FINAL REPORT:
GRIZZLY BEAR ECOLOGY IN THE SWAN MOUNTAINS, MONTANA[1]

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CHAPTER 1

INTRODUCTION

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INTRODUCTION

The Northern Continental Divide Ecosystem (NCDE) in western Montana is one of 5 areas in the contiguous 48 states where grizzly bears (*Ursus arctos horribilis*) still persist. The population status of grizzly bears in these 5 ecosystems varies from a remnant population in the Northern Cascades Ecosystem, to self-sustaining populations in both the NCDE and the Greater Yellowstone Ecosystem (Fig. 1.1). The species was listed as threatened under the Endangered Species Act in 1975, and a federal Grizzly Bear Recovery Plan (U.S. Dep. Interior, Fish and Wildlife Serv. 1993) outlines strategies for population and habitat conservation in each ecosystem.

Although not largest in area, the NCDE has the largest population of grizzly bears of the 5 ecosystems. Population estimates for the NCDE are believed to equal or exceed 500 grizzly bears (Dood et al. 1986). These bears occupy approximately 24,800 km^2 of habitat variously administered as National Park lands, designated wilderness, federal multiple-use lands, Native American reservations, private, corporate, and state lands.

The listing of the grizzly bear under the ESA provided the impetus for state, federal, private, and university research entities to examine life requisites and population status in the NCDE and elsewhere. In the early 1970's, a cooperative research program was developed between the State of Montana, the federal departments of Agriculture and Interior, and the University of Montana. This research program, known as the Border Grizzly Project, was the first study in the NCDE to incorporate radio-telemetry methods to determine ecological requirements of grizzly bears. The 1980's saw a flurry of habitat evaluation studies (e.g. U.S. Dep. Agri. 1985, Craighead et al. 1984) and the conception of cumulative effect models.

Using baseline information collected by the Border Grizzly Project, the Montana Department of Fish, Wildlife and Parks launched an ecological study of grizzly bears along the Rocky Mountain East Front in 1980. This area contains a unique transition between the Rocky Mountain Cordillera and the short-grass prairies of the great plains. This study ended in 1987 and provided information on the ecological requirements of grizzly bears along the eastern side of the NCDE, and their response to oil and gas development and other human activities (Aune and Kasworm 1989).

The Montana Department of Fish, Wildlife and Parks recognized that ecological requirements of grizzly bears differed between the more open and dry Rocky Mountain East Front and the moister habitats to the west of the Continental Divide. These differences, and the lack of ecological information on grizzly bears in western habitats suggested a west-side study would be necessary.

Studies of grizzly bears in the lower reaches of the South Fork Flathead River (this study) were initiated in 1987. This study, termed the "South Fork Project", was situated in the northern Swan Mountains. The goal of this research was to document factors limiting population size and to test methods for monitoring population trend. Habitat objectives included evaluation of seasonal habitat selection, and the effect of roads on grizzly bear distribution and survival.

This final report is a compilation of published and unpublished data obtained from radio-instrumented grizzly bears in the Swan Mountains. We have made an effort to publish information on the major topics of demography and resource selection in peer-reviewed journals. Several of the chapters have been published in wildlife journals while others have been submitted for publication. We have also included information on a variety of other topics that time did not allow us to prepare for publication.

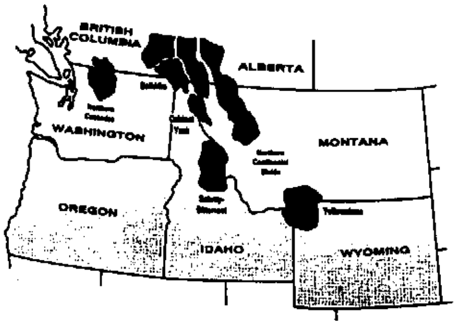
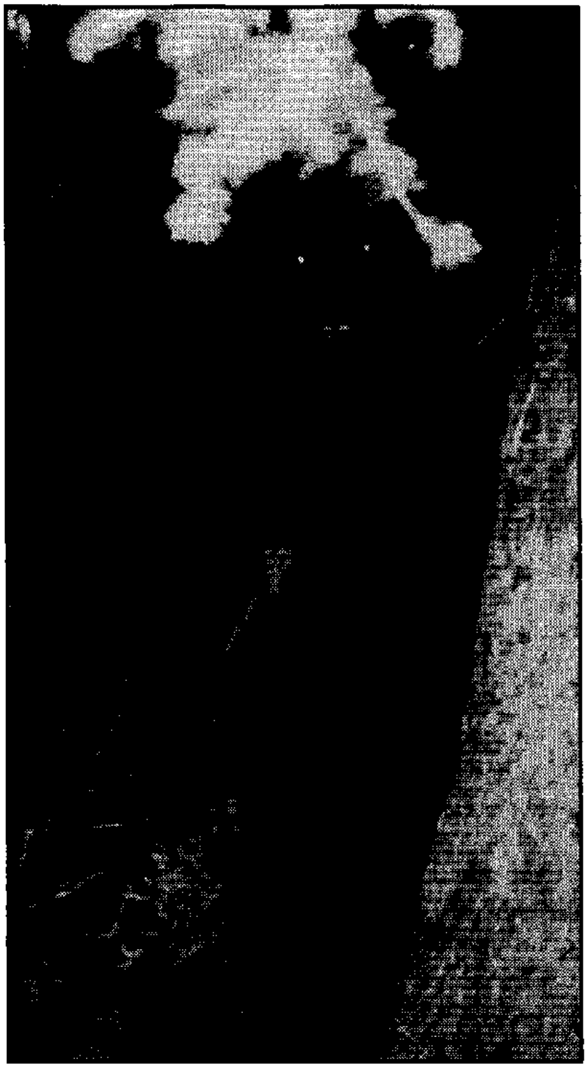


Figure 1.1. Grizzly bear recovery ecosystems in the conterminous 48 states (U.S. Dep. Agri. Fish and Wildlife Serv. 1993.) Grizzly bears persist in all but the Selway-Bitterroot Ecosystem.

CHAPTER 2

THE STUDY AREA



CHAPTER 2

THE STUDY AREA

The Study Area, located in the Swan Mountain Range of western Montana, extended from the northern terminus of the Swan Mountains on the north to the Bob Marshall Wilderness boundary on the south (Fig. 2.1). The 1,457 km^2 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 much of this western boundary because of its agricultural and suburban nature. The central portion of the Study Area was approximately 30 km from Glacier National Park. We defined two regions of the Study Area, the Core Area, where most grizzly bears were captured, and that area of the Study Area outside the Core termed the Peripheral Area (Fig. 2.1).

The topography of the Swan Mountains and adjacent area was formed by extensive glaciation during the Pleistocene (Alden 1953). During the Wisconsin and earlier periods of glaciation, a great cordilleran ice sheet extended from British Columbia into western Montana. One bifurcation of this ice sheet has been termed the Flathead Glacier and was estimated to be approximately 26 km wide near the towns of Columbia Falls and Whitefish. Mountain glaciers were also extensive in Glacier National Park and regions to the South. An abrupt transition exists between the Swan Mountains and valleys to the west; a result of scouring from the Flathead Glacier. This abrupt fault-line scarp affords little topographic separation between mountain grizzly bear habitat and valley habitats occupied by humans (Fig. 2.2). Most of the major drainages in the Study Area exhibited evidence of glaciation.

The Study Area was of broken mountain topography and was under the influence of Pacific maritime climate. Annual precipitation in the Study Area exceeded 70 cm, at least 50% as snow. Mountain snow, generally began to accumulate in October and persisted until mid May. In the Flathead Valley, snow began to accumulate in mid-November, and generally melted by mid-April. Southern exposures at low to mid elevations were generally the first areas to melt during spring in the Swan Mountains. Temperature extremes varied from -6° c in to 20° c in August. Variations in slope, aspect, elevation, fire history, moisture, and land use has resulted in a complex mosaic of vegetation communities. Hadden et al. (1987) described and mapped 51 community types within the Study Area. These community types ranged from dry grasslands on steep southerly aspects to moist Sitka alder/devil's club (*Alnus sinuata/Oplopanax horridum*) shrub fields in riparian areas.

Elevations varied from 870 m in the Flathead Valley to 2,421 m on Gildart Peak. We categorized the Study Area into 3 elevation zones that depicted differences in dominant coniferous trees (Fig. 2.3). 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). Common forest habitat type series (Pfister et al. 1977) of the low temperate zone included: *Abies lasiocarpa/Clintonia uniflora* (queencup beadlily), *Picea spp./Clintonia uniflora*, and *Pseudotsuga menziesii/Calamagrostis canadensis* (bluejoint reed grass). Habitat type series of the temperate zone included: *Abies lasiocarpa/Xerophyllum tenax* (beargrass), and *Abies lasiocarpa/Menziesia ferruginea* (fool's huckleberry). The *Abies lasiocarpa/Luzula hitchcockii* (smooth woodrush) and the *Pinus albicaulis/Abies lasiocarpa* were common series in the subalpine zone.

Vegetation in the Study Area was mapped using a 28 August 1988 Thematic Mapper (TM) satellite imagery scene (Manley et al. 1992). Our computer image processing procedures and final classification methods are given in Appendix D.

Using the satellite imagery, vegetation in the Study Area was first classified as either open ($\leq$ 10% conifer overstory), open-timbered (>10 and $\leq$ 40% overstory), or timbered (> 40% overstory). Open and open-timbered habitats were then classified as either nonvegetated rock lands, grass/forb lands, or shrub lands. Three additional landscape features were then combined with the satellite image (Fig. 2.4). Using 1:24,000 orthophoto quadrangles, we mapped avalanche chute and slabrock polygons. Finally, digitized maps of timber harvest units were

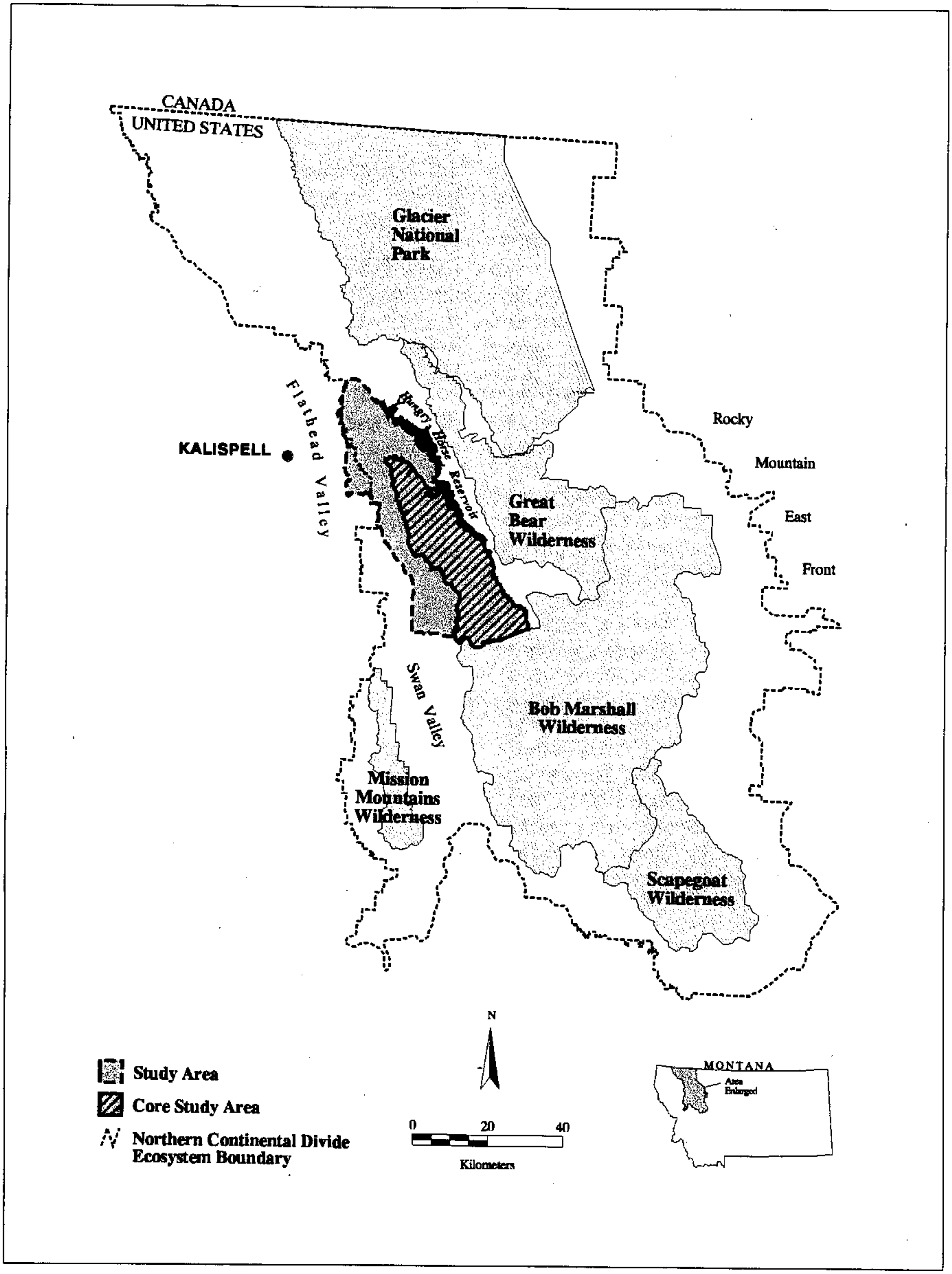


Figure 2.1. Location of Study Area in the Swan Mountains of western Montana.

added to the image. Dominant taxa of each cover type are given in Appendix D.

The Study Area was of mixed land ownership. Most (84%) of the land base was public lands administered by the Flathead National Forest (U.S.D.A Forest Service). Eight percent of the Study Area was private lands which occurred along the Flathead Valley-Swan Mountain interface. Private lands were generally developed for permanent homes, farms, and service facilities. The remaining land was either State or corporate timber lands.

Major communities in the Flathead Valley included Kalispell, Columbia Falls, and Whitefish. The Small town of Swan Lake along the upper reaches of the Swan Valley was within the Study Area. Human density in the Flathead Valley varied from > 39 humans/km^2 in the city of Kalispell, to < 10 humans/km^2 on private lands in more rural locations within or adjacent to the Study Area (U.S. Census data). Human density in the Swan Valley was approximately 0.4 humans/km^2. In 1995, the greater Kalispell area had 42,814 residents (Kalispell Bypass Feasibility Study, Boyer Consulting Services).

Public lands in the Study Area were administered by the USDA Forest Service under a multiple-use management strategy, and had a history of hydroelectric development, roading, and timber harvest since the early 1950's. The construction Hungry Horse Dam on the South Fork Flathead River was authorized by Congress in 1944. The area was cleared of timber during the period 1947 to 1952. Construction of Hungry Horse dam was initiated in 1948 and completed in 1953. The Reservoir, first reached full pool in 1954 (Casey et al. 1984), is 56 km long, and inundated 9,595 ha of riparian and upland habitat (Fig. 2.2)

Beginning in the late 1940's, a network of roads was established within the Study Area primarily to access 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. In the early 1980's, some roads were closed to improve wildlife security and other resources. A more aggressive closure program did not begin until approximately 1990. At present, there are 1,962 km of roads in the Study Area not reclaimed by natural vegetation. In 1990, 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 traveling by foot, bicycle, or horseback and some illegal vehicle use on closed roads occurred. Approximately 15% of the Study Area had been harvested for timber. Most timber harvest activity occurred in the low temperate and temperate zones. Further description of harvest activity in the Study Area can be found in Waller (1992).

Grizzly bears were studied in the Swan Mountains by researchers from the University of Montana from 1976-1978. The area was chosen as an example of "disturbed" habitat. The study was termed the Border Grizzly Project, and the team conducted periodic capture and telemetry studies. During this time, 12 grizzly bears were monitored for variable periods. Three theses were prepared during this period; a study of activity budgets (Sizemore 1980), the factors affecting huckleberry (*Vaccinium spp.*) production (Martin 1979), and a Ph.d thesis assessing the impacts of timber harvest on grizzly bears (Zager 1980).

Grizzly bears shared the Swan Mountains with other wildlife species. Ungulates included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*). Both deer species and elk wintered primarily at low elevations along the juncture of the Swan Mountains and the Flathead Valley. Small to mid-size carnivores present included pine marten (*Martes americana*), fisher (*Martes pennanti*), black bear (*Ursus americanus*), mountain lion (*Felis concolor*), bobcat (*Lynx rufus*), wolverine (*Gulo gulo*), and canada lynx (*Lynx canadensis*). Although transient wolves (*Canis lupus*) were observed by study personnel, no pack behavior or reproduction was observed.

CHAPTER 3
RESOURCE SELECTION

Grizzly bears respond to various natural resources in their environment. These natural resources include vegetation, food, and topography. Therefore, as the quality, quantity, and distribution of these resources varies across a landscape, one would expect selection by grizzly bears to vary. Even within the Swan Mountain study area, natural resources and topography varied geographically. Because of this geographic heterogeneity, resource selection often varied by individual grizzly bear, and depended on the age of the bear, its' gender or reproductive status, and its' relation to adjacent bears. For these reasons, and because grizzly bears are wide-ranging, intelligent, and omnivorous, one should not expect all bears to respond the same, even in an environment that seems to human eyes as similar.

In this chapter we have condensed our current knowledge of resource selection by Swan Mountain grizzly bears. We consider our findings to be a broad-scale approach to selection, as it was not an objective of our research to detail fine-grain or micro habitat selection parameters. The Chapter is composed of 4 sections: 1) seasonal habitat selection, 2) habitat characteristics of core home range areas, 3) the observed relationship between grizzly bears and timber harvest, and 4) resource selection at various landscape scales and bear densities. Most topics represent what has been termed "second-order selection" meaning that we estimated selection within grizzly bear home ranges. For each topic, resource selection was estimated using GIS technology, satellite imagery, and telemetry data obtained from instrumented animals.

SECTION 3.1

GRIZZLY BEAR HABITAT SELECTION IN THE SWAN MOUNTAINS, MONTANA[1]

J. S. Waller and R. D. Mace

ABSTRACT: In the contiguous United States grizzly bears (*Ursus arctos h.*) are classified as a threatened species, thus resource managers have a continuing interest in how grizzly bears use available habitats. We examined the use of satellite derived cover types by 19 individual radiomarked grizzly bears over 8 years and developed a hierarchial preference classification. We found that avalanche chutes were used in higher proportions than available during all seasons, along with slab rock. Shrub fields and timber harvest units were selected relative to availability during the summer and fall. Forested areas were among the least selected cover types during all seasons. Clear patterns of elevational movement were identified and were similar among most bears.

INTRODUCTION

Wildlife managers have sought to understand the seasonal patterns of grizzly bear habitat selection. Past grizzly bear habitat research efforts can be grouped into 2 categories. The first includes those that described the vegetative characteristics of grizzly bear habitat (Craighead et al. 1982, Blanchard 1983, Butterfield and Key 1985, Leach 1985, Mace and Bissell 1985, Aune and Kasworm 1989). The second group described habitat components and used telemetry data to examine selection patterns among the components (Servheen 1981, Kasworm 1985, Hamer and Herrero 1987, Hamilton and Bunnell 1987, Wielgus and Bunnell 1994b).

This study belongs to the second group, but was of longer duration and obtained larger sample sizes. We describe 7 broad cover types, derived from satellite imagery, and test for selection by grizzly bears among the cover types using telemetry data. We also describe patterns of seasonal elevational movement.

STUDY AREA

The 1,457 km^2 study area was located in the Swan Mountains of northwestern Montana. The study area was bordered by the Flathead River and the town of Hungry Horse to the north, Hungry Horse Reservoir to the east, the Bob Marshall Wilderness to the south, and the Swan and Flathead valleys to the west. Pacific maritime weather patterns prevailed. Average annual precipitation exceeded 250 cm, the majority being snow accumulation at higher elevations. The study area was characterized by rugged mountain topography with elevations varying from 915 m in the Flathead valley to 2,316 m along the crest of the Swan Mountains. Variations in slope, aspect, elevation, fire history, moisture, and land use has resulted in a complex mosaic of vegetation communities. Fifty-one community types were described and mapped within the study area (Hadden et al. 1987). These community types ranged from dry grasslands on steep southerly aspects to moist Sitka alder/devil's club (*Alnus sinuata/Oplopanax horridum*) shrub fields in riparian areas.

The primary land-uses were timber harvest and recreation. About 14% of the study area had been modified by timber harvest (Waller 1992). A network of roads existed in most drainages and was described in detail by Mace et al. (1996). Road construction began during the construction of Hungry Horse dam in the late 1940s. The dam permanently flooded 9,712 ha of riparian and upland habitats (Casey et al. 1984).

METHODS

Capture and Telemetry

Adult (≥ 5 years old) and subadult grizzly bears were captured and radiocollared (Table 3.1.1) as described by Mace et al. (1994). Radiocollared bears

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[1] Waller, J. S., and R. D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. J. Wildl. Manage. 64(4):00.00

Figure 2.2. The western border of the Study Area (top), looking north towards Glacier National Park, showing the abrupt transition between the Swan Mountains which are occupied by grizzly bears, and the rural Flathead Valley where bears occasionally ventured. Hungry Horse Reservoir (bottom), completed in 1953, was the eastern boundary of the Study Area.

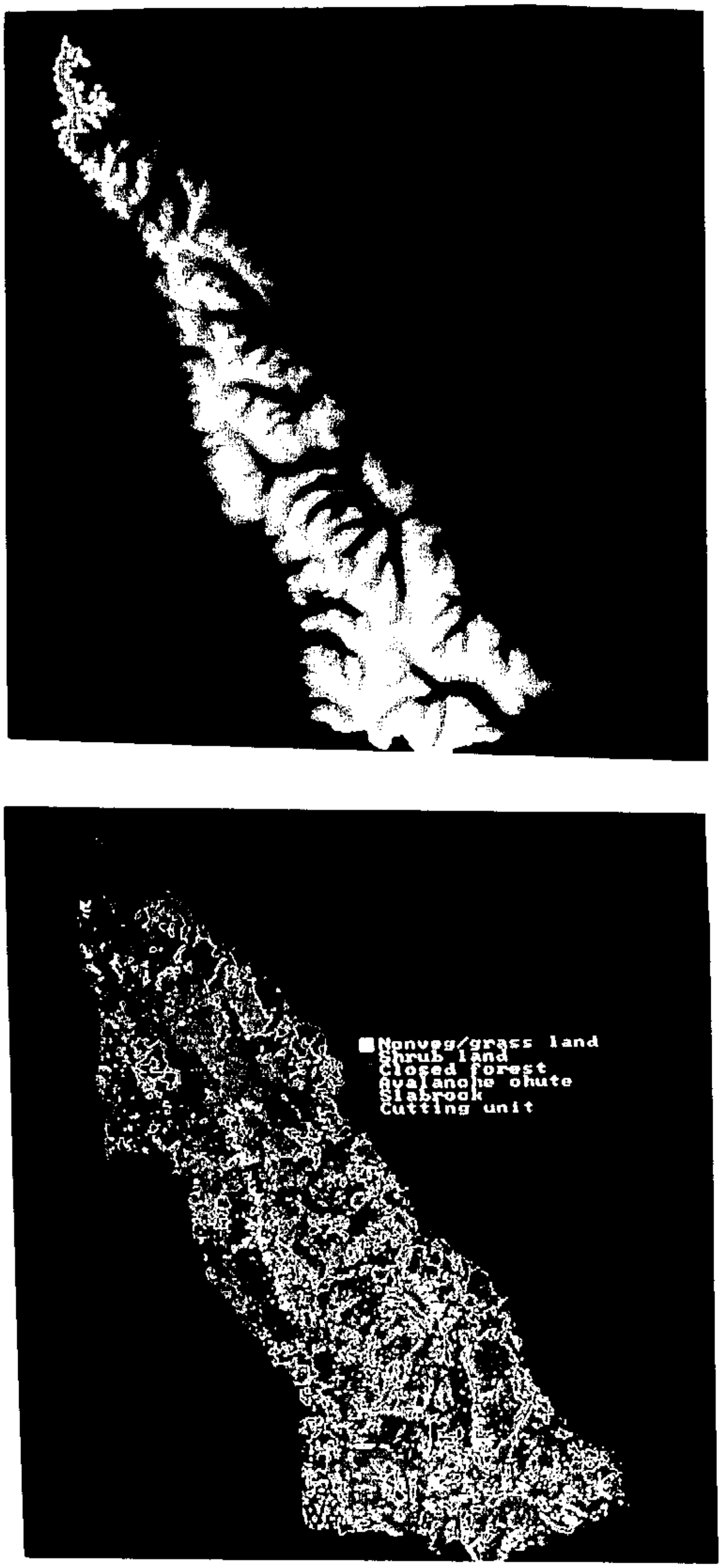

Figure 2.3. Digital elevation map (top) of the Swan Mountain Area depicting 3 elevation zones (low temperate, temperate, and subalpine) which were established based on dominant conifers. Thematic Mapper (TM) satellite map of the Study Area (bottom). Satellite data were classified into 7 dominant cover types based on field validation plots and aerial photographic interpretation.

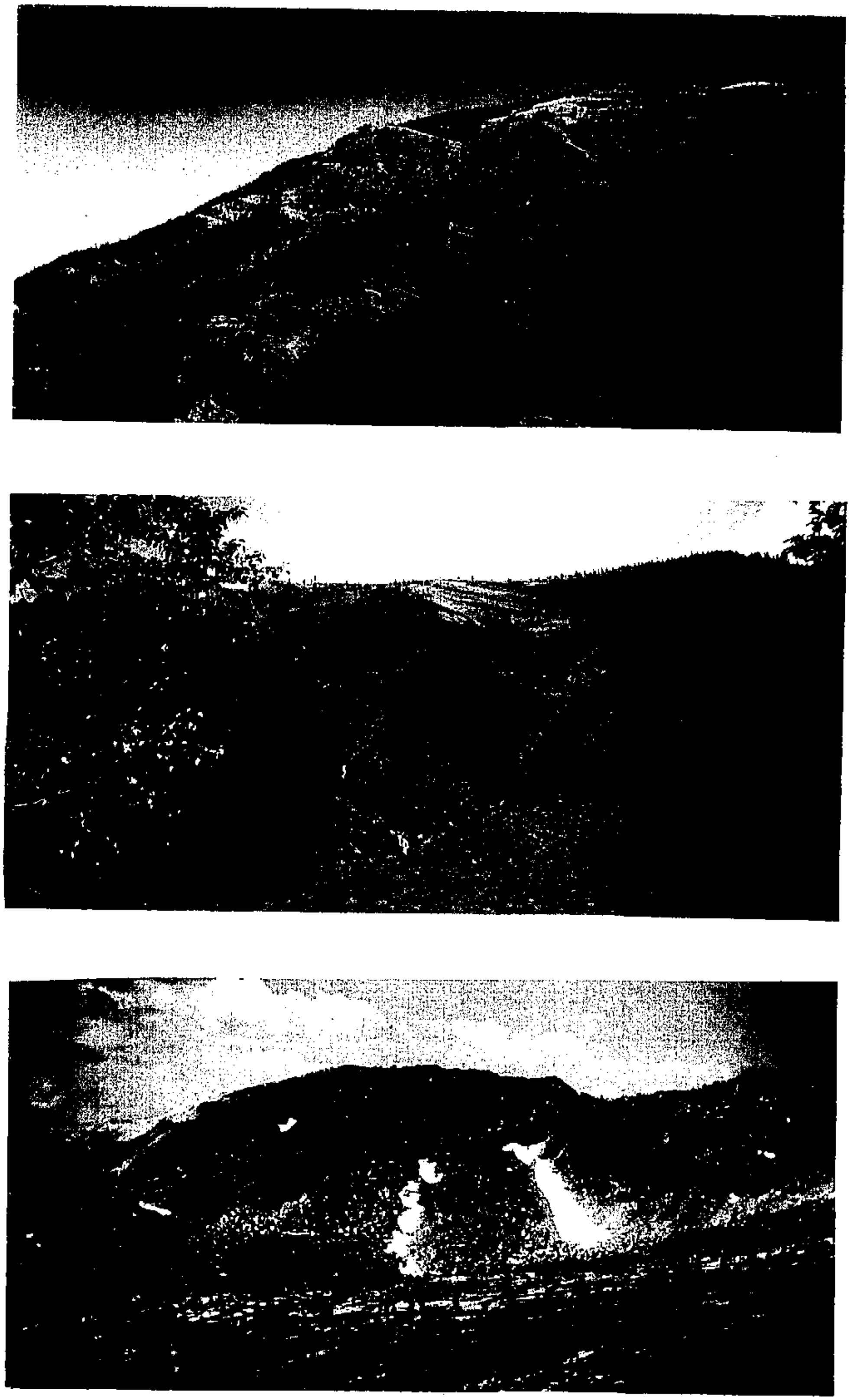

Figure 2.4. Photographs of 3 cover types important to grizzly bears in the Swan Mountains: the nonvegetated/grass land type (at top), avalanche chutes (center), and the slabrock cover type in foreground at bottom.

Table 3.1.1. Year and age at first capture, seasonal home range size, and percent of home range within the study area for each radiocollared grizzly bear, Swan Mountains, Montana.

Bear ID	Year	Age	Home range size (km^2) and percent within study area					
			Spring	%	Summer	%	Fall	%
F3	1987	1	667.5	67.2	287.0	90.1	324.4	76.9
F5	1987	7	206.6	92.2	107.9	100.0	62.6	100.0
F18	1989	2	61.9	100.0	109.8	100.0	74.6	99.8
F45	1990	19	143.4	97.6	156.0	100.0	124.3	100.0
F48	1990	10	107.5	100.0	154.0	100.0	82.7	100.0
F69	1992	3	301.5	77.0	192.8	95.7	80.6	90.9
F94	1988	8	80.1	93.0	87.2	99.2	117.3	100.0
F96	1988	15	149.0	100.0	151.8	100.0	119.8	99.6
F137	1988	1	136.0	90.4	182.3	98.9	92.7	100.0
F143	1988	5	136.4	100.0	75.8	100.0	86.7	100.0
F147	1987	1	387.5	68.0	270.9	72.9	314.4	74.3
M15	1993	7	448.9	65.2	582.8	87.0	379.5	94.3
M22	1989	3	1092.3	84.1	731.6	78.2	774.5	56.6
M25	1990	4	480.6	61.0	168.0	99.7	373.2	91.8
M71	1990	2	886.1	87.6	625.0	94.4	329.1	98.6
M144	1988	11	470.7	95.6	347.8	88.3	406.3	98.4
M146	1988	4	719.0	90.5	550.0	90.1	269.5	94.3
M149	1988	8	1178.5	60.0	993.0	62.5	918.2	64.2
M150	1988	6	480.1	88.5	517.7	90.8	438.2	99.9

were located from fixed-wing aircraft once per week in 1988 and 1989 and twice per week from 1990 through 1994. Optimal flying conditions, and thus our relocation flights, usually occurred between 0700 and 1100 hours. Each location site was photographed with self-developing film. Using these photographs and 1:24,000 orthophotographic quadrangles, we assigned each location a universal transverse Mercator (UTM) coordinate. Coordinates were then converted to map layers with EPPL7 (Minn. Land Manage. Info. Cent., 330 Centennial Building, 658 Cedar Street, St. Paul, MN 55155), a computerized geographic information system (GIS). Aerial telemetry locations were accurate to within 150 m, established by "blind" placement of radiocollars (Mace and Manley 1988).

Seasonal Home Range Estimates

We used the computer program CALHOME (Kie et al. 1996) to calculate seasonal multi-annual 95% adaptive kernel home ranges (Worton 1989) for 11 female and 8 male grizzly bears. We chose the 95% isopleth to measure potential grizzly bear occupancy but exclude short-term forreys. The home range polygons were then converted to GIS map layers.

Three seasonal foraging categories, (spring, summer, and fall), were defined based on observed changes in food habits, behavior, and prior literature (Craighead et al. 1982, Mace and Jonkel 1986). Spring was defined as the period from den exit to 15 July, summer as 16 July to 15 September, and fall as 16 September to den entrance.

GIS Mapping

A LANDSAT Thematic Mapper satellite image (Manley et al. 1992) was classified into 7 cover types based on spectral value, aspect, and aerial photo interpretation (Mace et al. 1996). These 7 classes were as follows: sites dominated by either rock or grass/forb communities (grass land/non-vegetated), natural shrub lands, sites with >40%

conifer overstory (forest), avalanche chutes (chutes), slabrock, timber harvest units (cuts), and those areas that could not be classified to a cover type due to shadow (unclassified). Unclassified areas consisted primarily of closed conifer forest and avalanche chutes on steep north and northwesterly aspects.

We used 1,416 rapid reconnaissance plots (Hadden et al. 1985,1987) to describe the vegetation in each cover type by 3 elevation zones; low temperate (870-1,494 m), temperate (1,495-1,981 m), and subalpine (>1,981 m). Each plot was assigned a GIS cover type based upon its UTM coordinates. Plant taxonomy followed Hitchcock and Cronquist (1973). Appendix D gives species lists for cover type and elevation zones, summarized by life form. Graminoids were ubiquitous in all cover types and zones, and were omitted. Each species' dominance (frequency of occurrence x mean canopy coverage) was standardized within cover type/elevation zones by: relative dominance = (dominance/ Σdominance) x 100.

To test the accuracy of the final cover type map we used 121 field plots (Manley et al. 1992). These plots, conducted to ground truth a previous satellite image classification, were selected to represent the geographic area, and the range of elevation and aspect of each spectral class. Ninety-one percent of the 121 plots were assigned a cover type consistent with the cover type map. Shrub land was misclassified as forest in 7 of the 11 classification errors. To address telemetry error, each 30-m pixel of the cover type map was assigned the dominant habitat within the surrounding 24 pixels (the telemetry error polygon) with a moving window routine.

Habitat Selection

We calculated selection indices for each bear during each season as the observed difference between the percent of each habitat used and the percent available. We ranked the indices from largest to smallest and used the Friedman nonparametric ANOVA on ranks to detect departures from random (Alldredge and Ratti 1986, 1992; White and Garrott 1990). If the test statistic exceeded the critical value ($1-\alpha$) of the F-distribution, selection was presumed to be occurring. If selection was detected, multiple comparisons were made to identify those habitats, or groups of habitats, that were significantly different (Conover 1980).

The elevation of each aerial telemetry location was recorded and entered into our database. We combined each bears average weekly elevation over all years to examine patterns of elevational movement. Box-whisker plots were used to display the median and range of average elevations for each sex by week. We used the computer program Statistica (Statsoft Inc., 2325 East 13th St., Tulsa, OK 74104) for all statistical tests.

RESULTS AND DISCUSSION

We found that cover type selection occurred during all 3 seasons ($P \leq 0.015$), despite variation among individual grizzly bears (Tables 3.1.2 - 3.1.4). Using multiple comparisons, we were able to group the 7 cover types into 3 to 4 distinct rankings, depending on sex and season. Although telemetry locations usually were during the morning, grizzly bears within our study area were crepuscular and moved little during the night (Mont. Fish, Wildl. and Parks, unpubl. data).

Males and females used avalanche chutes more than other cover types during each season (Tables 3.1.2- 3.1.4). During spring, avalanche chutes were selected significantly more than all other cover types by both sexes (Table 3.1.2). During summer, avalanche chutes again were selected by both sexes, but equally with slabrock and cuts, and for females, with shrub lands (Table 3.1.3). During fall, avalanche chutes and shrub lands were selected equally as the most used cover types, in addition to slabrock by females (Table 3.1.4). In the Northern Continental Divide Ecosystem (NCDE), avalanche chutes long have been recognized as preferred spring bear habitat, however they continued to be selected relative to availability through summer and fall. Continued use most likely is due to the presence of herbaceous forage associated with riparian areas in the chutes (Mace and Bissell 1985), and with the visual security and temperature moderation provided by dense stands of alder.

The slabrock cover type also remained important during each season. Slabrock is characterized by uplifted, exposed, and often terraced bedrock. Soil development has occurred between these terraces through erosion, and thus a unique vegetation community has been established. Vegetation composition in these terraces was variable, but often contained patches of preferred bear foods such as spring beauty (*Claytonia lanceolata*), glacier lily (*Erythronium grandiflorum*), and biscutroot (*Lomatium sandbergii*)(Mace 1985).

The increased use of shrub lands and cuts during the summer and fall could be explained by the

Table 3.1.2. Spring season differences between percent used and percent available cover types, rankings (in parentheses), selection groupings*, and telemetry sample sizes for female and male grizzly bears, Swan Mountains, Montana 1988-95.

Bear ID	Cover type							
	Unclassified	Grass/nonveg	Shrub land	Forest	Av. chute	Slabrock	Cutting unit	n
F3	-4.50 (3)	-2.68 (4)	13.78 (6)	-14.45 (1)	16.90 (7)	-2.21 (5)	-6.79 (2)	26
F5	2.62 (6)	-1.13 (3)	-1.01 (5)	-1.11 (4)	16.14 (7)	-2.12 (2)	-13.39 (1)	76
F18	-3.15 (3)	-0.58 (5)	-0.62 (4)	-14.50 (1)	29.56 (7)	0.97 (6)	-11.69 (2)	83
F45	1.19 (5)	-2.50 (4)	-4.17 (2)	-3.48 (3)	10.50 (7)	4.85 (6)	-6.14 (1)	72
F48	2.89 (6)	0.003 (5)	-2.16 (3)	-19.02 (1)	27.30 (7)	-0.91 (4)	-8.10 (2)	75
F69	-5.22 (1)	-3.95 (2)	10.10 (7)	0.65 (5)	-0.79 (4)	-3.79 (3)	3.01 (6)	14
F94	11.03 (7)	-2.17 (3)	-1.32 (4)	-7.02 (2)	9.68 (6)	0.00 (5)	-10.19 (1)	64
F96	-1.86 (5)	-2.42 (3)	-1.29 (6)	-16.37 (1)	26.74 (7)	-2.23 (4)	-2.53 (2)	88
F137	-4.66 (3)	-1.98 (5)	-1.75 (6)	-22.26 (1)	44.48 (7)	-2.17 (4)	-11.65 (2)	36
F143	4.08 (3)	4.19 (5)	-8.12 (2)	-39.65 (1)	36.12 (7)	10.82 (6)	0.72 (4)	30
F147	-0.24 (5)	1.56 (6)	-5.49 (1)	-2.70 (2)	9.11 (7)	-1.09 (4)	-1.64 (3)	65
All females*	B	B	B	C	A	B	C	
M15	-4.39 (2)	16.07 (7)	0.43 (4)	-13.01 (1)	2.53 (6)	-2.80 (3)	1.18 (5)	10
M22	-3.49 (2)	-0.32 (4)	3.76 (6)	-15.70 (1)	14.12 (7)	-1.30 (3)	3.50 (5)	82
M25	-8.23 (2)	-0.71 (3)	1.25 (5)	11.32 (6)	11.98 (7)	-0.22 (4)	-14.40 (1)	18
M71	-4.25 (2)	-1.69 (5)	-3.40 (3)	-21.19 (1)	8.18 (7)	0.89 (6)	-1.82 (4)	78
M144	-5.43 (3)	-2.15 (4)	-7.68 (2)	-13.96 (7)	13.60 (6)	-1.84 (5)	-9.43 (1)	16
M146	-4.58 (2)	-2.22 (3)	6.62 (6)	10.47 (7)	-0.61 (4)	3.01 (5)	-12.12 (1)	20
M149	-4.43 (3)	9.74 (6)	0.15 (4)	-6.91 (2)	10.18 (7)	2.37 (5)	-11.09 (1)	25
M150	-0.92 (4)	-2.10 (2)	-3.67 (1)	3.95 (7)	3.78 (5)	-1.81 (3)	3.94 (6)	20
All males *	C	B	B	B	A	B	C	

*Selection groupings: cover type groups that are used equally have the same alphabetic code, and are significantly different from those groups with a different code, for example: A is different from B and B is different from C, BC is different from A, but is not different from B or C. BC is different from A, but is not different from B or C.

availability of fruit-bearing shrubs that occurred in these cover types. Cuts and natural shrub fields created by fire often produced abundant crops of globe huckleberry (*Vaccinium globulare*), mountain ash (*Sorbus scopularum*), and serviceberry (*Amelanchier alnifolia*) (Martin 1979, Zager 1980, Waller 1992).

