly after den emergence they moved to the wide valley where they were often located in riparian habitats. Some bears, however, were mountain residents and remained in mountainous portions of the study area after den emergence, and there they selected avalanche chutes during spring. Some individuals, particularly males with large home ranges, exhibited both behaviors.

Low elevation riparian habitats in most other studies of southern grizzly bears had been degraded in various ways. In the Mission Mountains, Montana, low elevation riparian areas were interspersed with agricultural lands and settlement, yet some radiocollared grizzly bears used these habitats much like the elevational migrating bears in our study area (Servheen 1983). In the South Fork of the Flathead River, potential riparian habitat in the main valley was under a reservoir and unavailable to bears. Strong selection of avalanche chutes by grizzly bears during spring in that study area (Waller and Mace 1997) was similar to the pattern of mountain resident bears in our study. In the South Fork, Waller and Mace (1997) found that grizzly bears went up in elevation during spring to track optimum plant phenologies. This pattern was not clear in our study because most bears remained at low elevations and used riparian habitat throughout the spring.

During summer, huckleberries (*Vaccinium* spp.) and to a lesser extent buffaloberry (*Shepherdia canadensis*) dominated the diet of grizzly bears (McLellan and Hovey 1995). Buffaloberry shrubs occurred in a variety of habitats, but because fruit production is inversely related to conifer canopy cover (Hamer 1996), bears fed on buffaloberry in open timber and open timbered burns as was recorded in Banff National Park (Hamer and Herrero 1987). Huckleberry shrubs produced fruit almost exclusively in higher elevation areas that had been burned by wildfire 50–70 years previously (Martin 1983), and thus grizzly bears showed strong selection for open timbered burns and open burns during summer. Both elevational migrating and mountain resident grizzly bears used these higher-elevation burns in summer.

During summer in the South Fork, grizzly bears were frequently found in shrub fields caused by natural fire and cut-blocks due to the availability of fruit producing shrubs in these habitats (Waller and Mace 1997). In our study area, regenerating cut-blocks were rarely used by grizzly bears during any season. Many of the cut-blocks were logged to salvage dead or dying trees in response to insect outbreaks and were large and contained little bear food (Knight 1999).

During autumn, the diet of grizzly bears was more varied with huckleberries remaining a major food, but hedysarum roots, ungulates, clover (*Trifolium* spp.), and fruits of bearberry (*Arctostaphylos uva-ursi*), cranberry (*Viburnum edule*), and Rhamnus (*Rhamnus alnifolia*) also became important (McLellan and Hovey 1995). The variation in diet was reflected in the increased variety of habitats used by bears. Bears that remained in the mountains during spring and summer continued to do so in autumn whereas bears that used low elevations during spring usually returned to the low elevations during autumn.

MANAGEMENT IMPLICATIONS

Low gradient riparian areas were highly selected by grizzly bears during spring and autumn and these are important to many other terrestrial and aquatic organisms (Thomas et al. 1979, Naiman et al. 1993). We suggest that riparian habitats be kept undisturbed if possible by restricting road construction and reducing timber harvest in productive flood plains until research demonstrates that these activities are compatible with grizzly bear habitat use and requirements of other species. Avalanche chutes were also selected habitats by some bears in spring. Because bears avoided open roads by 100–250 m in the study area (McLellan and Shackleton 1988), we advise that road construction avoid avalanche chutes when possible. We further suggest that guidelines for managing forests adjacent to productive avalanche chutes be developed that include conifer retention by using a partial-cut silvicultrual system to maintain security cover. We believe that the high density of grizzly bears in the study area (McLellan 1989*a*) is related to the large pro-

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portion of the area that was burned by wildfire 50–70 years ago and now produce an abundance of huckleberries (Martin 1983) and buffaloberry (Hamer and Herrero 1987). Eventually, conifers will regenerate in these areas and berry production will decrease (Martin 1983, Hamer 1996). Maintaining or enhancing berry production will require (1) fires of suitable size and intensity, (2) reduction of conifer growth in existing burns by mechanical methods, or (3) learning how to produce sufficient berries using silvicultural methods and implementing this knowledge.

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MULTI-SCALE HABITAT PARTITIONING IN SYMPATRIC SUIFORMS

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Abstract: The native collared peccary (*Tayassu tajacu*) and the introduced feral pig (*Sus scrofa*) occur sympatrically in southern Texas. We examined habitat partitioning of these 2 species on the Chaparral Wildlife Management Area in southern Texas, from December 1993 through December 1995, at 3 scales of resource selection: seasonal home range, microhabitat, and temporal microhabitat. Seasonal habitat partitioning was observed at the home range level during and immediately subsequent to droughts. Microhabitat partitioning occurred in all seasons, regardless of precipitation. Temporal partitioning between species was observed in spring 1995. Partitioning of vegetation types at >1 level took place in 4 of 8 seasons. Multi-scale partitioning may provide additive, and possibly multiplicative, habitat partitioning between these species, and allow coexistence even during harsh environmental conditions such as droughts.

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A component of global change currently receiving attention is the proliferation of faunal and floral invasions due to anthropogenic influences (Vitousek et al. 1996), with recent calls for additional research by ecologists to describe and predict the outcomes of biological invasions (Carey et al. 1996, Kareiva 1996). The ecology of these invasions imparts new significance to the study of interspecific interactions because

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