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Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana

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Summary

1. Relationships between grizzly bears, habitat, and roads were investigated between 1990 and 1994 in the Swan Mountains, Montana. Relationships were examined at three levels of resource selection.

2. Differences existed between habitat and road features within, and those outside, the multi-year composite female grizzly bear home range. Using logistic regression, large resource selection probability functions were obtained for the subalpine zone within multiple-use lands having no roads. Selection probability was zero for private lands and declined as total road density increased.

3. Within seasonal ranges, most grizzly bears favoured low temperate and temperate elevation zones over the subalpine zone during all seasons. Relative to forested habitats, avalanche chutes were positively selected for during all seasons, but especially in spring. Shrub lands and cutting units were important to most bears during summer and autumn. Grizzly bears were more closely associated with higher total road densities during spring than during other seasons. When in low temperate habitats, most bears used habitats with lower total road density than occurred randomly.

4. Seasonal use by grizzly bears of areas within a 0·5 km buffer surrounding roads was evaluated. Most grizzly bears exhibited either neutral or positive selection for buffers surrounding closed roads and roads receiving <10 vehicles per day but avoided buffers surrounding roads having >10 vehicles per day.

5. Between 1988 and 1994, eight grizzly bears were killed by humans. These deaths were directly influenced by road access and unnatural food sources. These deaths, in addition to natural mortality, were too great to promote local population growth.

Key-words: GIS, grizzly bear, habitat, logistic regression, roads.

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Introduction

Grizzly bear (*Ursus arctos horribilis*) recovery programmes in the United States can be classified by two broad management goals. The first goal is to increase the number of grizzly bears within 'recovery areas' (designated areas having adequate space and habitat to maintain viable populations). The second involves managing habitat to maintain or improve conditions for grizzly bears to obtain life requisites including spatial, security, and energetic requirements.

One recovery area is the Northern Continental Divide Ecosystem (NCDE) in western Montana (USDI Fish & Wildlife Service 1993). The NCDE consists of national park, designated wilderness, private, Native American, and non-wilderness state and national forest lands. The non-wilderness land in the NCDE is accessed by a large network of roads and is managed for many uses including timber harvest, mining, and recreation. Published information on grizzly bear habitat selection in roaded multiple-use environments is minimal. Recent work has examined the impacts of roads and human settlement on grizzly bears in Yellowstone National Park (Mattson, Knight & Blanchard 1987) and in southern British Columbia (McLellan & Shackleton 1988). The studies in Yellowstone described grizzly bear response to a large number of people on a small network of roads where hunting and firearms were not allowed. Conversely, McLellan and Shackleton's work addressed grizzly bear response to roads during a high intensity, short duration petroleum extraction period. Their study area had few permanent developments and low levels of vehicular use compared with many areas in the NCDE. These and other studies (Archibald, Ellis & Hamilton 1987; Kasworm & Manley 1990) used distance measurements and univariate statistics to describe grizzly bear response to roads. In this paper, we explore nonlinear, multivariate data to characterize relationships among grizzly bears, habitat, and roads, in an area with a long history of legal and illegal killing of grizzly bears.

Study area

The study area was located in the Swan Mountain Range of western Montana (Fig. 1). The 1457 km^2 area was bounded on the north and south by US Highway 2 and the Bob Marshall Wilderness, respectively. The area was bounded on the east by Hungry Horse Reservoir and on the west by the edge of contiguous forest cover in the Flathead River and Swan River valleys. Grizzly bears are not tolerated by humans beyond this western boundary because of its agricultural and suburban nature.

The study area was composed of private, corporate, state and federal lands. State, corporate and federal lands were managed primarily for timber harvest, recreation, and wildlife values. Private lands (9% of area) were in the Flathead Valley east of the city of Kalispell and in a part of the Swan River Valley. Most private lands were developed for permanent homes, farms and service facilities.

Beginning in the late 1940s, a network of roads was established within the study area primarily to provide access to timber and to construct the Hungry Horse Dam. Two gravel roads, bordering the west and east side of the Reservoir, provide access to the study area, and a network of roads is present in most drainages. The Reservoir, completed in 1953, flooded 9712 ha of riparian and upland habitats (Casey, Yde & Olsen 1984).

Beginning in the early 1980s some roads were closed to improve wildlife security and other resources, and in 1990 a more aggressive closure programme was begun. At present, there are 1962 km of roads in the study area not reclaimed by natural vegetation. In 1990, the beginning of this investigation, 54% of the roads were continuously open to public travel by vehicle. The remaining 903 km were either permanently or seasonally closed to public vehicular travel. There were no restrictions on people travelling by foot, bicycle or horseback, and some illegal vehicle use on closed roads occurred.