Grizzly bears exhibited moderate selection for the grassland/non-vegetated cover type during each season. Fifty percent of this cover type occurred in the subalpine zone where food was generally less abundant (Craighead et al. 1982). Most bears selected the low temperate and temperate elevation zones during all seasons (Mace et al. 1996).

Forest was the least selected cover type among females during spring, and among males and females during summer and fall (Tables 3.1. 2- 3.1.4). During spring, the least selected cover types among males were cuts and unclassified areas, and among females, cuts and forest (Table 3.1.2). Unclassified and forested areas were among the least selected by both sexes during summer and fall (Tables 3.1.3 - 3.1.4). Other studies have shown an avoidance of timbered cover types (Servheen 1981, Almack 1985), while others suggest selection for this type (Blanchard 1983, Aune 1994). The forest cover type covered 62% of our study area. While we found that, statistically, forest was among the least selected cover types during all seasons, it is important to remember that about 50% of all radiolocations occurred in this type during all seasons.

During any particular day, grizzly bears could be found at any elevation (bounded by the availability of elevations within the individuals home range). However, after smoothing, clear patterns of elevational movement became apparent for both male and female grizzly bears (Fig. 3.1.1). The pattern of weekly movements were the same for males and females, but females were, on average, 95 m higher during spring and summer and 147 m higher during the fall. Use of lower elevations entailed greater risk of encountering humans (Mace et al. 1996). Our interpretation of these movements is that during spring bears moved to lower elevations, after emerging from their dens, to seek green vegetation and carrion. During mid-spring, median elevation then increased as bears tracked optimum plant phenologies (Mealey 1980, Sizemore 1980, Hamer and Herrero 1987). During early summer, median elevations dropped slightly as bears exploited early ripening huckleberries at lower elevations, then followed the pattern of ripening to higher elevations (Martin 1979). Median elevation then declined as food resources at higher elevations became unavailable due to frost and snow. Similar patterns of seasonal movement have been documented in Yellowstone National Park (Mealey 1980), Glacier National Park (Martinka 1972), Jasper National Park, Canada (Mundy and Flook 1973), Mission Mountains, Montana (Servheen 1981), and Denali National Park (Darling 1987). The observed pattern was hidden by daily and yearly variation among bears and substantial smoothing of our data was required to observe this pattern (Schooley 1994). However, this general pattern is appropriate to areas where topographic relief causes site

Table 3.1.3. Summer season differences between percent used and percent available cover types, rankings (in parentheses), selection groupings*, and telemetry sample sizes for female and male grizzly bears, Swan Mountains, Montana 1988-95.

Bear ID	Cover type							
	Unclassified	Grass/nonveg	Shrub land	Forest	Av. chute	Slabrock	Cutting unit	n
F3	-5.87 (2)	-2.85 (3)	14.39 (7)	-28.00 (1)	11.39 (6)	8.23 (5)	2.73 (4)	26
F5	-2.49 (2)	-2.29 (3)	1.43 (5)	-6.48 (1)	1.12 (4)	2.39 (6)	6.32 (7)	72
F18	1.72 (4)	-0.94 (3)	9.49 (6)	-18.19 (1)	10.51 (7)	2.34 (5)	-4.93 (2)	69
F45	-5.55 (1)	-0.006 (5)	1.13 (6)	-3.64 (3)	-0.94 (4)	13.84 (7)	-4.86 (2)	58
F48	-2.67 (2)	-0.44 (5)	0.46 (6)	-7.08 (1)	-1.40 (3)	-0.71 (4)	11.86 (7)	60
F69	2.91 (5)	-2.62 (3)	-1.20 (4)	-10.63 (1)	-4.69 (2)	11.48 (7)	4.75 (6)	24
F94	0.17 (5)	-3.43 (1)	4.32 (7)	-1.86 (2)	-1.68 (3)	0.00 (4)	2.46 (6)	52
F96	-3.66 (3)	-0.53 (4)	5.42 (5)	-18.46 (1)	5.61 (6)	16.41 (7)	-4.78 (2)	68
F137	-4.05 (2)	-2.06 (3)	-0.55 (5)	-6.69 (1)	15.34 (7)	-0.24 (6)	-1.75 (4)	41
F143	1.09 (4)	0.63 (3)	11.38 (7)	-14.85 (1)	3.40 (6)	-3.62 (2)	1.98 (5)	30
F147	-2.54 (2)	-0.35 (4)	5.24 (6)	-28.26 (1)	4.52 (5)	-2.16 (3)	23.55 (7)	44
All females*	C	BC	A	D	A	A	AB	
M15	10.45 (6)	5.21 (4)	6.24 (5)	-22.91 (1)	-6.85 (3)	21.12 (7)	-13.27 (2)	13
M22	-3.79 (2)	-0.08 (3)	6.45 (6)	-29.03 (1)	4.16 (4)	4.47 (5)	18.30 (7)	50
M25	-8.99 (2)	-0.28 (4)	6.08 (6)	-11.49 (1)	9.88 (7)	-0.28 (3)	5.09 (5)	32
M71	-4.25 (2)	-2.05 (3)	2.61 (5)	-28.21 (1)	4.09 (7)	-0.28 (4)	4.06 (6)	78
M144	-4.14 (2)	-1.66 (3)	-6.90 (1)	-1.24 (4)	13.62 (7)	-1.07 (5)	1.39 (6)	10
M146	-4.62 (2)	-2.00 (3)	-6.02 (1)	10.18 (7)	3.78 (6)	-1.42 (4)	1.12 (5)	13
M149	-2.31 (3)	2.26 (5)	3.57 (6)	-5.10 (2)	-1.21 (4)	5.54 (7)	-5.19 (1)	42
M150	-4.74 (3)	6.94 (6)	-8.88 (1)	2.71 (5)	-7.00 (2)	-1.68 (4)	12.66 (7)	11
All males *	C	B	B	C	A	A	A	

*Selection groupings: cover type groups that are used equally have the same alphabetic code, and are significantly different from those groups with a different code, for example: A is different from B and B is different from C, BC is different from A, but is not different from B or C.

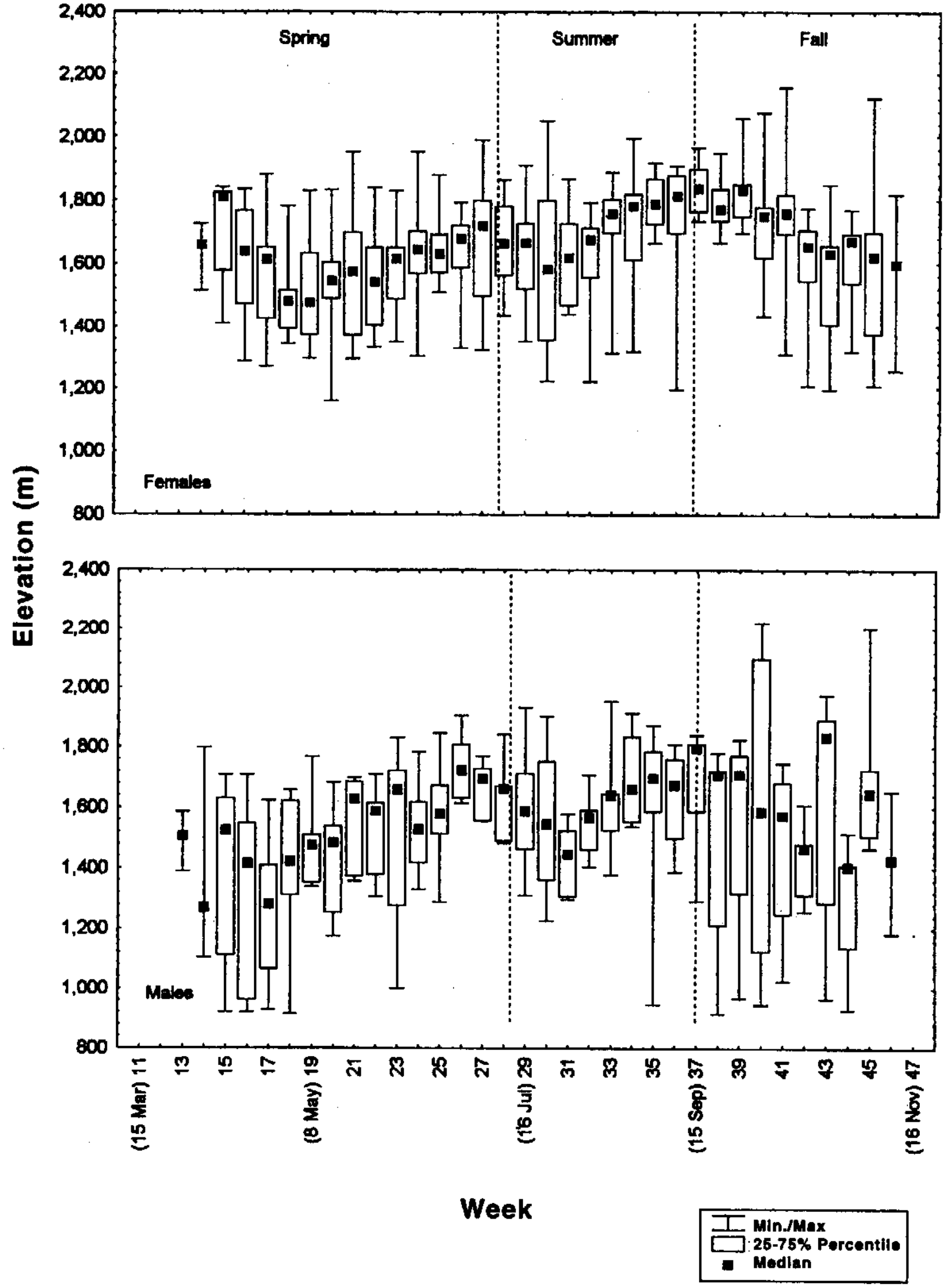

Figure 3.1.1. Median average elevation (m) by week for 12 female (top) and 8 male (bottom) grizzly bears 1988-94, Swan Mountains, Montana.

Table 3.1. 4. Fall season differences between percent used and percent available cover types, rankings (in parentheses), selection groupings*, and telemetry sample sizes for female and male grizzly bears, Swan Mountains, Montana 1988-95.

Bear ID	Cover type							
	Unclassified	Grass/nonveg	Shrub land	Forest	Av. chute	Slabrock	Cutting unit	n
F3	-4.49 (2)	-3.39 (3)	11.66 (7)	0.78 (5)	-0.06 (4)	4.05 (6)	-8.51 (1)	13
F5	-2.42 (2)	-0.67 (5)	-1.16 (3)	4.84 (6)	5.95 (7)	-0.75 (4)	-5.78 (1)	44
F18	5.79 (5)	-0.57 (3)	9.62 (6)	-21.73 (1)	10.42 (7)	-0.10 (4)	-3.44 (2)	40
F45	-6.05 (1)	-2.04 (3)	3.35 (6)	4.69 (7)	3.29 (5)	2.29 (4)	-5.53 (2)	45
F48	-2.34 (2)	-0.42 (6)	-1.62 (3)	-7.28 (1)	-1.13 (4)	-0.43 (5)	13.22 (7)	37
F69	-0.19 (3)	-3.18 (2)	2.86 (5)	-14.85 (1)	-5.05 (6)	10.16 (7)	0.15 (4)	19
F94	-2.45 (4)	-2.58 (3)	12.60 (7)	-4.61 (2)	-4.76 (1)	0.00 (5)	1.81 (6)	27
F96	2.38 (4)	-1.37 (3)	8.85 (6)	-19.61 (1)	14.40 (7)	4.81 (5)	-5.25 (2)	42
F137	0.04 (3)	-1.66 (2)	13.86 (6)	-31.89 (1)	17.24 (7)	1.92 (5)	0.51 (4)	23
F143	-1.10 (5)	-2.62 (4)	28.38 (7)	-24.33 (1)	13.29 (6)	-3.08 (3)	-10.55 (2)	19
F147	-2.59 (2)	-0.88 (4)	7.61 (7)	-1.32 (5)	5.32 (6)	-2.51 (3)	-10.03 (1)	25
All females*	C	BC	A	C	A	AB	C	
M15	-4.21 (3)	-2.75 (4)	-9.89 (1)	-0.53 (6)	-7.82 (2)	-2.24 (5)	27.43 (7)	5
M22	-4.80 (2)	-2.18 (3)	10.06 (7)	-9.23 (1)	2.02 (5)	-1.77 (4)	6.92 (6)	31
M25	-1.05 (3)	-0.88 (4)	22.75 (7)	-21.07 (1)	5.52 (6)	-0.51 (5)	-3.57 (2)	19
M71	1.84 (6)	-2.22 (4)	1.65 (5)	-6.63 (1)	10.47 (7)	-2.33 (3)	-2.78 (2)	42
M144	-6.32 (3)	-1.83 (4)	22.50 (6)	-27.40 (1)	25.70 (7)	-1.80 (5)	-10.85 (2)	6
M146	-4.93 (1)	-2.57 (3)	2.30 (6)	10.24 (7)	-2.96 (2)	-2.54 (4)	2.02 (5)	11
M149	-4.56 (2)	-2.55 (4)	13.81 (6)	-29.03 (1)	27.21 (7)	-1.71 (5)	-3.16 (3)	9
M150	-4.98 (2)	-3.04 (3)	4.54 (5)	-5.10 (1)	48.94 (7)	-2.59 (4)	5.09 (6)	7
All males *	D	C	A	D	A	B	BC	

*Selection groupings: cover type groups that are used equally have the same alphabetic code, and are significantly different from those groups with a different code, for example: A is different from B and B is different from C, BC is different from A, but is not different from B or C.

specific variation in food plant phenology. Grizzly bears are a widely distributed holarctic species capable of exploiting a wide variety of habitats within large home ranges. Thus, departures from this general pattern are certain to be found, as documented by Hamer and Herrero (1987). Furthermore, grizzly bears are not always feeding, and do not forage necessarily where the probability of food occurrence or optimum phenology is highest. Furthermore, grizzly bears have physiological and behavioral requirements other than feeding - such as thermal regulation, security, and breeding.

MANAGEMENT IMPLICATIONS

Bear foods occur in relatively small microsites within broad cover types. This patchy distribution of foods, combined with the grizzly bear's capacity for learning and tradition, make modeling difficult. However the selection of avalanche chutes over other cover types in this study area transcends analysis technique. Avalanche chutes clearly are an important habitat component, even in proximity to roads (Mace et al. 1996). Management should be structured to protect avalanche chutes that produce preferred bear foods from human disturbance.

We have ranked cover types in order of use, but we do not imply that this ranking is in order of importance. Cover types that rank low in use may be critical environmental components for grizzly bears. The juxtaposition of human activity and environmental condition related to demography is the ultimate test of how effective the study area is, and how effectively we are ensuring the continued survival of the grizzly bear.

SECTION 3.2

CHARACTERISTICS OF GRIZZLY BEAR CORE HOME RANGE AREAS IN WESTERN MONTANA[1]

R. D. Mace and J. S. Waller

INTRODUCTION

The Northern Continental Divide Ecosystem (NCDE), identified as 1 of 6 grizzly bear (*Ursus arctos horribilis*) recovery areas (U.S. Dep. Int. Fish and Wildl. Serv. 1993), was composed of private, corporate, state, federal, and tribal lands. A significant portion of the NCDE has been altered by timber harvest, grazing, hydroelectric development, agriculture, and road and trail development.

Management of human access on federal multiple-use lands within the NCDE has been identified as a key element of habitat and population management programs for grizzly bears (U.S. Dep. Int. Fish and Wildl. Serv. 1993). Interim human access guidelines in the NCDE are composed of 2 primary elements: standards based on the density of roads and associated levels of vehicular use, and the maintenance of "core areas" that would provide security to grizzly bears for each season. Road standards are based on published information for the species (Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996). Habitat managers have found it difficult to create and manage core areas within management units for lack of definition. Recurring management questions regarding core areas for grizzly bears include: how large should they be?, which seasonal habitats need be present?, and what types and levels of human access can occur in core areas while maintaining effectiveness?

In this paper we describe some attributes of core areas within seasonal home ranges of grizzly bears. We describe habitat and road characteristics within core areas and compare them to peripheral portions of the home range.

METHODS

Capture, Telemetry, and Home Range Parameters

Beginning in 1988, adult (≥ five years old) and subadult grizzly bears were captured and radio-collared (Mace et al. 1994). Radio-collared grizzly bears were located once per week during 1988 and 1989, and twice each week during 1990-1994 from fixed-wing aircraft. Each relocation was assigned a universal transverse Mercator (UTM) coordinate using 1:24,000 orthophotographic quadrangles. Other aspects of the capture and telemetry program are provided in Mace et al. (1994) and Mace et al. (1996). Grizzly bears averaged 179 days near, or in, winter dens and were therefore active 186 days of the year on average (Mace and Waller 1997c). During the active period, seasons were short (spring = 81 days, summer = 63 days, and autumn = 42 days). Ground telemetry was hindered by rugged mountain topography and poor access, and aerial telemetry was limited by inclement weather especially during spring and autumn. For these reasons, we were unable to estimate core home ranges for each individual annually, and therefore combined the summer and autumn seasons into 1 period (late season) to attain a minimum sample of 50 locations per individual each season.

We used the 95% adaptive kernel method (Worton 1989) to estimate the home ranges of grizzly bears during two seasons, early and late, using the program CALHOME (Kie et al. 1996). The early season was defined as the period following emergence from winter dens to 15 July when bears foraged primarily on succulent vegetation such as graminoids and cow parsnip (*Heracleum lanatum*). The late season was from 16 July to den entry when bears fed primarily on the fruit of globe huckleberry

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[1] Mace, R. D. and J. S. Waller. In Press. Characteristics of grizzly bear core home range areas in western Montana. Wildl. Soc. Bull.

(*Vaccinium globulare*), mountain ash (*Sorbus* spp.), and service berry (*Amelanchier alnifolia*).

We used the methods of Bingham and Noon (1997) to estimate seasonal core areas for those individuals with ≥ 50 seasonal telemetry relocations. Seasonal telemetry relocations were pooled across years for each individual to attain adequate samples for each season. For each individual, we constructed 9 home range isopleths from 10% to 90%. We then determined the size (km^2) of these isopleths, and for each, the percent area of the 95% isopleth.

We used the exponential regression ($y = e^{bx}$) procedure of Bingham and Noon (1997) to compute the % seasonal home range isopleth at which utilization was distributed as expected under a uniform random distribution. For each bear and season, we regressed x (% isopleth) on y (ln % of the 95% range) to determine the slope (b) of the line. Using this exponential regression procedure for 100 replicates of 50 random coordinates, Bingham and Noon (1997) determined that 90% of the slope parameters (b) were ≥ 0.051. Therefore, when regressions of seasonal bear home range data resulted in slopes of < 0.051, we concluded that seasonal locations were concentrating in a portion of the home range in a non-random fashion. Solving for x as: $x = (\ln(1/b))/b$, the % isopleth at which utilization was as expected under the uniform distribution was determined. This value of x represented the core isopleth for each grizzly bears' seasonal range, and the remainder of the 95% seasonal range was termed the peripheral area.

The core and peripheral areas for each individual were then converted to Geographical Information System (GIS) maps using the program EPPL7 (Minnesota Land Management Information Center. 300 Centennial Building, 658 Cedar Street. St. Paul, MN 55155). Core areas for each pair of grizzly bears were classified as overlapping, adjacent, or enclosed. Adjacent pairs were those individual pairs of grizzly bears having core areas within 3 km of one another. When one seasonal core area was entirely within another core, the core areas were termed enclosed (Mace and Waller 1997a). Percent overlap in core areas for each adjacent pair of grizzly bears was calculated as (overlap size/core size of animal A * overlap size/core size of animal B)$^{0.5}$

We were unable to build seasonal core areas for each bear by year because of small sample sizes, and therefore could not investigate annual shifts in core areas. As an indication of core area fidelity within individual among years, we determined the percentage of each years locations that occurred within the multi-year seasonal core for each bear.

Habitat Variables

The habitat characteristics of the core and peripheral home range areas of each individual were compared seasonally using 6 cover types, 3 elevation zones, and the density of roads. The cover types used were rock/grass land, shrub lands, forest, avalanche chutes, cutting units, and slabrock. Elevation zones used were the low temperate (< 1,494 m), the temperate zone (1494-1981 m), and the subalpine zone (> 1,981 m) (Mace et al. 1996).

The density of roads (km/km^2) within each seasonal core and peripheral area were calculated using digitized linear road maps. Roads were placed into 2 classes based on observed vehicular traffic levels. Low-use roads were those that were either closed to public vehicular travel or received ≤ 10 vehicle trips/day. High-use roads were those receiving > 10 vehicle trips/day (Mace et al. 1996). The variable "total road density" was the sum of low- and high-use density. We also calculated the percentage of "unroaded habitat"; those areas of core and peripheral areas that were > 0.5 km from any road.

Comparisons of variables between core and peripheral ranges were conducted using analysis of variance. Arcsine transformations were used for percentage data (Sokal and Rohlf 1981). Statistical significance was accepted at $\alpha = 0.05$.

RESULTS

We evaluated the characteristics of core and peripheral home range areas for 11 and 15 grizzly bears during early and late seasons respectively. The age and length of time grizzly bears were monitored varied by individual (Table 3.2.1.).

Grizzly bears did not move through their environment in a random fashion. Exponential regressions for each bear during both seasons fit the telemetry data well (Fig. 3.2.1). The slopes of all seasonal home range regressions were ≤ 0.051 and core areas were estimated.

Core isopleths were $\geq 70\%$ of the 95% home range for both sexes during both seasons (Table. 3.2.2.). Female core areas were smaller than those of males during both seasons (Table 3.2.2, Fig. 3.2.2). The percent core isopleths did not vary by sex or season ($P > 0.05$). Female early season core isopleths averaged 58 km^2 ± 38 (sd) and 74 km^2 ± 32 during the late season. We observed annual variability in the amount of time (% locations) individual bears spent in seasonal cores (Fig. 3.2.3). Percent time spent in seasonal cores varied from 29% to 100% and was ≥ 73% each year when individuals were pooled (Table 3.2.2).

We evaluated the extent of core area overlap between individual grizzly bears for 25 early season and 67 late season pairs. Seventy-three of 92 (79%) core ranges exhibited some overlap. Percent overlap of core areas for all combinations of male and female pairs averaged ≤ 28% during both seasons (Table 3.2.3). Percent overlap did not vary by pair type during early or late season ($P > 0.05$).

We evaluated the extent of early and late season core area overlap for 7 female and 3 male grizzly bears. Overlap between female early and late season core areas averaged 61% ± 10 (47 km^2 ± 26), and averaged 67% ± 7 (215 km^2 ± 78) for males.

Habitat and road variables differed between core and peripheral areas during the early season, but not during late season. During the early season, core areas had significantly greater proportions of avalanche chutes than the peripheral areas. During this season, core areas also exhibited signifi-

Table 3.2.1. Sex, age and seasonal telemetric sample size for grizzly bears in the Swan Mountains, Montana.

Bear	Sex (Age)[a]	Early Season Sample Size		Late Season Sample Size	
		Telemetry pnts	Months/yrs	Telemetry pnts	Months/yrs
5	F (7-13)	102	20/6	126	27/7
14	F (11-18)	88	26/8	122	32/8
18	F (2-10)	99	27/8	135	31/8
22	M (2-10)	108	33/8	136	35/8
25	M (4-5)			56	9/2
45	F (20-25)	84	19/6	115	25/6
48	F (10-16)	93	23/7	126	29/7
69	F (3-7)			55	16/5
71	M (2-8)	90	26/7	130	32/7
94	F (8-16)	103	27/8	103	30/8
96	F (15-23)	113	28/8	138	34/9
137	F (2-4)			64	11/3
143	F (5-7)			53	13/3
147	F (2-7)	99	20/7	85	21/5
149	M (8-15)	52	17/6	78	26/8

[a] Minimum-maximum age.

Table 3.2.2. Summary statistics for the core and 95% peripheral home range isopleths for male and female grizzly bears during 2 seasons. Size units are in km^2. Swan Mountains, Montana.

Sex	Early season Averages[a]				Late season averages[a]			
	Core Isopleth %	Core Size	Periphery Size	Annual % Use of Core	Core Isopleth %	Core Size	Periphery Size	Annual % Use of Core
Male	73 ± 12	404 ± 235	474 ± 175	73 ± 21	74 ± 3	235 ± 114	227 ± 85	82 ± 15
Female	70 ± 10	58 ± 38	74 ± 33	76 ± 18	83 ± 10	74 ± 32	64 ± 44	87 ± 15

[a] Mean ± Sd.

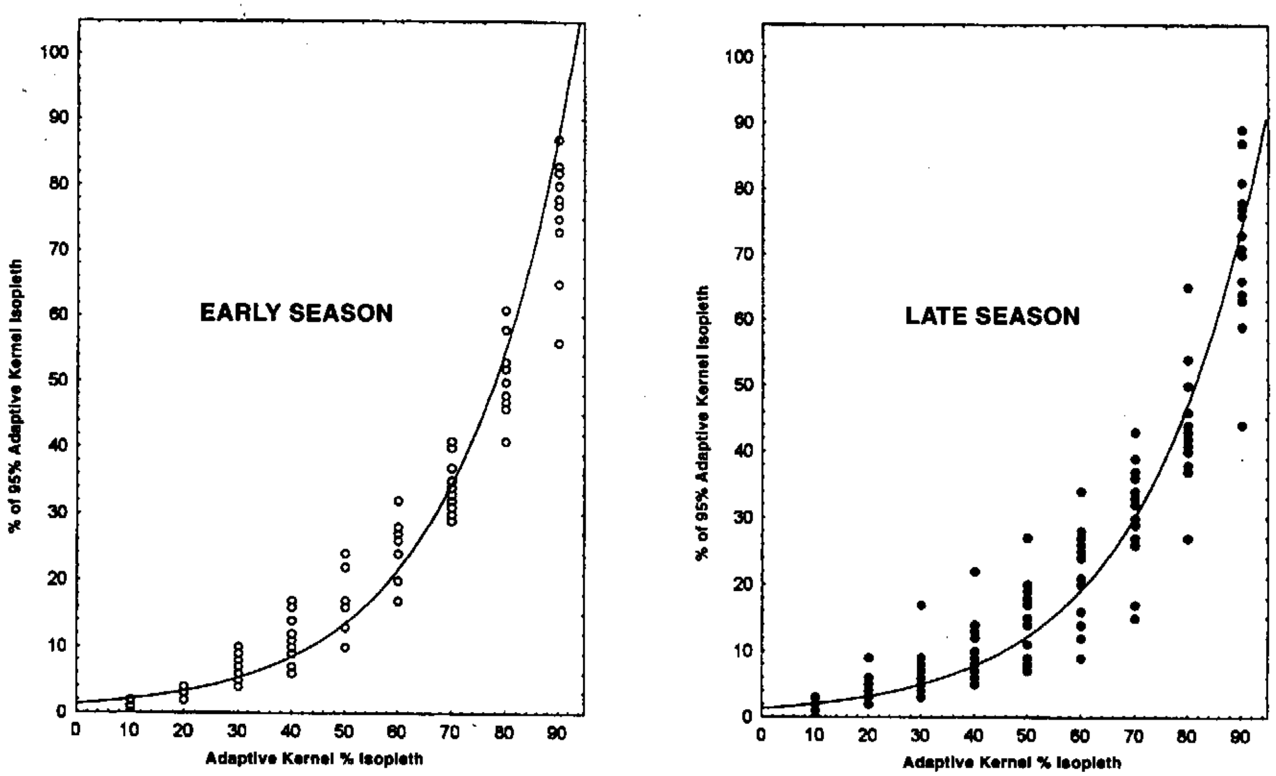


Figure 3.2.1. Relationship between the 95% adaptive kernel home range and 10% increments of the range for grizzly bears in the Swan Mountains, Montana.

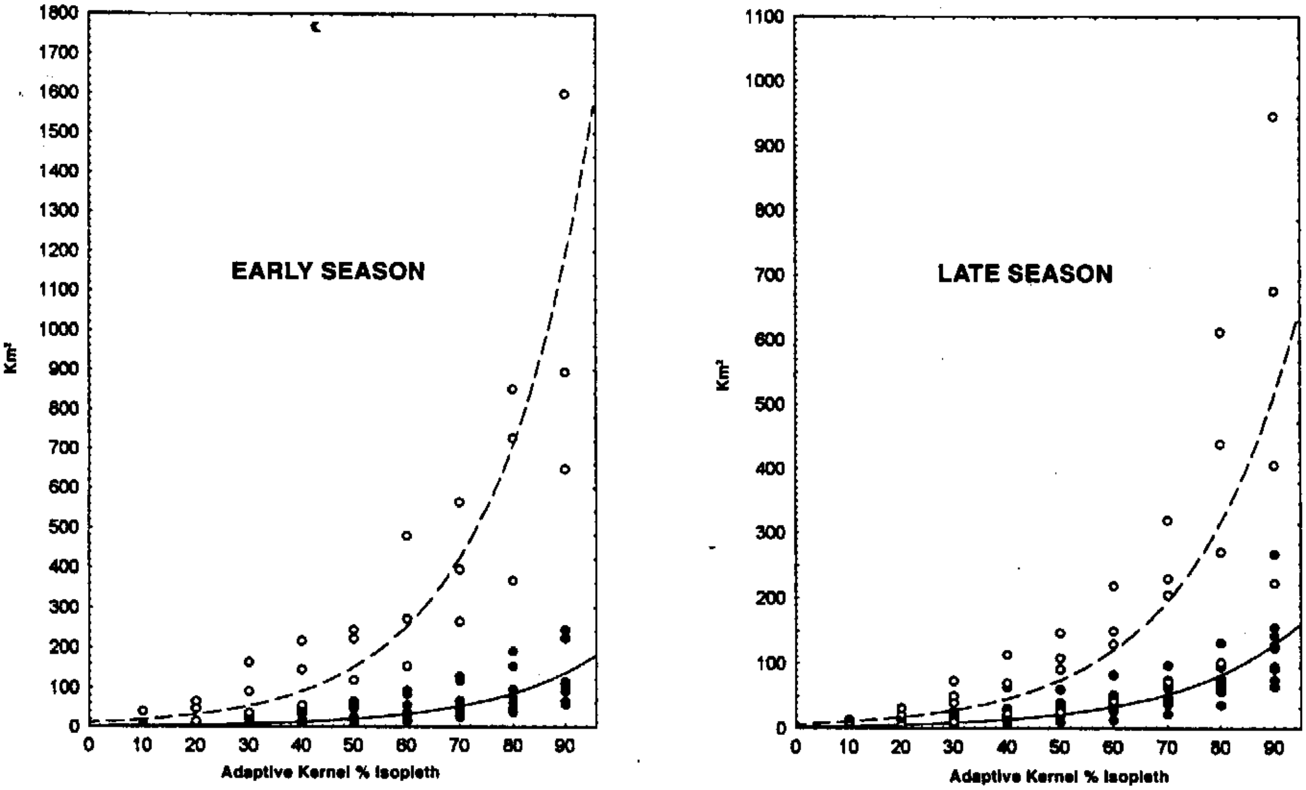


Figure 3.2.2. Size of each 10% increment of the 95% seasonal home range for grizzly bears in the Swan Mountains of Montana. Closed circles are females and open circles are males.

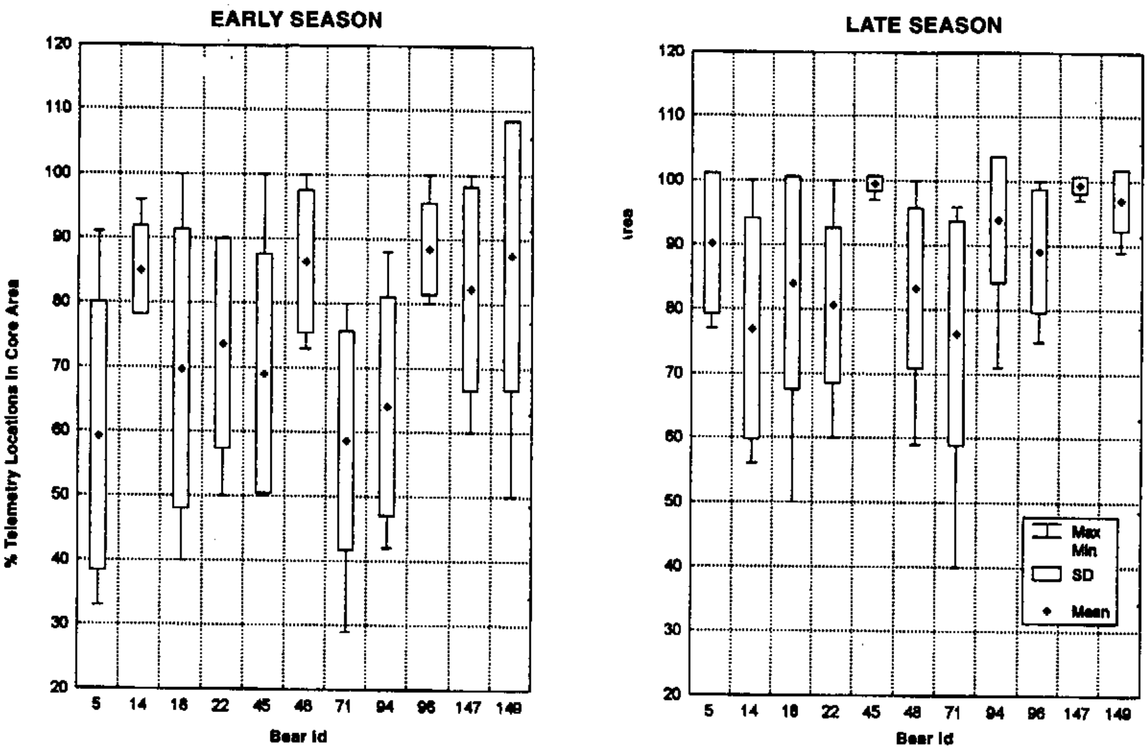


Figure 3.2.3. Percent of telemetry locations of each grizzly bear in the core area each year as an indication of annual fidelity to the core area.

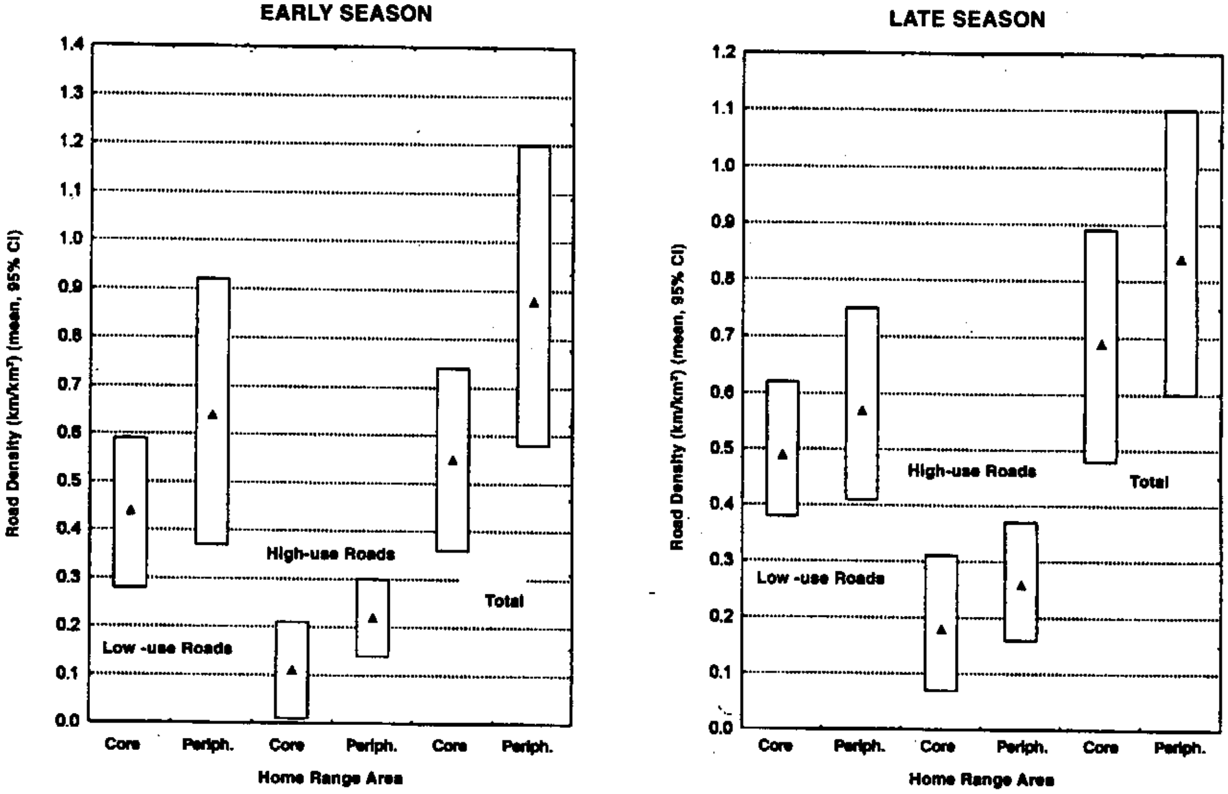


Figure 3.2.4. Mean and 95% confidence intervals for low-use, high-use and total road density in seasonal core and peripheral home ranges of grizzly bears, Swan Mountains, Montana.

Table 3.2.3 Percent of core overlap between male and female grizzly bears during each season. Swan Mountains, Montana.

Pair Type	Seasonal Overlap Statistics					
	Early season			Late season		
	% Overlap[a]	Overlap Size[a] (km^2)	Spatial Relationship[b]	% Overlap[a]	Overlap Size[a] (km^2)	Spatial Relationship[b]
Fem/fem	13 ± 17	6 ± 7	5,3,0	15 ± 16	13 ± 17	27,5,0
Fem/male	25 ± 20	35 ± 37	12,0,5	20 ± 17	35 ± 34	23,6,2
Male/male	28 ± 25	97 ± 51	3,0,0	21 ± 31	68 ± 98	3,1,0

[a] Mean ± Sd.

[b] Number of core areas that were adjacent, overlapping, or enclosed.

Table 3.2.4. Characteristics of grizzly bear core and peripheral home range areas, Swan Mountains, Montana.

Variable	Characteristics of core and peripheral home range areas[a]			
	Early season		Late season	
	Core	Periphery	Core	Periphery
Grass/rock	2.9 ± 2.0	2.8 ± 1.0	2.8 ± 2.0	3.1 ± 2.0
Shrub land	13.4 ± 3.0	12.4 ± 4.0	15.0 ± 3.0	14.0 ± 3.0
Forest	62.0 ± 5.0	62.0 ± 3.0	61.0 ± 4.0	62.0 ± 4.0
Chute	9.0 ± 5.0 [b]	4.0 ± 2.0	7.0 ± 3.0	6.0 ± 1.0
Slabrock	1.4 ± 1.0	1.3 ± 0.01	2.2 ± 2.0	2.0 ± 2.0
Cutting unit	11.0 ± 7.0	17.0 ± 7.0	12.0 ± 6.0	13.0 ± 5.0
Low temperate zone	25.2 ± 10.0 [b]	43.0 ± 11.0	24.0 ± 14.0	31.0 ± 12.0
Temperate zone	62.0 ± 9.0 [b]	47.4 ± 8.0	58.0 ± 15.0	55.0 ± 7.0
Subalpine zone	13.3 ± 6.0	9.7 ± 5.0	13.3 ± 9.0	14.0 ± 7.0
Low-use rds (km/km^2)	0.44 ± 0.2	0.64 ± 0.4	0.50 ± 0.2	0.58 ± 0.3
High-use rds (km/km^2)	0.11 ± 0.1 [b]	0.22 ± 0.1	0.19 ± 0.2	0.26 ± 0.2
Total road density (km/km^2)	0.54 ± 0.3 [b]	0.88 ± 0.4	0.69 ± 0.4	0.84 ± 0.4
Unroaded	64.4 ± 13.0 [b]	50.5 ± 14.0	62.0 ± 11.0	58.0 ± 11.0

[a] Mean percent of area of habitat, unroaded, and road density variables ± Sd.