Methods

CAPTURE, TELEMETRY, AND HOME RANGE

Beginning in 1988, adult ($\geqslant$5 years old) and subadult grizzly bears were captured and radio-collared (Mace *et al.* 1994). Use of a 3·2 km capture grid throughout the study area for 3 years with variable snaring methods reduced capture bias (White *et al.* 1982). We used telemetry data from 1990 to 1994 when radio-collared grizzly bears were located twice each week from fixed-wing aircraft. Most locations were obtained during the morning when flight conditions were best. We photographed each location from the air with a Polaroid camera, enabling us immediately to record locations. We documented an average aerial telemetry error of 75 m (150 m^2) (Mace & Manley 1988). Using these photographs and 1:24 000 orthophotographic quadrangles, we assigned a universal transverse Mercator (UTM) coordinate to each relocation and converted locations to GIS maps.

The adaptive kernel method (Worton 1989) was used to estimate home ranges using CALHOME (US Department of Agriculture, Forest Service, Pacific South-west Forest Experimental Station, 2081 East Sierra, Fresno, CA 93701). Home ranges of individuals were then converted to Geographical Information System (GIS) maps.

STUDY DESIGN

We evaluated the relationships among grizzly bears, roads and habitat using univariate and multivariate statistics with GIS map layers (Pereira & Itami 1991). Relationships were evaluated at three orders of resource selection (Johnson 1980), hereinafter referred to as second-, third-, and fourth-order selections. We first compared habitat and road features within a composite 95% multi-year annual home range of radio-collared female grizzly bears to accessible habitats within the study area but outside the composite home range (second-order selection); recognizing that the study area boundaries did not include urbanized areas to the west where grizzly bears no longer occurred. The composite home range was developed by overlaying the 95% multi-annual ranges of 14 adult and subadult female grizzly bears. We chose the 95% isopleth to exclude short-term forays.

For third-order selection we compared use of habitat and road features from telemetry data to random expectation within 100% seasonal home ranges. We chose the 100% isopleth at this selection level so as to better estimate home ranges that were based on sample sizes that, for some bears, were less than optimal (Table 1) (Worton 1989). Other authors studying low-density and highly mobile species have also acknowledged difficulties obtaining large sample sizes (Joshi, Garshelis & Smith 1995; Weilgus & Bunnell 1995).

In fourth-order selection we investigated the response of grizzly bears to roads of differing traffic volume. We tested whether use by bears of 0·5 km buffers surrounding roads of each class differed from availability within seasonal home ranges. Multivariate tests were not used because of a limited telemetry sample size near roads.

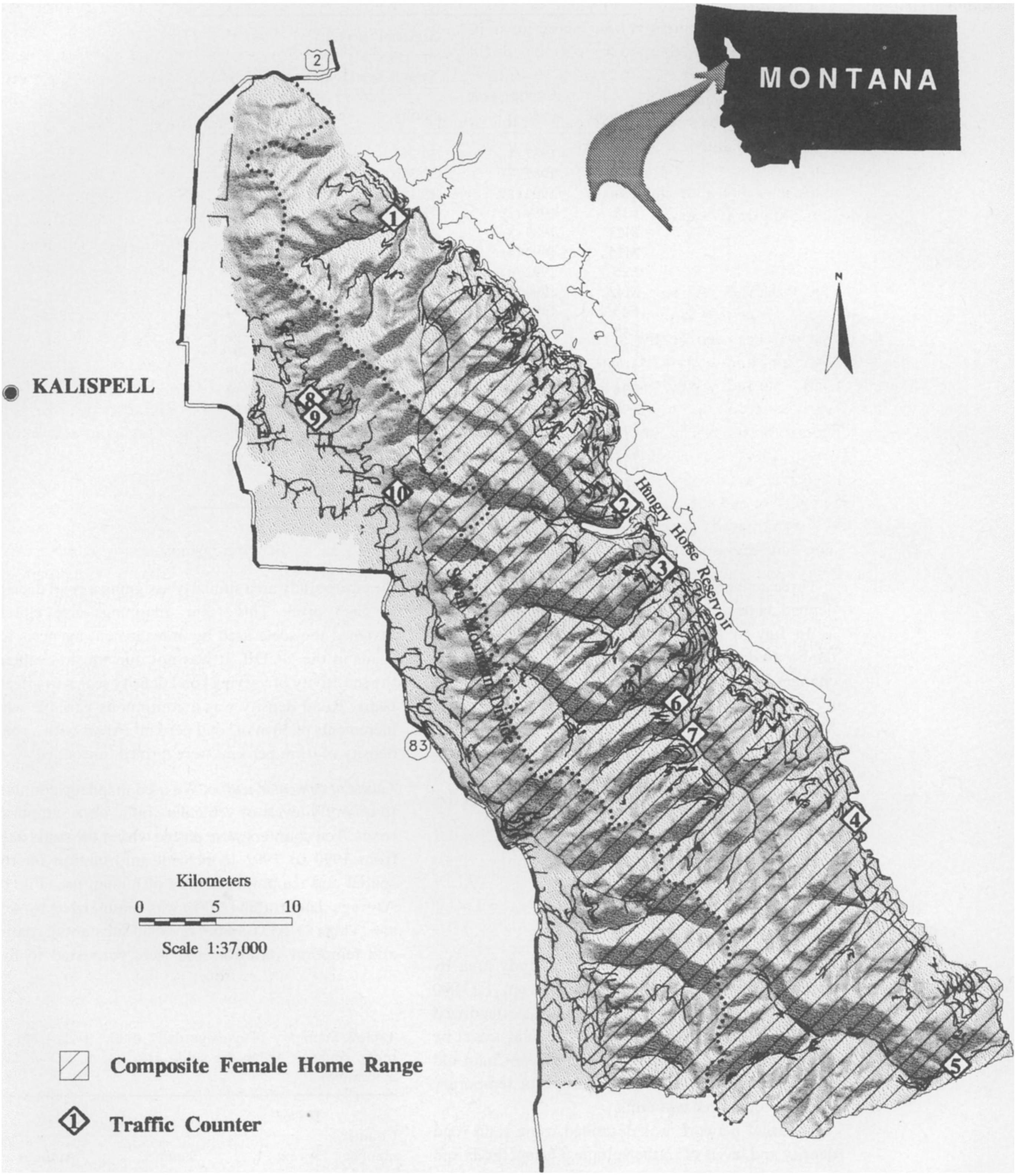

Fig. 1. Relief map of study area in the Swan Mountains, Montana showing distribution of roads, location of traffic counters, and the composite 95% multi-annual home range of female grizzly bears.

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Table 1. Year of capture, age at capture, seasonal sample size, and 100% adaptive kernel home range size for grizzly bears in the Swan Mountains, Montana (1990–94). Sample sizes represent the number of telemetry points used for estimating home range and habitat selection using logistic regression

Bear Id	Capture year (age)	Seasonal telemetry Sample size/Home range (km²) Spring	Summer	Autumn
F3	1987 (1)	30/251	15/204	18/329
F5	1987 (7)	57/380	52/181	45/81
F8	1993 (2)	18/187		
F18	1989 (2)	79/155	57/174	37/125
M22	1989 (3)	82/1267	49/668	30/658
M25	1990 (4)	20/337	33/190	20/542
F26	1992 (4)		16/32	
M42	1990 (1)	31/79	34/31	15/12
F45	1990 (19)	61/303	62/250	47/174
F48	1990 (10)	60/226	65/173	42/182
F69	1992 (3)	15/333	26/317	20/70
M71	1990 (2)	74/1091	62/701	40/496
F94	1988 (8)	36/225	37/110	31/119
F96	1988 (15)	83/197	63/249	42/141
F137	1988 (1)	39/169	35/202	23/89
F143	1988 (5)	19/155	16/92	19/78
F147	1987 (1)	50/343	31/160	25/229
M149	1988 (8)	26/970	38/1181	

Three active seasons were categorized: 'Spring' was defined as den exit to 15 July; 'Summer' was defined as 16 July to 15 September; 'Autumn' was 16 September to den entry. Categories were based on major changes in consumption of the primary food plants by grizzly bears (Craighead, Sumner & Skaggs 1982; Mace & Jonkel 1983). We used the GIS software EPPL7 (Minnesota State Planning Agency, 300 Centennial Building, 658 Cedar Street, St Paul, MN 55155). Maps were in a raster format with a pixel size of 30 × 30 m.

Map layers

ROADS

We constructed a road map for the study area by digitizing all roads present in 1990 from 1:24 000 orthophotographic quads. Each road was categorized as being either open or closed to vehicular travel by the public during each season. We did not map old roads reclaimed by natural vegetation or temporary roads in timber harvest units.

The road network was described using total road density and levels of traffic volume. Our methods and mapping process for road variables were as follows.

Total road density. The linear road map was converted to a total road density (road density) map using a moving window having an area of 1 km². The moving window routine in EPPL7 assigned the centre pixel of a 1-km² window the total kilometers of roads present within the window. The window then moved across the entire study area similarly assigning a road density to each pixel. This 1-km² mapping scale closely matched the scale used by management agencies for roads in the NCDE. It was not our aim to evaluate the sensitivity of varying road density scales to grizzly bears. Road density was a continuous variable with increments of 30 m of road per km². Areas with a road density of 0 km per km² were termed 'unroaded'.