[b] Core significantly different than periphery ($P < 0.05$).

cantly lower proportions of low temperate and higher proportions of temperate zone habitats than did the peripheral areas.

High-use and total road density were significantly lower, and unroaded area significantly greater, in the core than in the peripheral home range areas during the early season (Table 3.2.4, Fig. 3.2.4). No difference was observed between the 2 home range areas in low-use road density. Road variables were not different during the late season.

DISCUSSION

Information on the seasonal habitat requirements of grizzly bears in the Swan Mountains accumulated slowly. As a result, our core and peripheral area analyses represented grizzly bear selection over several years.

Core area size varied among individuals and season, yet the percent of the 95% seasonal range estimated as core varied relatively little. Core isopleths for males were larger during the early season relative to the late season. The converse was found for females. We believe the larger core size for males during the early season was due primarily to increased movements by reproductively active males during the breeding season. The extent of early season movements for females each year depended on whether they had young, and the age of the young. Daily movement rates of females with cubs-of-the-year were less than other classes of bears during this time (Appendix E).

During the late season, male core areas were smaller, a result of more restricted and concentrated foraging behavior. Female core areas were larger during the late season relative to the early season. It was during this season that bears fed extensively on the fruit of several shrubs to gain necessary fat reserves for denning.

Early season core areas differed from peripheral areas for several habitat features. Core areas tended to be at mid- to high-elevation sites (temperate and subalpine zones) during this season. These early season core areas were higher in proportional availability of avalanche chutes and lower in high-use road density and total road density than peripheral portions of the seasonal range. Core and peripheral areas could not be differentiated in terms of low-use roads; roads that were generally closed to public vehicular traffic or received low vehicular use. These data suggest during the early season, bears were concentrating their use in areas having minimum human disturbance. This displacement occurred at a time when much of the higher elevation habitat was still covered with winter snow.

We found no significant differences in habitat and road attributes between the core and peripheral areas during the late season. This was undoubtedly due to the larger core isopleths relative to the early season, and bear foraging activity in lower elevation shrub lands as fruit began to ripen.

Habitat management emphasis in the NCDE is placed on protection of female grizzly bears (Dood et al. 1985 , U.S. Dep. Agri. Fish and Wildl. Serv. 1993), and it seems logical that identification of female core areas should receive high priority for habitat conservation. Seasonal core areas for female grizzly bears were small (x = 58 km^2 during early season and x = 74% during the late season) relative to the entire seasonal home range and as such would be more easy to identify and protect. Further, seasonal core areas of individuals females overlapped extensively (x = 61%), suggesting that contiguous blocks of core habitat meeting the annual needs of females could be identified.

We believe that core areas should transcend elevation zones, and be composed of at least 9% avalanche chute habitat. The high forage value and security of avalanche chutes were described previously (Mace et al. 1996). Access management, typically through seasonal or permanent road closures, would be necessary within core areas to minimize disturbance and illegal mortality. At least 60% of core areas should be 0.5 km from the nearest road. As suggested by Mace et al. (1996), road density standards could be relaxed somewhat those areas with less suitable seasonal habitat. However, one must recognize that the peripheral areas described herein were not unused by grizzly bears. Peripheral areas were used less intensively by grizzly bears yet may have contained necessary elements for survival.

SECTION 3.3

GRIZZLY BEARS AND TIMBER HARVEST

J. S. Waller and R. D. Mace

Two events that probably had a large impact on the South Fork grizzly bear population were the construction of Hungry Horse reservoir and timber harvest. Hungry Horse dam, constructed between 1948 and 1953, flooded 9,712 ha of riparian and upland habitat. Accelerated timber harvest began during the early 1950's with the removal of approximately 90 million board feet (mbf) of timber that would soon be flooded by Hungry Horse reservoir. In 1947 the maximum allowable cut (MAC) on the Flathead National Forest (FNF) was 65 mbf. New silvicultural technologies, and the increasing postwar demand for timber, increased the FNF's MAC to 127 mbf. In 1963 144 mbf was harvested on the FNF, nearly double the 1953 harvest of 75 mbf. In 1898 only 3 sawmills operated in the area with timber harvested primarily from private lands. Private timber reserves supplied local mills until the second world war. By 1953 20 mills operated in the area, and increased to 36 mills and 4 plywood plants by 1965. The forest road system expanded with the increased timber harvest. In 1939 there were 458 km of roads in the FNF, and by 1965 there were over 2,763 km of road. After the completion of the west-side reservoir road in 1953, roads were built to the heads of every major drainage in the study area from Doris Mountain near the northern terminus of the Swan Mountains to the northern boundary of the Bob Marshall Wilderness. Expansion of the road system into the Bunker Cr. drainage on the northern boundary of the Bob Marshall was controversial and hotly contested during the mid 1950's (Shaw 1967).

From the inception of the South Fork Grizzly Project, the effects of roads on grizzly bears were recognized as being an important area of research. By 1990 it was apparent that timber harvest units were a large component of the grizzly bears' environment, and thus a suitable subject for research as well. In September 1990 a graduate student was employed to document the nature and extent of cutting unit use by grizzly bears. This work culminated in 1992 with a thesis entitled "Grizzly bear use of habitats modified by timber management" (Waller 1992).

This study employed a sample of 22 radio-collared grizzly bears to document the extent to which grizzly bears used harvested habitats on a seasonal and annual basis, and how this use compared to the availability of harvested habitats. Use sites within harvested stands were sampled and compared to random sites within the same stand to determine if grizzly bears were selecting unique microsites within stands or if use sites were representative of the stand as a whole.

Thesis results indicated that grizzly bears significantly avoided cutting units, during all seasons, at the study unit level of selection. However, study animals used cutting units in proportion to their availability within their seasonal 95% minimum convex polygon home ranges. No differences in use of cutting units by age or sex class were observed. Use of cutting units increased during the summer, and clearcuts were used less than other harvest types. Grizzly bears were more likely to use cutting units harvested 30-40 years ago than older or newer cutting units. Also cutting units at higher elevations were more likely to be used than those at lower elevations.

Also in 1992 the SFGP released it's Progress Report for 1992 which addressed annual patterns of grizzly bear selection for or against cutting units by elevation class. Again, only univariate tests were conducted (Mace and Manley 1993). Results of this analysis differed only slightly from those in Waller's thesis. No preference or avoidance of specific cutting unit types was observed. Females were found to avoid cutting units at lower elevations. Cutting units less than 12 years old were used less than expected.

In 1996, we published the results of our research concerning the interaction between grizzly bears and roads (Mace et al. 1996). This multivariate analysis incorporated habitat and elevation to assess the seasonal interactions between grizzly bears and roads at 3 levels of selection. One of the habitat classes in the analysis was cutting units. This analysis found that cutting units were avoided at the 2nd order of selection (within a composite home range). However, we observed stronger selection for cutting units within seasonal home range polygons; logistic regression coefficients were positive for cutting units for 67%, 79%, and 54% of radio collared bears during spring, summer, and fall respectively.

In 1997 we published a paper addressing univariate habitat selection, and again, cutting units were one of the habitat types in the analysis (Waller and Mace In Press). Cutting units were found to be among the least preferred habitat types for both sexes during spring and fall within 95% home ranges. Conversely cutting units were among the most preferred habitat types for both sexes, within 95% home ranges, during summer.

During 1996, we attempted to publish a paper describing in greater detail the factors affecting how grizzly bears select cutting units. This publication failed the peer review process due to shortcomings in the data. Specifically, reviewers questioned the accuracy of the U.S. Forest Service records used to classify cutting units by harvest method and scarification type. No field verification of this database was performed, or was possible due to the ages of the cutting units involved. Further, the functional relationship between U.S.F.S. classification and actual ground condition was not clear. Several silvicultural systems were used on the FNF, such as clearcutting, seed tree cutting, and shelterwood cutting. Although these cutting units were classed differently, the actual condition may have been functionally the same. We made an attempt to classify cutting units by current condition using satellite imagery, but we were forced to pick one dominant cover type to represent the cutting unit. In reality, cutting units could be mosaics of several cover types, and thus have different values to grizzly bears. No relationship was found between current dominant overstory and bear use.

Another serious shortcoming that has affected other analysis efforts is the small telemetry sample sizes involved. By 1994 we had amassed 2,248 useable aerial telemetry locations on 20 individual grizzly bears, but only 254 (11%) occurred within cutting units, an average of 2 locations per bear per year. There were 1,503 cutting units within the study area, but bears were relocated in only 188 of these units (12%). One may perceive this as avoidance of cutting units, however cutting units comprise only 15% of the study area. Given these figures, it is clear that bi-weekly aerial telemetry flights were insufficient to accumulate the telemetry sample sizes necessary to analyze fine scale patterns of habitat selection.

The error associated with aerial telemetry locations further compounds the problem. About 50% of the locations in cutting units were within 75 m of the edge of that unit. Our telemetry was accurate to 75 m, thus for 127 locations classed as being in a cutting unit, we were uncertain as to whether or not the bear was actually in the cutting unit or not. In these cases the resolution of our habitat mapping exceeds the resolution of our telemetry. However, it appeared that grizzly bear distance from, or into, a cuting unit is as expected relative to the availability of distances (Fig. 3.3.1).

Despite these problems, certain aspects of this database appeared robust, and recurred in the analyses described above. The first of these is the apparent avoidance of cutting units at large scales or lower orders of selection. As selection order increased, from landscape or geographic levels to seasonal selection within home ranges, avoidance of cutting units decreased. This probably reflects the selection that occurred at lower orders and not high Type II error rates. Although the number of telemetry points was low, the number of individuals was high enough to minimize Type II errors (Alldredge and Ratti 1986).

The data indicated, and personal observations confirmed, that use of cutting units increased during the summer when huckleberries (*Vaccinium globulare*) became available. Some cutting units supported large patches of huckleberry, but there is no research that explained or predicted the spatial distribution or productivity of these patches. We have also found a consistent negative relationship between the age of cutting units and the amount of use they received. Cutting units less than 12 years old were much less likely to be used than older units.

We found that certain cutting units seemed to have seasonal concentrated use by grizzly bears. To date we have been unable to attribute this use to any factors within our databases. We suspected that concentrated use was a function of abundant food resources (these cutting units seemed to have lots of huckleberries), security (not necessarily related to proximity to open road, rather freedom from human disturbance), and the cutting units' spatial location within the study area. This last factor deserves some discussion. We believe that use was also related to a cutting units topographic position. Cutting units that had high security, abundant food, and occurred along major drainages or ridgetops received more use from resident females and males that traveled through the corridor. Also units that occurred at the intersection of several home ranges could be expected to be used by more bears than those within the core home range of a resident female.

Grizzly bears have survived and successfully reproduced within the study area despite 50 years of timber harvest (Mace and Waller 1997b). However our studies of timber harvest/grizzly bear interactions are observational and no companion study in adjacent wilderness is available to compare survival and reproductive parameters. No empirical studies of the response of bear foods to timber harvest have been conducted. Observational studies (Zager 1980, Waller 1992, Anderson 1993) suggest wide variation in responses exist. Timber harvest in other ecosystems may have a more severe effect on bear food abundance than in our study area (Anderson 1993). Ecosystem specific food studies, combined with baseline population data, would help managers deduce the effects of various land management strategies on resident grizzly bear populations.

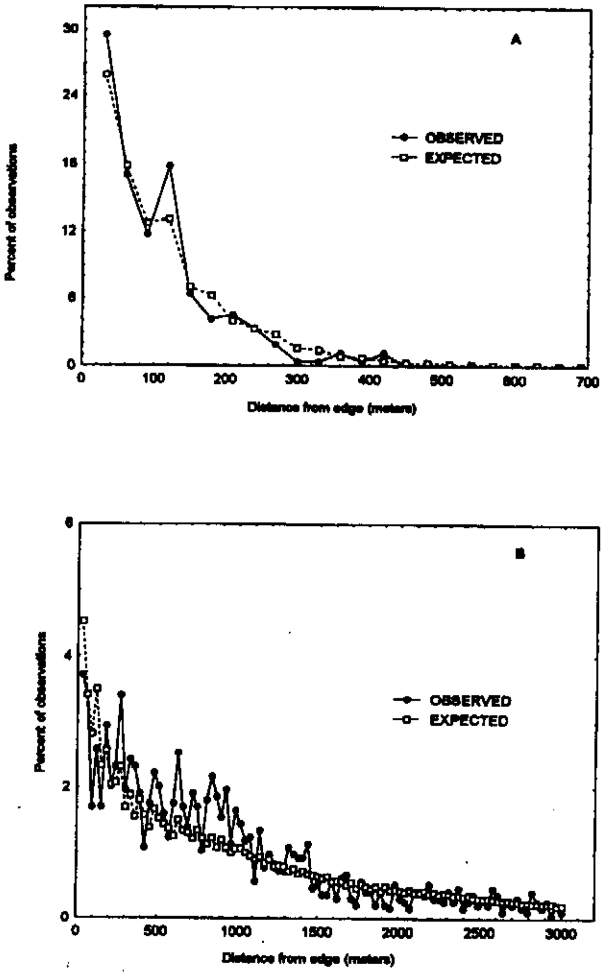


Figure 3.3.1. Distribution of observed and expected (available) distances to edge of cutting units from; A) within cutting units, and B) outside cutting units, Swan Mountains, Montana.

SECTION 3.4

RELATIONSHIPS BETWEEN GRIZZLY BEAR DENSITY AND HABITAT COMPOSITION AT VARIABLE LANDSCAPE SCALES

R. D. Mace and J. S. Waller

INTRODUCTION

Hierarchial levels of selection by wildlife exist (Owen 1972, Weins 1973, Pedlar et al. 1996) because the availability of natural resources and degree of habitat patchiness often varies with scale (Turner et al. 1991, Allen and Starr 1982). For grizzly bears, Mace et al. (Chapter 3.1) demonstrated changes in resource use at 3 levels of selection and concluded that resource selection and avoidance of roads appeared weakest at the home range level relative to both finer and broader levels.

In this section, we evaluate selection for cover types and road densities at 7 landscape scales. Additionally, habitat and road variables are examined relative to gradients of increasing grizzly bear density. At each scale we compare the differences in road densities in those locations where bears were absent, to those locations utilized by the maximum number of individual bears.

METHODS

We used aerial telemetry locations from 1987-1996 to ascertain the distribution and density of grizzly bears in the Swan Mountains. Telemetry locations were stratified by season: spring (den emergence - 15 July), summer (16 July - 15 September), and autumn (16 September - den entry). All seasonal telemetry coordinates were entered into a GIS data base using each bears' tag number as the coordinate identifier. Using a "jumping window" GIS routine (EPPL7, Minnesota Land Management Information Center. 300 Centennial Building, 658 Cedar Street. St. Paul, MN 55155), bear density, road density, and proportional habitat availability were calculated within square blocks of 7 different sizes (scales): 0.15 km^2, 0.5 km^2, 1 km^2, 2 km^2, 3 km^2, 4 km^2, and 5 km^2. Grizzly bears were termed "absent" from those blocks at each scale that received no documented use (Fig. 3.4.1).

Habitat and road features within the highest bear density blocks per scale (used) were compared to availability using selection indices (% use - % available). The study area was partitioned into the 7 block scales. Within each used and available block at each scale, we determined the proportional availability of dominant cover types. Cover types were mapped using Thematic Mapper satellite imagery (Mace et al. 1996) and included: sites dominated by either rock or grass/forb communities, shrub lands, forest (> 40% conifer overstory), snow chutes, slabrock, and timber harvest units (cutting units). The density of forest roads were determined for each scale and bear density. Road density was calculated as the linear kms of roads/block size. Roads were classified as either open to vehicular travel by the public (regardless of traffic volume) or closed to vehicular travel by the public during each season. Total road density was the sum of open and closed road density. Least squares linear regression was used to assess the relationships between grizzly bear density and open and closed road density at each scale.

RESULTS

Habitat Composition

Forty-three, 39, and 35 individual grizzly bears were radio monitored during spring, summer, and autumn respectively, from 1987-1996. For each season, the number of individual grizzly bears detected in landscape blocks increased with scale (Fig. 3.4.2). At a scale of 5 km^2, we observed a maximum of 16, 18, and 15 individual grizzly bears during spring, summer, and autumn. Grizzly bears were absent from blocks of the study area at all scales during each season (Fig 3.4.2). Large selection indices for cover types were observed during each season.

During spring, the largest positive selection index observed was 55.5% for snow chutes at a density 6 grizzly bears/0.5 km^2. Selection indices were

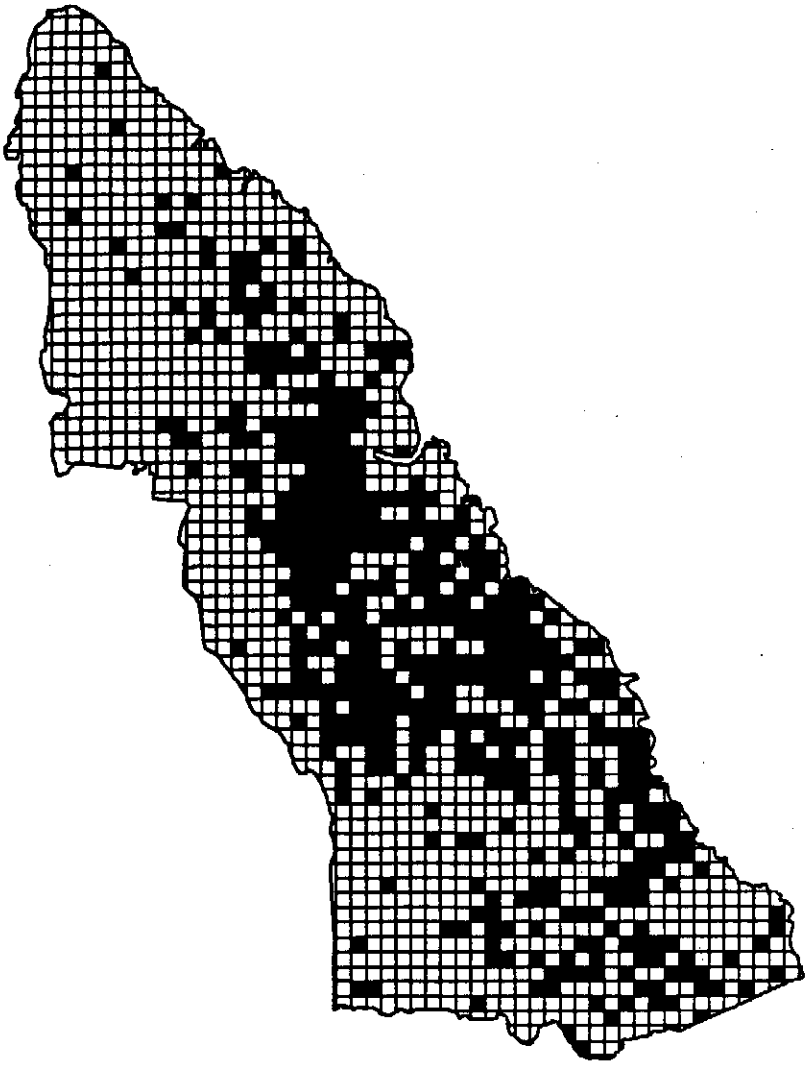


Figure 3.4.1. Example of grizzly bear density map for landscape scale of 1 km^2 during spring. Bear densities varied by block from 0 or absent (white) to 10 individuals/1 km^2.

strongly negative for the forest and cutting unit cover types up to 3km^2 scale (Fig 3.4.3). During spring, selection indices were strongly positive for snow chutes relative to other cover types and were maximized at 0.50 km^2. Univariate tests showed that all classes of grizzly bears were more often within 0.5 km of a snow chute during spring (Appendix E, Table E.10). Selection indices for all cover types approached zero (no selection) at a scale of 3 km^2.

During summer, selection indices for cover types were neutral or positive for all but the forest cover type to a scale of 3 km^2 (Fig. 3.4.3). The largest selection index observed was 67.43% for cutting units at a density 6 grizzly bears/0.5 km^2. During summer, a density of 6 (3 m, 3 f) individual grizzly bears/0.50 km^2 was observed for a single cutting unit in the central portion of the study area. Clear-cut in 1973, this northeast facing unit consistently produced high volumes of globe huckleberry (*Vaccinium globulare*) fruit. Selection indices were strongly negative at 0.5 km^2 for the forest cover type. Selection indices for all cover types approached zero (no selection) at a scale of 5 km^2.

The strongest negative selection index during autumn was for the forest cover type at a density of 3 grizzly bears/0.15 km^2 (Fig. 3.4.3). As during summer, autumn indices were neutral or positive for all other open- to open-timbered cover types out to 5 km^2. The shrub land cover type exhibited the strongest positive selection (37.82%) during autumn at a density of 7 grizzly bears/1 km^2. During autumn, cutting units, and snow chutes also exhibited positive selection indices at finer scales, and re-

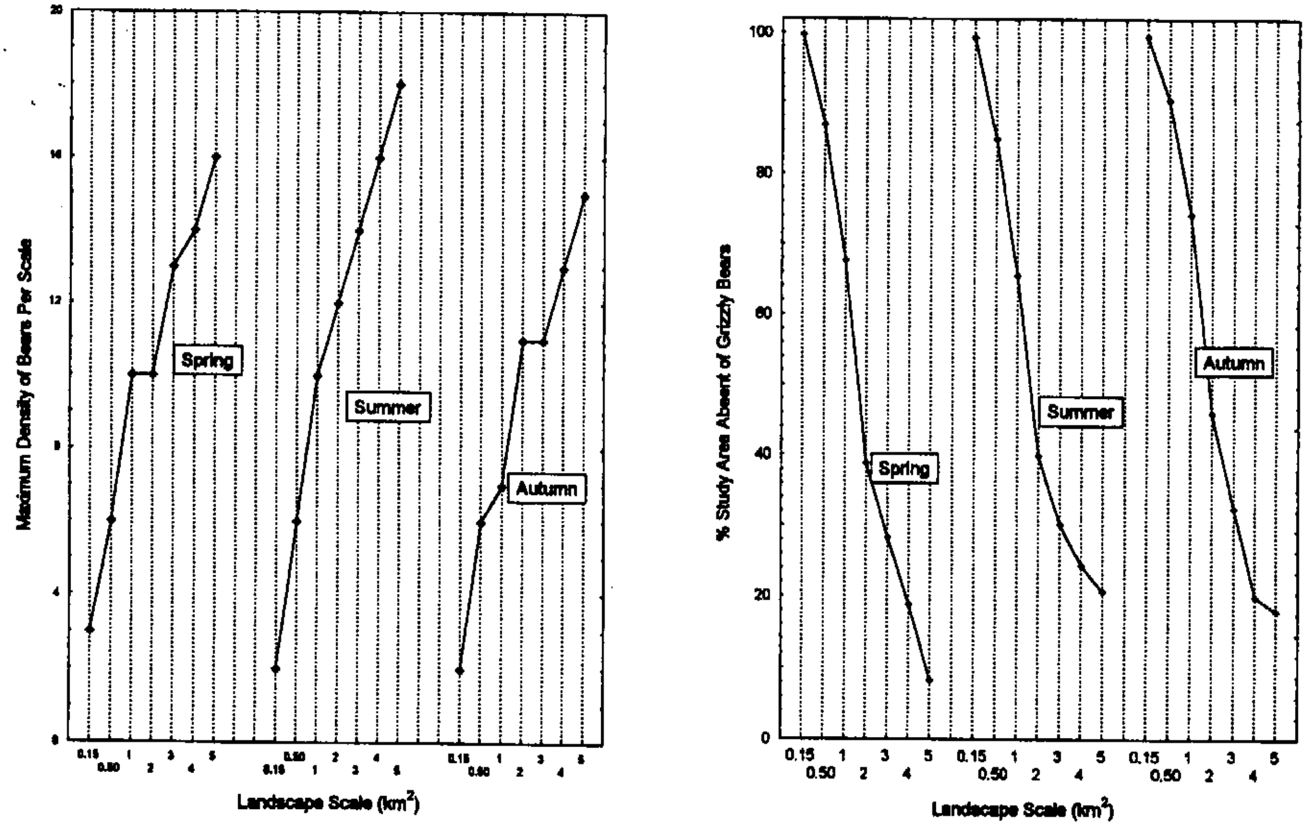


Figure 3.4.2. Density of grizzly bears at 7 landscape scales for 3 seasons (left). Percent of the study area absent of grizzly bears at 7 landscape scales for 3 seasons (right).

mained important during this season for bears consuming fruit.

Road Composition

Bear density varied with open and closed road density at all scales. During spring, open road density exceeded closed road density where grizzly bears were absent at all scales (Fig. 3.4.4). Open road density during this season declined with increasing densities of bears at all scales. Grizzly bear density declined significantly as open road density increased during spring for all but the 0.50 km^2 scale (Table 3.4.1). Total road densities were 0 km/km^2 where bear densities were highest between 0.15 - 2 km^2 scales. Closed road density generally exceeded open road densities at all scales where bears were present.

During summer, open road densities exceeded closed road densities where bears were absent at all landscape scales (Fig. 3.4.4). Open road density declined as bear density increased out to 1 km^2. We observed an open road density of 0 km/km^2 for the highest density of bears from 0.50 - 2 km^2. Significant relationships between bear density and open road density were observed for all but the 0.15 km^2 scale (Table 3.4.1). A significant negative relationship between bear density and closed road density was observed for the 0.50 km^2 scale.

During autumn, open road density exceeded closed road density where bears were absent at all scales (Fig. 3.4.4). Significant negative relationships between bear density and open road density were observed at most landscape scales during autumn (Table 3.4.1). No significant relationship was observed between closed road density and bear density during autumn. The maximum closed road density was observed at a landscape scale of 0.5 km^2 in an area used by 4 grizzly bears.

DISCUSSION

Grizzly bears are wide ranging and occupy large home ranges. Therefore we should not expect that each location represents active selection; there are for example, those locations obtained while

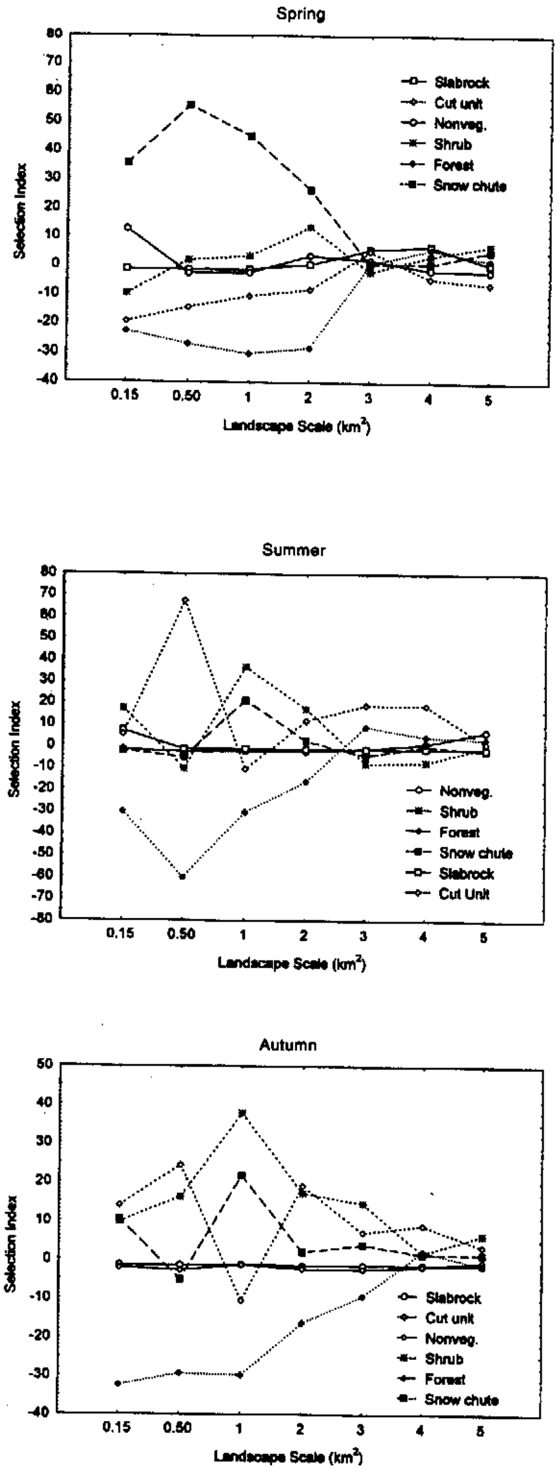


Figure 3.4.3. Selection indices for cover types during 3 seasons at 7 landscape scales. Indices were calculated for those blocks having the maximum density of bears.

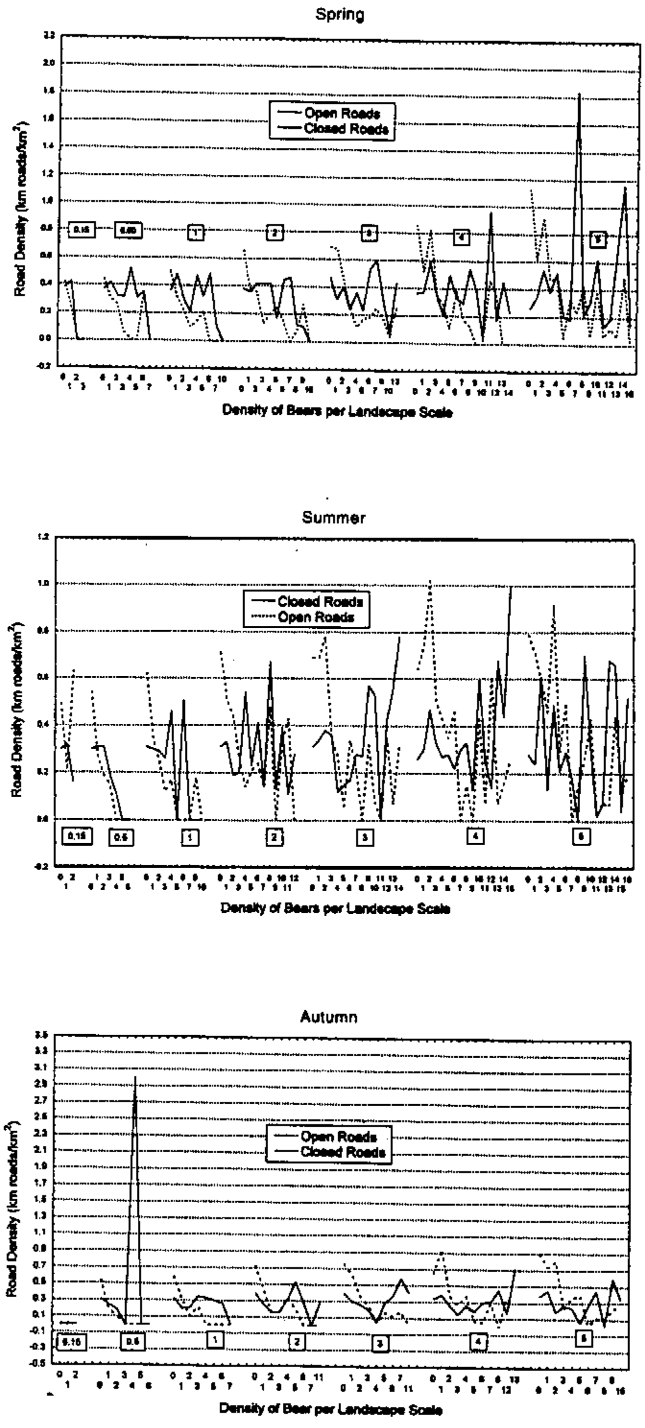


Figure 3.4.4. Relationships between open and closed road density and density of grizzly bears at 7 landscape scales during 3 seasons. Zero bear density were those blocks where bears were absent.

a bear is simply moving from one foraging area to another. Selection by individual bears is often inferred from a repeated pattern of use of specific habitat types or specific areas (White and Garrott 1990). Therefore, the density of grizzly bears over time in particular areas may be a stronger index of habitat selection than are each location obtained from individual bears. Areas with high grizzly bear densities provide additional information on habitat needs, social interaction and habitat selection for this species. We evaluated the effects of landscape scale and bear density for 2 habitat variables: roads and cover types. We do not imply that these are the only 2 variables affecting bear distribution and density. Rather, these are 2 variables that we believed would transcend landscape scale (Pedlar et al. 1997). Relative availability of vegetal foods can be inferred from cover types (see Appendix D), and the density of open and closed roads address displacement and survival parameters (Mace et al. 1996).

During each season, selection indices were strongly negative for forested habitats at scales < 4 km^2. Therefore, during each season, the highest bear densities obtained over time were in those locations with $\leq$ 40% overstory canopy. Vegetal foods sought by grizzly bears are more common in open to open-timbered habitats. Grizzly bears are recognized as less a forest dwelling species than black bears (*Ursus americanus*) (Herrero 1978).

Relationships among open roads and grizzly bear density on public lands were observed at all scales. Open road density declined as density of bears increased during all seasons, even at the broadest scales (5 km^2). Conversely, no strong relationships were observed for closed road density and bear density. These data show that the areas utilized by most bears at all landscape scales were those with minimal disturbance from vehicular traffic. These data emphasize that road closure programs are effective in minimizing motorized disturbance of

Table 3.4.1. Least squares linear regression summaries (R^2, slope, and p-value) for relationships between grizzly bear density and open and closed road density at 7 landscape scales. Negative slopes were obtained when road density declined with increasing bear density. Swan Mountains, Montana.

Scale	Spring						Summer						Autumn					
(km^2)	Open Rds.			Closed Rds.			Open Rds.			Closed Rds.			Open Rds.			Closed Rds.		
	R^2	β	P	R^2	β	P	R^2	β	P	R^2	β	P	R^2	β	P	R^2	β	P
0.15	0.89	-0.15	**0.05**[b]	0.76	-0.16	0.13	0.11	-0.70	0.79	0.64	-0.07	0.42	na[a]			na[a]		
0.50	0.35	-0.04	0.12	0.29	-0.03	0.17	0.84	-0.08	**0.00**	0.90	-0.06	**0.00**	0.65	-0.07	**0.03**	0.01	0.05	0.83
1	0.72	-0.04	**0.00**	0.38	-0.03	0.08	0.54	-0.43	**0.02**	0.33	-0.03	0.08	0.73	-0.07	**0.01**	0.20	-0.02	0.27
2	0.58	-0.04	**0.01**	0.45	-0.03	0.24	0.30	-0.03	**0.05**	0.00	-0.00	0.83	0.62	-0.06	**0.01**	0.02	-0.01	0.72
3	0.47	-0.04	**0.02**	0.01	-0.00	0.77	0.42	-0.04	**0.00**	0.19	-0.02	0.10	0.67	-0.06	**0.01**	0.13	-0.02	0.34
4	0.49	-0.04	**0.00**	0.00	-0.00	0.87	0.38	-0.04	**0.01**	0.24	0.02	**0.05**	0.24	-0.03	0.12	0.16	0.02	0.23
5	0.50	-0.04	**0.00**	0.01	0.01	0.73	0.46	-0.04	**0.00**	0.01	0.01	0.67	0.43	-0.05	**0.03**	0.00	0.00	0.83

[a] No variance in estimate. Road densities were 0 km roads/km^2 at all densities of bears.

[b] Bold p-values ($\leq$ 0.05) indicate significant reduction in road density as bear density increased, except during summer for closed roads at a scale of 4 km^2 where the converse was true.

grizzly bears at both fine and broad landscape scales. Similar findings were presented in Chapters 7.1 and 7.3. Managers seeking to establish road density standards for this species on public lands should recognize the inverse relationship between open road density and bear density. Road management programs should evaluate open road density at scales relevant to habitat selection, e.g. <3 km^2. Broader scale management may fail to address problems in areas of preferred habitat. In our study area, we noted some illegal motorized use of closed roads. An effective enforcement program should be implemented to ensure that closed roads effectively minimize displacement and risk. Our study was conducted in an area of relatively low human density. High levels of non-motorized use on closed roads in areas adjacent to high human population densities may negate the results found here.

CHAPTER 4

DENNING ECOLOGY OF GRIZZLY BEARS IN THE SWAN MOUNTAINS, MONTANA

CHAPTER 4

DENNING ECOLOGY OF GRIZZLY BEARS IN THE SWAN MOUNTAINS, MONTANA

R. D. Mace and J. S. Waller

ABSTRACT: Grizzly bear (*Ursus arctos horribilis*) denning ecology in the Swan Mountains of northwestern Montana was evaluated from 30 radio-collared grizzly bears from 1988-1994. All bears denned each year. Mean den entry and exit dates were 5 Nov and 11 Apr respectively. As found elsewhere in North America, females denned earlier and left their dens later in the spring than males. On average, females with cubs denned the longest of all age, sex, and reproductive classes (x = 177 days). The average elevation of 78 dens was 1,974 m (95% confidence interval 1,942-2,005 m), and there was no difference among classes of grizzly bears. Dens were situated on all aspects, and did not vary significantly among bear classes. Mean slope for the pooled sample was 63%. Eighty-two percent of the dens were located in habitats having a conifer overstory of < 60%. Denning habitat did not appear to be limiting because new dens were used each year. Denning habitat and chronology found in the Swan Mountains were compared to 2 other studies in Montana. Chronology of denning was similar among areas while topographical variables differed somewhat. Implications for improved habitat and population management are given.

INTRODUCTION

Grizzly bears spend nearly half of their lives in winter dens (Folk et al. 1980), yet denning ecology is poorly documented in Montana. Only 2 studies of grizzly bear den ecology have been conducted in the Northern Continental Divide Ecosystem (NCDE) (USDI 1993). Servheen and Klaver (1983) evaluated characteristics of grizzly bear dens in the Mission Mountains, and Aune and Kasworm (K. E. Aune and W. F. Kasworm, Final Rep.-East Front Grizzly Bear Study. Mont. Dep. fish, Wildl., and Parks, Helena) located dens along the Rocky Mountain East Front (RMEF) portion of the NCDE. Our study, in the western portion of the NCDE, provides additional knowledge of grizzly bear denning ecology.

METHODS

Grizzly bears were captured in snares and fitted with radio collars as described by Mace et al. (1994). Individuals were classified as adults (≥ 5 years old) or subadults. Adult females were further classified by reproductive status; those that did not give birth in dens, females with cubs (0.5 years old) and those females with young > 1 years old (females with young). Weather permitting, each bear was located once per week from 1987-1989 and twice per week from 1990-1992 from fixed-wing aircraft. Telemetry procedures were described by Mace et al. 1996). Each den location was plotted on a 1:24,000 orthophoto quadrangle and assigned a Universal Transverse Mercator coordinate. Elevation, aspect, and percent slope measurements were recorded. Aspect was categorized as: northern (315^0 - 45^0), eastern (45^0 - 135^0), southern (135^0 - 225^0), or western (225^0 - 315^0). Each den site occurred in either an open habitat (< 40% conifer overstory), open-timbered (41% - 60%), or a timbered (> 60%) habitat. From these physiographic characteristics, we estimated the forest habitat series near each den (Pfister et al. 1977). Comparisons among or between age and sex classes for continuous data were made using either ANOVA or Student's T procedures, and for categorical data using X^2 statistics (Sokal and Rohlf 1969).

Aerial telemetry flights were too infrequent to ascertain the exact day of den entry in the autumn and den exit in the spring and were therefore estimated. Each bear was classified as either away from its' den (> 500 m), in the vicinity of the den (<500 m), or in the den for the winter. We used the formulas of Schartz et al. (1987) to estimate the minimum, maximum, and mean days in the den per individual each year. These estimates were based on autumn and spring telemetry flights. For autumn, we used the last julian date that a bear was not denned (PD) and the first known julian date a bear was denned (FID). For spring, we used the last known julian date a bear was still denned (LID), and the first date a bear was known to be out of the den (OD). The minimum days each bear was denned was calculated as (365-FID)+ LID. Maximum days denned was calculated as (365-PD)+OD. Mean number of days denned was estimated as (minimum days + maximum days)/2. The maximum number of days that bears could be in the vicinity of the den in autumn and spring was estimated as (FID-1)-(PD+1), and (OD-1)-(LID+1) respectively.