Levels of vehicular traffic. We used magnetic counters to quantify levels of vehicular traffic on a sample of roads. Ten counters were placed within the study area from 1990 to 1992 to provide information on the spatial and temporal patterns of human use (Fig. 1). Average daily traffic (ADT) was summarized by season (Table 2). ADT values revealed substantial spatial and temporal variation and were converted to five

Table 2. Summary of average daily traffic levels from 10 traffic counters within the study area (mean, SD, *n* days monitored)

Counter number	Season Spring	Summer	Autumn
1	201, 183, 253	471, 207, 135	97, 54, 122
2–3	38, 42, 37	32, 15, 62	8, 8, 76
4	22, 22, 211	57, 21, 136	26, 20, 152
5	7, 7, 166	10, 8, 123	10, 7, 152
6–7	3, 5, 346	6, 5, 272	7, 9, 348
8–9	12, 16, 424	22, 18, 249	22, 19, 302
10	27,28,363	70, 34, 186	25, 20, 178

broad classes: Class 1 = < 1 vehicle per day, Class 2 = 1–10 vehicles per day, Class 3 = 11–60 vehicles per day, Class 4 = 61–300 vehicles per day, and Class 5 = > 300 vehicles per day. Class 1 roads were roads closed to the public. We coded all roads in the study area by these classes for each season, based on their proximity to roads with counters and whether they were open to vehicular travel.

Elevation zone. The study area was categorized into three elevation zones describing differences in dominant coniferous trees. The categories were developed from unpublished vegetation data and transferred to a GIS format using a digital elevation map at 1:24 000. The low temperate zone extended from 870 m to the lower limit of subalpine fir (*Abies lasiocarpa*) at 1494 m. The temperate zone extended to the upper limit of Douglas fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) at 1981 m. Elevations above 1981 m were classified as the subalpine zone. There was no distinguishable alpine zone in the study area (Mace *et al.* 1994). Using the moving window routine, the final map represented the dominant elevation zone within a 150 m^2 area.

Cover type. A 28 August 1988 LANDSAT Thematic Mapper image of the study area was classified into 30 spectral classes that were vegetatively described using field plots and aerial photo interpretation (Manley, Ake & Mace 1992). The 30 classes were then grouped into three broad cover types: sites dominated by either rock or grass/forb communities (non-vegetated); shrubs (shrub land); or forest (>40% conifer overstorey). We then overlaid three digitized physiographic features on the satellite image: avalanche chutes, slabrock (Mace 1986), and timber harvest units (cutting units). Using the moving window GIS routine, the dominant cover type was assigned to the 150 m^2 telemetry error unit. Lakes and those habitats obscured by shadow were omitted from the final map.

Land ownership. We divided the study area into two zones based on land-ownership and predominant land-use patterns. The multiple-use zone (code = 1) included areas managed by state or federal agencies and corporate timber lands. The private zone (code = 0) included lands under private ownership.

Model building strategies and statistical methods

Our model building strategy varied by order of resource selection. Statistical analyses were conducted using STATISTICA (Statsoft Inc., 2325 East 13th St, Tulsa, OK 74104, USA).

For second and third-order selection, we used logistic regression (maximum likelihood estimates) to predict the probability of occurrence of grizzly bears as a function of map variables. Logistic regression was selected over discriminant analysis because variables were a mixture of continuous and categorical data (Press & Wilson 1978). Our goal was to compare the importance of variables among individuals by examination of the sign (negative or positive trajectory) and significance (*P*-values) of regression coefficients, and not to construct the simplest model possible. The most parsimonious strategy, as outlined by Hosmer & Lemeshow (1989) reduces the content of a model and would omit information important to habitat managers.

In second-order selection we compared the characteristics of 4668 random coordinates within the composite female home range to characteristics of 2447 random coordinates outside the range.

Because each coordinate represented a 1 km^2 area, the two areas were sampled in a 5:1 ratio to their size. Random coordinates within the composite home range estimated characteristics of female home ranges, and those outside the composite home range characterized unused habitat by females from 1990 to 1994. We calculated resource selection probability functions (RSF) using the following equation from Manly, McDonald & Thomas (1993; p. 128)

$$w^*(x_i) = \frac{\exp\{\log_e(P_{\hat{u}}/P_u) + \beta_0 + \beta_1 x_{i1} + \ldots \beta_p x_{ip}\}}{1 + \exp\{\log_e(P_{\hat{u}}/P_u) + \beta_0 + \beta_1 x_{i1} + \ldots \beta_p x_{ip}\}}$$

where $w^*(x_i)$ was the RSF, $P_{\hat{u}}$ and P_u were sampling probabilities of unused and used units, β_0 was the intercept, and $\beta_1 x_{i1} + \ldots \beta_1 x_{ip}$ represented the available resource units divided into I groups.

RSF values represented the relative probability (0–1) of variable combinations occurring within the composite female home range. We did not investigate second-order selection for males, as their composite range enveloped the entire study area.

We compared the characteristics of telemetry coordinates of individuals to random coordinates within seasonal home ranges for third-order selection. The number of random coordinates used equalled home range size (e.g. 200 random coordinates for a home range of 200 km^2).

We developed 'standard variables' for categorical maps (Hosmer & Lemeshow 1989). Standard variables, from which other members of the category were allowed to differ, were the subalpine zone for the elevation map, and forest for the cover type map. We developed an interaction term between the low temperate zone and road density (LOTEMPXRD) to investigate the influence of road density on RSF values in this zone. We chose this interaction term above all other possible combinations because the low temperate zone was available to all bears and contained the majority of roads.

The significance of logistic models was ascertained by comparing the log-likelihood χ^2 value for the model fitted to each individual parameter against the χ^2 value for the model fitted only to the intercept β_0 (Hosmer & Lemeshow 1989; Manly *et al.* 1993). Variables were then considered either significant ($P < 0{\cdot}10$) or not significant to the final model. Variable coefficients and their standard errors were calculated. Final models exhibiting a *P*-value ≤0·10 were considered significant.

For fourth-order selection, we compared use and availability of road ADT classes within 0·5 km buffers, for each bears' seasonal home range. A 0·5 km buffer surrounding roads was narrow enough to detect selection, yet sufficiently wide to include an adequate sample of telemetry points for chi-square tests using Bonferroni simultaneous confidence intervals (Byers, Steinhorst & Krausman 1984). Individuals were classified as exhibiting negative, neutral, or positive selection toward road buffers of each ADT class.

Results

SECOND-ORDER SELECTION: FEMALES

The area within the composite female home range differed from the area outside of the range. The composite range was positively associated with multiple-use lands (Table 3). RSF values were zero for all combinations of habitat and road variables on private lands.

The area outside of the composite range was dominated (71%) by low temperate habitats while most of the composite range occurred within the temperate zone (Table 3). Further, there was more subalpine zone habitat within the range than outside. Logistic regression coefficients were negative for the low temperate and temperate zones relative to the subalpine. The maximum RSF value possible in the low temperate, temperate, and subalpine zones was 0·12, 0·85, and 1·0, respectively.

The composite range differed from the non-range relative to cover types (Table 3). RSF values were highest for the slabrock cover type and lowest for cutting units.

Road density was lower (= 0·6 km km^{-2}) within the composite range than outside (= 1·1 km km^{-2}). Fifty-six per cent of the composite range was unroaded (0 km km^{-2}) compared to 30% outside the range. The female composite home range was negatively associated with increasing values of road density (Table 3). An RSF value of 1·0 was achieved at a road density of 0 km km^{-2}. RSF values declined to zero as road densities approached 6·0 km km^{-2}.

RSF values for the temperate zone demonstrated the relationship between road density and cover type (Fig. 2). Selection in this elevation zone was greatest at a road density of zero for all cover types. As road density increased, RSF values declined.

THIRD-ORDER SELECTION

We compared telemetry data to random coordinates for road and habitat features within the 100% seasonal home ranges of individual grizzly bears. We did not conduct cohort analyses because seasonal ranges varied by individual in the availability of elevation and dominant cover types, and in the amount of unroaded habitat.

SPRING

Logistic models were significant for 15 out of 17 bears radio tracked during spring. Positive selection for the

Table 3. Summary statistics and multivariate logistic regression results for second-order of selection, where the composite female home range was compared to area outside of home range. Swan Mountains, Montana

	Summary statistics (final model) Within composite range				Outside composite range				Multivariate statistics‡		
	Min–max	Mean	S.E.	%†	Min–max	Mean	S.E.	%†	Coefficient	S.E.	*P*
Road density	0–6·3	0·6	0·014		0–5·2	1·1	0·022		−0·16	0·06	0·02
Nonvegetated				3				4	0·57	0·22	0·01
Shrub land				14				10	0·23	0·10	0·02
Forest*				59				67			
Chute				7				2	0·47	0·15	0·00
Slabrock				2				0·2	1·38	0·46	0·00
Cutting unit				15				17	0·14	0·08	0.11
Low temperate				31				71	−1·32	0·12	0·00
Temperate				54				24	−0·15	0·12	0·20
Subalpine*				15				5			
Ownership				100§				75†	5·60	0·58	0·00
LOTEMPXRD									0·12	0·07	0·08

*Standard variables.
†Percentage of total for categorical variables.
‡Constant = −3·99, sampling fraction = 1·91.
§Percentage multiple-use lands.