We compared site characteristics of grizzly bear dens in our study to 2 other studies in Montana. Aune and Kasworm (1989) presented data for 70 dens along the (RMEF), and Servheen and Klaver (1983) listed characteristics for 15 dens in the Mission Mountains of western Montana. To aid in comparisons, we categorized elevation into 100 m increments, aspect was compared using 8 categories, and slope by 10% increments.

RESULTS

Thirty radio collared grizzly bears provided information on 78 denning episodes between 1987 and 1994 (Fig 4.1). The number of den episodes per individual varied from 1-6. All bears denned each year. One instance of reuse of a den was documented for an adult male. We twice documented sisters denning together the winter following dispersal as 2-year olds. Sample sizes were not adequate to assess annual variation in denning attributes. Although we did not visit many dens on the ground, visual observations from fixed-wing aircraft suggested most dens were excavated. No radio collared bears died during the denning period.

Denning Chronology

Den entry and exit dates were obtained for 59 and 53 den episodes respectively (Table 4.1). When bear classes were pooled, the mean dates of den entry and exit were 5 Nov. (sd = 11 days) and 11 Apr. (sd = 13) respectively. The earliest recorded entry date was 17 October for a female with cubs, and the latest was 16 Dec. for an adult male. The earliest den exit date was 13 Mar for a male, while the latest was 12 May for a female with cubs. On average, females denned earlier (4 days) and left the den area later (13 days) than males. Females with cubs entered dens earlier and emerged later than other sex and age classes (Table 4.1). Females with young entered dens later on average than other female classes. There was snow upon the ground when bears moved to the den vicinity during autumn in all but 3 of 78 cases (3 females, 2 of which were pregnant).

The estimated minimum, maximum, and mean days that grizzly bears were in dens varied by sex and age class (Table 4.2). Regardless of estimation procedure, females with cubs denned the longest x = 177 days), and adult males the shortest period (x = 148 days) of all sex and age classes. Using the mean estimate, subadult males were in dens 2 weeks longer than adult males.

Grizzly bears did not immediately enter dens following construction in the autumn, nor did they immediately leave the den vicinity after exiting dens during spring. During autumn, the maximum number of days bears were in the vicinity of dens prior to finally staying in dens averaged 11 days (SD = 7) for all classes of grizzly bears; females with cubs were in the vicinity of their den longer prior to den-

Table 4.1. Mean den entry and exit dates for grizzly bears in the Swan Mountains, Montana.

Class	First Date Of Den Entry				First date den exit			
	N	Mean	SD	Range	N	Mean	SD	Range
Female	39	4 Nov	10	17 Oct-24 Nov	37	15 Apr	12	25 Mar-12 May
Subad f	12	1 Nov	8	22 Oct-15 Nov	11	15 Apr	12	2 Apr-8 May
Sol f	5	5 Nov	14	25 Oct-15 Nov	3	18 Apr	5	14 Apr-24 Apr
Fc	10	2 Nov	6	17 Oct-8 Nov	12	21Apr	12	3 Apr-12 May
Fy	12	7 Nov	11	24 Oct-24 Nov	11	7 Apr	11	25 Mar-28 Apr
Male	20	8 Nov	13	21 Oct-16 Dec	17	2 Apr	11	13 Mar-17 Apr
Ad m	15	9 Nov	13	21 Oct-16 Dec	12	2 Apr	11	13 Mar-17 Apr
Subad m	5	5 Nov	12	21 Oct-24 Nov	5	2 Apr	14	13 Mar-16 Apr
All	59	5 Nov	11	17 Oct-16 Dec	54	11 Apr	13	13 Mar-12 May

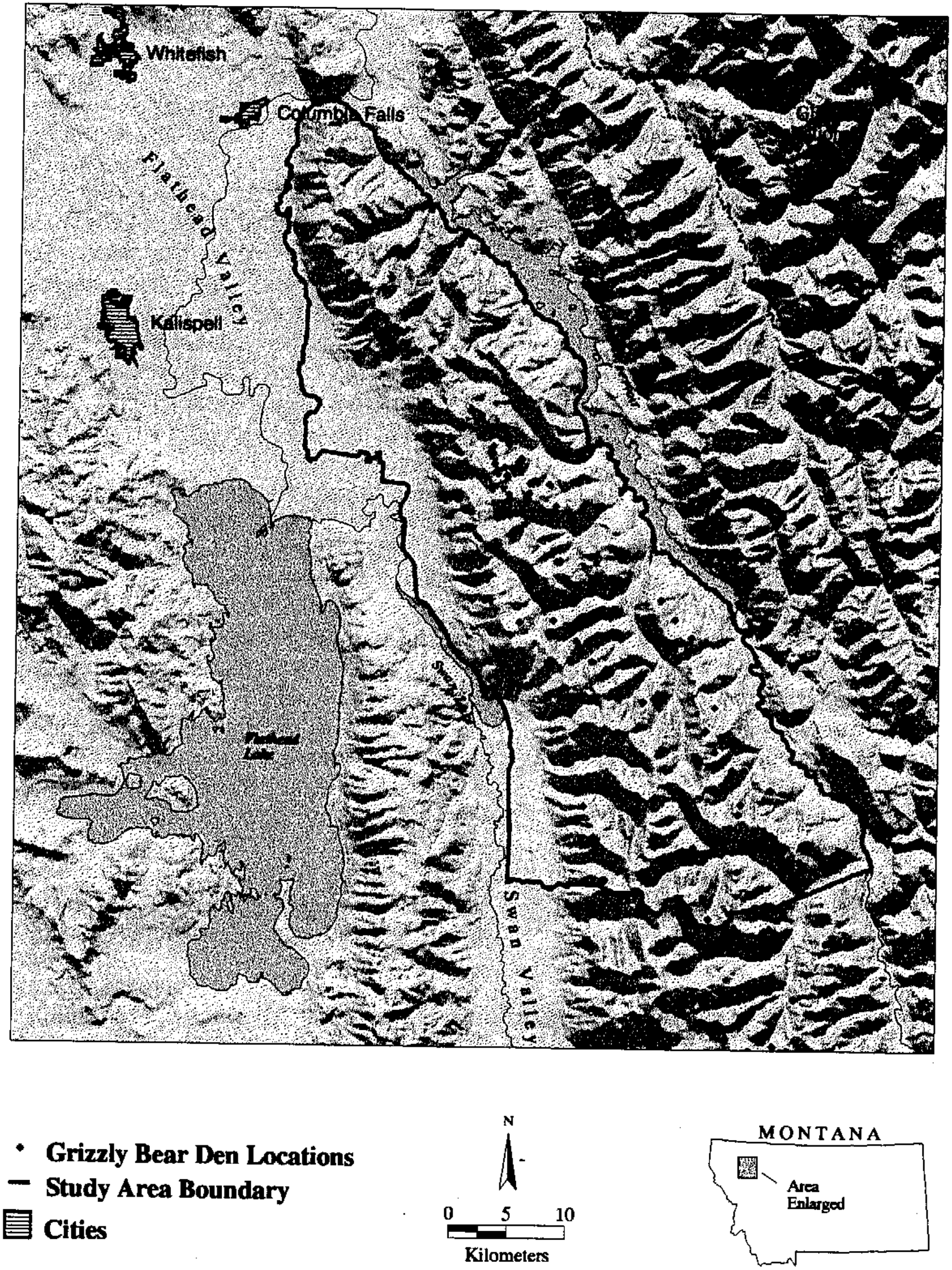


Figure 4.1. Topographic representation of the Swan Mountain study area showing locations of dens.

Table 4.2. The minimum, maximum, and mean number of days grizzly bears were in dens. Swan Mountains, Montana.

Class	Number of Days In Den								
	Minimum			Maximum			Mean		
	N	Mean	SD	N	Mean	SD	N	Mean	SD
Female	29	153	19	50	179	16	28	168	16
Subad f	9	156	14	14	181	13	8	168	12
Sol f	3	160	6	6	179	18	3	177	2
Fc	9	160	15	14	190	10	9	177	10
Fy	8	138	24	16	169	18	8	154	19
Male	12	137	19	25	158	22	12	152	16
Ad m	9	134	18	19	156	21	9	148	15
Sub m	3	145	24	6	162	27	3	162	18
All	41	147	20	75	172	21	40	163	17

ning during autumn (x = 15 days). Subadult males and adult males remained in the vicinity of their dens longer after spring exit than other sex and age classes (Table 4.3).

Location of Dens

Elevation, aspect, percent slope, and site canopy characteristics were recorded for all 78 den episodes. Average elevation of dens for the pooled sample was 1,974 m (95% confidence interval of 1,942 m - 2,005 m) (Table 4.4). The average elevation of male and female dens were 2,012 m and 1,957 m respectively, but differences were not significant (t = 1.6, 76 df, P = 0.11). There was no significant difference among the 6 age and sex classes relative to den elevation (P > 0.05). On average, dens were 110 m (sd = 99 m) from the nearest ridgetop.

Grizzly bears selected a variety of aspects for denning, although most (36%) dens were located on easterly aspects (Table 4.4). Females and males tended to use eastern and western aspects respectively, but differences were insignificant ($x^2 = 2.5$, 3 df, P = 0.47). Choice of aspect was not significant among sex and age classes ($x^2 = 17$, 15 df, P = 0.33).

Grizzly bears denned on relatively steep slopes; mean slope for the pooled sample was 63%. Average slope for males was greater than for females (Table 4.4), but differences were not significant (t = 0.84, 76 df, P = 0.40). The 6 classes of grizzly bears did not differ from one another relative to percent slope of dens (F = 2.03; 5, 72 df, P = 0.08).

Grizzly bears denned more often in open (40%) and open-

Table 4.3. The maximum number of days that grizzly bears were in the vicinity of dens (<500 m) but had not permanently entered during autumn, nor had permanently left the den vicinity during spring. Swan Mountains, Montana.

Class	Maximum Number Of Days In Vicinity Of Den					
	Autumn			Spring		
	N	Mean	SD	N	Mean	SD
Female	52	9	8	39	14	10
Subad f	12	11	6	11	12	6
Sol f	5	14	10	3	14	9
Fc	10	15	5	14	16	10
Fy	12	11	9	11	14	12
Male	26	7	7	19	18	11
Ad m	15	9	7	14	17	11
Subad f	5	12	5	5	21	11
All	59	11	7	58	15	10

Table 4.4. **Physiographic characteristics of grizzly bear dens in the Swan Mountains, Montana.**

Class	N	Elevation		Aspect (% of Categories)				% Slope		Site Canopy[a] (% of Categories)		
		Mean	Sd	N	W	S	E	Mean	Sd	O	OT	T
Female	54	1957	142	13	22	26	39	62	15	42	42	17
Subad F	16	1990	102	0	19	38	44	66	8	50	38	13
Sol F	6	1982	101	17	33	17	33	68	10	33	68	0
Fc	15	1961	140	33	13	20	33	66	15	47	33	20
Fy	17	1913	182	6	29	24	41	53	18	31	44	25
Male	24	2012	134	21	33	17	29	65	17	36	46	17
Ad m	17	2010	134	18	24	18	41	65	17	47	41	12
Subad m	7	2014	144	29	57	14	0	66	22	14	57	29
All	78	1974	141	15	27	23	36	63	16	40	43	17

[a] O = open , OT = open timbered, and T = timbered habitat.

timbered (42%) habitats than in timbered areas. No difference was found between male and female grizzly bears ($x^2 = 0.13$, 2 df, P = 0.93), or among the classes ($x^2 = 7$, 10 df, P = 0.76) in cover type selection. Most dens (74%) were located within or adjacent to the *Abies Lasiocarpa/Luzula hitchcocki*, or the *Abies Lasiocarpa/Xerophyllum tenax* (15%) climax habitat type series. Seven percent and 1% of the dens were located within the *Abies Lasiocarpa/ Menziesia ferruginea* and the *Abies Lasiocarpa/ Clintonia uniflora* series.

Comparisons to Other Studies in Montana

The elevation of dens in the Swan Mountains were most similar to those described by Servheen and Klaver (1983) for the Mission Mountains of Montana (Table 4.5). Few dens were located at elevations < 1,700 m in either the Swan Mountains or the RMEF. Most grizzly bears denned at higher elevations in the EF relative to the Swan Mountains.

Differences in aspect selection for denning areas were apparent in the 3 areas (Table 4.5). Bears in the Swan Mountains were most likely to den on

Table 4.5. Comparison of den location attributes (percent of observations) in the Swan Mountains (n = 78), the Rocky Mountain East Front (n = 70, Aune and Kasworm 1989), and the Mission Mountains (n = 15, Servheen and Klaver 1983).

Elevation (m)				Aspect				Percent Slope			
Category	Swan	RMEF	Missions	Category	Swan	RMEF	Missions	Category	Swan	RMEF	Missions
1500	1	1		N	4	30		5	.01	0	
1600	3	0		NE	14	19	33	15	.01	2	
1700	8	1		E	22	15	7	25	4	3	87
1800	15	3		SE	15	4		35	4	16	13
1900	19	8		S	12	8	7	45	10	20	
2000	40	23	80	SW	5	6	27	55	31	26	
2100	12	23	13	W	22	4	27	65	21	22	
2200	1	21		NW	6	14		75	28	11	
2300	1	15									
2400	0	5									
2500+	0	5	7								

either eastern or western aspects. Conversely, most dens in the RMEF and Mission Mountains were on northern to northeastern aspects.

Dens in the Swan Mountains tended to occur on steeper slopes then the other 2 areas (Table 4.5). Dens in the Mission Mountains tended to be on gentler slopes (<45%) relative to the other areas.

Aune and Kasworm (1989) reported a median date of den entry during autumn of 6 Nov which is similar to our mean date of 4 Nov for all classes of grizzly bears. Bears in the Mission Mountains may den at a slightly later date; Servheen and Klaver (1983) report that most bears denned during the third week of Nov. The timing of den exit during spring was similar among areas. In the RMEF, median date of exit was 7 Apr compared to our mean date of 14 Apr. Mission Mountain grizzly bears also emerged during the early part of April.

DISCUSSION

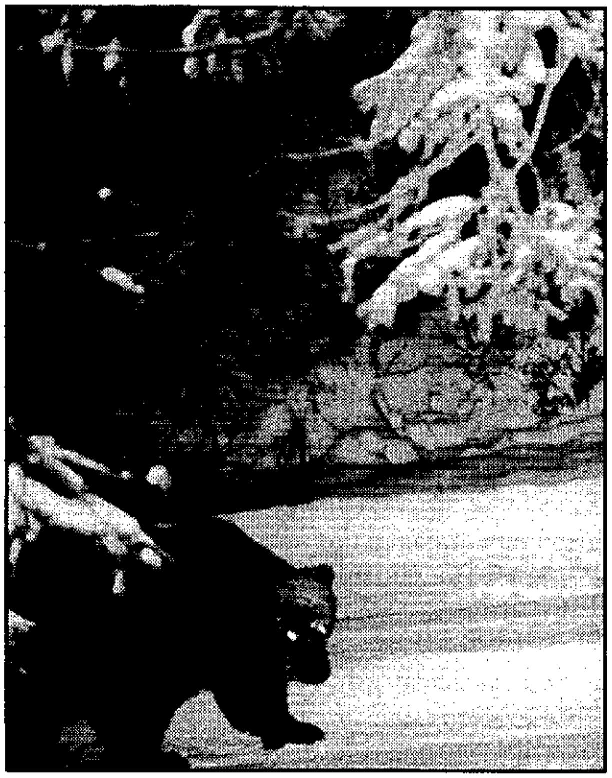
Our goal was to complement existing information on the denning ecology of grizzly bears in western Montana. Our analyses and comparisons with existing information suggested that den site selection varied within the NCDE. Grizzly bears on the RMEF tended to den at higher elevations than in the Swan or Mission Mountains. This is undoubtedly due to higher elevation mountains in this area as described elsewhere (IGBC, 1987). However, the timing of the denning period appeared to be similar across the NCDE.

As elsewhere in North America, grizzly or brown bears den at high elevations and on steep slopes (Pearson 1975, Harding 1976, Vroom et al. 1980, Judd et al. 1986, Schoen et al. 1987). Craighead and Craighead (1972) reported that grizzly bears prefer remote areas for denning, and our studies concur. We documented only one case of reuse of a den by an adult male, suggesting that denning habitat is not limited in the study area.

The impacts of resource development on denning brown bears was discussed in IGBC (1987) and Schoen et al. 1987). Possibly the greatest potential threat to security for denning grizzly bears in our area was off-trail, high-elevation snowmobiling. However, we routinely observed snowmobile activity within 2 km of denning grizzly bears, yet did not observe den abandonment. Although den abandonment, a severe form of disturbance, was not noted, physiological stress as described by Reynolds et al. (1986) could not be discounted. Dens in the Swan Mountains were typically on steep slopes that would be nearly impossible for snowmobilers to traverse. We believe the greatest potential for disturbance from snowmobile activity occurs when females with cubs are still confined to the den vicinity during spring, and when bears descend to lower elevations and more gentle terrain which is more suitable to snowmobiling.

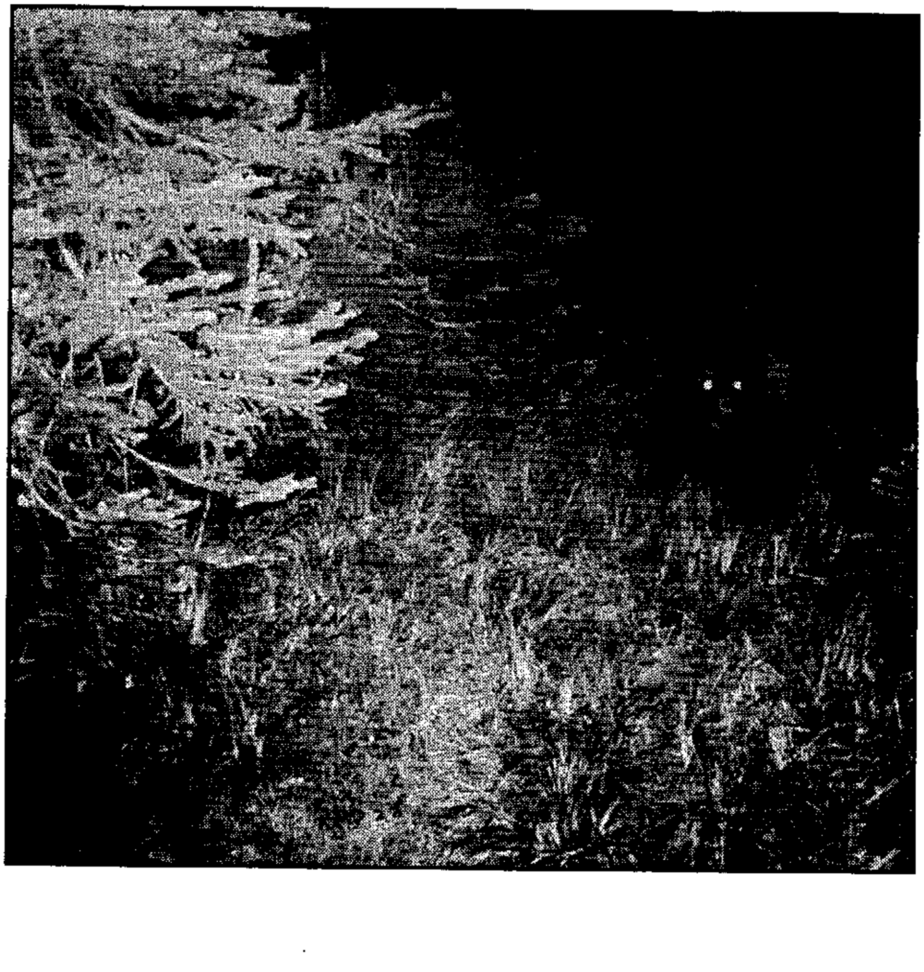
Denning activity of grizzly bears is of importance to habitat and population managers. In the NCDE, seasonal habitat effectiveness models have been constructed for each season, including the denning season. Season dates were based on unpublished information or publications having small sample sizes. We recommend that the denning season for cumulative effects models in the western portion of the NCDE be based on the dates when females were first noted in the vicinity of their dens during the autumn (8 Oct), and the last date when females were near the den during spring (26 May). These dates would insure that the "walking hibernation" physiological stage (Nelson et al. 1983), where bears were anorectic, was included in the denning period. Our observations of bears during this period suggested that grizzly bear movement was quite confined and bears were very lethargic and approachable. All areas above 1,942 m should be considered denning habitat.

Population management programs for grizzly bears throughout the sympatric range of both species in North America have recognized the need to minimize illegal grizzly bear mortality from mistaken identity during these spring and autumn black bear hunting seasons (Peek et al. 1987). Season structure for bear hunting should be designed to minimize mortality of female grizzly bears especially.



CHAPTER 5

SPATIAL AND TEMPORAL INTERACTION OF MALE AND FEMALE GRIZZLY BEARS IN NORTHWESTERN MONTANA



CHAPTER 5

SPATIAL AND TEMPORAL INTERACTION OF MALE AND FEMALE GRIZZLY BEARS IN NORTHWESTERN MONTANA[1]

R. D. Mace and J. S. Waller

ABSTRACT: Spatial requirements of grizzly bears (*Ursus arctos horribilis*) in Montana are poorly understood, yet habitat management is based on attributes of female home ranges. We evaluated home range size, overlap, and spatial/temporal use of overlap zones (OZ) of grizzly bears inhabiting the Swan Mountains of Montana. Annual home ranges of adult males were larger ($x = 768$ km^2), and adult female ranges smaller ($x = 125$ km^2), than those of subadults. Overlap in annual home ranges of adjacent female grizzly bears averaged 24% (37 km^2), varied from 0 to 94%, and was less when one or both females had young. Female home range overlap was greatest when one of both members of a pair were subadults. Male home range overlap with females averaged 19% for adult males and 30% for subadult males. Most simultaneous use of the OZ occurred during summer. We investigated both spatial and temporal interaction of grizzly bears having overlapping home ranges. Thirty-seven of 49 (76%) adjacent female pairs showed a symmetrical and random spatial use of the OZ indicating lack of territoriality. In one of 49 (2%) cases, simultaneous use of the OZ exceeded solitary use. Temporal use of the OZ was random in 44 of 49 (90%) female interactions. Avoidance behavior within the OZ of home ranges was indicated for 1 of 2 pairs of sisters following dispersal from their mother. Most male/female pairs exhibited a symmetrical and random use of the OZ. In 12 of 21 (57%) cases where the female home range was enclosed within a male range, the male exhibited spatial attraction to the female range. There was no evidence of spatial avoidance of the OZ for male pairs. Habitat availability in different portions of overlapping home ranges helped explain the observed patterns of spatial and temporal interaction among grizzly bears. The overlap zone of home ranges had higher proportional availability of avalanche chutes, rock/forb lands, and slabrock than home range areas outside the OZ. These home range and behavioral characteristics occurred at a female-dominated population density of 2-3 solitary grizzly bears/100 km^2.

INTRODUCTION

Grizzly bears currently inhabit a small portion of their original range in North America (Storer and Tevis 1955) and are classified as a threatened species under the Endangered Species Act. Only 2 areas exist in the contiguous 48 states of the United States where population densities are sufficient (U.S. Dep. Agric., Fish and Wildl. Serv. 1993) to study spatial interactions among individuals: the Greater Yellowstone Ecosystem (GYE), and the Northern Continental Divide Ecosystem (NCDE). Telemetry studies of grizzly bears in Yellowstone began in the early 1950s, but not until the late 1970s in the NCDE. Home range characteristics of grizzly bears in the contiguous 48 states are documented for the GYE (Craighead 1976, Blanchard and Knight 1991) yet remain poorly understood for much of the NCDE. Servheen (1983) reported the home range sizes of 6 grizzly bears in the Mission Mountains, and home range size for 24 grizzly bears in the Eastern Rocky Mountain Front (ERMF) area of the NCDE were evaluated (K. E. Aune and W. F. Kasworm, unpubl. data).

Interaction studies are rare for most wildlife species, and are not quantitatively described for grizzly bears. There is a lack of quantitative tools (White and Garrott 1990) to describe interaction, and studies are difficult to design that test hypotheses regarding the interaction of adjacent individuals. To be meaningful, intraspecifc interaction studies should include simultaneously derived elements of time, space, and habitat.

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[1] Mace, R. D., and J. S. Waller. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. J. Wildl. Manage. 61:39-52.

Temporal and spatial interaction among individuals has direct application to habitat management of grizzly bears. Spatial requirements and interaction addresses social behavior (White and Garrott 1990), and ultimately population density. An understanding of the spatial organization of grizzly bears in the NCDE should help wildlife managers frame realistic population recovery goals that are based on habitat condition and ecosystem size.

We evaluated spatial characteristics of male and female grizzly bear annual home ranges, evaluated both spatial and temporal patterns of overlap at the home range scale of selection, and characterized habitat attributes associated with those overlapping ranges.

METHODS

Capture and Telemetry

We captured grizzly bears in leg-hold snares between 1987 and 1992 with a 3.2 km^2 capture grid, and fitted them with radiocollars (Mace et al. 1994). Bears were classified as belonging to one of 5 groups: adult (ad) male and solitary adult female ($\geq$5 yr old), subadult (subad) male or female (<5 yr old), and adult females with attendant young (family). We located each bear once per week in 1988 and 1989 and twice each week from 1990 through 1992 from fixed-wing aircraft, weather permitting. Most flights occurred from 0600 to 1030 Mountain Standard Time. We photographed the location with a Polaroid camera and identified the location of each bear on the photograph before resuming the flight. We assigned Universal Transverse Mercator coordinates to each location from 1:24,000 orthophoto quadrangles. We evaluated telemetric error by placing radiocollars in the field and locating them from fixed-wing aircraft. The average error of 150 m was not large enough to significantly affect home range estimators.

Annual Home Range Size

We estimated annual home range size with the adaptive kernel methods (Worton 1989) using one location/week per grizzly bear during the period 1988-92. We chose the adaptive kernel home-range estimator based on the comparison of techniques by Worton (1987), Boulanger and White (1990), White and Garrott (1990), and Minta (1992). The adaptive kernel method is a nonparametric estimator that uses a probability density function that varies across an animal's distribution. In our judgement, this method most accurately estimated the size and shape of annual home ranges in the study area. Ninety-five percent isopleths were constructed to estimate each individual's annual home range during the non-denning period (generally Apr-Nov) with the program CALHOME (Kie et al. 1996). The number of annual home ranges constructed varied by individual (n = 1-4). In those cases where several annual home ranges of an individual of a given age-class or reproductive status were available, we used the average home range size because we were interested in comparing home range size of cohorts, and not in annual variability in home range size of individuals. Comparisons among groups were made with the Kruskal-Wallis 1-way ANOVA. When Kruskal-Wallis tests were significant ($P \leq 0.05$), we used Mann-Whitney U statistics to determine which groups differed.

Spatial and Temporal Interaction

We evaluated spatial and temporal patterns of home range interaction from 1990 to 1992 for each pair (α, β) of overlapping grizzly bears using 2 locations/week/bear. We included spatially adjacent yet nonoverlapping ($\leq$ 3 km) pairs in estimates of home range overlap. We used the 95% adaptive kernel isopleth to estimate annual home ranges and assessed the spatial and temporal interactions (Minta 1992) and simultaneous locations for each member of a pair. Minta's method reduces observations (telemetry locations) over space and time to a binomial distribution incorporating used and expected frequencies in different areas of a home range. The technique replaces zero cells with pseudo-Bayes estimates that improves the stability of small-sample chi^2 inference from probability values. We defined simultaneous locations as those obtained within one hour of each other from fixed-wing aircraft. Locations were classified as occurring in one of 3 seasons: spring (den emergence-15 Jul), summer (16 Jul-15 Sept), or autumn (16 Sept-den entry).

We evaluated spatial and temporal interaction between pairs of grizzly bears using raster-based Geographical Information System computer program EPPL7 (Minnesota Land Management Information Center. 300 Centennial Building, 658 Cedar Street. St. Paul, MN 55155). Overlap of 2 home ranges could take 2 forms. The entire home range of β could be enclosed within the range of α termed an enclosed pair), or the OZ could be only a portion of each bear's range (termed an overlapping pair). For each pair, 3 areas of the combined ranges were mapped: the home range area unique to α

($area_A$), that unique to β ($area_B$), and the OZ of α and β ($area_{AB}$). For pairs with an enclosed range, $area_{AB} = area_B$. Simultaneous locations were overlaid on the combined home range map to determine where the simultaneous locations occurred relative to the 3 areas. For overlapping ranges, 4 possibilities existed for each pair of simultaneous locations: both bears were in the OZ, α alone was in the OZ, β alone was in the OZ, or neither bear was in the OZ. For enclosed ranges we needed to determine only the number of times α occurred in $area_B$. Percent overlap in home ranges was calculated as $[(area_{AB}/home\ range_A) * (area_{AB}/home\ range_B)]^{0.5}$.

Each pair was classified as belonging to a group depending on the gender, age, and reproductive status of both α and β. When both individuals were female, 6 groups were delineated; pairs consisting of 2 solitary adults, solitary adult-subadult, solitary adult-family, subadult-family, 2 subadults, and 2 families. Six groups were delineated when pairs consisted of a male and a female: adult male-solitary adult female, subadult male-solitary adult female, adult male-subadult female, 2 subadults, adult male-family, and subadult male-family. The basic sampling unit for all analyses were these groups. Because of mortality and loss of functional radiocollars, it was not possible to ascertain changes in spatial and temporal interactions of each unique pair over the course of the study.

Our first hypothesis concerned only the spatial interaction between α and β. For overlapping ranges, we tested whether α and β influenced each other's spatial use of the OZ. That is, from location data, did α and β use their respective areas as expected in relation to the size of the OZ? Spatial relation to the OZ by each individual was categorized as either random, attraction, or avoidance with Minta's (1992) coefficients of interaction ($L_{A:A}$ for α and $L_{B:B}$ for β). As coefficients approached zero, use of the OZ became random. Coefficients >0 suggested attraction, and coefficients <0 suggested spatial avoidance. Probabilities of these coefficients ($p_{A:A}$ and $p_{B:B}$) were also calculated with α set at 0.05. Spatial response by each pair was further classified as symmetrical (same response by the pair), asymmetrical (opposite response), or singular (only 1 individual showing a significant departure from random use). In cases where β's range was enclosed within α's range, we tested the hypothesis that α used the OZ in a nonrandom fashion. Minta (1992) considered symmetrical avoidance of α and β evidence of territoriality, or defense of an area.

Our second hypothesis for overlapping ranges concerned temporal interaction between α and β in the OZ. The null hypothesis was phrased as follows; α and β's simultaneous use and non-use of the OZ equal the solitary use of the OZ by each member of the pair. We calculated Minta's (1992) coefficient of temporal interaction (L_{ixn}) and its associated probability (p_{ixn}) to determine if the joint use of the OZ was random, simultaneous, or solitary. Temporal use of the overlap area is random as L_{ixn} approaches zero, simultaneous use is greater than solitary use when $L_{ixn} > 0$, and solitary use is greater than simultaneous use when $L_{ixn} < 0$. Departures from random expectation (odds for each of the 4 cells) were calculated as suggested by Minta (1992). Spatial and temporal interactions among pairs were evaluated with SAS (SAS Inst. Inc. 1988).

We evaluated the habitat composition of $area_A$, $area_B$, and the OZ for each pair of grizzly bears. Proportional availability of 6 cover types within the 3 home range areas were determined with GIS and a classified LANDSAT Thematic Mapper image (Mace et al. 1997). Habitats were classified as: rock/forb land, shrub land, closed forest (>40% conifer overstory), avalanche chute, slabrock, or timber harvest units (cutting units). Proportional availability of cover types was normalized with the arcsine transformation (Sokal and Rohlf 1969), and ANOVA was used to investigate the effects of group, home range area, and the proportional availability of cover types. Separate analyses were conducted for each cover type as not all cover types were available to all groups. We used Tukey's statistic for post hoc analyses when significant ANOVAs were obtained ($P \leq 0.05$).

RESULTS

Annual Home Range Size

We estimated 67 annual home ranges of 24 individual grizzly bears (Table 5.1), varying is size from 35 km^2 for a subadult female to 1114 km^2 for an adult male. On average, adult males had the largest ranges ($x = 768\ km^2$, $n = 15$) and solitary adult females the smallest ranges ($x = 121\ km^2$, $n = 11$). No females were known to cross the 1-3 km wide Hungry Horse Reservoir to suitable habitat on the other side although males did (Fig. 5.1).

Our sample of subadult males included 2 annual ranges from one individual who was orphaned as a yearling. This individuals ranges were smaller ($x = 47\ km^2$) than other members of the cohort ($x =$

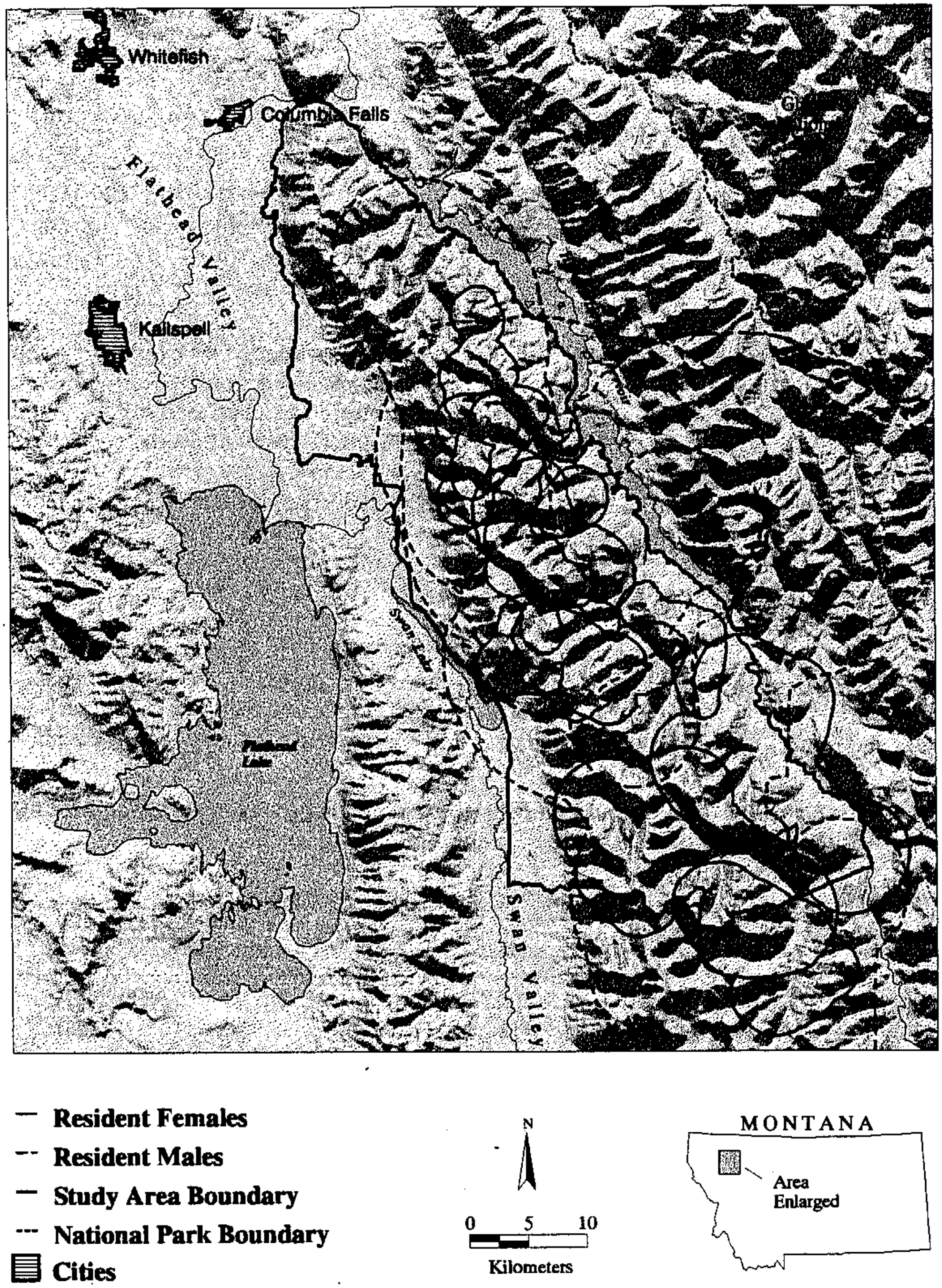


Figure 5.1. The Swan Mountain study area in Montana showing 11 female and 3 male grizzly bear 95% annual home ranges during 1990. The shaded area is the primary study area where all bears were captured.

Table 5.1. Annual home range size (km^2) for grizzly bears in the Swan Mountains, Montana. 1988-92.

Age/gender class	No. individuals	No. ranges	Av	SE	Range
Ad F	10	29	125	12	46-272
Family	8	18	127	17	59-272
Solitary Ad F	9	11	121	19	46-229
Ad M	8	15	768	73	420-1114
Subad F	9	16	228	40	35-456
Subad M	4	7	379	118	47-799

512 km^2 , SE = 118, n = 5), and were excluded from further analyses.

The 4 groups were significantly different in home range size (H = 37.0, 5 df, P = 0.00). Solitary adult females differed from adult males (z = -4.3, P = 0.00), adult males differed from families (z = -0.5, P = 0.00), subadult females differed from subadult males (z = -2.06, P = 0.03) and families (z = -2.07, P = 0.03), and subadult males differed from families (z = -2.30, P = 0.02).

Spatial and Temporal Interaction Between Females

Extent of Home Range Overlap. Annual home range overlap of 49 overlapping and 4 adjacent pairs of female grizzly bears were evaluated. Females were well distributed throughout the study area (Fig. 5.1). Percent overlalp varied from 0 to 94% and averaged 24% (Table 5.2). The size of the OZ for all overlapping female pairs averaged 37 km^2 (n = 49, SE = 6.2, 95% CI = 25-50 km^2).

Percent overlap was greatest (x = 30%, n = 11) for the solitary adult-subadult group, and the least (x = 10%, n = 10) for the family-solitary adult group (Table 5.2). Percent overlap varied by the 6 groups (H = 11.3, 5 df, P = 0.04). Percent overlap varied significantly between the solitary adult-subadult group and the family-solitary adult group (z

Table 5.2. Spatial interactions of adjacent and overlapping female grizzly bears.Swan Mountains, Montana, 1990-92. (No.in parentheses indicates column percentages).

Spatial interaction[a]	No. of pairs in each group						
	2 families	Family - solitary ad	2 subads	Subad- solitary ads	Both solitary ads	Family- subad	All pairs
No. overlapping pairs	11	7	5	8	7	11	49
Symmetrical:	10 (91)	6 (86)	4 (80)	5 (63)	4 (57)	8 (73)	37 (76)
Random	10	6	3	4	4	8	35
Attraction				1			1
Avoidance			1				1
Asymmetrical:			1 (20)				1 (2)
Singular:	1 (9)	1 (14)		3 (37)	3 (43)	3 (27)	11 (22)
Attraction		1		3	2	3	9
Avoidance	1			0	1		2
% overlap[b]							
Av	15	10	30	39	25	30	24
SE	4	5	16	11	8	4	3
Range	1-43	0-45	8-94	3-74	0-64	6-53	0-94

[a] Spatial interaction towards OZ were symmetrical when α and β had same response, asymmetrical when α and β exhibited opposite response, and singular when only 1 individual exhibited spatial response to OZ.

[b] % overlap statistics includes an additional 4 pairs that were adjacent but nonoverlapping.

= -2.5, P = 0.01), and between the family-subadult group (z = -2.6, P = 0.00).

Spatial/temporal Interaction of Females. Forty-nine of 53 pairs of female grizzly bears exhibited some spatial overlap. There were no enclosed ranges for female pairs. When pooled, 76, 22, and 2% of the pairs, respectively, exhibited symmetrical, singular, and asymmetrical spatial responses to the OZ (Table 5.2). Thirty-five of 37 (95%) symmetrical responses were random.

Eleven singular responses to the OZ were calculated (9 positive, 2 negative), and they exhibited greater percent overlap (x = 41, SE = 6, n = 11) than symmetrical groups (x = 22, SE = 4, n = 37) (H = 8.03,1 df, P = 0.00). Two of these singular and positive responses were adult female/daughter pairs. In all other singular and positive cases, the younger of the 2 individuals was positively attracted to the OZ.