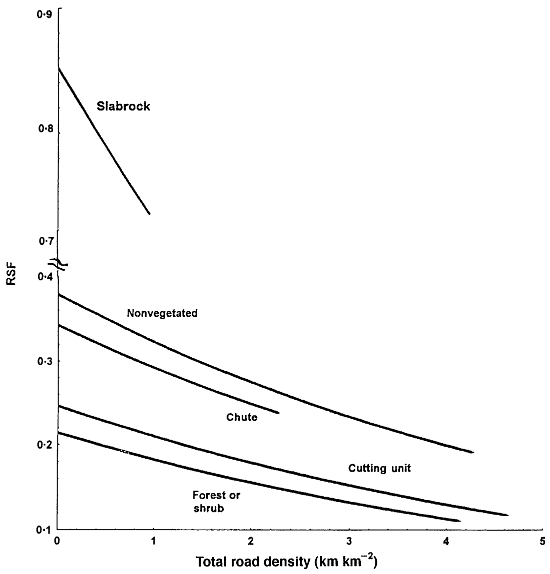

Fig. 2. Resource selection probability functions (RSF) for second-order selection, Swan Mountains, Montana. RSF values depict changes in the relative probability of temperate elevation zone cover types occurring within the composite 95% female home range relative to total road density. Logistic curves for each cover type show only the maximum total road density present in the study area. For example, the cover type Slabrock most distinguished the composite home range from non-range area, and occurred at a maximum total road density of 1 km km^{-2}.

low temperate and temperate zones relative to the subalpine was evident for 14 and 13 individuals, respectively (Table 4). A positive relationship for chutes was observed for all 15 bears, 14 of which were significant. Most bears were positively associated with cutting units during this season.

Coefficients for road density were negative or positive for eight and seven individuals, respectively. Road density was significantly negative for two and significantly positive for three bears. Coefficients for the interaction term LOTEMPXRD was negative for 10 of the 15 grizzly bears during spring. Thus, most bears utilized areas with lower road densities while in the low temperate zone (Table 4). Road density averaged 0·57 km km^{-2} (SD = 0·87) for the pooled sample. On average, 53% (SD = 9·0) of the spring home ranges were unroaded.

SUMMER

Seventeen bears were evaluated for summer, and logistic models were significant in 14 cases. Coefficients were positive for the temperate zone for 10 grizzly bears during summer (Table 4). Four bears selected the subalpine zone over the two lower elevation zones during this season.

Grizzly bears exhibited positive selection for more cover types than during spring (Table 4). Coefficients for shrub lands, slabrock, and cutting units were positive relative to forest for most bears. Significant positive selection for chutes declined from spring.

Table 4. Summary of multivariate logistic regression coefficients for third order selection within seasonal home ranges, Swan Mountains, Montana. Spring (n = 15 ranges), summer (n = 14), and autumn (n = 13) data are given by row per variable

	Number of grizzly bears having negative or positive logistic regression coefficients within seasonal home ranges (number of significant ranges)	
Parameter	Negative	Positive
Low temperate	1 (0)	14 (11)
	8 (1)	6 (3)
	7 (3)	6 (1)
Temperate	2 (0)	13 (7)
	4 (0)	10 (1)
	8 (2)	5 (0)
Chute	0	15 (14)
	7 (1)	7 (5)
	2 (0)	11 (5)
Shrub land	7 (1)	8 (1)
	4 (0)	10 (6)
	2 (0)	11 (5)
Slabrock	9 (0)	5 (3)
	2 (0)	9 (6)
	6 (0)	6 (2)
Cutting unit	5 (2)	10 (2)
	3 (0)	11 (5)
	6 (2)	7 (5)
Nonvegetated	8 (1)	7 (1)
	7 (2)	6 (0)
	10 (1)	3 (0)
Road density	8 (2)	7 (3)
	11 (5)	3 (0)
	9 (2)	4 (0)
LOTEMPX	10 (2)	5 (0)
TOTRD	6 (1)	8 (2)
	8 (2)	5 (0)

*The sum of negative and positive coefficients for each parameter may not equal total number of individuals evaluated per season. For some bears, parameters were unavailable within home ranges. Coefficients were considered significant at $P \leqslant 0{\cdot}10$.

Road density was negative and positive for 11 and 3 bears during summer, respectively. Five of the negative associations were significant. During summer, the road density use averaged 0·4 km^{-2} (SD = 0·8) from the pooled telemetry sample. When pooled, summer home ranges were on average 59% unroaded (SD = 8·0).

AUTUMN

Fifteen grizzly bears were evaluated for autumn and significant models were obtained for 13 individuals. Six and five bears exhibited positive coefficients for the low temperate and temperate zones, respectively, during autumn (Table 4). Three bears were positively associated with the subalpine zone relative to the lower elevation zones. Chutes and shrub lands were selected by most bears during autumn. Most bears selected against the nonvegetated cover type.

Nine of 13 bears exhibited negative selection for road density during autumn, two of which were significant. Average road density from the pooled telemetry sample was 0·34 km km^{-2} (SD = 0·69), and autumn home ranges averaged 62% unroaded (SD = 14·0).

FOURTH-ORDER SELECTION

Few seasonal home ranges contained Class 4 or Class 5 roads. All bears having these two types within their home range exhibited negative selection towards them (Table 5). All grizzly bear spring home ranges contained Class 1 roads. Most bears showed neutral or positive selection towards Class 1 road buffers during spring (Table 5). The number of bears exhibiting positive selection for road buffers decreased as traffic volume increased. Seven of 11 bears showed negative selection towards Class 3 roads during spring. One bear exhibited positive selection for Class 3 roads during this season; an adult female conditioned to human and livestock food located near a Class 3 road.

Most grizzly bears were either negative or neutral towards Class 1, Class 2, and Class 3 during summer (Table 5). Two of the three bears positively associated with Class 1 roads were males. No positive selection was observed for Class 2 or Class 3 roads.

Twelve of 14 individuals exhibited neutral selection for Class 1 roads during autumn. No bears were positively associated with Class 2 or Class 3 roads during this season.

Discussion

Grizzly bears historically occupied much of the western United States but were extirpated as human populations grew and tolerance diminished (Storer & Tevis 1955; Mattson 1990). Currently, grizzly bears still persist in areas where habitat is relatively secure and human-induced mortality is low. Management of human access in grizzly bear habitat has become critical as these remnant wildlands become increasingly accessible to humans via roads.

This study has demonstrated complex spatial and temporal relationships between grizzly bears and habitat resources. Resource selection was expressed relative to the strength (power) and association (negative, positive) of several road and habitat parameters. These relationships varied by landscape scale, level of selection, season, and individual.

Differences between used and unused habitats were demonstrated for female grizzly bears at the second-order of selection. The outermost boundary of the 95% composite multi-annual home range confirmed our knowledge of the western distribution of females observed in our capture/resight studies using snare and camera grids (Mace *et al.* 1994). No females were captured or photographed outside the composite range. The composite multi-annual home range of females did not contain private lands. Such lands contain high-quality seasonal habitat for grizzly bears living in the Swan Mountains, including ungulate winter ranges and riparian areas valuable to grizzly bears during spring. However, these areas also have high densities of humans and roads. Illegal killing, and sanitation problems which attract and habituate grizzly bears, are on-going management concerns on or adjacent to private lands.

Female grizzly bears occupied ranges having lower total road densities than unused areas. Female home range selection was high for subalpine habitats that were unroaded, and low for low temperate zone habitats with roads. Selection was greatest for unroaded cover types and declined as road densities increased. A total road density on multiple-use lands of $<6·0$ km km^{-2} differentiated the used from unused areas. More dramatic selection against human activities would have been demonstrated had we extended the study area boundaries further into urbanized areas. These findings support the conservation value of unroaded habitats as found elsewhere. Thiel (1985) and Mech *et al.* (1988) studied the relationship between wolves and road densities and agreed that higher road densities generally did not support wolves. Mech (1989) found that low densities of wolves can persist in areas of greater densities of roads if adjacent habitats have few roads. In Florida, translocated mountain lions (*Felis concolor*) established home ranges in areas having approximately one-half the road density relative to the entire study area (Belden & Hagedorn 1993).