Solitary female pairs were least symmetrical in their response to the OZ relative to other pair groups (Table 5.2). Rather, the spatial relation between solitary females was more singular (43%).

We evaluated changes in interaction among members of 2 families after breakup when young were 2 years old. Two daughters were followed as 2 and 3 year olds relative to their mother. One daughter reduced spatial overlap with her mother from 56% as a 2 year old, to 30% as a 3 year old. The second daughter reduced overlap with mother from 45% to 38%. As 2 year olds, these sisters represented the only case of asymmetrical interaction where one spatially avoided and the other was spatially attracted to the OZ. As 3 year olds, this pair exhibited the only case of symmetrical avoidance of the OZ, and overlap decreased from 26 to 16%. Two 2 year old daughters of a second family generally stayed together during the entire year of dispersal as 2 year olds, and exhibited a spatial overlap of 94%.

Forty-four of 49 (90%) female pairs exhibited a random temporal pattern of use of the OZ ($p_{ixn} > 0.05$). The null hypothesis that $\alpha$and β's simultaneous use and non-use of the OZ equaled the solitary use of the zone by each individual was not rejected in most cases. We rejected this hypothesis in the remaining 5 instances, 4 of which where simultaneous use exceeded solitary use of the OZ.

Twenty-six of 49 female pairs exhibited some simultaneous use of the OZ. Most simultaneous use occurred during summer. We accepted the hypotheses that proportional use of the OZ during each of 3 seasons did not vary by group (P > 0.05). When groups were pooled, we rejected the hypothesis that proportional use of the OZ did not vary by season (H = 12.7, 2 df, P = 0.00). Proportional use differed significantly between spring and summer (z = -2.68, P = 0.01), and between summer and autumn (z = -3.26, P = 0.00).

Spatial and Temporal Interaction Between Males

Five cases of male-to-male interaction involving 3 individuals were evaluated from 1990 to 1992. There were no instances of enclosed ranges for males, and percent overlap averaged 51% (range 40-69%). No cases of symmetrical/random interaction were observed. Three of 5 pairs exhibited singular/positive interaction towards the OZ, while remaining 2 pairs exhibited symmetrical and positive interaction to the OZ. One pair exhibited a significant and positive coefficient of temporal interaction ($p_{ixn} < 0.05$) which suggested that simultaneous use was greater than solitary use.

Spatial and Temporal Interaction Between Males and Females

Extent of Home Range Overlap. The mean percent overlap in annual home range for all male/female pairs was 30% (n = 51, SE = 1.9). Subadult males exhibited significantly greater overlap with females than did adult males (Table 5.3) (H = 4.47, 2 df, P = 0.03). For adult males, the amount of overlap did not vary by female group (H = 2.6, 2 df, P = 0.27). Similarly, no difference in percent overlap was observed for subadult male relative to female group (H = 4.2, 2 df, P = 0.12).

Spatial/temporal Interaction. Home range overlap was ascertained for 52 male/female pairs, 21 of which were cases where the female range was enclosed within the males' range. No male home range was enclosed in a female range. There were no instances of non-overlapping but adjacent ranges for male/female pairs.

Patterns of spatial/temporal use of the OZ were evaluated for 24 adult male/female pairs: 13 were overlapping ranges and 11 were enclosed ranges. Ten of 13 adult male/female pairs exhibited symmetrical and random use (P > 0.05) of the OZ (Table 5.3). The remaining adult male/female pairs were singular, 2 were singular attraction by males to the OZ, and one was singular avoidance of the OZ by a family/adult male pair. Temporal use of the OZ was random for 12 of 13 adult male/

Table 5.3. Spatial interactions of overlapping male and female grizzly bears. Swan Mountains, Montana, 1990-92.(No. in parentheses indicates column percentages).

Spatial interaction[a]	No. of male-female pairs			
	Family	Solitary ad	Subad	All pairs
Ad M				
No. pairs	6	3	4	13
Symmetrical:	5 (83)	2 (67)	3 (75)	10 (90)
Random	5	2	3	10
Attraction				
Avoidance				
Singular:	1 (17)	1 (33)	1 (25)	3 (10)
Attraction	0	1	1	2
Avoidance	1	0	0	1
% overlap				
Average	16	16	33	19
SE	4	7	10	4
Range	2-35	0.6-23	23-42	0.6-42
Subad M				
No. pairs	9	5	3	17
Symmetrical:	5 (56)	3 (60)	2 (67)	10 (59)
Random	5	3	2	10
Avoidance				
Asymmetrical	1 (11)			1 (6)
Singular:	3 (33)	2 (40)	1 (33)	6 (35)
Attraction	1	1	1	3
Avoidance	2	1		3
% overlap				
Average	29	24	39	30
SE	5	3	2	3
Range	7-44	15-33	35-43	7-44

[a] Spatial interaction towards OZ were symmetrical when α and β had same response, asymmetrical when α and β exhibited oppositeresponse, and singular when only 1 individual exhibited spatial response to OZ.

female pairs ($p_{ixn} > 0.05$), thus rejecting our second hypothesis concerning temporal interaction.

The home ranges of 11 adult male/female pairs was enclosed. In 5 and 6 instances respectively, the adult male used the OZ (the entire female range) randomly, or was spatially attracted to the OZ (Table 5.4). No spatial avoidance of a female range was observed for adult males.

Ten of 17 subadult male/female pairs exhibited symmetrical and random spatial use of the OZ (Table 5.3). One subadult male (positive spatial interaction) and family (negative spatial interaction) pair were asymmetrical. The remaining 6 pairs of subadult male/female were singular. Temporal use of the OZ was random for 16 of 17 subadult male/female pairs ($p_{ixn} > 0.05$), thus rejecting our second hypothesis concerning temporal interaction. Solitary temporal use was greater than simultaneous use in one instance ($p_{ixn} < 0.05$).

The home range of 10 subadult male/female pairs was enclosed. In 4 and 6 instances respectively, the adult male used the OZ (the entire female range) randomly, or was spatially attracted to

Table 5.4. Spatial interaction of male grizzly bears to enclosed home ranges of female grizzly bears. Swan Mountains, Montana, 1990-92.

Spatial interaction of males[a]	Female age and reproductive class			
	Family	Solitary ad	Subad	All pairs
Ad M				
Random	1	2	2	5
Avoidance	0	0	0	0
Attraction	3	1	2	6
% overlap (mean, SE, range)	35, 6, 19-47	25, 1, 23-26	38, 5, 25-46	34,3,19-47
Subad M				
Random	1	2	1	4
Avoidance	0	0	0	0
Attraction	0	3	3	6
% overlap (mean, SE, range)		36,2,30-42	44,7,33-66	40,3,30-66

[a] Spatial response towards of males towards OZ was random when males used OZ in proportion to their home range size. They were attracted to OZ when use was significantly greater than expected, and they avoided the OZ when use was less significantly less than expected.

the OZ (Table 5.4). No spatial avoidance of the female range was observed for subadult males.

Forty-two of 51 male/female pairs used the OZ simultaneously. Most overlap of occurred during summer (Table 5.5). Simultaneous seasonal use of the OZ did not vary by male/female group ($P > 0.05$). When groups were pooled, the percent simultaneous use of the OZ differed by season ($H = 37.0$, 2 df, $P = 0.00$). Simultaneous use differed between spring and summer ($z = -4.91$, $P = 0.00$), and between summer and autumn ($z = -5.3$, $P = 0.00$).

HABITAT CHARACTERISTICS OF HOME RANGE AREAS

Female Pairs. The proportional availability of several cover types within combined home ranges varied by female groups. Significant differences were observed for shrub lands ($P = 0.04$) and avalanche chutes ($P = 0.00$)(Table 5.6). Post hoc comparisons showed that the solitary adult-subadult group had more ($P = 0.01$) shrub lands ($x = 14\%$) in their ranges than did the family-solitary adult group ($x = 8\%$). The family-solitary adult group and 2-family group had significantly less ($P < 0.05$) proportional availability of avalanche chutes in their home ranges ($x = 6$ and 7%, respectively) than did the solitary adult-subadult group ($x = 13\%$). The family-solitary adult group had less proportional availability of avalanche chutes than did the 2-subadult group ($P = 0.02$). The unique portion of each pairs home range differed significantly for avalanche chutes ($P = 0.04$). There was a higher proportion of avalanche chutes within the OZ ($x = 10\%$) relative to areas of the home ranges outside of the OZ ($x = 8\%$). We conducted ANOVA tests on the relations among the area of the home range, spatial pattern of interaction (symmetrical or singular), and proportional availability of each cover type. No significant interactions were observed ($P > 0.05$)(Table 5.7).

Male/Female Pairs. The shrub land, avalanche chute, and slabrock cover types differentiated male and female ranges. The proportional availability of shrub lands and avalanche chutes varied by male/female group (Table 5.8). Subadult-subadult pairs had more shrub land ($x = 12\%$) than adult-subadult pairs ($x = 8\%$), and the subadult-subadult pairs had more ($x = 9\%$) of the avalanche chute cover type than did the subadult-family pairs ($x = 6\%$). The proportional availability of avalanche chutes and slabrock did vary by area of the combined ranges. There was a higher proportion of these 2 cover types in the OZ ($x = 9$ and 3%) than in the unique portions of each bears home range ($x = 6$ and 2%). The interaction of home range area, cover type, male/female group was not significant ($P > 0.05$).

We conducted ANOVA tests on the relations among the area of the home range, spatial pattern

Table 5.5. Simultaneous seasonal use of the OZ by pairs of male and female grizzly bears. Swan Mountains, Montana, 1990-92.

Male-female group	Mean percent simultaneous use of OZ per season								
	Spring			Summer			Autumn		
	Mean	SE	No. pairs[a]	Mean	SE	No. pairs	Mean	SE	No. pairs
Female pairs:									
Solitary ad (n = 7)	24	14	3	18	10	3	15	7	3
Sol ad-family (n = 7)	12	8	2	31	16	3	0	0	0
Sol ad-subad (n = 8)	15	6	5	27	9	5	20	7	5
Subad (n = 5)	8	8	1	29	19	2	13	10	2
Subad-family (n = 11)	19	8	4	26	12	5	17	9	4
Family (n = 11)	8	6	2	33	12	5	5	5	1
Pooled	15	3		28	5		12	3	
Male/female pairs:									
Ad M:									
Family (n = 10)	22	10	5	62	12	8	6	4	3
Sol. ad (n = 6)	17	17	1	31	19	2	3	3	1
Subad (n = 8)	11	5	4	44	11	6	20	8	4
Pooled	17	6		48	8		10	3	
Subad M:									
Family (n = 10)	23	10	6	45	12	7	12	6	4
Sol. ad (n = 10)	11	10	3	45	12	7	34	11	6
Subad (n = 7)	14	7	3	75	11	7	12	6	4
Pooled	16	5		53	7		20	5	
Male pairs:									
Ad-ad (n = 1)	4			82			13		
Ad-subad (n = 4)	35	22	4	59	20	3	6	4	2

[a] No. of pairs exhibiting simultaneous overlap during each season.

of interaction (symmetrical or singular), and proportional availability of each cover type. A significant interaction was observed for the shrub land type only (P = 0.00)(Table 5.9). Pairs exhibiting a symmetrical interaction had more proportional shrub lands in the OZ than outside the OZ (x = 11 and 8%). Pairs exhibiting a symmetrical interaction had more shrub land in the OZ than the unique portion of the home range for singular pairs (x = 7%).

DISCUSSION

Population size, demography, and habitat condition can influence home range size and extent of overlap (Sanderson 1966, Rogers 1977, Young and Ruff 1982). Home range size and overlap data for grizzly bears in the Swan Mountains were difficult to compare with those from other areas because of variable data collection methods and lack of a standard home range estimator (Interagency Grizzly Bear Comm. 1987). However, it is apparent from published literature that the size of grizzly bear home ranges varies in North America by region, age, gender, and reproductive status (Interagency Grizzly Bear Comm. 1987, Nagy and Haroldson 1989). Our results concur with other findings that the home ranges of males were larger than females, and that subadult ranges were larger than those of adult females (Interagency Grizzly Bear Comm. 1987). Even though we used a different home range estimator than did Blanchard and Knight (1991) for grizzly bears in the GYE, and Aune and Kasworm (1987) for the RMEF, the magnitude of differences suggests that they can be compared generally. Both

Table 5.6. Mean squares (MS), degrees of freedom (df), and probability levels (P) for cover type comparisons among overlapping female home ranges relative to group and area of overlapping range. Swan Mountains, Montana, 1990-92.

	Dependent habitat variables												
	Rock/forb			Shrub		Forest		Avalanche chute		Slabrock		Cutting Unit	
Source	df	MS	P	MS	P	MS	P	MS	P	MS	P	MS	P
Female group [a]	5	21	0.32	41	0.04	29	0.24	105	0.00	16	0.85	94	0.13
Area of home range[b]	1	57	0.10	0.2	0.91	9	0.52	68	0.10	170	0.04	101	0.20
Group x area	5	46	0.03	11	0.67	8	0.84	27	0.36	67	0.20	69	0.30
Error		107,17[c]		113,17		116,22		112,24		92,41		114,55	

[a] Six female groups were evaluated: 2 ads, 2 subads, solitary ad-family, solitary ad-subad, 2 families, subad-family.

[b] Two areas of the overlapping home range were considered: the unique portion of each individuals range, and the OZ.

[c] df error, MS error.

Table 5.7. Mean squares (MS), degrees of freedom (df), and probability levels (P) for cover type comparisons among overlapping female home ranges relative to spatial interaction and area of overlapping range. Swan Mountains, Montana, 1990-92.

	Dependent habitat variables												
	Rock/ forb			Shrub		Forest		Avalanche chute		Slabrock		Cutting unit	
Source	df	MS	P	MS	P	MS	P	MS	P	MS	P	MS	P
Spatial interaction[a]	1	0.00	0.05	0.00	0.42	0.00	0.81	0.00	0.46	0.00	0.70	0.00	0.74
Area of home range[b]	1	0.00	0.80	0.00	0.91	0.00	0.93	0.00	0.53	0.00	0.72	0.20	0.24
Interaction x area	1	0.00	0.10	0.00	0.97	0.00	0.96	0.00	0.17	0.00	0.84	0.10	0.32
Error		112,0.00[c]		118,0.00		121,0.20		117,0.00		97,0.02		119,0.01	

[a] Symmetrical or singular spatial interaction.

[b] Two areas of the overlapping home range were considered: the unique portion of each individuals range, and the OZ.

[c] df error, MS error.

Table 5.8. Mean squares (MS), degrees of freedom (df), and probability levels (P) for cover type comparisons among male and female home ranges relative to group, and area of overlapping range. Swan Mountains, Montana, 1990-92.

		Dependent habitat variables											
		Rock/forb		Shrub		Forest		Avalanche chute		Slabrock		Cutting unit	
Source	df	MS	P	MS	P	MS	P	MS	P	MS	P	MS	P
Male-female group [a]	5	12	0.30	58	0.05	153	0.19	55	0.04	4	0.87	51	0.43
Area of home range[b]	1	9	0.34	0.0	0.99	0.3	0.95	123	0.02	85	0.01	171	0.07
Group x area	5	15	0.21	15	0.73	10	0.99	23	0.45	23	0.07	52	0.42
Error		119,10[c]		120,26		120,101		116,24		103,11		119,52	

[a] Six male-female groups were evaluated: 2 ads, 2 subads, ad M-sub F, sub M-ad F, ad M-family, subad M-family

[b] Two areas of the overlapping home range were considered: the unique portion of each individuals range, and the OZ.

[c] df error, MS error.

Table 5.9. Mean squares (MS), degrees of freedom (df), and probability levels (P) for cover type comparisons among male and female home ranges relative to spatial interaction and area of overlapping range. Swan Mountains, Montana, 1990-92.

		Dependent habitat variables											
		Rock/ forb		Shrub		Forest		Avalanche chute		Slabrock		Cutting unit	
Source	df	MS	P	MS	P	MS	P	MS	P	MS	P	MS	P
Spatial interaction[a]	1	26	0.09	0.52	0.86	10	0.54	59	0.09	13	0.27	5	0.74
Area of home range[b]	1	0.42	0.83	9.7	0.45	0.0	0.99	27	0.25	27	0.12	19	0.51
Interaction x area	1	33	0.06	175	0.00	0.10	0.96	3	0.72	1.0	0.76	11	0.62
Error		84,8[C]		85,17		85,26		81,20		70,11		84,44	

[a] Symmetrical or singular spatial interaction.

[b] Two areas of the overlapping home range were considered: the unique portion of each individuals range, and the OZ.

[c] df error, MS error

male and female grizzly bears in the GYE occupied areas that were at least 5 times the size of grizzly bear ranges in the Swan Mountains. Adult male annual ranges in the RMEF and Swan Mountains were generally of the same size, while female ranges were 2-3 times larger in the RMEF depending on age and reproductive status. If home range size and habitat quality are inversely related (Ford 1983), then one could conclude that the moist maritime climate of the Swan Mountains may provide grizzly bears with higher quality habitat than exists in the drier GYE and RMEF areas.

The spatial extent of home range overlap among female grizzly bears in this study varied among individual pairs similar to findings in other areas (Interagency Grizzly Bear Comm. 1987). Overlap was greatest for solitary adult/subadult pairs, and least between adjacent family groups. Our 4 instances of adjacent but non-overlapping home ranges indicated that drainage bottoms with roads may serve as home range boundaries for some females. Further, our data suggest that Hungry Horse Reservoir may serve as a physical barrier to females.

Minta's (1992) coefficients of spatial and temporal interactions allowed us to judge grizzly bear use of space at a female-dominated population density of 2-3 solitary bears/100 km^2 (Mace et al. 1994). However, as Minta (1992) discussed, we were able to assess only interaction between 2 individuals at a time, and could not quantify simultaneous interaction among >2 individuals even though such overlap occurred. However, the overall pattern of random symmetry in spatial and temporal use of home range, especially for female pairs, increased our confidence in the accuracy of observed interactions. For example, in 1990 adult female No. 5 overlapped with 6 other radioed females and 3 radioed males. Her response to other females was a symmetrical/random interaction in 5 of 6 cases. During the same year, her home range was enclosed within 2 subadult male ranges, both of which were spatially attracted to her range. Similar patterns were observed for other females.

Spatial interaction of males and females has been documented for many species (Main and Coblentz 1990), and segregation between sexes varies by species and scale. Because segregation is scale-dependent (Bowyer and Kie 1996), strict comparisons among local populations should be confined to similar scales.

Gender interactions could feasibly vary with demographic differences among local populations. For example, in local populations skewed towards females, the probability of a female encountering a male would be low relative to a population dominated by males. Two recent publications by Wielgus and Bunnell (1994b, 1995) highlight the importance of scale and demography in interaction studies.

Wielgus and Bunnell studied the seasonal habitat use of grizzly bears in Alberta, Canada and tested hypotheses regarding gender segregation (1994b). The population under study had a female:male ratio of about 1:3, which was nearly the opposite of our Swan Mountain population (4:1 ratio). The authors proposed that female avoidance of males would be manifested by increasing differences in habitat selection between sexes as male use increased in areas occupied by females. Using telemetry data, the authors compared use of habitat between sexes among seasons and not within seasons. Based on differences in specific use of habitat between the sexes in different seasons, the authors concluded that females avoided males due to the presence of immigrant males (Weilgus and Bunnell 1994b).

At the home range scale of selection, female spatial avoidance of males would be suggested by significant negative coefficients for females towards the OZ shared with males. We did not observe such evidence of sex segregation relative to the use of space within home ranges in a female-dominated population. Therefore, female avoidance behavior towards males appeared to be minimal in the Swan Mountains as indicated by the preponderance of a symmetrical/random spatial and temporal interaction among overlapping male/female pairs. Where female ranges were enclosed within male ranges, males commonly exhibited spatial attraction to the female range. Two of 3 males in our study were young and considered resident, and were probably familiar to most if not all females (at least through scent). Conversely the third male, considered a transient adult, was implicated in the death of a yearling male and a 2-year-old female in 1990. Aggressive interactions such as this, which resulted in death, occurred at finer scales of space and time would not be detected by our methods.

Most female pairs exhibited a symmetrical/random spatial interaction, although there were relatively more singular responses observed than with male/female pairs. Most singular responses were cases where one female was attracted to the OZ, and the other used the OZ randomly. Avoidance of the OZ, either singular or symmetrical, was observed in only 3 of 49 female pairs (6%). These data suggest that competition for space among females is minimal in the Swan Mountains.

The importance of cover type availability in different portions of overlapping home ranges helped explain the patterns of spatial and temporal interaction among individual grizzly bears (Brown and Orians 1970). The OZ of all pairs had higher proportional availability of avalanche chutes than home range areas outside the OZ. Avalanche chutes are forage-rich areas during all seasons and provide both thermal and security cover. Although all individuals had avalanche chutes outside of OZ's, forage quality varied widely for this cover type (Mace and Bissell 1986). Areas where numerous bears overlapped were often distinguished by numerous and productive avalanche chutes. These findings lend further evidence that this cover type is a vital and shared component of grizzly bear habitat throughout the year in the Swan Mountains. Mace et al. (1996) found that the generally negative response of grizzly bears to roads was lessened for bears using avalanche chutes. For female pairs, the rock/forb land cover type was more prevalent in the OZ than in the individual portion of the home range. Rock/forb lands are also food-rich areas, and were used by females while foraging and for digging underground roots and bulbs.

Although simultaneous use of the OZ occurred during all seasons, use was greatest during summer for both male/female and male/male pairs. Food is most abundant during summer (Mace and Jonkel 1983) while grizzly bears consumed fruit (primarily globe huckleberry [*Vaccinium globulare*] and serviceberry [*Amelanchier alnifolia*]). Males and females were routinely observed in separate areas of large berry fields during this season. Sexual segregation during summer in Canada but not in Idaho (Weilgus and Bunnell (1995).

Our study design to assess spatial and temporal interaction was conducted over 3 years. The design would have been improved if the same focal individuals were maintained longer. If this had been possible, we would have treated the individual bear as the basic analysis unit. Unfortunately mortality, loss of functional collars, and budgets required that we pooled data within cohorts. Interpretation of our results was also hampered for other reasons. We did not know the lineage of all individual bears in the study area. For example, the relation between a 22- year-old adult female and 4 overlapping younger females was unknown. Likewise, we could not confirm the birthplace or mother of any of the males. We recommend that future studies of this type incorporate genetic testing for lineage (Craighead et al. 1995).

Our data support that grizzly bears in the Swan Mountains are not territorial in the classic sense at the home range level of resource selection (Craighead and Mitchell 1982). Although we quantified some differences in habitat availability between the OZ and areas outside of OZ, we conclude, as hypothesized by Stirling and Derocher (1990), that overlap is extensive when food and other resources are widely distributed and undefendable. These data do not imply however, that competition for resources is not present at finer scales of selection, that differences in microhabitat selection between sexes does not occur, nor that aggressive inter-sex interactions do not occur. Further, one should be careful not to assume similar interactions are present in all grizzly bear populations. Because of the high mobility of this species, long-term studies at finer spatial and temporal scales are untenable.

MANAGEMENT IMPLICATIONS

Land management agencies in the contiguous 48 states manage habitat for grizzly bears using rough estimates of home range size and habitat preference because little detailed information is available on the spatial requirements of grizzly bears. Occupied habitat is partitioned into "subunits" that are intended to mimic the home range size of female grizzly bears and are often drawn without overlap with watershed boundaries. Within these arbitrary subunits that environmental assessments for grizzly bears are prepared for all human activities including timber harvest, road and trail access, recreation activities, and hydrocarbon exploration and development. Our studies suggest that habitat management for this species would be improved if, in addition to current management guidelines, localized areas about the size of the OZ and having mixtures of avalanche chutes, grass/rock lands, and shrub lands were identified and protected as crucial habitat for numerous individual grizzly bears.

CHAPTER 6

GRIZZLY BEAR CAPTURE PROGRAM

CHAPTER 6

GRIZZLY BEAR CAPTURE PROGRAM

R.D. Mace and J. S. Waller

CAPTURE METHODS

Grizzly bears were opportunistically captured from 1987-1996. Intensive capture effort was conducted during May and June, although several short-term snaring sessions were conducted during other seasons to recapture bears that lost radio collars.

The location and intensity of capture effort varied somewhat each year. During 1988 and 1989, a 3.2-km systematic capture grid was placed over the Core Area and portions of the Peripheral Area to identify accessible snare sites. Although the same snare sites were used in 1988 and 1989, snare placement was changed. After 1990 we stopped snaring in the Peripheral Area because of lack of captures, and sampled primarily in the Core Area.

We designed initial capture sessions to mark as many bears as possible by modifying snaring methods and placement (White et al. 1982). Two Aldrich foot snares (Aldrich Animal Trap Co., Clallam Bay, WA 98326) were placed at each site and checked daily. About 23 kg of wild ungulate bait was maintained at all sites, and sites were prebaited for 3-5 days before snares were set. We used different combinations of wooden cubbies (Jonkel and Cowan 1971) and trail sets each year.

We marked each bear with an ear tag and a 16.5- x 5-cm Armortite (Cooley Inc., Pawtucket, RI 02862) ear streamer with a unique symbol in each ear. Ear streamers were color-coded for gender. A premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966), and individuals ≥5 years old were classified as adults. Physical measurements were obtained from captured bears. Actual scale weights were not obtained for larger bears. We used the method of Nagy (1984) to estimate body weight of larger bears based on chest circumference (behind the hump) and scale weights of smaller bears. The linear equation we used was: $\log_{10}(\text{weight}) = \text{intercept} + (\text{slope}*\log_{10}(\text{chest}))$.

Grizzly bears were immobilized with either Telazol (tiletamine HCL/zolazepam HCL) or the mixture of ketamine/Rompun (ketamine HCL/xylazine HCL). A premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966). Bears were divided into 6 classes: adult (≥ 5 years old) males and females, subadult (2-4 years old) males and females, cubs (0.5 years old), and yearlings (1.5 years old). We fitted captured grizzly bears with motion-sensitive radio collars. We generally used 2.5 cm cotton spacers to close the collar belting thus ensuring that collars would not be worn permanently (Hellgren et al. 1988). We defined capture rate as the number of snare-nights/capture. A convex polygon was constructed from snare locations each year, from which the density of snares used each year (snares/100 km^2) was calculated.

RESULTS

Capture Success

Fifty individual grizzly bears were captured in 108 capture episodes between 1987-1996 (Table 6.1). We accumulated 8,627 snare-nights during the study. Capture success ranged from 20-113 snare-nights/capture and averaged 80 snare-nights/capture.

No new adult females were captured after 1990 (Table 6.1). Most adult males were also captured early in the study. The one adult male captured in 1993 left the study area immediately after capture and was never relocated again. New subadult males and females continued to be captured throughout the period. No females with cubs of the year were captured during the study.

Our sample of 50 individual grizzly bears was 58% female and 42% male. Median age of females at capture was 3.5 years and varied from one to 19 (Fig. 6.1). Thirty-eight percent of the female captures were adults, 38% were subadults, and 24% were one year-olds. Median age of males at capture was 4.5 years and varied from one to 11 years. Forty-three percent of the male captures were adults, 38% were subadults, and 19% were one year-olds. Most recaptures were of adult male grizzly bears, followed by adult females (Table 6.2).

Distribution of Grizzly Bear Captures

Three grizzly bears were captured outside of

Table 6.1. Grizzly bear capture effort and success from 1987-1996. Swan Mountains, Montana.

Characteristic	Year										Total
	87	88	89	90	91	92	93	94	95	96	
Capture polygon size (km^2)	101	866	866	518	560	999	559	425	37	30	
No. snares	14	61	60	44	42	44	32	23	4	8	
Snare-nights	142	2196	2100	1296	750	789	814	402	40	98	8627
Snares/100 km^2	14	7	7	8	8	4	6	5	11	27	
No. grizzly captures	6	25	19	15	12	7	16	5	2	1	108
No. individuals	4	15	15	12	8	6	13	5	2	1	
Snare-nights/capture[a]	24	88	111	86	63	113	51	80	20	98	
No. new individuals[b]	4	13	5	8	5	3	6	4	1	1	50
No. new ad f	2	4	1	3	0	0	0	0	0	0	10
No. new ad m	0	6	1	0	0	0	1	0	0	0	8
No. new subad f	2	2	2	1	3	3	3	2	1	0	19
No. new subad m	0	1	1	4	2	0	2	2	0	1	13

[a] Snare-nights/no. individuals.

[b] New individuals are defined as those grizzly bears not previously captured.

the Core Area (Fig. 6.2). Two of these 3 captures were male grizzly bears that periodically left the Swan Mountains. The third capture in the Peripheral Area was a subadult female. The remaining 105 captures were generally well distributed throughout the Core Area from Graves Creek south to Bunker Creek (60 snare-nights per capture).

Capture-Related Injuries

In 29% of 108 capture episodes, we observed slight abrasions and/or swelling of the snared leg. We observed the loss of a front claw from being snared in 1 instance. In 3 of 108 captures (2.7%) minor cuts were observed. No grizzly bears attempted to chew off the snared foot.

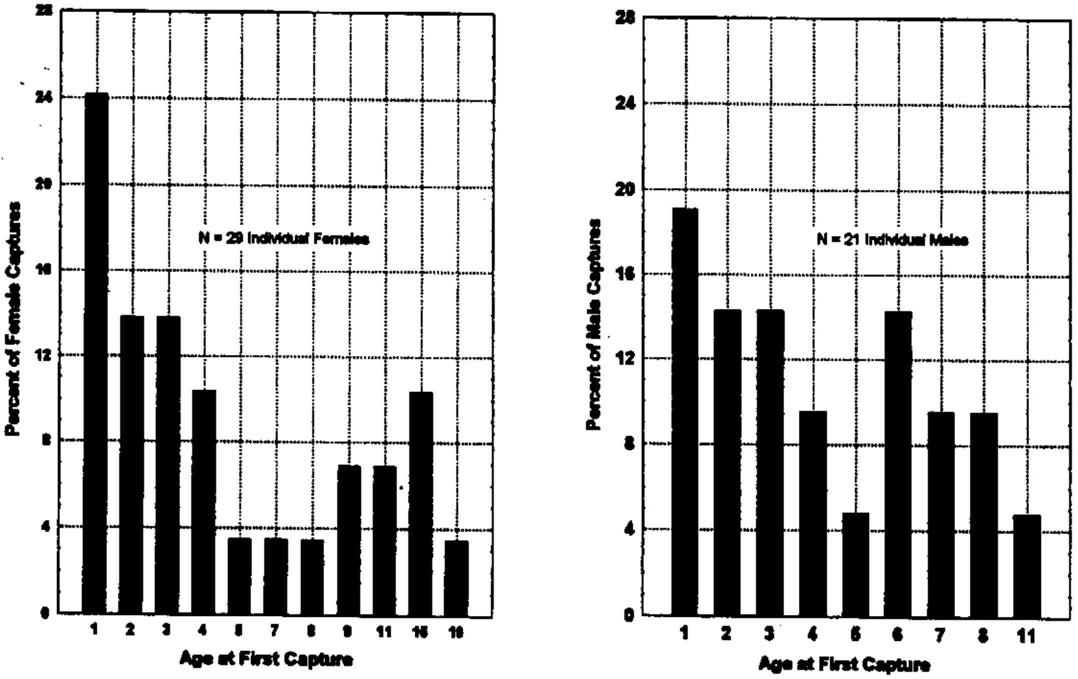


Figure 6.1. Age structure of 50 grizzly bears captured in the Swan Mountains between 1988 and 1996.

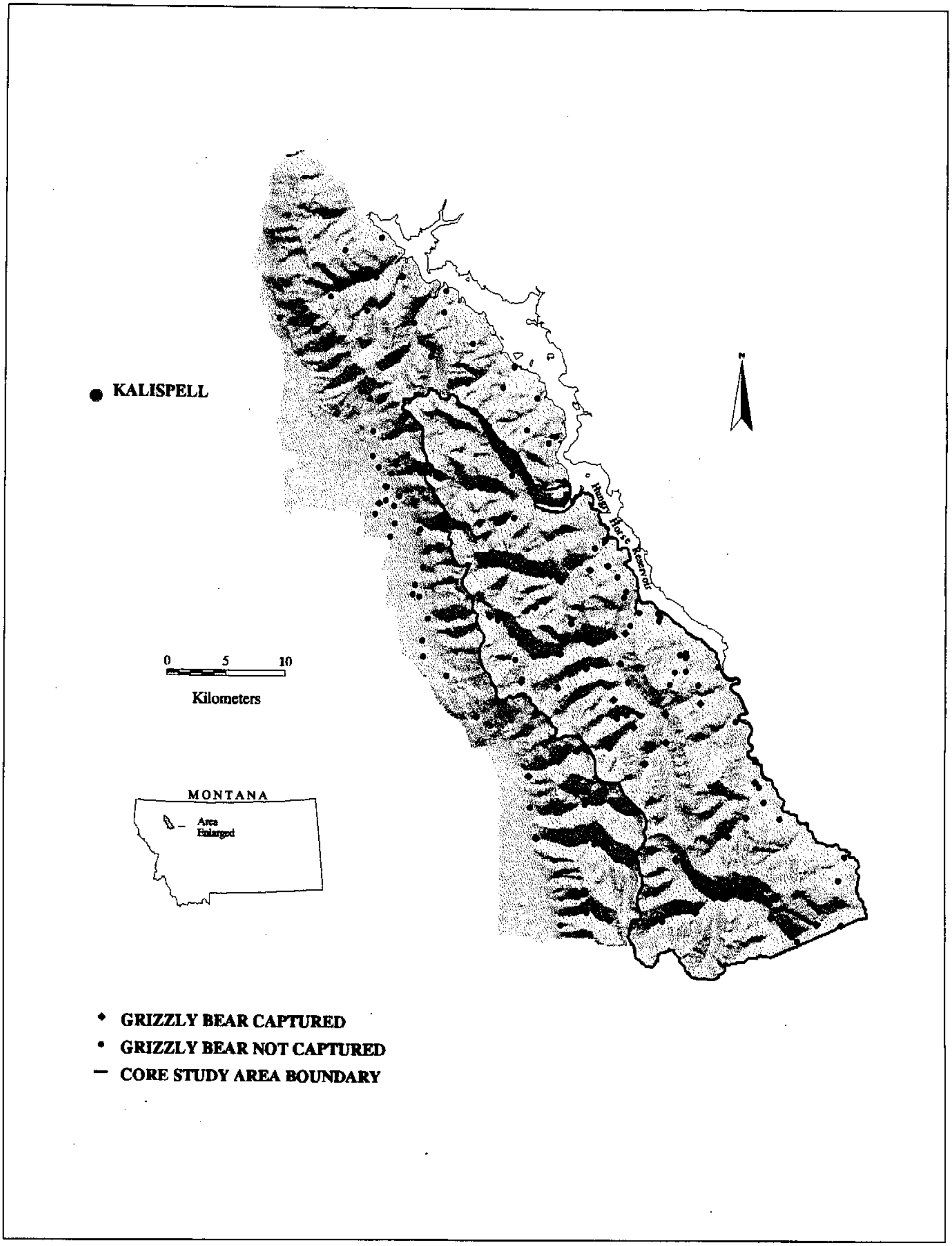


Figure 6.2. Location of snare-sites where we were successful and unsuccessful in capturing grizzly bears relative to the Core and Peripheral portions of the study area.

One grizzly bear death was classified as a research mortality. This 1 year-old male was killed by an adult male within several hours after being successfully released by the field team. Additionally, one subadult female grizzly bear was illegally shot while in a snare; a mortality that was classified as "illegal."

Morphology

Scale weights (kg) for age classes of male and female grizzly bears at first capture are given in (Table 6.3). Using the chest circumference from known-weight grizzly bears, we predicted weights for those animals we could not weight. The linear equation derived from 26 female captures was: $\log_{10}(\text{weight}) = -2.691 + (2.358*\log_{10}(\text{chest}))$. The prediction equation for spring weight from 17 male captures was: $\log_{10}(\text{weight}) = -3.801 + (2.908*\log_{10}(\text{chest}))$. The R^2 values were 0.82 and 0.95 for females and males respectively, confirming as found elsewhere that male grizzly bears attain greater body weight then females as they mature (Fig. 6.3). Similar differences between males and females was observed for zoological length (Fig. 6.4).

Table 6.2. Capture-recapture statistics for grizzly bears snared in the Swan Mountains Montana. 1987-1996.

Sex	Age Class			
	Adult	Subadult	Yearling	Total
Captures:				
Male	9 (18)[a]	8 (16)	4 (8)	21
Female	11 (22)	11 (22)	7 (14)	29
Recaptures:				
Male	24 (41)[b]	8 (14)	1 (2)	33
Female	15 (26)	3 (5)	7 (12)	25
Total:	60	35	15	108

[a] Percent of 50 captures.

[b] Percent of 58 recaptures.

Table 6.3. Selected morphological measurements of grizzly bears in the Swan Mountains, Montana. Measurements given are from the initial capture of each individual.

Measurement	Male			Female		
	Ad[a]	Subad	Yrlng	Ad	Subad	Yrlng
Weight (kg)	156,25,3[b]	81,7,7	37,10,4	88,4,6	60,5,9	35,2,4
Front foot:						
Pad length	8,0.4,9	7,0.4,7	5,0.3,5	7,0.2,11	6,0.2,11	5,0.2,6
Pad width	15,0.3,10	12,0.5,7	10,0.6,5	12,0.2,11	12,0.3,11	11,0.2,7
Foot length	13,0.7,9	12,.02,7	10,0.5,5	12,0.5,11	11,0.3,11	9;0.2,7
Claw length (arc)	5,0.2,10	6,0.5,6	5,0.2,5	5,0.2,11	5,0.1,6	5,0.3,11
Rear foot:						
Pad length	19,0.5,10	17,0.8,7	13,1,5	16,0.4,11	15,0.3,11	12,1,6
Pad width	14,0.3,11	12,0.6,7	10,0.7,11	11,0.3,10	11,0.3,7	11,0.3;5
Foot length	24,0.6,10	21,0.3,7	17,1.4,7	21,0.8,11	20,0.4,11	17,1.3,5
Claw length	3,0.1,9	3,0.1,6	3,0.1,4	3,0.3,11	3,0.3,10	3,0.3,6
Neck circumference	77,3,10	59,3,7	44,2,5	56,1.3,11	50,1.6,11	44,2,7
Zoological Length (w/tail)	191,5,6	158,3,5	137,4,3	173,4,4	153,3,9	133,7,6
Chest circumference (behind hump)	119,4,10	92,4,7	71,4,5	95,1.4,11	82,3,10	69,5,6

[a] Ad = adult (≥ 5.0 years), subad = subadult (2-4 years), yrlng = 1-year old.

[b] Mean, SE, N. Scale weight given in kg, all other measurements in cm.