Within seasonal ranges, we did not pool individuals because resource availability and selection was unique to the individual (White & Garrott 1990). Grizzly bear selection tended to be strongest for elevation and

Table 5. Selection within seasonal home ranges of 0·5 km buffers surrounding roads of 5 ADT classes. Selection was defined as negative (−), neutral (=), or positive (+). Swan Mountains, Montana

	Selection towards 0·5 km buffer proximate to road classes (number of bears)														
	Class 1			Class 2			Class 3			Class 4			Class 5		
Season	−	=	+	−	=	+	−	=	+	−	=	+	−	=	+
Spring	3	8	6	6	8	2	7	3	1	4	0	0	4	0	0
Summer	6	8	3	11	6	0	6	4	0	4	0	0	4	0	0
Autumn	1	12	1	6	7	0	8	1	0	3	0	0	2	0	0

cover type variables relative to total road density. Both positive and negative relationships were observed for each season for total road density but were rarely significant in multivariate models. Thus, road density did not strongly influence bear use of habitats within established home ranges as was documented by Brody & Pelton (1989) for black bears. However, grizzly bear seasonal ranges were composed mostly of roads closed to vehicles or those driven infrequently by humans. Interestingly, avoidance of areas having a high total road density was evident for some bears, even though roads were closed to public travel.

During each season, most grizzly bears selected cover types below the subalpine zone. During spring, much of the subalpine zone was either unavailable or undesirable to grizzly bears because of snow. It is less apparent why most bears showed selection against the subalpine zone during summer and autumn. However, it is possible that food resources at higher elevations were less abundant than in lower elevation areas as documented by Craighead *et al.* (1982). These authors concluded that: 'The high quality of the temperate zone forests as grizzly bear habitat suggests that the species would have difficulty surviving wherever this habitat component is lacking or was heavily exploited.'

All grizzly bears exhibited strong selection for chutes during spring, and selection continued for many bears throughout the year. During spring in particular, selection was stronger for chutes than for other variables including total road density. Chutes have high coverage and availability of vegetation sought by bears, such as *Heracleum lanatum*, *Angelica* spp., *Erythronium grandiflorum* and *Claytonia* spp. (Mealey, Jonkel & Demarchi 1977; Mace 1986; Korol 1994). Further, visual security in this habitat is often high because of dense stands of *Alnus* spp. shrubs, which may attain a height of >5 m.

Increased use of cutting units and shrub lands in the low temperate and temperate zones during summer and autumn was evident for bears eating the fruit of *Vaccinium* spp. and *Sorbus* spp. Certain harvest methods at specific successional stages (Waller 1992) may promote fruit production in these shrubs (Zager, Jonkel & Habeck 1983; Martin 1983).

Neutral use, or positive selection towards habitats near roads implies that important habitat resources occur near roads. Such selection was found in our fourth-order analyses during all seasons, but especially during spring, for areas proximate to closed roads and roads with <10 vehicles per day. This was partially due to bears utilizing cutting units, or avalanche chutes which often terminated near roads. Few bears exhibited selection towards habitats near roads having >60 vehicles per day. This proximal avoidance of roads has been demonstrated elsewhere (Tracey 1977; Harding & Nagy 1980; Archibald, Ellis & Hamilton 1987; Mattson *et al.* 1987; McLellan & Shackleton 1988; Kasworm & Manley 1990).

McLellan & Shackleton (1988) demonstrated avoidance of areas close to roads yet survival rates were high and demographic consequences were minimal. Conversely, our results are biased towards those radio-collared grizzly bears that survived long enough for us to obtain an adequate sample of telemetry data. During the period 1988–94, eight marked grizzly bears in the study area were killed by humans. These deaths were directly influenced by road access through illegal killing, and through the management removal of bears conditioned to human foods in developed areas. Mace *et al.* (1994) reported a population size of 15–21 solitary ($\geqslant 2$ years old) grizzly bears present in the study area. The mortalities associated with road access, coupled with a high number of natural mortalities ($n = 7$, 1988–94), inhibited the growth of this local population in the Swan Mountains.

All three levels of selection suggested that grizzly bears can utilize roaded habitats, but spatial avoidance will increase and survival will decrease as traffic levels, road densities, and human settlement increases. Long-term survival of grizzly bears in the Swan Mountains will depend on their ability to utilize and survive in lower elevation, mixed-ownership habitats. Access management through road use restriction on multiple-use lands will be of limited mitigative value if habituation and mortality levels are not minimized on or adjacent to private lands.

Road closure programmes in the NCDE are extremely controversial because traditional access by vehicle for recreation or resource extraction is reduced. An important balance must be met between grizzly bear security and survival, and human sociological and economic concerns. We maintain that road density standards and road closure programmes should incorporate seasonal habitat requirements of grizzly bears. A properly implemented programme would minimize road density and traffic volume in watersheds having highly preferred habitats such as those with avalanche chutes during spring. Based on local knowledge of grizzly bear habitat selection patterns, road density standards could then be relaxed somewhat in less suitable habitats, allowing increased public use while minimizing threats to the local grizzly bear population. Innovative road access programmes that allowed short-term (e.g. 2 weeks during summer) access by humans during periods when displacement impacts to grizzly bears are minimal, would serve to build public acceptance towards this species.

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