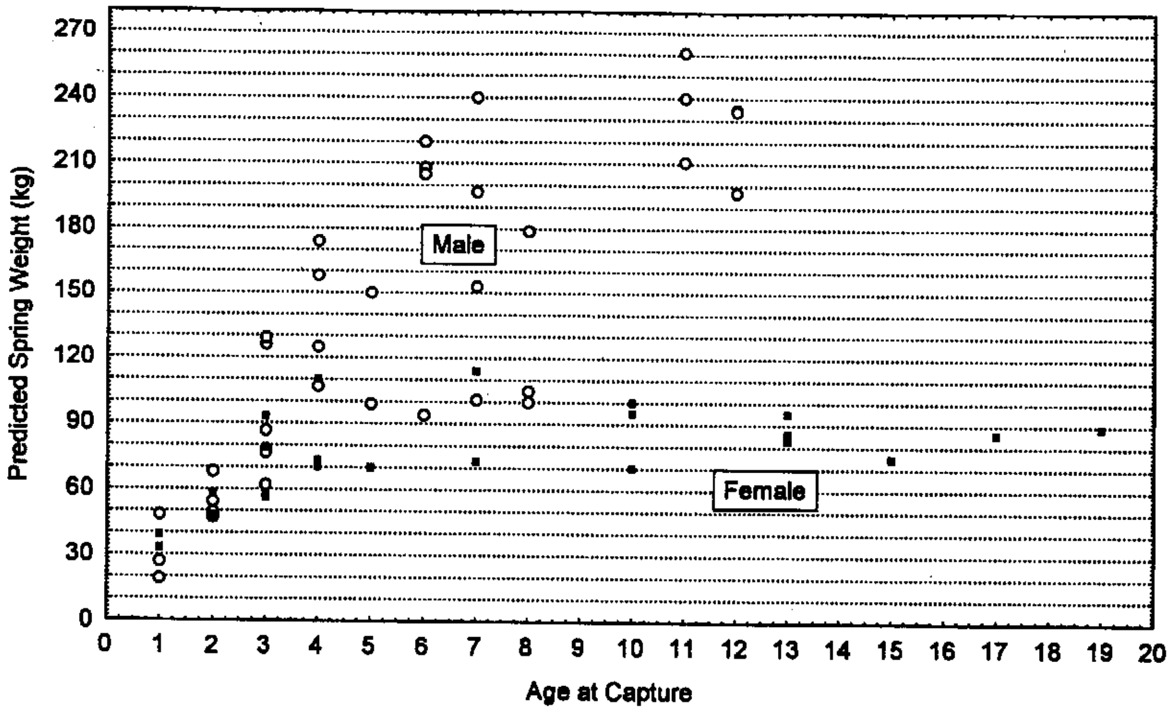


Figure 6.3. Estimated spring body weight of male and female grizzly bears using the $\log_{10}$ transformation of chest circumference (Nagy 1984). Data included capture and recapture measurements. Swan Mountains, Montana.

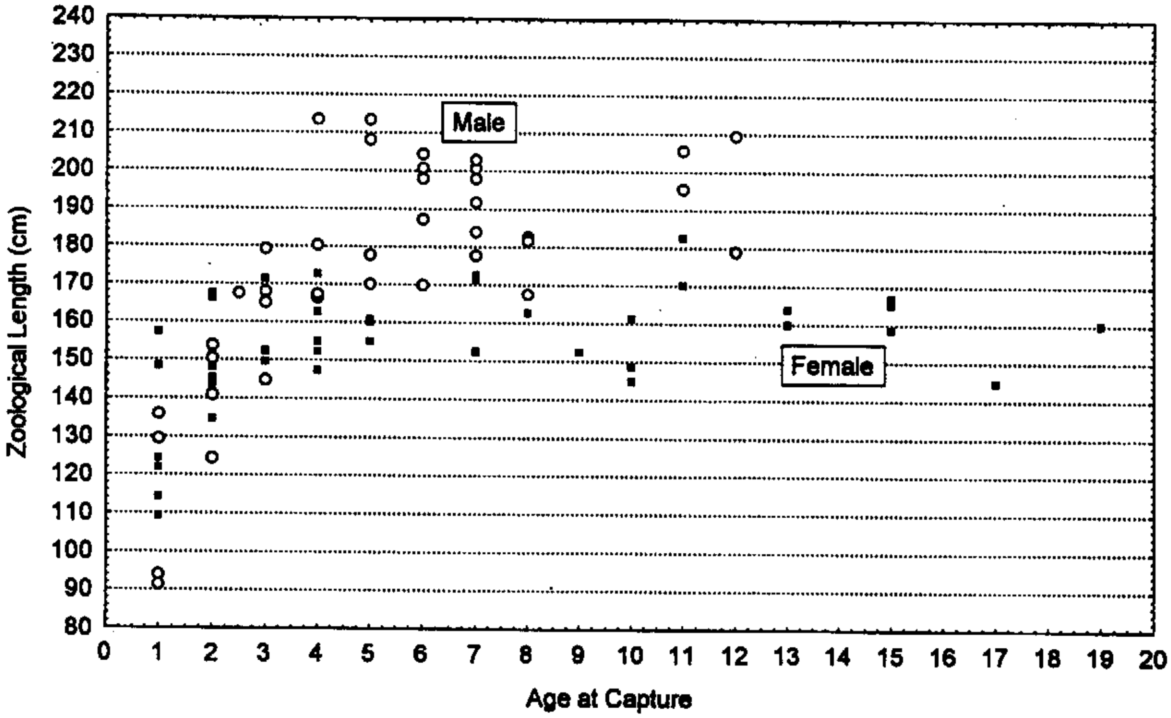


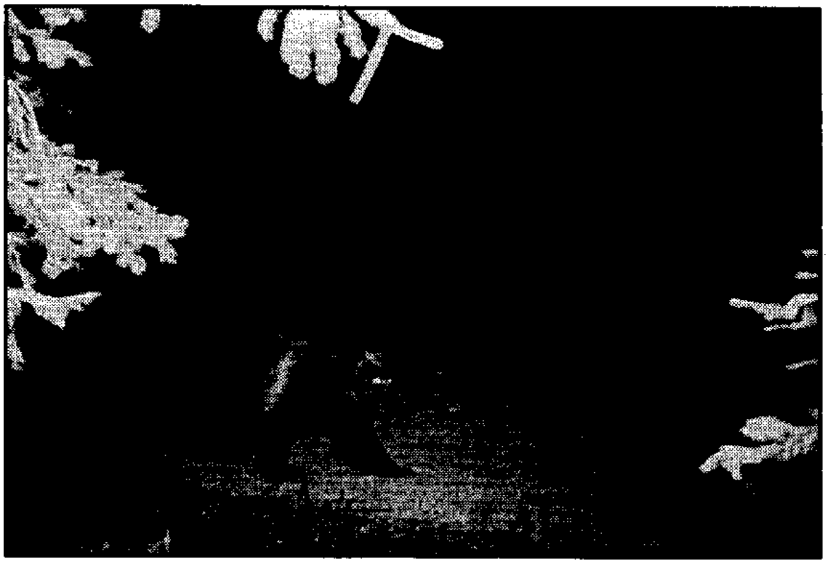
Figure 6.4. Zoological length of male and female grizzly bears from capture and recapture data. Swan Mountains, Montana.

CHAPTER 7

GRIZZLY BEAR RELATIONSHIPS TO THE HUMAN ENVIRONMENT

Grizzly bear habitat selection in relation to both the natural environment and to the human environment is an exceedingly important topic in remaining grizzly bear habitat. History has clearly shown that grizzly bear populations were extirpated or severely reduced from much of their historic range because of conflicts with humans. These conflicts often resulted in death for grizzly bears, or large-scale conversion and loss of previously suitable habitats. Even today, humans are an omnipresent component of remaining grizzly bear habitat. It is important that we understand the role humans play in grizzly bear ecology, because grizzly bears directly compete with man for space and resources, and because human attitudes and actions influence bear distribution and survival.

In this chapter we summarize our knowledge of human-grizzly bear interactions in the Swan Mountains. The chapter is composed of 3 sections. The first and second sections describe the influence of road and trails respectively on grizzly bear distribution. In section three, we outline our procedures for evaluating the cumulative impacts of human activities on grizzly bear habitat effectiveness.



SECTION 7.1

RELATIONSHIPS AMONG GRIZZLY BEARS, ROADS, AND HABITAT IN THE SWAN MOUNTAINS, MONTANA[1]

R. D. Mace, J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring

SUMMARY:

1. Relationships among grizzly bears, habitat, and roads were investigated between 1990-94 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 favored 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 random.
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/day but avoided buffers surrounding roads having >10 vehicles/day.
5. Between 1988-1994, 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 excessive to promote local population growth.

INTRODUCTION

Grizzly bear (*Ursus arctos horribilis*) recovery programs in the western 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 and 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 et al. 1987) and in southern British Columbia (McLellan and 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.

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[1] Mace, R. D., J. S. Waller, T. L. Manley, L.J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. J. Appl. Ecol. 33:1395-1404.

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 et al. 1987, Kasworm and Manley 1990) used distance measurements and univariate statistics to describe grizzly bear response to roads. In this paper, we explore nonlinear, multivariate methods to characterize relationships among grizzly bears, habitat, and roads in an area with a long history of legal and illegal mortality of grizzly bears.

STUDY AREA

The study area was located in the Swan Mountain Range of western Montana (Fig. 7.1.1). The 1,457 km^2 area was bounded on the north and south by U.S. 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 1940's, a network of roads was established within the study area primarily to access 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, inundated 9,712 ha of riparian and upland habitats (Casey et al. 1984).

Beginning in the early 1980's some roads were closed to improve wildlife security and other resources. A more aggressive closure program did not begin until approximately 1990. At present, there are 1,962 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 traveling by foot, bicycle, or horseback and some illegal vehicle use on closed roads occurred.

METHODS

Capture, Telemetry, and Home Range

Beginning in 1988, adult ($\geq$ five 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 1990-1994 when radio-collared grizzly bears were located twice each week from fixed-wing aircraft. Most locations were obtained during morning when flight conditions were best. We photographed each location with a Polaroid camera from the aircraft enabling us to immediately record locations. We documented an average aerial telemetry error of 150 m^2 (Mace and 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 (U.S. Department of Agriculture, Forest Service. Pacific Southwest 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 and Itami 1991). Relationships were evaluated at three orders of resource selection (Johnson 1980). We first compared habitat and road features within a composite 95% multi-year annual home range of radio-collared female grizzly bears to habitats within the study area but outside the composite home range (second-order selection). The composite home range was developed by overlaying upon each other, the 95% multi-annual ranges of 14 adult and subadult female grizzly bears. We chose the 95% isopleth to omit short-term forreys. Further, the 95% isopleth confirmed the distribution of females observed from our capture/resight results using snare and camera grids: no females were captured or photographed outside the composite range

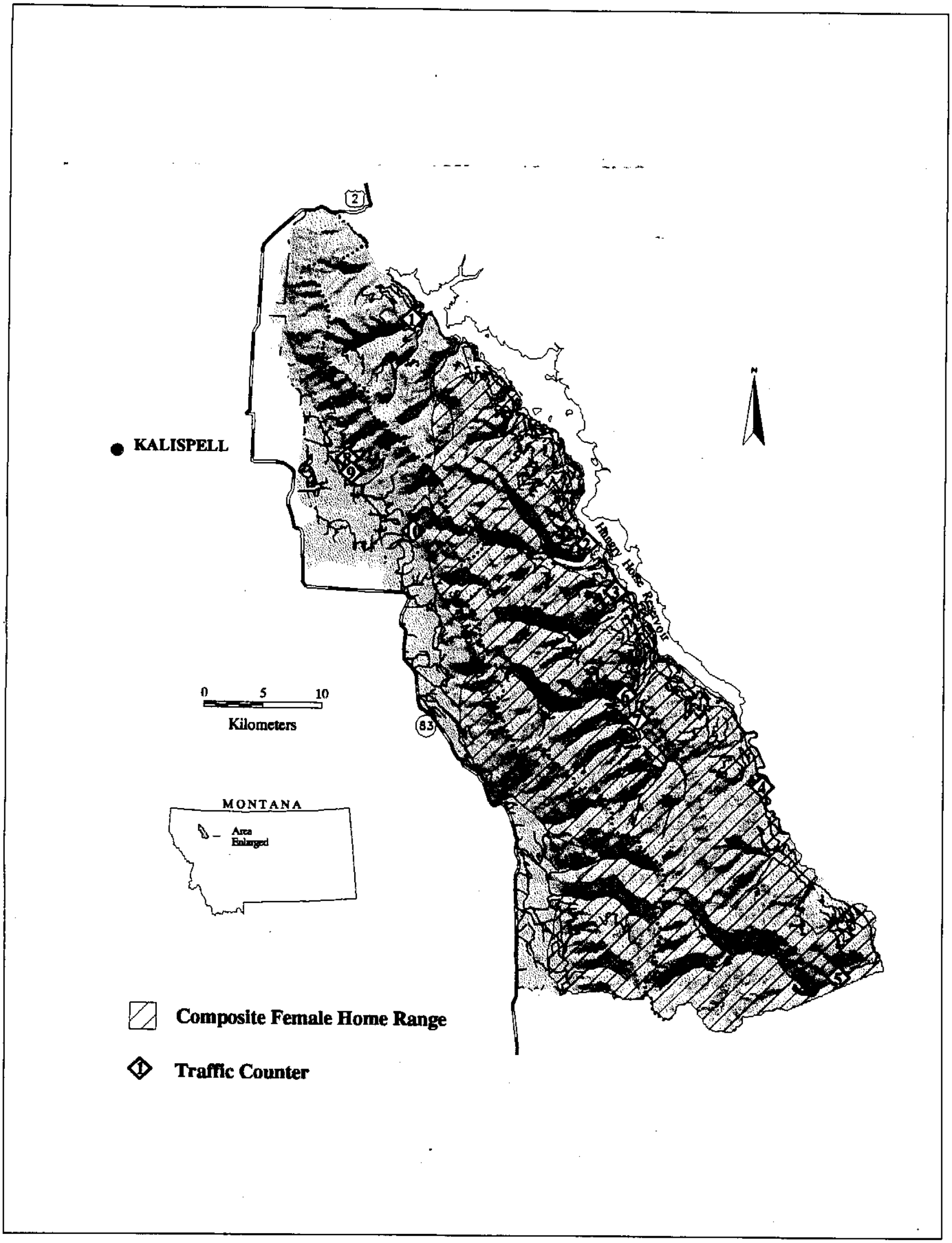

Figure 7.1.1. Relief map of study area in the Swan Mountains, Montana, showing distribution of roads, location of traffic counters, and the composite 95% multi-annual home range of female grizzly bears.

(Mace et al. 1994).

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 to conservatively estimate home ranges that were based on sample sizes that, for some bears were less than optimal (Table 7.1.1) (Worton 1989). Other authors studying low-density and highly mobile species acknowledged difficulties obtaining large sample sizes (Joshi et al. 1995, Weilgus and Bunnell 1995).

In fourth-order selection we investigated the response of grizzly bears to roads of several traffic volume classes. We tested whether bear use of 1/2 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.

Three seasons were used. 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 et al. 1982, Mace and 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 x 30 m.

Table 7.1.1. Year of capture, age at capture,seasonal sample size, and home range size for grizzly bears in the Swan Mountains, Montana (1990-1994). Sample sizes represent the number of telemetry points used for estimating home range and habitat selection using logistic regression.

Bear Id	Capture Year-Age (km^2)	Seasonal Telemetry Sample Size/Home Range		
		Spring	Summer	Autumn
F3	1987-1	30/251	15/79	18/329
F5	1987-7	57/380	52/70	45/81
F8	1993-2	18/187		
F18	1989-2	79/155	57/67	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	62/97	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	

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 km^2. The moving window routine in EPPL7 assigned the center pixel of a 1 km^2 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 km^2 mapping scale closely matched management standards for roads in the NCDE. It was not our intent 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/km^2. Areas with a road density of 0 km/km^2 were termed "unroaded."

Levels of Vehicular Traffic. We used magnetic counters to quantify levels of vehicular traf-

Table 7.1.2. Summary of average daily traffic levels from 10 traffic counters within the study area (mean, SD, n days monitored).

Counter No.	Season		
	Spring	Summer	Autumn
1	201,183,253	471,207, 35	97,54, 22
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, 72	7,9,348
8-9	12,16,424	22, 8,249	22,19,302
10	27,28,363	70,34,186	25,20,178

fic on a sample of roads. Ten counters were placed within the study area from 1990-92 to provide information on the spatial and temporal patterns of human use (Fig. 7.1.1). Average daily traffic (ADT) was summarized by season (Table 7.1.2). ADT values revealed substantial spatial and temporal variation and were converted to 5 broad classes: Class1 = <1 vehicle/day, Class2 = 1-10 vehicles/day, Class3 = 11-60 vehicles/day, Class4 = 61-300 vehicles/day, and Class5 = >300 vehicles/day. Class1 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 depicting 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 et al. 1992). The 30 classes were then grouped into three broad cover types: sites dominated by either rock or grass/forb communities (nonvegetated), shrubs (shrub land), or forest (> 40% conifer overstory). We then overlaid three digitized physiographic features on the satellite image: avalanche chutes, slabrock (Mace 1986), and timber harvest units where the overstory canopy had been removed (cutting units). Using the moving window GIS routine, each pixel was assigned the dominant cover type within 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).

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 and Wilson 1978). Our goal was to contrast the significance of variables among individuals by examination of the sign (negative or positive) and magnitude (p value) of associated regression coefficients, and not to construct the simplest model possible. The most parsimonious strategy, as outlined by Hosmer and 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 4,668 random coordinates within the composite female home range to characteristics of 2,447 random coordinates outside the range. This number of random points represented five times the size of the two areas relative to the road density map. 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 1990-1994. We calculated resource selection probability functions (RSF) using the following equation from Manly et al. (1993, p. 128)

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

where $w^*(x_i)$ was the RSF, $P_{\bar{u}}$ and P_u were sampling probabilities of unused and used units, β_o 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 of variable combinations occurring within the composite female home range, and were scaled from 0 - 1.0. 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 equaled home range size (e.g. 200 random coordinates for a home range of 200 km^2).

We developed "dummy variables" for categorical maps (Hosmer and Lemeshow 1989). Standard variables 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.

The significance of logistic models was ascertained by comparing the log-likelihood X^2 value for the model fitted to each individual parameter against the X^2 value for the model fitted only to the intercept β_0 (Hosmer and Lemeshow 1989, Manly et al. 1993). Variables were then considered either significant ($P < 0.10$) 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 a 0.5 km buffer surrounding roads of each ADT class within each bears seasonal home range. A 0.5 km buffer surrounding roads was small enough to detect selection, yet sufficient for chi-square tests using Bonferroni simultaneous confidence intervals (Byers et al. 1984). Individuals were classified as exhibiting negative, neutral, or positive selection toward road buffers of each ADT class.

Table 7.1.3. 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.

Parameter	Summary Statistics								Multivariate Statistics[c] (Final Model)		
	Within Composite Range				Outside Composite Range						
	Minimum-maximum	Mean	S.E.	%[b]	Minimum-maximum	Mean	S.E.	%[b]	Coefficient	S.E.	P
Road density	0 - 6.3	0.6	.014		0 - 5.2	1.1	.022		-0.16	.06	.02
Nonvegetated				3				4	0.57	.22	.01
Shrub Land				14				10	0.23	.10	.02
Forest[a]				59				67			
Chute				7				2	0.47	.15	.00
Slabrock				2				0.2	1.38	.46	.00
Cutting Unit				15				17	0.14	.08	.11
Low temperate				31				71	-1.32	.12	.00
Temperate				54				24	-0.15	.12	.20
Subalpine[a]				15				5			
Ownership				100[d]				75[c]	5.60	.58	.00
LOTEMPXRD									0.12	.07	.08

[a] Standard variables

[b] Percent of total for categorical variables

[c] Constant= -3.99, sampling fraction= 1.91

[d] Percent multiple-use lands

RESULTS

Second-order Selection-Females

The composite female home range differed from the area outside of the range. The composite range was positively associated with multiple-use lands (Table 7.1.3). 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 7.1.3). 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 7.1.3). 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 percent 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 7.1.3). 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. 7.1.2). Selection in this elevation zone was greatest at a road density of zero for all cover types. As road density increased, RSF values declined.

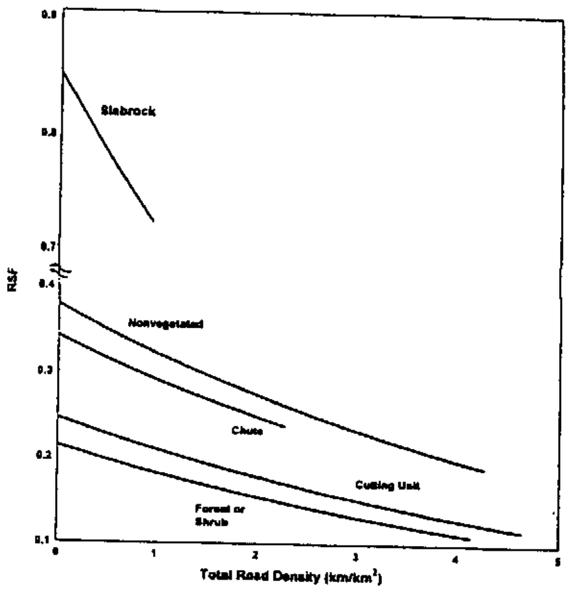

Figure 7.1.2. Resource selection probability functions (RSF) for second-order selection, Swan Mountains, Montana. RSF values depict changes in the relative probability of temperate elevation zone cover types occurring within the composite 95% female home range relative to total road density. Logistic 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 a non-range area, and occurred at a maximum total road density of 1 km/km^2.

Third-Order Selection

We compared telemetry 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 of 17 bears during spring. Positive selection for the low temperate and temperate zones relative to the subalpine was evident for 14 and 13 individuals respectively (Table 7.1.4). 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 8 and 7 individuals respectively. Road density was significantly negative for 2 and significantly positive for 3 bears. Coefficients for the interaction term LOTEMPXRD was negative for 10 of 15 grizzly bears during spring. Thus most bears utilized areas with lower road densities while in the low temperate zone (Table 7.4). 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 7.1.4). Four bears selected the subalpine

Table 7.1.4. 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.

Parameter	Number of Grizzly Bears Having Negative or Positive Logistic Regression Coefficients Within Seasonal Home Ranges (Number of Significant Ranges)[a]	
	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 TOTRD	10 (2)	5 (0)
	6 (1)	8 (2)
	8 (2)	5 (0)

[a] 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.

zone over the two lower elevation zones during this season.

Grizzly bears exhibited positive selection for more cover types than during spring (Table 7.1.4). Coefficients for shrub lands, slabrock, and cutting units were positive relative to Forest for most bears. Significant positive selection for chutes declined from spring.

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 7.1.4). 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 fall, 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 Class4 or Class5 roads. All bears having these two types within their home range exhibited negative selection towards them (Table 7.1.5). All grizzly bear spring home ranges contained Class1 roads. Most bears showed neutral or positive selection towards Class1 road buffers during

Table 7.1.5. 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.

Season	Selection Towards 0.5 Km Buffer Proximate To Road Classes (Number of Bears)														
	Class1			Class2			Class3			Class4			Class5		
	-	=	+	-	=	+	-	=	+	-	=	+	-	=	+
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

spring (Table 7.1.5). The number of bears exhibiting positive selection for road buffers decreased as traffic volume increased. Seven of 11 bears showed negative selection towards Class3 roads during spring. One bear exhibited positive selection for Class3 roads during this season; an adult female conditioned to human and livestock food located near a Class3 road.

Most grizzly bears were either negative or neutral towards Class1, Class2, and Class3 during summer (Table 7.1.5). Two of the three bears positively associated with Class1 roads were males. No positive selection was observed for Class2 or Class3 roads.

Twelve of 14 individuals exhibited neutral selection for Class1 roads during autumn. No bears were positively associated with Class2 or Class3 roads during this season.

DISCUSSION

We 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. 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, yet also have high densities of humans and roads. Illegal mortality and sanitation problems which attract grizzly bears are ongoing 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. 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 study area (Belden and Hagedorn 1993).

Within seasonal ranges, resource availability and selection was unique to the individual. For this reason, we could not pool individuals as is typically done (Harding and Nagy 1980, Tracey 1977, Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990). Seasonal coefficients tended to be strongest (either positively or negatively significant) for elevation and cover type variables relative to road density. Both positive and negative multivariate relationships were observed for each season for total road density but coefficients 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 and Pelton (1989) for black bears. However, grizzly bear seasonal ranges were comprised mostly of Class1 and Class2 roads. Thus total road density measurements within these ranges reflect either roads closed to vehicles or roads driven infrequently by humans. Interestingly, avoidance of high total road densities areas was evident for some bears, even though roads were closed to public travel.

During each season, most grizzly bears were positively associated with the cover types below the subalpine zone. During spring, much of the subalpine was either unavailable or undesirable to grizzly bears because of snow. It is less apparent why most bears showed multivariate selection against the subalpine zone during summer and autumn. However, it is possible that food resources in this higher elevation band were less abundant than in lower elevation areas as documented by Craighead et al. (1982). These author's 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 were positively and significantly associated with chutes during spring. Multivariate selection for this cover type continued for many bears throughout the year. During spring in particular, logistic regression coefficients were stronger for chutes than other variables including road density. Chutes have high coverage and frequency of vegetal foods sought by bears such as *Heracleum lanatum*, *Angelica spp.*, *Erythronium grandiflorum*, and *Claytonia spp.* (Mealey et al. 1977, Mace 1986, Korol 1994). Further, visual security is chutes 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 et al. 1983, Martin 1983).

Neutral use of, or positive selection towards habitats near roads implies that important habitats occur near roads. Such selection was found in our fourth-order analyses during all seasons for areas proximate to closed roads (Class1) and roads with < 10 vehicles/day (Class2) during spring. This was partially due to bears utilizing cutting units, or avalanche chutes which often terminated near roads. Few bears exhibited positive selection towards areas near roads having >60 vehicles/day. This proximal avoidance of roads has been demonstrated elsewhere (Tracey 1977, Harding and Nagy 1980, Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990).

McLellan and Shackleton (1988) demonstrated avoidance of areas proximate 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, development of grizzly bear habitat, and conditioning of grizzly bears to unnatural food sources near roads. Mace et al. (1994) reported a population size of 15-21 solitary (≥ 2 y ears old) grizzly bears present in the study area. The mortalities associated with road access, coupled with a high number of natural mortalities (n = 7, 1988-1994), inhibited the growth of this local population in the Swan Mountains.

All three levels of selection suggested that grizzly bears can persist in areas with roads, 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 programs in the NCDE are extremely controversial because traditional public access by vehicle to favorite locations is reduced. Further, local economies, generated from recreation and timber harvest activities are affected. 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 programs should incorporate seasonal habitat requirements of grizzly bears. A properly implemented program would minimize road densities and traffic volumes in highly preferred habitats. Road density standards could then be relaxed somewhat in less suitable habitats, allowing increased public use of public lands while minimizing threats to the local grizzly bear population. Innovative road access programs that allow short-term (e.g., 2 weeks) access by humans would serve to build public acceptance towards this valuable wildlife species.

SECTION 7.2

GRIZZLY BEAR DISTRIBUTION AND HUMAN CONFLICTS WITHIN JEWEL BASIN HIKING AREA, SWAN MOUNTAINS, MONTANA.[1]

R. D. Mace and J. S. Waller

ABSTRACT: Telemetry data obtained from grizzly bears (*Ursus arctos horribilis*) were used to evaluate resource selection within the Jewel Basin Hiking Area (JBHA) of western Montana. Logistic regression models were constructed using Geographic Information System maps of elevation zones, dominant cover types, and distance to hiking trails and lakes. Fourteen radioed grizzly bears used the JBHA between 1987-1994 primarily during summer. Using univariate statistics, we determined that grizzly bears were significantly further than expected from trails, and from lakes with camp-sites during spring, summer, and autumn. In multivariate models however, distance to trails and/or lakes were significant variables only during summer and autumn. During these 2 seasons the relative probability of grizzly bear selection increased as distance to trails and lakes with camp-sites increased. For each season, grizzly bears selected open habitats relative to the forest cover type which contained most of the trail system. We found no historical records of conflicts between grizzly bears and recreationists in the JBHA, nor did bears appear to be food-conditioned or habituated. No radioed bears lived solely within the JBHA, each individual's home range was also composed of multiple-use lands that were roaded and where many other human activities occurred. We concluded that several factors together precluded human-bear conflict in the JBHA. These include low visitor use levels, trail placement, an educated public, and negative conditioning towards a host of human activities occurring within and outside the area. Therefore, while in the JBHA, grizzly bears minimized their interaction with recreationists by spatially avoiding high use areas.

INTRODUCTION

The largest population of grizzly bears in the contiguous 48 states is found in an area termed the Northern Continental Divide Ecosystem (NCDE) in western Montana. Over 50% of the NCDE is roadless, including Glacier National Park and 4 congressionally designated wilderness areas. Access to these roadless areas is by an extensive trail system. Except for Glacier National Park where hunting is not allowed, this trail system is used for big game hunting, fishing, and other activities involving hiking, horseback riding, and camping.

Confrontations and conflicts between grizzly bears and recreationists are reported most frequently in national parks or wildlife sanctuaries where firearms are often not allowed, where big game hunting is not allowed, and where brown bear hunting in particular is not permitted (Martinka 1982, Noble 1972). Therefore, much of our current knowledge on the effects of recreational activities on grizzly bears has been gained in "protected areas" (Faro and Eide 1974, Chester 1980, Post 1982, Schleyer 1983, McCrory et al. 1986). There is little information on the impacts of recreational activities on brown bears inhabiting multiple-use areas. In this paper we examine the spatial and temporal distribution of radio-collared grizzly bears relative to trails and camp-sites in a popular recreation area. The area abuts managed forest and private lands where big game hunting is allowed, and where there is a long history of legal hunting of grizzly bears.

STUDY AREA

The JBHA, designated in 1970, was located in the Swan Mountains approximately 44 km east of Kalispell, Montana (Fig. 7.2.1). The 6,212 ha area was managed by the USDA Forest Service for

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[1] Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. Wildl. Soc. Bull. 24:461-467.

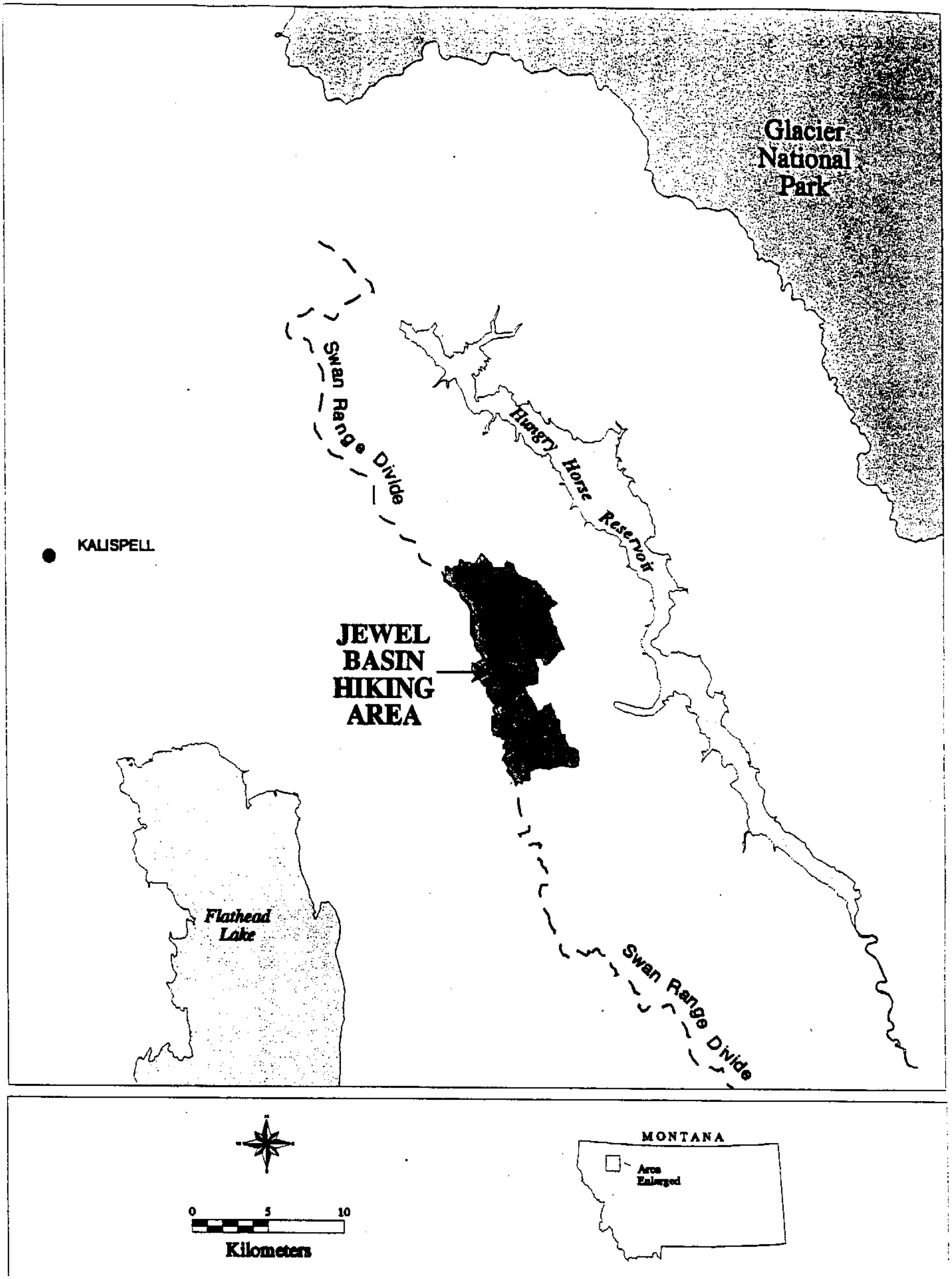

Figure 7.2.1 Location of the Jewel Basin Hiking Area in the Swan Mountains, Montana.

hiking and camping activities and contained 28 mountain lakes and over 100 unimproved camp sites. There were 55 km of trails in the JBHA. Packstock and mechanized equipment were prohibited but big game hunting was allowed. Access to the JBHA was by road, but no roads existed within the hiking area proper. Elevation varied from 1,360 to 2,310 m.

Visitor use of the JBHA was not well documented prior to 1990. Because of lingering snowpack and frozen lakes, visitation was relatively low until mid-June to early July. The USDA Forest Service (Flathead National Forest) estimated that an average of 90 people/day used the JBHA during the period June-August. They further estimated that approximately 80% of this use was for day-trips. Mace et al. (1996) reported that an average 27, 70, and 25 vehicles/day traveled the primary road leading to the JBHA during spring, summer, and autumn respectively. McCool and Braithwaite (1989) reported that most visitors to the JBHA were from the local area.

METHODS

Grizzly bear telemetry coordinates were compared to 2431 random coordinates within the JBHA using Geographical Information System (GIS) maps. Random coordinates were used to ascertain resource availability (Marcum and Loftsgaarden 1980). Grizzly bears were captured and radio-collared between 1987 and 1994 as described by Mace et al. (1994). Aerial telemetry procedures were described by Mace et al. (1996). Telemetry coordinates were compared to availability relative to 5 cover types, 3 elevation zones (Mace et al. 1996), and distance to trails and lakes. The cover types used were rock/grass lands, shrub lands, forest, avalanche chutes, and slabrock. The low temperate zone included those habitats below 1494 m. The temperate zone extended from the low temperate zone to 1981 m. Areas above 1981 m were termed the subalpine zone. We incorporated an aerial telemetry error of 75 m into each map using a GIS moving window routine (Mace et al. 1996). Thus the distance maps represented the average distance to trails and lake shores within 150 m^2, and the cover type and elevation maps were the dominant category within the error polygon.

Historical records of grizzly bear conflicts with humans in the NCDE were obtained from local offices of state (Montana Department of Fish, Wildlife, and Parks) and federal (USDA Forest Service, Flathead National Forest) agencies.

Trail and camp-site locations were obtained from the USDA Forest Service, Flathead National Forest in digital format. These features were then validated by ground reconnaissance. All camp-sites were located along the shores of lakes, and anglers used the entire shoreline of lakes. Using EPPL7 software (Minnesota State Planning Agency. 300 Centennial Building, 658 Cedar Street. St. Paul, MN 55155), we developed 10 distance isopleths from trails and lake shores. Categories used were <210 m, 211-450 m, 449-690 m, 689-930 m, 931-1,170 m, 1,169-1,410 m, 1,409-1,650 m, 1,649-1,890 m, 1,889-2,130 m, and >2,130 m. We designated 3 seasons: spring (den emergence-15 July, summer (16 July-15 September),and autumn (16 September-den entry).

The pooled sample of grizzly bear telemetry coordinates from 1987 to 1994 were compared to available map layer combinations using maximum-likihood logistic regression. Random coordinates were generated from the uniform random distribution. We developed 0-1 indicator variables for categorical variables (Hosmer and Lemeshow 1989). Logistic regression procedures followed those of Manly et al. (1993, formula 8.6, p. 127) for used and available habitat resources. For each season, we developed a full model (Model 1) that contained all map variables. A second and final model (Model 2) was then developed using those variables that were significant ($P \leq 0.10$) from Model 1. Model fit was ascertained by comparing the model containing all variables to the "no selection model" (Hosmer and Lemeshow 1989). For each season, we calculated resource selection functions (RSF) that were scaled between 0-1. An RSF value of 0 represented a zero probability of use while an RSF of 1.0 represented a 100% relative probability of use of a habitat combination by grizzly bears. For categorical and parametric statistical tests, we used Pearson's Chi-square and Student's T, respectively with alpha set at 0.05. We used the computer software STATISTICA (Statsoft Inc. 2325 East 13th. St. Tulsa, OK 74104) for data analyses.

RESULTS

Habitat Selection Based on Univariate Statistics

Between 1987 and 1994, 14 radioed grizzly bears (8 m, 6 f) were located 185 times within the JBHA. Locations were recorded during spring (33%), summer (45%), and autumn (22%).

Table 7.2.1. Univariate statistics describing the availability and seasonal use of elevation zones, dominant cover types and distance to trails and lakes for grizzly bears using the Jewel Basin Hiking area, Montana. 1988-1994.

Availability and Use	Percentage Availability and Grizzly Bear Use of Elevation Zones and Cover Types								Distance to (m) :			
	Elevation Zone			Dominant Cover Type					Trails		Lakes	
	Low Temperate	Temperate	Subalpine	Nongrass	Shrub land	Forest	Avalanche Chute	Slabrock	Av	Sd	Av	Sd
Available	4	70	26	6	26	50	11	8	617	565	1133	878
Spring Use	13	78	8	2	13	40	38	7	813	619	1378	944
Summer Use	18	79	4	2	18	33	17	30	878	511	1376	686
Autumn Use	5	83	12	2	29	22	39	7	1129	544	2031	1060

Grizzly bears were significantly further than available (Table 7.2.1) from trails during spring (T = 2.64, 2489 df, P = 0.00), summer (T = 4.17, 2513 df, P = 0.00), and autumn (T = 5.76, 2470 df, P = 0.00). Grizzly bears were also significantly further than available from lakes shorelines with camp-sites during spring (T = 2.12, 2489 df, P = 0.03), summer (T = 2.50, 2513 df, P = 0.01), and autumn (T = 6.46, 2470 df, P = 0.00). Grizzly bear distances from both lakes with camp-sites and trails generally increased as the seasons progressed (Table 7.2.1). The data suggest that grizzly bears positioned themselves further from lakes with campsites than from trails (Table 7.2.1).

Most of the trail system within the JBHA was in the temperate (73%) and subalpine (26%) elevation zones, and in either forested (66%) or shrub land (24%) habitats (Table 7.2.2). Fifty-one percent of the trail system was in forested habitats within the temperate zone (Table 7.2.2).

Table 7.2.2. Distribution of trails in the JBHA by elevation and cover type.

	Percent of Trail System In Each Elevation Zone and Cover Type			
Cover Type	Elevation Zone			
	Low Temperate	Temperate	Subalpine	Row Total
Nongrass		1	2	3
Shrub land		15	9	24
Forest	1	51	14	66
Avalanche chute		1	1	2
Slabrock		5		5
Column Total:	1	73	26	

The JBHA was composed primarily of temperate (70%) and subalpine (26%) habitats (Table 7.2.1). Grizzly bear distribution relative to elevation zone differed significantly from available during spring ($X^2 = 22$, 2 df, P = 0.00) and summer ($X^2 = 57$, 2 df, P = 0.00), but not during autumn ($X^2 = 4$, 2 df, P = 0.13). Grizzly bear use of the low temperate zone was greatest during summer, and use of the subalpine zone was greatest during autumn. Cover types were not equally available within the JBHA: forest (50%) and open shrub lands (26%) predominated (Table 7.2.1). Avalanche chutes were important to grizzly bears during spring and autumn, as were slabrock habitats during summer. Use of dominant cover types by grizzly bears was different than available during all 3 seasons (P = 0.00).

Habitat Selection Based on Multivariate Analysis

Model 1 for each season revealed the strength (p-value) and association (coefficient sign) of resource variables to grizzly bears in the JBHA. Model 1 was significant over the no selection model for spring ($X^2 = 44$, 8 df, P = 0.00), summer ($X^2 = 93$, 8 df, P = 0.00), and autumn ($X^2 = 51$, 8 df, P = 0.00). However, for each season there were several variables that did not contribute significantly to habitat selection ($P \geq 0.10$) (Table 7.2.3) and were omitted

Table 7.2.3. Logistic regression coefficients for Model number 1 (Full model) for each season, using all variables in the logistic equation.

Variable[a]	Seasonal Logistic Regression Coefficient Estimates, Standard Errors and P-values								
	Spring			Summer			Autumn		
	Est	SE	p	Est	SE	p	Est	SE	p
Constant	-4.88	0.54	0.00	-6.40	0.68	0.00	-7.08	0.69	0.00
Low temperate	1.94	0.62	0.00	3.49	0.67	0.00	0.22	0.88	0.80
Temperate	1.11	0.48	0.02	2.03	0.61	0.00	0.85	0.50	0.09
Nongrass	-0.56	1.04	0.59	0.36	0.76	0.64	0.13	1.10	0.91
Shrub land	-0.38	0.42	0.36	0.23	0.34	0.50	0.99	0.45	0.03
Avalanche chute	1.32	0.33	0.00	0.24	0.36	0.52	1.33	0.45	0.00
Slabrock	-0.04	0.53	0.95	1.79	0.30	0.00	0.58	0.68	0.39
Distance to trails	0.07	0.07	0.32	0.11	0.06	0.05	0.13	0.07	0.08
Distance to lakes with camp-sites	-0.05	0.06	0.40	0.05	0.05	0.33	0.19	0.07	0.01

[a] Standard variables were the subalpine elevation zone and the forest cover type.

from the final model.

Model 2 was significant over the no selection model for spring ($X^2 = 42$, 3 df, P = 0.00), summer ($X^2 = 91$, 4 df, P = 0.00), and autumn ($X^2 = 50$, 5 df, P = 0.00). During spring, grizzly bears selected the low temperate or temperate elevation zones over the subalpine zone (Table 7.2.4). Higher RSF values were achieved for the avalanche chute cover type over all other cover types. Distance to trails and lakes did not enter into Model 2 during spring.

During summer, grizzly bears again selected the low temperate and temperate elevation zones over the subalpine zone (Table 7.2.4). Only the slabrock cover type entered into the final model. Distance to trails was a significant variable during summer but distance to lakes with camp-sites was not. The highest RSF value was achieved when the distance to trails exceeded 2,130 m.

Grizzly bears exhibited selection for the temperate elevation zone during autumn (Table 7.2.4). Only the shrub land and avalanche chute cover types entered into the final model for this season and both remained significant (Table 7.2.4). Grizzly bears selected areas at a maximum distance to trails (> 2,130 m). The distance to lakes was nearly significant (P = 0.11).

Table 7.2.4. Final logistic regression coefficients for the final Model Number 2 for each season, where only significant variables ($P \leq 0.10$) from Model Number 1 were entered into the logistic equation.

Variable[a]	Seasonal Logistic Regression Coefficient Estimates, Standard Errors and p-values								
	Spring			Summer			Autumn		
	Est	SE	p	Est	SE	p	Est	SE	p
Constant	-5.06	0.46	0.00	-6.13	0.63	0.00	-6.93	0.61	0.00
Low temperate	2.02	0.59	0.00	3.46	0.65	0.00			
Temperate	1.15	0.47	0.02	2.00	0.60	0.00	0.80	0.43	0.06
Shrub land							0.86	0.41	0.04
Avalanche chute	1.44	0.28	0.00				1.21	0.41	0.00
Slabrock				1.67	0.26	0.00			
Distance to trails				0.15	0.05	0.00	0.13	0.07	0.07
Distance to Lakes with camp-sites							0.19	0.07	0.11

Grizzly Bear/Human Conflicts

No human has been killed by a grizzly bear in the NCDE, outside of Glacier National Park, since the early 1900's. There are no records of bear-inflicted human injury in the JBHA. We were unable to find a single instance of aggressive, habituated, or food-conditioned behavior by grizzly bears in the JBHA.

DISCUSSION

The behavioral response of grizzly bears to humans varies widely by the type, timing, placement, and predictability of the activity. Under most circumstances, bears flee upon detecting humans (Herrero 1985, Revenko, 1994). However, as suggested by Mattson (1990), individual and population response to human activity is a function of several factors including the nature and extent of historical interaction with humans, availability of human foods to bears, demographics and size of the population, and the distribution of native habitats and foods. Under some circumstances, grizzly bears may become habituated to human activities, loose their overt fear of humans, and no longer avoid people. Much of our understanding of the processes and motivation behind habituation of brown bears to human activity comes from direct observation of animals at concentrated foraging areas such as salmon streams (Egbert and Stokes 1976, IGBC 1987, Olson and Gilbert 1994), or from areas where human garbage was available (Hornocker 1962, Jope 1983, Mattson 1990, Craighead et al. 1995). These studies suggest that there are differences among age, sex, and reproductive classes in the likelihood and level of habituation to humans. Unfortunately, we were unable to assess these differences because of the relatively small sample of telemetry locations per individual bear within the JBHA. The small sample sizes were a result of the small size of the JBHA relative to the home ranges of study animals. Annual home ranges for males and females in the Swan Mountains were approximately 12 and 2 times larger than the JBHA for males and females respectively (Mace and Waller 1996).

Habituation, in the absence of artificial food reward or excessive negative stimuli, occurs most frequently under circumstances where human activity is predictable and controlled. Bears are termed "food-conditioned" when consumption of human food or garbage is involved. To our knowledge, none of the radio-collared grizzly bears in this study had a history of serious conflict with humans and were not considered habituated or food-conditioned.

Grizzly bears in the JBHA did not position themselves in a random fashion relative to trails and lakes with camp-sites. During each season, bears were significantly further from areas frequented by humans. Our analyses suggested that grizzly bears responded seasonally to habitat and topographic variables in addition to trails and campsites. Similar relationships between habitat and hiking trails were suggested in the work of Gunther (1990), Kasworm and Manley (1990), and Nadeau (1987).

During all seasons, grizzly bears in the JBHA selected for open cover types (< 40% overstory of conifers) relative to the forest cover type. Open habitats generally contained more forage preferred by grizzly bears (Mace and Jonkel 1986). Most of the trail system (66%) in the JBHA occurred in the forest cover type which may partially explain the lack of confrontations between hikers and grizzly bears. McLellan and Shackleton (1989) studied the immediate response of grizzly bears to off-trail hikers, heavy machinery, fixed-wing aircraft, and helicopters. They observed grizzly bears fleeing >1 km from hikers in both open and forested habitats, and the response to off-trail hikers was greater than that observed for the other types of disturbances. Comparing their findings to those of Jope (1985), who studied bear response to humans along the trail system of Glacier National Park, McLellan and Shackleton (1989b) concluded that the flight response appeared stronger outside of the Park reserve where bears were less habituated to humans.

The lack of confrontation and habituation in the JBHA was undoubtedly a result of several factors. We were unable to document a single case that would indicate a food-conditioning problem with grizzly bears in the JBHA. Habituated or food-conditioned brown bears are most often involved in injury or death to human recreationists (Herrero and Fleck 1990). The density of grizzly bears and humans is relatively low in the JBHA compared to other studies. From our sample of radio-collared bears, we estimate that a maximum of 5 individual grizzly bears and < 100 recreationists might be present in the JBHA on any particular day during the peak of summer activity. Martinka (1982) noted that confrontation between bears and humans was directly related to the number of people in bear habitat. Most recreational activity in the JBHA is confined to well-defined, historical hiking trails and camp-sites. Because of steep terrain and heavily forested habitats, little off-trail hiking occurs in the area. Although human activity centers are well-defined, temporal use of many camp-sites and trails by humans is unpredictable because of low numbers of recreationists. McCool and Braithwaite (1989) found that recreationists in the JBHA tended to be from the local area and had some knowledge of proper hiking and camping etiquette in grizzly bear habitat. Also, much of the trail system in the JBHA is through forested areas that are not preferred habitat for grizzly bears. Such placement of trails has been identified (Herrero 1985) as an important management strategy in areas occupied by grizzly bears.

McCullough (1982) suggested that negative conditioning of bears to humans was caused by hunting which involved removal of aggressive or unwary individuals. Herrero (1985) argues this by stating: "Death isn't an instructor-it is an eliminator." Our sample of radioed grizzly bears that use the JBHA occupied ranges that were administered for multiple uses (Mace et al. 1996). They and their recent ancestors were frequently confronted with both concentrated and dispersed human activity associated with timber harvest, road traffic, recreation, and disturbance associated with conversion of habitat to agricultural and residential use. Outside of Glacier National Park, grizzly bears in the NCDE are confronted with black bear and ungulate hunters for one half of their active period, and grizzly bears were legally hunted in the NCDE until 1991. Conversely, most of these activities, including public use of firearms and hunting are not permitted in parks and sanctuaries where habituation has historically been most pervasive. While it is true that grizzly bears within national parks are not totally protected from human-caused mortality, most mortalities were due to management actions targeted towards food-conditioned, habituated, or aggressive bears (Craighead 1995, Gunther 1994, Herrero 1994).

We suggest that most grizzly bears surviving in multiple-use and other highly impacted habitats in the NCDE have become negatively conditioned to humans. This negative reaction may reduce human-caused mortality, but also results in loss of habitat, loss of foraging opportunity, and may upset the spatial distribution of individuals. The level of this negative conditioning, and thus displacement, may be based on the amount and nature of human stimuli to which an individual is subjected. It is clear that management programs that discourage food-conditioning and habituation, encourage public education, and direct the placement of facilities away from preferred bear habitat, together with low levels of human use, have prevented human-bear conflicts in the JBHA.

SECTION 7.3

LANDSCAPE EVALUATION OF GRIZZLY BEAR HABITAT IN WESTERN MONTANA[1]

R. D. Mace, J. S. Waller, T. L. Manley, K. Ake, W. T. Wittinger

ABSTRACT We present a methodology for evaluating the cumulative effects of human activity on grizzly bear habitat in the Northern Continental Divide Ecosystem (NCDE) of western Montana. We used logistic regression to model the relative probabilities of female grizzly bear resource selection from telemetry data, TM satellite imagery (greeness), elevation, human activity points, roads, and trails. Selection models were then extrapolated to other portions of the NCDE where no telemetry data existed. During spring, adult female grizzly bears were positively associated with low and mid-elevation habitats having high values of deciduous green vegetation. Logistic regression coefficients were negative for all road and human activity variables. Summer and fall coefficients were also negative for road, human activity, and trail variables. During summer and fall, females were positively associated with mid to high elevations. Coefficients were positive for greeness during all seasons. Extrapolations of seasonal potential and realized habitat models were made to other areas on the western side of the NCDE. Realized habitat values declined on northwest to southeast gradients during all seasons. During spring, mean habitat potential values decreased from northwest to southeast, with much of the Bob Marshall Wilderness exhibiting a relatively low probability of use by female grizzly bears. Conversely, during summer and fall the Bob Marshall area exhibited a greater extent of high probability functions. The mapping and extrapolation process highlighted areas where habitat restoration would have the greatest benefit. These areas were typically low elevation spring habitats where high road densities and urbanization occurred.

INTRODUCTION

Wildlife managers have long sought to understand how human activities effect the suitability of habitat for various wildlife species. The literature abounds with references which assess the impacts of land conversion, land use practices, urbanization, and pollution on wildlife demography, energetics, nutrition, and survival (Berry 1986). The majority of these references emphasized animal response to a single variable. Early efforts to incorporate multiple factors included "habitat suitability models" which were generally a series of univariate models that were combined into a single suitability model.

Significant improvements in habitat suitability models were made following advances in spatial statistics, habitat selection statistics, satellite imagery, and computer mapping (Stormer and Johnson 1986). These advances allowed more effective evaluations of the impacts of human occupation on wildlife at landscape and ecosystem scales (Craighead et al. 1982). Population Viability Analysis techniques that link animal demographics and habitat condition will require sound evaluations of landscape scale habitat selection processes (Boyce 1992).

Models that evaluate the effects of multiple human activities on grizzly bear habitat suitability have been termed "cumulative effects models" (CEM), and were first conceptualized in the early 1980's (Christensen 1986). Early CEM efforts relied heavily on the "Delphi Method" where group consensus was used to quantify relationships between human activities and grizzly bear habitats. CEM models improved significantly with additional knowledge of habitat requirements and factors limiting effective habitat use by grizzly bears. Recent studies of grizzly bear demography (Mace et al. 1994, Mace and Waller, In Press) and habitat selec-

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[1] Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1997. Landscape evaluation of grizzly bear habitat effectiveness in western Montana. Paper submitted to Conserv. Biol. June 1997.

tion (Mace et al. 1996, Waller and Mace, In Press) have formed the foundation for a more comprehensive CEM.

Here we present a landscape-scale evaluation of grizzly bear habitat suitability by modeling potential and realized habitat effectiveness using resource selection probability functions (Manly et al. 1993). We define potential habitat effectiveness as the relative probability of grizzly bears using landscape features in the absence of human activity. The relative probability of use of landscape features in the presence of human activities is termed realized habitat effectiveness. Further, we present an analytical method that will enable managers to more easily interpret CEM outputs, and will direct managers to those areas of occupied grizzly bear habitat that have the greatest potential for restoration or protection efforts. We also demonstrate the usefulness of this technique by extrapolating model parameters to evaluate habitat suitability within a portion of the western NCDE.

STUDY AREAS

The 24,262 km^2 NCDE is located in the Rocky Mountain Cordillera of western Montana and is one of 6 designated grizzly bear recovery areas (U.S. Dep. Int. 1993). The Continental Divide bisects the ecosystem and each side differs in climate, constituent habitat types and mountain structure. Those portions west of the Divide are characterized by a Pacific Maritime climate (cool, wet summers and warm, wet winters), mesic habitats, and lower average elevations. Those portions east of the Divide have a continental climate (hot, dry summers and cold, dry winters), with more xeric habitats (Pfister et al. 1977), and higher average elevations.

Bears within the NCDE are currently managed in geographical units termed "Bear Management Units" (BMU) and "subunits". Twenty-three BMU's form the basis for grizzly bear habitat and population management activities in the NCDE. BMU's were drawn by group consensus and were intended to represent areas of contiguous habitat that met the yearlong needs of grizzly bears. They incorporate several drainages and range from 435 to 1,658 km^2 and average 1,000 km^2. Subunits are subsets of BMUs that provide greater landscape resolution. They were also drawn by group consensus and typically encompass major drainages and portions of intervening ridges and serve to group smaller areas of seasonal habitats.

Telemetry Study Area

The 1,457 km^2 telemetry study area (TSA) was located in the Swan Mountain Range of the NCDE (Fig. 7.3.1), and included portions of 3 BMU's and 12 complete subunits. Although heavily forested, the higher elevations contained mixtures of natural burns, avalanche chutes, rock lands, and grass lands.

The TSA was composed of private, corporate, state, and federal land ownerships. 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 parts of the Swan River Valley. Most private lands were developed for permanent homes, farms, and service facilities.

Extrapolation Area

The 4,690 km^2 extrapolation area (EA) included portions of 8 BMU's on the western side of the NCDE, and comprised 36 complete subunits having similar climate and vegetation. All 8 BMU's used in the EA were utilized to some extent between 1987 and 1995 by either radio collared male or radio collared female grizzly bears. In addition to private, state, tribal, and corporate lands, the EA included portions of the Mission Mountain Wilderness, the Bob Marshall Wilderness, and the Great Bear Wilderness. The western boundary of the EA could be characterized as rural or agricultural. Private lands within the EA occurred primarily in the Swan Valley and between Glacier National Park and the Great Bear Wilderness. Together, the TSA and EA constituted approximately 25% of the NCDE.

METHODS

Capture and Telemetry

Beginning in 1987, adult ($\geq$ 5 years old) and subadult grizzly bears were captured and radio-collared in the TSA (Mace et al. 1994). Radio-collared grizzly bears were diurnally located 1-3 times each week from fixed-wing aircraft. Our radio-collared bears tended not to be active at night (MFWP, Unpublished data). We used telemetry data collected from 1987 through 1996 from 8 adult females. Telemetry sample size was similar for each of the 8 individuals (within 2 standard deviations of the group mean each season). Relocations were grouped into seasons based on major changes in consumption of the primary food plants consumed by grizzly bears (Craighead et al. 1982, Mace and Jonkel 1986). Spring was defined as that period

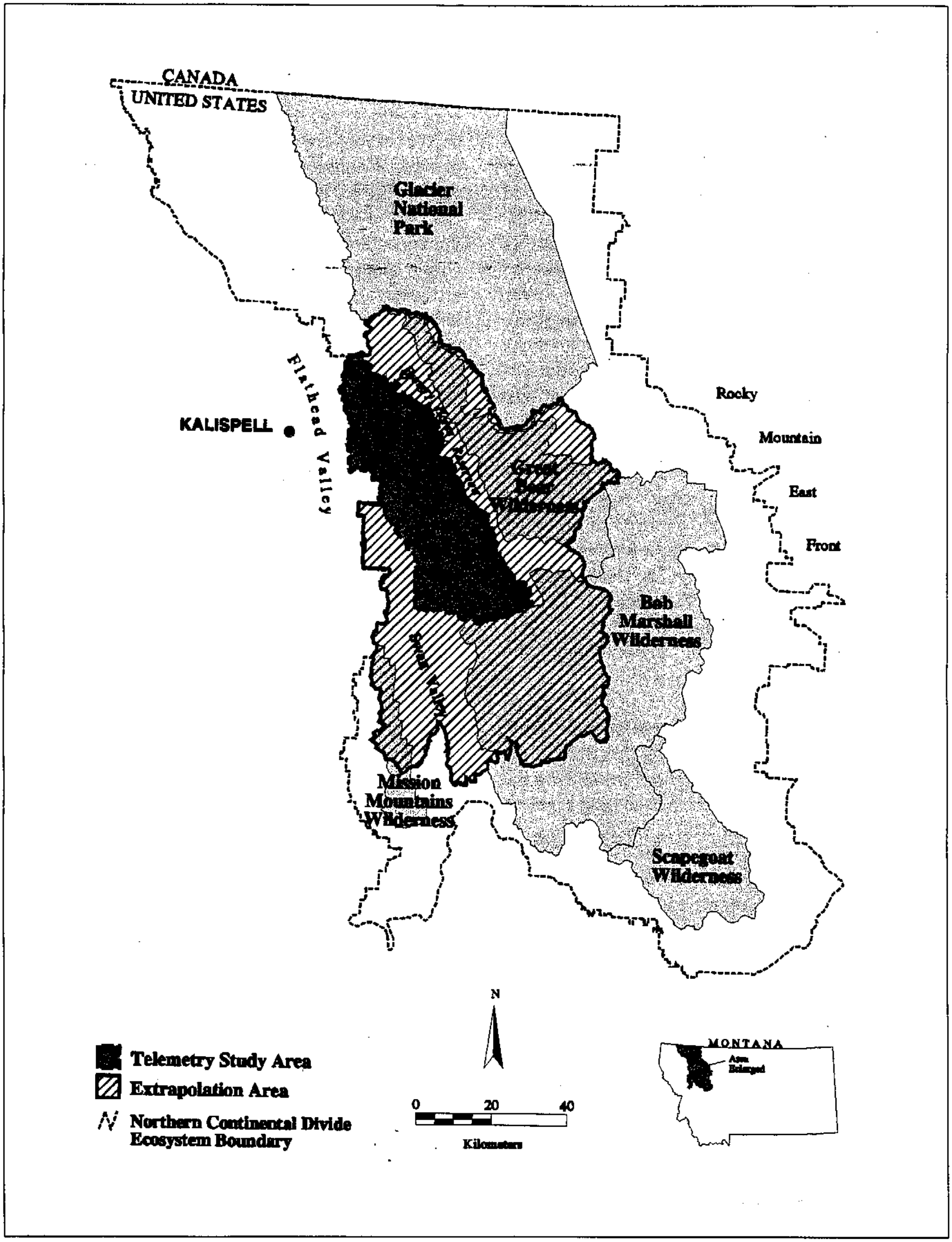


Figure 7.3.1. Location of telemetry study area in the Swan Mountains of western Montana and area of extrapolation relative to the NCDE boundary.

after each bear left the vicinity (500 m) of their winter den until 15 July. Summer was defined as 16 July to 15 September. Fall was 16 September to that time when each grizzly bear denned. Seasonal telemetry sample sizes were 517 during spring, 412 during summer, and 244 during fall. A universal transverse Mercator (UTM) coordinate was assigned to each relocation. Relocations were then converted to computer geographic information system (GIS) maps using 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 x 30 m. The denning season was excluded from analysis because of low sample sizes and lack of human activity in the study area during the denning period.

Map Layers

Roads and Trails. All roads and trails in the study area in 1990 were digitized from 1:24,000 orthophotographic quads and verified in the field. Each road was categorized as being either legally open or closed to vehicular travel by the public during each season. Old roads reclaimed by vegetation and temporary roads in timber harvest units were not mapped. Only those trails maintained by the USDA Forest Service were used.

We used 10 magnetic counters to quantify levels of vehicular traffic on a sample of roads from 1990-92 (Mace et al. 1996). Using this traffic volume data, and extrapolations based on knowledge of the study area, we categorized each road segment into 3 levels of vehicular traffic for each season: low = < 1 vehicle/day, moderate = 1-10 vehicles/day, and high = > 10 vehicles/day. The road network of each traffic volume class was then converted to a road density map using a 1-km^2 moving window GIS routine. The EPPL7 moving window routine calculated road km/km^2 for each pixel in the study area. This 1-km^2 mapping scale closely matched the scale used by management agencies for roads in the NCDE. It was not our intent to evaluate the sensitivity of grizzly bears to varying road density scales. Road density maps were categorized as 0 = 0 km roads/km^2 (unroaded), 1 = > 0 and $\leq$ 0.5 km road/km^2, 2 = > 0.5 and $\leq$ 1.0 km road/km^2, 3 = > 1.0 and $\leq$ 1.5 km road/km^2, 4 = >1.5 and $\leq$ 2.0 km road/km^2, and 5 > 2.0 km road/km^2. We did not have detailed knowledge of seasonal human use levels on the trail system in the study area. Therefore, to match the mapping scale used for roads, we buffered the trail system by 0.5 km (Kasworm and Manley 1990, Mace et al. 1996, Mace and Waller 1996).

Human Point Disturbance. All known points of human use were digitized as sources of disturbance. Point disturbances varied from periodically used camping areas to permanently occupied residences. We subjectively grouped the points as having low or high impacts on grizzly bear distribution based on the following criteria: amount of human activity, the probable activities that humans would engage in at each point type, presence of attractants (i.e. food, garbage, livestock), noise levels, and whether disturbances were long- or short term. Low and high disturbance point maps were then buffered by 0.5 km to match road and trail layers.

Pseudo-Habitat and Elevation. A classified, validated habitat map for the NCDE did not exist, therefore we used a 28 August, 1988 Thematic Mapper satellite image to develop a pseudo-habitat map. Following atmospheric corrections (Jensen 1986), the image was transformed into brightness, wetness, and greenness bands using the tasseled cap transformation (Crist and Cicone 1984, Manley et al. 1992). We selected the greenness band, categorized into 10 classes of increasing greenness, as an indicator of grizzly bear habitat. Increasing values of greenness related to increased reflectance of deciduous, green vegetation (e.g. leaf area index).

We classified a digital elevation map into 3 elevation zones based on changes in conifer species composition (MFWP, Unpublished data). The low temperate zone extended from 914 m to the lower limit of subalpine fir (*Abies lasiocarpa*) at 1,494 m.. The temperate zone extended to the upper limit of Douglas fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) at 1,981 m. Elevations above 1,981 m were classified as the subalpine zone. There was no discernible alpine zone in the study area (Mace et al. 1996). In the logistic models, we used the subalpine zone as the standard against which the low temperate and temperate zones varied (Hosmer and Lemeshow 1989).

Model Building Methods

We used logistic regression, seasonal telemetry locations, and an equal number of random coordinates to model the probability of occurrence of adult female grizzly bears as a function of map variables (Pereira and Itami 1991, Manly et al. 1993, Mace et al. 1996). For each season we calculated resource selection probability functions (RSF) for used and available resources using the following equation from Manly et al. 1993 (p. 127):

$$\tau_i = \frac{\exp\{\log_e(P_u/P_a)+\beta_o+\beta_1 x_{i1}+\ldots+\beta_{ip} x_{ip}\}}{1 + \exp\{\log_e(P_u/P_a)+\beta_o+\beta_1 x_{i1}+\ldots+\beta_{ip} x_{ip}\}}$$

where τ_i was the RSF, P_u and P_a were sampling probabilities of used and available units, β_o was the intercept, and $\beta_1 x_{i1}+\ldots+\beta_{ip} x_{ip}$ represented the available resource units divided into i groups. RSF values represented the relative probability of an adult female grizzly bear using each map combination.

Logistic regression modeling usually includes univariate tests of variables and the derivation of a final model that is composed of only the most significant variables (Hosmer and Lemeshow 1989). However, we were interested in the cumulative effect of all the chosen variables on grizzly bear habitat selection and therefore did not omit variables that were either univariately or multivariately insignificant. While inclusion of insignificant variables reduced the efficiency of the model, parameter estimates remained unbiased (Menard 1995). The logistic regression coefficients represented the relative contribution of each variable in explaining grizzly bear resource selection relative to random availability. The association and power of each variable was ascertained by each coefficient's sign (negative or positive) and strength (p value). Significant negative coefficients implied avoidance, while significant positive coefficients suggested attraction. Seasonal models that significantly reduced the -2log-likelihood ratios ($P \leq 0.05$) from the null models were considered suitably fitted (Hosmer and Lemeshow 1989, Menard 1995).

RSF values were scaled from 0 to 100% by dividing each unscaled RSF value by the largest unscaled RSF value. Scaled RSF values from the model were then used to create 2 GIS maps. The "Potential" map represented the probability of occurrence of adult female grizzly bears in the absence of human activity. To develop the potential map, all coefficients for human activities, roads, and trails in the logistic model were replaced with zero. The "Realized" map included the coefficients for human activities, roads and trails. The difference in RSF values between the 2 maps was considered to be the reduction in habitat potential due to human development.

The pooled sample of 8 adult females was used to create the coefficients. We derived 95% confidence intervals for each coefficient each season by creating a separate model for each n-1 sample of individuals (jackknifing). This process allowed assessment of model stability and resource selection variability among individual bears. The significance of each coefficient was determined by it's p-value, calculated by dividing the coefficient by it's asymptotic standard error (computed by finite differencing, Statistica 1994). Squaring the resulting quotient produces the Wald statistic which follows a chi-square distribution.

Standardized residuals (Menard 1995) were used to examine the distribution of errors and to detect cases where the model fit poorly. To establish the model's substantive significance, we calculated coefficients of determination (R^2) for each seasonal model by regressing use against predicted values (Menard 1995). Pearson 2*2 contingency tables were used to measure classification accuracy using a predicted value of 50% probability as a decision point (Statistica 1995).

We developed potential and realized habitat effectiveness maps for each season for the EA by applying TSA coefficients. We used mean subunit RSF values to compare habitat potential and realized habitat effectiveness across the EA. Declines in habitat potential could be calculated as potential minus realized RSF values. However, because declines in areas of high potential have a greater impact on bears than similar declines in areas of low potential, a simple weighing algorithm was used to calculate an adjusted percent change:

$$\text{adj. \% change} = \frac{(\text{potential RSF} - \text{effective RSF})*\text{potential RSF}}{100}$$

This process ranked declines in areas of high potential greater than similar declines in areas of lower potential. Average subunit values were combined into various subdivisions to compare: the TSA to the EA, designated wilderness to non-wilderness, and the Bob Marshall Wilderness to the Great Bear Wilderness. The Mission Mountains wilderness made up only small portions of 3 subunits, comprised only 2% of the total area, and was therefore treated as non-wilderness. The Bob Marshall and Great Bear wilderness areas comprised 17 complete subunits and a much larger portion of the EA (24% and 13% respectively). We used Krukal-Wallis nonparametric ANOVA to test comparisons between subdivisions. Significance was accepted at $\alpha = 0.05$.

The Swan Valley was not statistically compared to other subunits because it overlaps with other non-wilderness subunits and is clearly different from wilderness subunits. We compared the areal extent of high value habitats each season by calculating the percent of each subdivision having RSF values >70% (arbitrarily chosen to represent areas having high probabilities of use).

RESULTS

Telemetry Study Area

Spring. The spring logistic model was significant (-2LL = 1250.8, X^2 = 182.6, 8 d.f., P = 0.000, R^2 = 0.16), and all variables except low-impact human activities made significant contributions. Errors were normally distributed with mean = -0.005 and s.d. = 1.003. The model correctly classified 72% of used sites and 57% of random sites.

Our sample of adult female grizzly bears was most strongly associated with areas of high greenness in the temperate zone. They were significantly and negatively associated with increasing densities of all roads and presence of high-impact human activity points (Table 7.3.1). Adult females were least effected by the presence of low-impact human activity points (Table 7.3.1).

Spring mean subunit habitat potential averaged 78% and ranged from 60-87%, while realized values averaged 55% and ranged from 33-78% (Table 7.3.4). Reductions (% adjusted change) from spring habitat potential averaged 21% and ranged from 0 to 46%. Spring habitat potential values of >70% occurred in 83% of the TSA, but realized values >70% occurred in only 42% of the TSA (Fig. 7.3.2). Across all levels of greenness, the greatest average reduction from potential was due to high-impact activities in low-temperate and temperate elevation zones, followed by moderate-use roads in low temperate and temperate elevation zones (Fig. 7.3.3). Low-impact activities had little effect during spring.

Summer. The summer logistic model was significant (-2LL = 965.4, X^2 = 176.9, 9 d.f., P = 0.000, R^2 = 0.19), and significant variables were greenness and road density. Errors were normally

Table 7.3.1. Mean spring logistic regression model coefficients, +/-95% confidence intervals, range, standard error (S.E.) and significance levels from 8 adult female grizzly bears, Swan Mountains, Montana.

	Coefficients							
Variable	Mean	-95%	+95%	Min.	Max.	S.E.	t	P
Constant_Bo	0.8604	-0.9870	-0.7432	-0.9749	-0.5878	0.2837	-3.0329	0.0024
Greenness	0.1026	0.0784	0.1284	0.0660	0.1539	0.0320	3.2040	0.0014
Low temperate zone	1.4095	1.2275	1.5866	0.9954	1.7140	0.2842	4.9586	0.0001
Temperate zone	0.8224	0.6874	0.9510	0.5524	0.9860	0.2316	3.5510	0.0004
Low-use road density	-0.5019	-0.5654	-0.44 73	-0.6 36	-0.4356	0.0614	-8.1705	0.0000
Moderate-use road density	-0.5462	-0.6412	-0.4650	-0.7401	-0.3986	0.1104	-4.94 73	0.0001
High-use road density	-0.50 65	-0.5751	-0.4510	-0.6365	-0.4254	0.1352	-3.7452	0.0002
Low-impact activity points	-0.0703	-0.1871	0.0409	-0.2869	0.0569	0.2562	-0.2743	0.7839
High-impact activity points	-1.5706	-1.2256	-0.9057	-1.6752	-0.9838	0.6007	2.3180	0.0207

distributed with mean = 0.000 and s.d. = 0.993. The model correctly classified 76% of used sites and 60% of random sites.

During summer, as in spring, sample bears were strongly associated with high greenness. Elevation coefficients were negative for the low temperate zone and positive for the temperate relative to the subalpine, but were not significant. Coefficients were negative for all human variables during summer, but only road density variables were significant (Table 7.3.2). Summer habitat potential averaged 66% and ranged from 61-75%, while summer realized values averaged 47% and ranged from 38-66% (Fig. 7.3.4). Percent adjusted change from summer habitat potential averaged 12% and ranged from 6-17%. Summer habitat potential values of >70% occurred in 42% of the TSA, and realized values >70% occurred in 27% of the TSA (Fig. 7.3.2). Across all levels of greenness, the greatest mean reduction from habitat potential was due to increasing high and moderate-use road densities in low temperate and temperate elevation zones. Trails and low-impact human activities had little effect (Fig. 7.3.3).

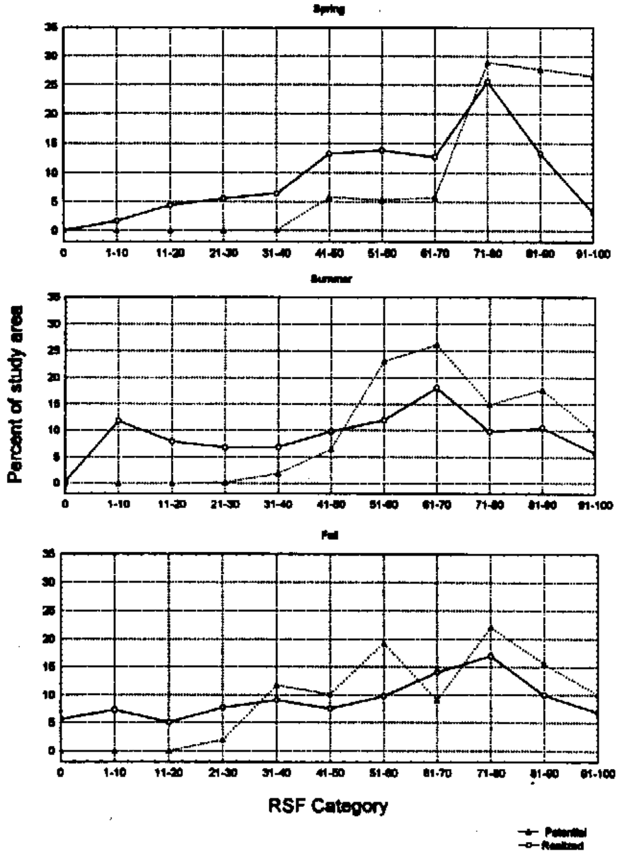


Figure 7.3.2. Percent of telemetry study area (TSA) in each potential and realized resource selection function (RSF) category. Swan Mountains, Montana.

Fall. The fall logistic model was significant (-2LL = 576.1, X^2 = 100.4, 8 d.f., P = 0.000, R^2 = 0.19), and correctly classified 77% of use sites and 58% of random sites. However, model instability was observed due to the absence of bear use in areas with high-impact human activities and very limited bear use of areas with high-road density. High-impact use areas were omitted from the model, and areas on the maps where they occurred were assigned an RSF value of zero. Only 1 individual female used areas of high road density resulting in a wide confidence interval for this variable (Table 7.3.3). Had she not been detected in areas of high-road density, this variable would also have been omitted from the model and coded as zero RSF.

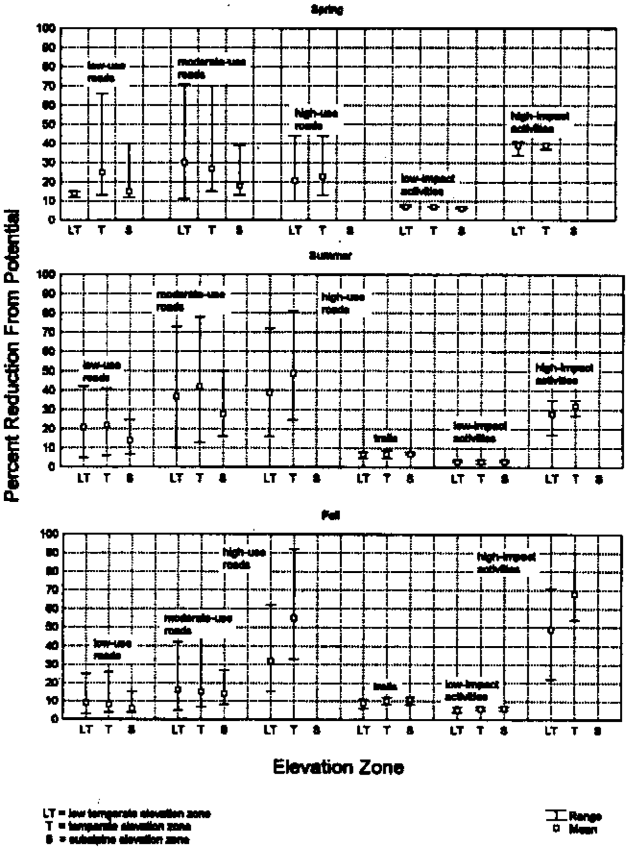
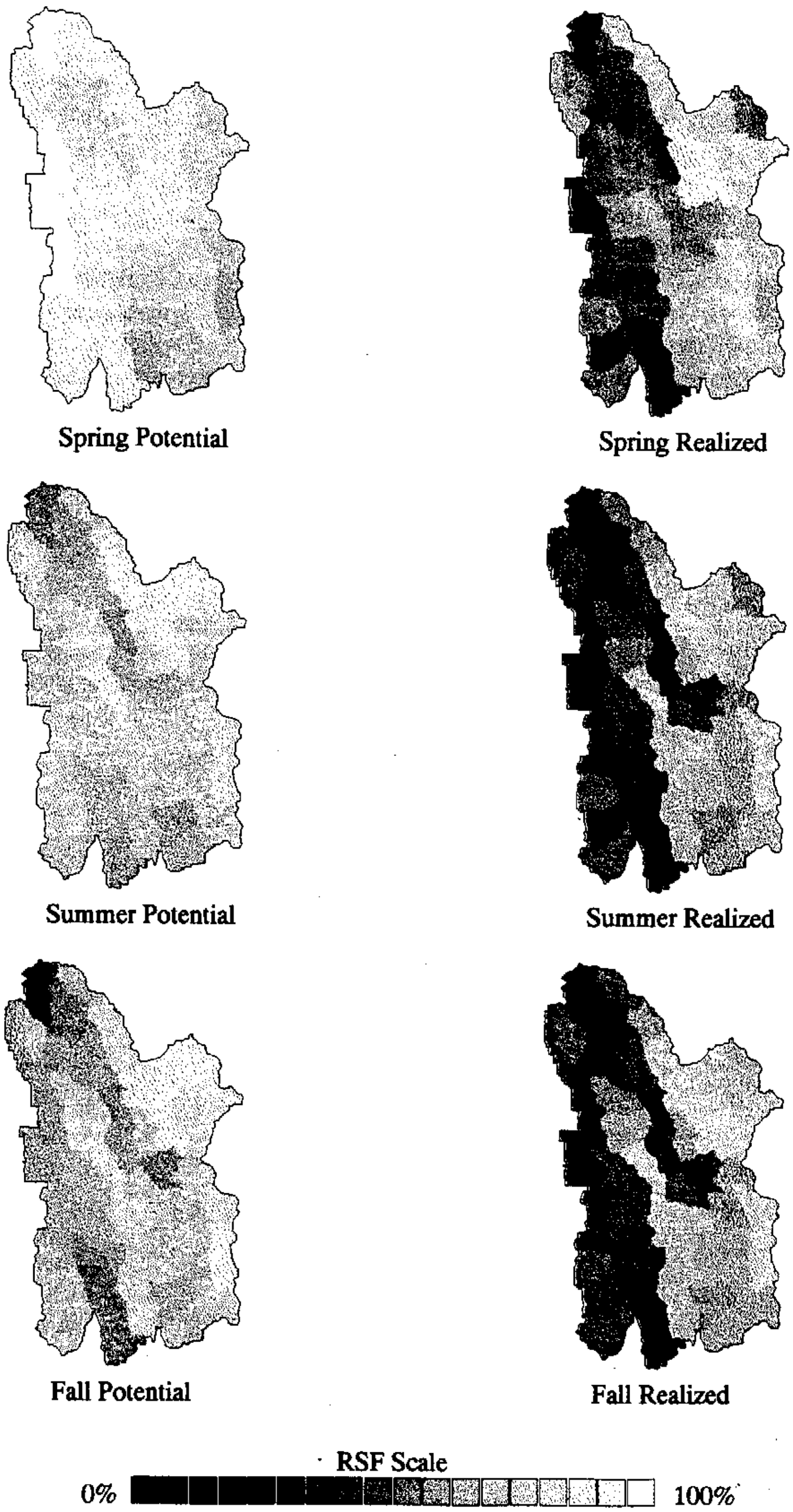


Figure 7.3.3. Mean percent reduction in habitat effectiveness in the telemetry study area (TSA) during each season within each elevation zone due to roads, trails, and low and high impact human point activities. Percentages represent reduction in effectiveness when all other human activity variables are absent and across all levels of greenness. Swan Mountains, Montana.



Spring Potential

Spring Realized

Summer Potential

Summer Realized

Fall Potential

Fall Realized

Figure 7.3.4. Habitat potential and effectiveness maps for female grizzly bears for the extrapolation area during each season. Swan Mountains, Montana.

Table 7.3.2. Mean summer logistic regression model coefficients, +/-95% confidence intervals, range, standard error (S.E.) and significance levels from 8 adult female grizzly bears, Swan Mountains, Montana.

	Coefficients							
Variable	Mean	-95%	+95%	Min.	Max.	S.E.	t	P
Constant_Bo	-1.1371	-1.3375	-0.9448	-1.5301	-0.8522	0.3300	-3.4461	0.0006
Greenness	0.2351	0.2175	0.2552	0.2056	0.2751	0.0405	5.7970	0.0000
Low temperate zone	-0.3569	-0.6062	-0.1308	-0.8587	0.1376	0.3027	-1.1790	0.2388
Temperate zone	0.2167	0.0711	0.3536	-0.0444	0.5436	0.2285	0.9483	0.3433
Trail buffer	-0.2620	-0.3652	-0.1827	-0.5269	-0.1821	0.1863	-1.4064	0.1601
Low-use road density	-0.2790	-0.3213	-0.2375	-0.3539	-0.2008	0.0993	-2.8100	0.0051
Moderate-use road density	-0.5912	-0.7637	-0.4643	-1.0022	-0.4150	0.1303	-4.5359	0.0001
High-use road density	-1.0372	-1.2428	-0.8943	-1.4742	-0.8246	0.3545	-2.9255	0.0036
Low-impact activity points	-0.1114	-0.2185	0.0082	-0.2925	0.0787	0.3105	-0.3586	0.7200
High-impact activity points	-1.1627	-1.4568	-0.8666	-1.7187	-0.6093	0.7863	-1.4788	0.1397

Significant fall variables were greenness, elevation, and high-use road density. Moderate-use road density approached significance at $P = 0.07$ (Table 7.3.3). Our sample of females significantly avoided the low temperate elevation zone during this season.

Fall habitat potential averaged 63% and ranged from 56-72%, and fall realized values averaged 49% and ranged from 35-68% (Table 7.3.4). Percent adjusted change from fall habitat potential averaged 8% and ranged from 4-12%. Fall habitat potential values >70% occurred in 47% of the TSA and realized values >70% occurred in 34% of the TSA (Fig. 7.3.2). Across all levels of greenness, the greatest mean reductions from potential were due to high impact human activities and increasing densities of high-use roads at low temperate and temperate elevation zones (Fig. 7.3.3). As in spring and summer, trails and low-impact human activities had little effect.

Extrapolation Area

The application of TSA coefficients to the EA insured that the same factors controlled RSF levels in the EA. Thus those areas having the greatest potential were those areas similar to areas of high potential within the TSA. Potential was reduced by increasing road densities and high impact human activity points.

Average subunit habitat potential values in the EA were 74%, 66%, and 65% during spring, summer, and fall respectively (Table 7.3.4). Percent adjusted change from potential in the EA was greatest (13%) during spring, and declined as the seasons progressed. There was no significant difference in mean subunit habitat potential or realized values between the EA and the TSA within seasons ($P > 0.05$). However, the TSA and the EA differed significantly ($H = 5.78$, 1 d.f., $P = 0.02$) in the percent adjusted change during summer, but not during spring and fall. The reduction in potential was greater during spring than other seasons in both the TSA (21%) and the EA (13%).

The average potential RSF value of non-wilderness subunits was significantly greater than that of wilderness subunits during spring ($H = 15.8$, 1 d.f., $P = 0.00$); was the same during the summer, and significantly lower during fall ($H = 14.4$, 1 d.f., $P = 0.00$). The average realized RSF value of non-wilderness subunits was significantly lower than that of wilderness subunits ($H \geq 23.3$, 1 d.f., $P \leq 0.01$) during all seasons (Table 7.3.4). Not surprisingly, reductions from potential in non-wilderness were significantly greater than in wilderness during spring and summer ($H \geq 32.4$, 1 d.f., $P \leq 0.01$).

The Great Bear wilderness had significantly higher potential and realized RSF values than the Bob Marshall during spring and summer ($H \geq 7.7$, 1 d.f., $P \leq 0.01$), but not during fall (Table 7.3.4). Average reduction from potential in the Great Bear was significantly greater ($H \geq 3.9$, 1 d.f., $P \leq 0.05$) than in the Bob Marshall wilderness during spring and summer, but not during fall.

Within the EA, the areal extent of habitat potential values >70% was within 15% of that within the TSA during all seasons. The areal extent of realized habitat values >70% were within 5% of those within the TSA during all seasons. The areal extent of habitat potential values >70% in non-wilderness was higher during spring and lower in summer and fall. Realized RSF values >70% comprised less area in non-wilderness during all seasons (Table 7.3.5).

DISCUSSION

Our modeling methodology clearly showed the cumulative impacts of human activity on grizzly bear habitat. Model outputs were easily interpreted as the relative probability of use. During spring, female grizzly bears utilized low elevation habitats. It is in these low elevation habitats that winter snow first melts and favored succulent vegetation first

Table 7.3.3. Mean fall logistic regression model coefficients, +/-95% confidence intervals, range, standard error (S.E.) and significance levels from 8 adult female grizzly bears, Swan Mountains, Montana.

	Coefficients							
Variable	Mean	-95%	+95%	Min.	Max.	S.E.	t	P
Constant_Bo	-0.7181	-0.9848	-0.4652	-1.1746	-0.2974	0.3569	-2.0119	0.0449
Greenness	0.1989	0.1739	0.2272	0.1660	0.2501	0.0499	3.9840	0.0001
Low temperate zone	-1.0481	-1.2659	-0.8471	-1.4066	-0.6511	0.3146	-3.3319	0.0010
Temperate zone	0.0001	-0.1498	0.1442	-0.3128	0.1816	0.0202	0.0070	0.9944
Trail buffer	-0.3500	-0.4423	-0.2711	-0.4828	-0.1558	0.2410	-1.4520	0.1473
Low-use road density	-0.1637	-0.2234	-0.1046	-0.2509	-0.0661	0.1188	-1.3774	0.1691
Moderate-use road density	-0.2862	-0.3607	-0.2141	-0.4106	-0.1509	0.1565	-1.8286	0.0682
High-use road density	-1.3110	-11.676	2.9960	-26.057	-1.0996	0.5881	-2.2294	0.0263
Low impact activity points	-0.1994	-0.3543	-0.0496	-0.5187	0.0136	0.3920	-0.5086	0.6113

Table 7.3.4. Average seasonal mean subunit Resource Selection Function (RSF) values, mean adjusted differences, and ranges (in parentheses) by research and management subdivisions, Western Montana.

Subdivision	Spring			Summer			Fall		
	Potential	Realized	Difference	Potential	Realized	Difference	Potential	Realized	Difference
Telemetry Area (TSA)	78 (72-84)	55 (44-66)	21 (11-30)	66 (61-75)	47 (38-66)	12 (6-17)	63 (56-72)	49 (35-68)	8 (4-12)
Extrapolation Area (EA)	74 (60-87)	59 (33-78)	13 (0-46)	66 (51-76)	53 (18-72)	8 (2-26)	65 (41-79)	54 (16-74)	6 (2-18)
Wilderness[a]	70 (60-81)	69 (60-78)	0.5 (0-6)	68 (62-76)	63 (58-72)	2 (2-6)	70 (62-79)	65 (57-74)	3 (2-6)
Non-wilderness[b]	78 (71-87)	52 (33-71)	23 (7-46)	65 (51-76)	45 (18-66)	13 (6-26)	62 (41-74)	46 (16-68)	8 (4-18)
Bob Marshall[a]	67 (60-73)	66 (60-73)	0 (0-0)	65 (59-72)	61 (58-69)	2 (2-3)	69 (62-79)	64 (57-70)	3 (2-4)
Great Bear[a]	76 (71-81)	75 (70-78)	1 (0-6)	73 (69-76)	68 (63-72)	3 (2-6)	73 (65-76)	67 (59-70)	4 (3-6)
Swan Valley[c]	90 (82-92)	32 (23-45)	53 (38-60)	59 (56-63)	19 (14-27)	24 (21-28)	46 (43-49)	17 (11-23)	13 (11-16)

a. Includes portions of the EA.
b. Includes portions of the TSA.
c. Includes portions of the EA and TSA.

appears. These lower elevation habitats also contain most of the human activities and roads during spring, thus reductions from potential are highest during this season.

During summer, females generally shifted to mid elevations, however use of other elevation zones continued, thus coefficients for elevation during summer were insignificant. Female grizzly bears continued to avoid all road classes. In our study area, low-volume roads were closed to public travel by vehicle, although some administrative use by agency personnel and illegal public use was noted. No strong avoidance of high-impact human activity points was noted during summer because of their absence from the mid-elevation zones preferred during this season.

During fall, female grizzly bears continued to utilize mid and high elevation habitats while avoiding low elevation habitats. High volume road densities and high impact human activity points were strongly avoided. These results suggest that there is value in road closure programs that minimize traffic volume. Avoidance of habitats adjacent to roads and the negative impacts of increasing road volume have been documented elsewhere for grizzly bears (McLellan and Shackleton 1988, Mattson et al. 1987, Kasworm and Manley 1990, Mace et al. 1996). No avoidance of low-impact human activity points was observed during any season because, by definition, these points were assumed to have minimal impact on bears.

Extrapolation of TSA coefficients revealed a general decline in habitat potential from NW to SE during all seasons, but most noticeably during the spring (Fig. 7.3.4). This was caused by gradients of increasing elevation and decreasing greenness. The decline in greenness was related to the topographic position of the Mission Mountains, which created a rain shadow effect within portions of the Bob Marshall wilderness. Decreased precipitation in the Bob Marshall resulted in more contiguous dry forest cover, especially at lower elevations. Although closed-canopy timber was often used by grizzly bears for both refuge and foraging, vegetal foods attractive to grizzly bears were generally less abundant in the dry

Table 7.3.5. Percent of subdivision with resource selection function (RSF) values >70%. Western Montana.

	Potential (%)			Realized (%)		
Place (subdivision)	Spring	Summer	Fall	Spring	Summer	Fall
Extrapolation Area (EA)	70	33	48	46	23	35
Telemetry Study Area (TSA)	83	42	43	42	27	34
Wilderness	62	36	60	62	29	46
Non-wilderness	80	34	40	35	20	27
Bob Marshall Wilderness	47	27	57	45	22	42
Great Bear Wilderness	72	51	66	72	43	53
Swan Valley	97	13	0.25	12	1	0.25

forest types of the Bob Marshall Wilderness than elsewhere (Craighead et al. 1982, Servheen 1983, Mace 1986, Aune and Kasworm 1989). Further, much of the documented grizzly bear use of closed timber habitats in the NCDE was adjacent to open canopy habitats with abundant succulent vegetation such as avalanche paths, meadows, rock lands, or timber harvest units (Aune and Kasworm 1989, MFWP Unpublished data). In fact, the high greenness values in the TSA were due in part to past timber harvest activities which removed overstory conifers. Grizzly bears in the TSA generally used timber harvest units in proportion to availability within seasonal home ranges (Zager et al. 1983, Waller 1992). Additionally, during spring telemetry flights we observed that much of the EA retained winter snow longer than more northerly areas, thus decreasing habitat availability.

Conversely realized habitat effectiveness increased on a northwest to southeast gradient due to lower levels of human development within the designated wilderness areas. The lower habitat potential in the Bob Marshall Wilderness during spring corroborates our knowledge of bear density and home range size. Bear densities were higher, and home ranges smaller, in the TSA than in the higher elevation and drier habitats to the east of the Continental Divide (Aune and Kasworm 1989, Eberhardt and Knight 1996, Mace and Waller In press).

The Swan Valley exhibited very high spring selection potential for female grizzly bears. This valley lay between the Bob Marshall and Mission Mountain wilderness areas and has been proposed as a linkage zone between these 2 wilderness areas (Sandstrom and Servheen, In Press). However, grizzly bear observations and conflicts were rare in this valley, suggesting a relatively low density of bears (Mace and Waller, In Press). The high road densities and numerous human activity centers in the Swan Valley, which were avoided by female grizzly bears in the TSA, made this an obvious area for habitat and security restoration. Obtaining full grizzly bear occupancy in the western portion of the NCDE will require management attention to these and other low-elevation spring habitats. However, merging management philosophy and action in this mixture of state, federal, private, and corporate lands will be a continuing challenge.

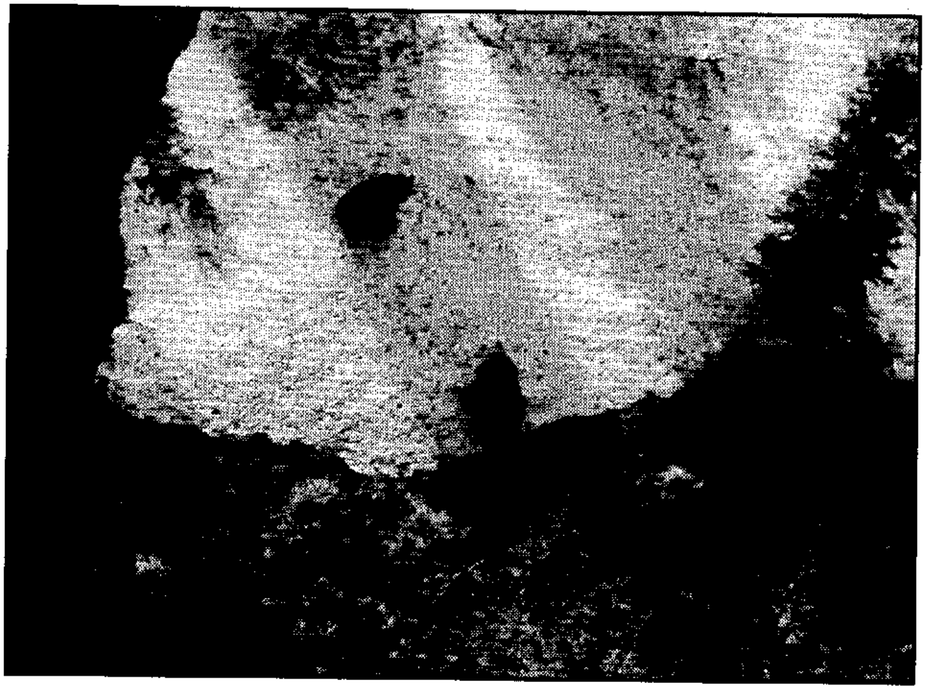
The greenness band derived from tasseled-cap transformation of TM satellite imagery was a powerful pseudo-indicator of habitat. Strong selection for greenness was observed during all seasons. We do not suggest that our use of a pseudo-habitat map would be superior to a well constructed and validated cover type map. Rather each mapping method has its own strengths and weaknesses. Because we used an unsupervised classification of a satellite image, our greenness map was repeatable. Updates could be made as often as every 2 weeks, thus allowing measurement of change through time. However, there is no clear connection between greenness and vegetation composition. Similar greenness values can be obtained for vastly different physiographic features (for example, cutting units and avalanche chutes). Thus habitat management decisions may be difficult to derive. Craighead et al. (1982) suggest that conversion of satellite imagery to a validated map with vegetal and physiographic descriptions should be the ultimate goal of habitat managers in the NCDE.

The CEM process outlined here does not include several resources valuable to grizzly bears in some areas of the ecosystem. Seasonal concentrations of grizzly bears exist in areas that could not be mapped accurately. These included spring livestock and wildlife carcass areas and domestic fruit orchards used by some bears during summer and fall. Incorporation of these source attractants could improve the model.

Further, the sample of female grizzly bears used to build seasonal coefficients are those bears that have survived. Thus the model is biased towards those behaviors that contribute to longevity. Most of the grizzly bears that occupied the valley bottoms were killed during Anglo-american settlement, and selection pressure still operates against bears showing preference for low elevation habitats.

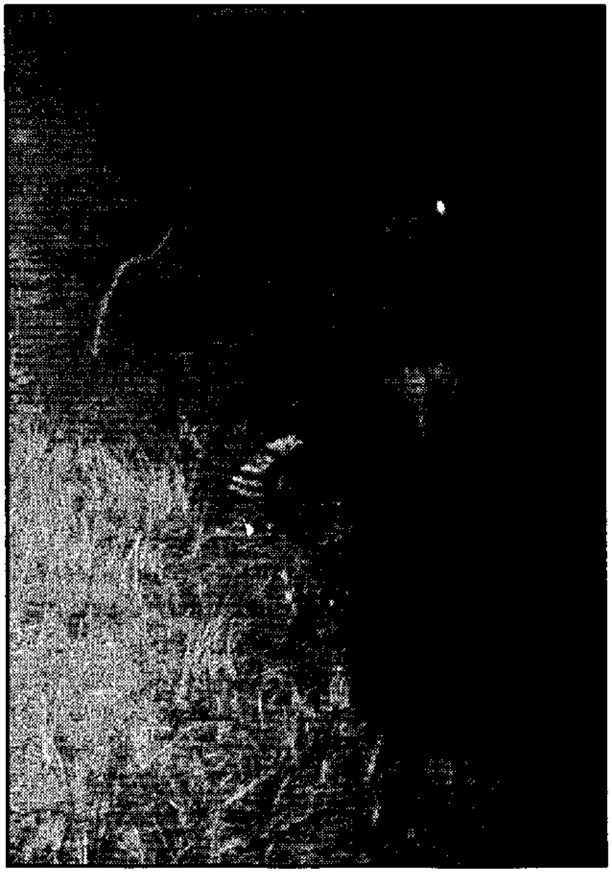
We believe that the TSA population is stable (Mace and Waller, In press). However, the link between demography and habitat effectiveness is tenuous at best. Until such a linkage is made, structured population viability analyses, as suggested by Boyce (1995) will not be possible. For the NCDE, habitat condition assessments will proceed in the absence of population assessments sufficient for viability analyses.

Other authors have presented similar concepts using different mathematical methodologies. These include Mahalanobis distance (Clark et al. 1993), discriminant function analysis (Capen et al. 1986), Bayesian probability (Aspinall and Veitch 1993), proximity analysis (Breininger et al. 1991), and logistic regression (Pereia and Itami 1991). We believe our method has some advantages over previous methods. Model outputs are easily interpreted in terms of relative probability of use, not an arbitrary score. Mathematically, the process of logistic regression is well understood, though it's application to GIS data is new. Most readily available statistical software performs logistic analysis. We recommend that habitat managers in other ecosystems having telemetry information from grizzly bears consider using methods similar to ours for deriving CEM coefficients and mapping the relative probability of use on a seasonal basis. A standardized statistical and mapping method would greatly aid in comparisons among ecosystem. Our statistical technique, using RSF values derived from logistic regression appear superior to the "delphi system" currently in place to assign response coefficients. Negative coefficients represent avoidance of resources by grizzly bears, while positive coefficients represent attraction by grizzly bears. These positive attractions towards human development areas, although sometimes insignificant statistically, drew our attention to areas of increased risk of mortality.



CHAPTER 8

ACTIVITY PATTERNS AND TIME BUDGETS OF GRIZZLY BEARS IN THE SWAN MOUNTAINS OF MONTANA: A SYNOPSIS



CHAPTER 8

ACTIVITY PATTERNS AND TIME BUDGETS OF GRIZZLY BEARS IN THE SWAN MOUNTAINS OF MONTANA: A SYNOPSIS[1]

Erik Wenum

INTRODUCTION

The continued existence of many grizzly bear populations will depend on their ability to coexist with man. Previous studies indicated that grizzly bears were able to adjust their activity rhythms to avoid direct conflicts with humans by either avoiding areas of predictable human use or by shifting their activity rhythms to periods of low human disturbance (Gunther 1991, McCann 1991, Aune and Kasworm 1989).

There is a need for greater understanding of how and when bears alter their activity rhythms to avoid conflicts with humans, and how age, sex, reproductive status, and season relate to the ability or need for behavioral adjustment.

The activity rhythms of a species are of interest for several reasons (Roth 1983). Most importantly, once activity rhythms have been quantitatively described, they may be used to help interpret the level of stress the population is experiencing.

There are 2 aspects of an activity rhythm, activity budgets and activity patterns. Activity budgets refers to the amount of the diel period spent in an active state. Activity patterns refers to the diel rhythms of activity.

The specific objectives of this study were to:

1. Determine seasonal activity budgets and patterns of 6 focal adult female grizzly bears.
2. Determine as possible, activity budgets and patterns, among various sex, age, and reproductive classes.
3. Determine if differences exist between activity budgets and patterns of 6 focal adult female grizzly bears when using roaded and unroaded habitats.

METHODS

Field Procedures

South Fork Grizzly Project personnel fitted captured grizzly bears with motion sensitive radio collars (Telonics Inc. Mesa, AZ.). Each collar was equipped with a 10° mercury tip switch, which changed the emitted radio signal from a slow pulse rate (≈60 signals/minute) to a fast pulse rate (≈90 signals/minute) when the collar was tilted >9° from vertical. Reset to the slow pulse rate was instantaneous when the collar returned to the upright position.

Activity budgets and patterns were recorded using a LOTEK SRX 400 telemetry scanner/receiver unit (LOTEK Engineering Inc. Ontario, Canada) with a Telonics omni-directional whip antennae. This unit was capable of continuously scanning multiple radio frequencies and storing the following parameters: time, date, frequency, pulse rate, and signal strength. With the addition of 2 12-volt dry cell batteries, the unit was capable of continuously recording for 10 days.

Activity data were collected during 3 seasons: spring, summer, and fall of 1992, 1993 and 1994. Spring was defined as 8 May - 15 July (68 days) from den emergence until the end of breeding season. Also signifying the end of spring was a change in food habits, from grasses and forbs, notably cow parsnip (*Heracleum lanatum*) and angelica (*Angelica arguta*) to globe huckleberries (*Vaccinium globulare*) and serviceberry (*Amelanchier alnifolia*). Summer was defined as 16 July - 15 September (61 days) during which berry use was continuous (Mace and Manley 1990). Fall was defined as 16 September - 15 November (60 days) beginning when food habits changed from huckleberries to mountain ash (*Sorbus* spp.) berries and gut piles from hunter kills and ending when denning occurred.

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[1] Wenum, E. 1997. Activity patterns and time budgets of grizzly bears in the Swan Mountains of Montana. M.S. thesis. Montana State Univ., Bozeman. In Prep.

Bears ≤ 4.5 years old were classified as sub-adults, and bears > 4.5 years old were classified as adults. Due to the length of the study, several individuals changed from sub-adult to adult and/or changed reproductive classes. Bears that occurred in more than one classification over time were treated as independent individuals each year.

Bears were located through aerial telemetry flights twice per week, weather permitting, and through ground telemetry. Relocation flights generally occurred between 0700 and 1200 hours, with some occurring between 1700 and 2100 hours. Location information was used to determine which bear was in an accessible location in which to deploy the LOTEK unit. The unit was placed as close to the focal bear as possible in a location to optimize continuous monitoring without influencing bear activity. Location information was also used to determine the focal bear's location relative to the 2 habitat types (roaded, unroaded) and to other bears. While monitoring bears in roaded habitats the LOTEK was checked at regular intervals. While monitoring bears in unroaded habitats the LOTEK was attended continuously. Throughout each sampling bout the LOTEK unit was moved as needed according to the focal bears movements. Once deployed, the unit was checked periodically and was retrieved when the memory banks were full, the batteries had died, or the bear had left the area.

During 1992, 8 bears were monitored, representing 5 age, sex, and reproductive classes: adult females, adult females with yearlings, adult males, sub-adult males and sub-adult females.

Thirteen bears were monitored in 1993, representing 4 age, sex, and reproductive classes: adult females, an adult female with 2 2-year olds, adult males, and sub-adult females.

Sixteen bears were intensively monitored during the 1994 field season representing 5 age, sex, and reproductive classes: adult females, adult females with cubs of the year, adult males, sub-adult males, and sub-adult females. Six adult females, 3 solitary and 3 with cubs of the year, were selected as focal animals. These individuals were selected based on the location of their home ranges relative to roads. The study area was divided into 2 major habitat types: those that were "roaded" and those that were "unroaded". These 2 habitat groups were defined by road density (miles of road/mi^2) as described by Mace and Manley (1993). Each focal bear had both roaded and unroaded areas within their home range.

Focal bears were continuously monitored for a sampling bout of 72 hours. Focal bear sampling order was generated using a randomized block design. Each focal bear was monitored a minimum of 2 72-hr bouts per season. Non-focal bears were monitored as available.

Determining Activity

Raw activity data were downloaded in ASCII format to a laptop computer at the end of each sampling bout and transferred into a database management program. Programs written in dBASE III Plus (Ashton-Tate 1985, 1986) were used to edit and collate activity data. Radio collar pulse and modulation rates, and signal strength were used to categorize data sets as active or inactive. Field tests revealed that a stationary collar would exhibit variable signal strength due to atmospheric and vegetative interference. It was determined that a signal strength standard deviation of < 10 could be used as a corrective factor for these atmospheric and vegetative variables. Consecutive activity data were combined into 15-minute blocks. For each 15-minute block, changes in modulation and signal strength were summarized. The pulse rate range (60-90 signals/minute) was divided into 3 quartiles, 60-70, 70-80 and 80-90 signals/minute. A 15-minute block was categorized as inactive if the mean pulse rate was between 60-70 or 80-90 signals/minute and the signal strength standard deviation was < 10. Fifteen minute blocks were categorized as active if the mean pulse rate was between 60-70 or 80-90 signals/minute and the signal strength standard deviation was ≥ 10 or if the mean pulse rate was between 70-80 signals/minute regardless of the signal strength standard deviation. Activity data were collected from test collars to verify activity determination methods during each collection season. Grizzly bear activity data were validated through direct observations, when possible.

Explanation of the statistical methods used and the results concerning the seasonal effects on females of differing reproductive status, sub-adults (male and female), and adult males, and the discussion of these results may be found there.

RESULTS

Distribution of Data

Grizzly bear activity data were collected from 19 grizzly bears between 1992 and 1994, resulting in 21,538 quarter hrs (5,384.5 hrs) of observations. Over 47% (10,249 quarter hrs or 2,562.25 hrs) of the data were collected in 1994 when monitoring was most intensive.

During 1992, 4,478 quarter hrs (1,119.50 hrs) of activity data were collected on all age and sex classes. Over 52% (2,330 quarter hrs or 582.50 hrs) of the data were for adult females (Table 8.1).

During 1993, 6,811 quarter hrs (1,702.75 hrs) of activity data were collected on all age and sex classes (Table 8.2).

During 1994 a total of 10,251 quarter hours (2,562.75 hours) of activity data were collected on all age and sex classes. Over 54% (5,537 quarter hrs or 1,384.25 hrs) of the data collected were from adult females (Table 8.3).

A total of 9,863 quarter hrs (2,465.75 hrs) were collected from adult females, 5276 quarter hrs (1,319.00 hrs) for adult males and 6,399 quarter hrs (1,599.75 hrs) were collected from subadult bears.

Table 8.1. Total quarter hours of activity monitoring during 1992.

Bear Class	Spring	Summer	Fall	Total
Adult Female[a]	65	1298	390	1753
Adult Female[b]	467	-	110	577
Adult Female Total (n=5)	532	1298	500	2330
Adult Male Total (n=1)	3	48	33	84
Sub-adult Total (n=2)	819	644	601	2064
Total	1354	1990	1134	4478

[a] accompanied by 1 or more yearlings.
[b] solitary female.

Table 8.2. Total quarter hours of activity monitoring during 1993.

Bear Class	Spring	Summer	Fall	Total
Adult Female[a]	83	-	-	83
Adult Female[b]	1150	730	33	1913
Adult Female Total (n=7)	1233	730	33	1996
Adult Male Total (n=4)	539	816	1441	2796
Sub-adult Total (n=2)	-	1414	605	2019
Total	1772	2960	2079	6811

[a] accompanied by 2 2-year olds.
[b] solitary female.

Activity Budgets

On an annual basis, adult females were active 78.96% (±0.83) of the time. For adult female grizzly bears, percent time active (PTA) during spring, summer and fall was 76.47% (±1.31), 84.13% (±1.16), and 72.37% (±2.28) respectively (Table 8.4).

PTA gradually increased as spring progressed. A post-denning lethargy period was observed. This period lasted several days and resulted in a lower PTA until the bear left the den site. As this lethargy period ended, bears continued to increase activity with a seasonal mean PTA of 76%.

Bears were most active during the summer, spending as much as 85% of time in an active state. This increase in activity was reflective of a hyperphagic state during the berry season, a time when bears were experiencing the greatest weight gain per unit time over the course of a year.

In early fall, season bears were highly active (PTA = 78%) due to continued hyperphagic activity. As fall progressed, PTA levels decreased as more bears prepared for the onset of the denning period. This decrease in PTA may have due in part to bears entering a pre-denning lethargy period prior to den entrance. Two adult females displayed a decreasing PTA, from 54% to 38%, as they neared den entrance.

Although this is only a brief summary of the activity budgets for adult females (Fig. 8.1), the pattern remained constant for all age, sex, and reproductive classes, with the exception of sub-adult females that showed no significant change from summer (75%) to fall (76%).

Table 8.3. Total hours of activity monitoring during 1994.

Bear Class	Spring	Summer	Fall	Total
Adult Female[a]	1290	948	907	3145
Adult Female[b]	987	862	543	2392
Adult Female Total (n=6)	2277	1810	1450	5537
Adult Male Total (n=4)	642	407	1347	2396
Sub-adult Total (n=6)	963	729	624	2316
Total	3882	2946	3421	10249

[a] accompanied by 1 or more cubs of the year.

[b] solitary female.

Table 8.4. Proportion of time spent in an active state for adult female grizzly bears.

Season	n[a]	Lower C.I.[b]	Mean	Upper C.I.
Overall	9360	0.78138	0.78964	0.7979
Spring	4042	0.75164	0.76472	0.7778
Summer	3838	0.82975	0.84132	0.85289
Fall	1480	0.70084	0.72365	0.74646

[a] number of quarter hour samples.

[b] 95% confidence interval

Activity Patterns

During each season, adult female grizzly bears were strongly diurnal in their activity patterns. Overall activity began at approximately 0515 hours and ended at approximately 2145 hours, resulting in 16.5 (±0.5) hours of near continuous activity (Fig. 8.2).

During spring, the onset of activity was strongly correlated to sunrise, beginning at 0445 hours (sunrise = 0445 hours) and continuing until 2200 hours, resulting in 17.25 ±0.5) hours of activity. The cessation of activity however, did not appear to be as strongly related to sunset, as bears were active for 1.5 to 1.75 hours after sunset (2015 hours)(Fig. 8.3).

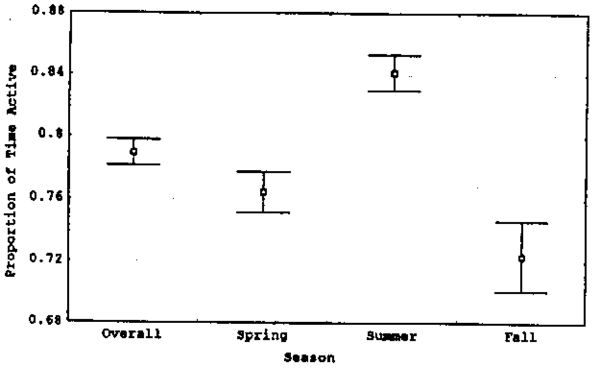

Figure 8.1. Proportion of time active for adult female grizzly bears in the Swan Mountains.

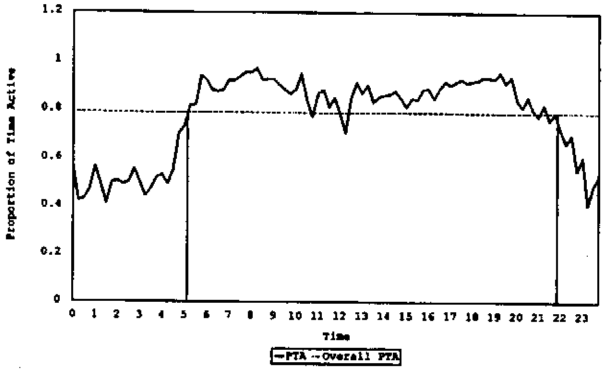

Figure 8.2. Proportion of time active during each hour over all seasons for female grizzly bears in the Swan Mountains.

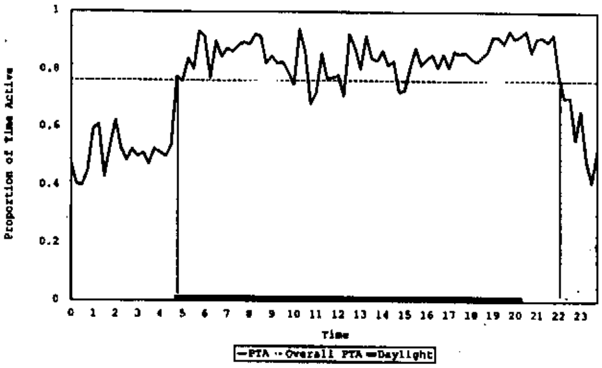

Figure 8.3. Proportion of time active during each hour during spring for female grizzly bears in the Swan Mountains.

Summer activity began at 0500 hours, approximately 0.5 hours before sunrise (0530), and continued for 16.25 (±0.5) hours until 2130 hours. Activity continued for approximately 2 hours after sunset (1930 hours)(Fig. 8.4). Although the active period was shorter during summer than spring, the level of activity increased by over 8%, due to hyperphagic activity.

During fall, there was a general decrease in both the level of activity (a decrease of 12% from summer) and the amount of time spent active (14 ±0.5 hours). This active period however, was longer than the daylight period by 3 hours (Fig. 8.5).

The diurnal activity pattern remained constant for adult females regardless of their reproductive status. Both sub-adult males and females followed similar diurnal patterns, although their total time spent active was less than adult females. While adult males had strongly diurnal activity patterns during the summer season, there were no discernible patterns during the spring and fall seasons.

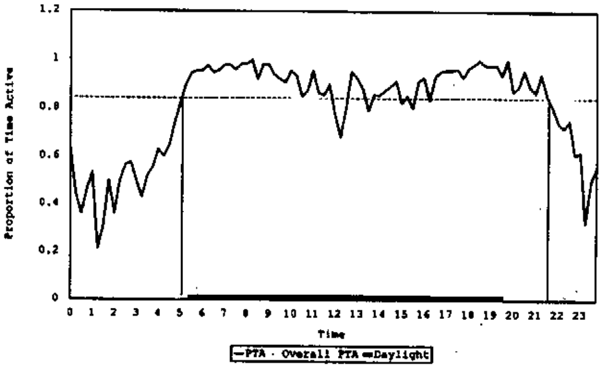

Figure 8.4. Proportion of time active during each hour during summer for female grizzly bears in the Swan Mountains.

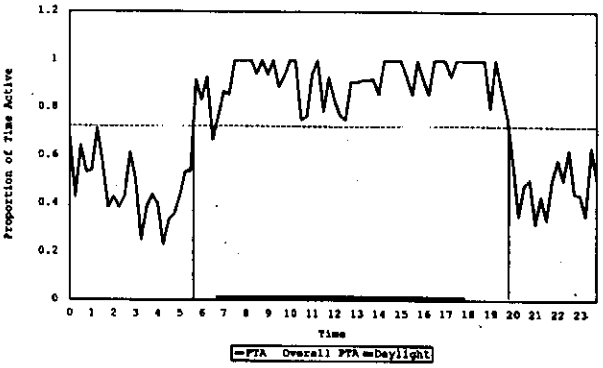

Figure 8.5. Proportion of time active during each hour during fall for female grizzly bears in the Swan Mountains.

CHAPTER 9

DEMOGRAPHY AND TREND OF SWAN MOUNTAIN GRIZZLY BEARS

In the previous chapters, information was provided on various aspects of grizzly bear ecology. We described their relationship to, and selection for and against habitat resources. We further described the characteristics of grizzly bear home ranges and their spacing patterns across the landscape. Finally we described how grizzly bears used their environment relative to the activities of humans. We believe these topics are useful for the management the species, as they have pointed to several factors that limit population size in the Swan Mountains. However, knowledge of the population size, productivity, and trend is necessary to place those habitat-based findings in perspective. It is this demographic perspective that is needed to more accurately judge the consequence of the various limiting factors described, and which serves as the final and most important parameter from which to judge the overall health of the Swan Mountain system.

In this chapter we describe the demography and trend of grizzly bears in the Swan Mountains. The chapter was built upon many of the analyses, conclusions, and recommendations presented previously. The chapter incorporates our knowledge of population size, density, productivity, mortality, and ultimately trend.

CHAPTER 9

DEMOGRAPHY AND TREND OF A LOCAL GRIZZLY BEAR POPULATION IN A SOURCE-SINK LANDSCAPE[1]

R. D. Mace and J. S. Waller

ABSTRACT: Demographic characteristics and local population trend of grizzly bears (*Ursus arctos horribilis*) were studied in the Swan Mountains of western Montana from 1987-1996 using capture and telemetry methods. We captured 50 grizzly bears in 108 capture episodes (1 bear/72 snare-nights). Using radiocollared bears only, there were between 19 and 30 bears in the 1,457 km^2 study area each year (x = 1.6 bears/100 km^2). Density of bears in a 692 km^2 high-use area termed the Core Area averaged 2.5 bears/100 km^2. Twenty-eight cubs were produced from 17 litters for a mean litter size of 1.64 ± 0.12 cubs/litter. The reproductive rate for female cubs was estimated to be 0.389 ± 0.104. We obtained 170 bear/years of censored telemetry data from all classes of radioed grizzly bears, 25 of which died. The observed annual total mortality rate of 13.4% for all classes was higher than found in expanding brown bear populations. Most mortalities occurred in roaded areas near private lands at the edge of the study area (Rural Zone) that exhibited a lower bear density than the Core Area. Dispersal movements of young females were confined to areas near the natal home range, away from the Rural Zone, while young males were more likely to utilize the Rural Zone. Using a derivation of Lokta's equation, our estimate of lambda during the entire study was 1.009 (95% confidence interval = 0.896 - 1.096). There was a 59% probability that the population was stable to increasing, a 55% probability that the population was increasing, and a 41% probability of population decline. The spatial occupancy of the Core Area suggested that the study area was at or near capacity under present landscape conditions. Differential bear densities within the study area, movement patterns, spatial occupancy, and vital rate characteristics suggested a "source-sink" situation. Recommendations to manage grizzly bears along fringe habitats are provided.

INTRODUCTION

Little information exists on the demography, fecundity, survival, and trend of grizzly bears in the Northern Continental Divide Ecosystem (NCDE) of Montana (U.S. Dep. Agric., Fish and Wildlife Serv., 1993). There has been no effort to collect such data at the ecosystem scale because of its' large size (≈ 22,000 km^2) and limited access (> 50% roadless). Rather, past research emphasis has been placed on local populations within the NCDE, where demographic studies were secondary to other objectives (Servheen 1981, K. A. Aune and W. F. Kasworm, unpubl. data).

In 1987, the Montana Department of Fish, Wildlife and Parks began a study of grizzly bears in the Swan Mountains in the western portion of the NCDE. The study area was placed on the western side of the Continental Divide to complement previous work along the Rocky Mountain East Front (RMEF)(K. A. Aune and W. F. Kasworm, unpubl. data). The objective of the study was to identify those factors that may be limiting local population growth. The evaluation of limiting factors required that we estimate vital population rates and assess population trend. We present our findings regarding population size and density, trend, age structure, survival, fecundity, and dispersal.

STUDY AREA

The study area, located in the Swan Mountain Range of western Montana, extended from the northern terminus of the Swan Mountains on the north to the Bob Marshall Wilderness boundary on the south (Fig. 9.1). The 1,457 km^2 area was bounded on the east by Hungry Horse Reservoir and

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[1] Mace, R. D., and J. S. Waller. Demography and trend on a local grizzly bear population in a source-sink landscape. In Press Conserv. Biol.

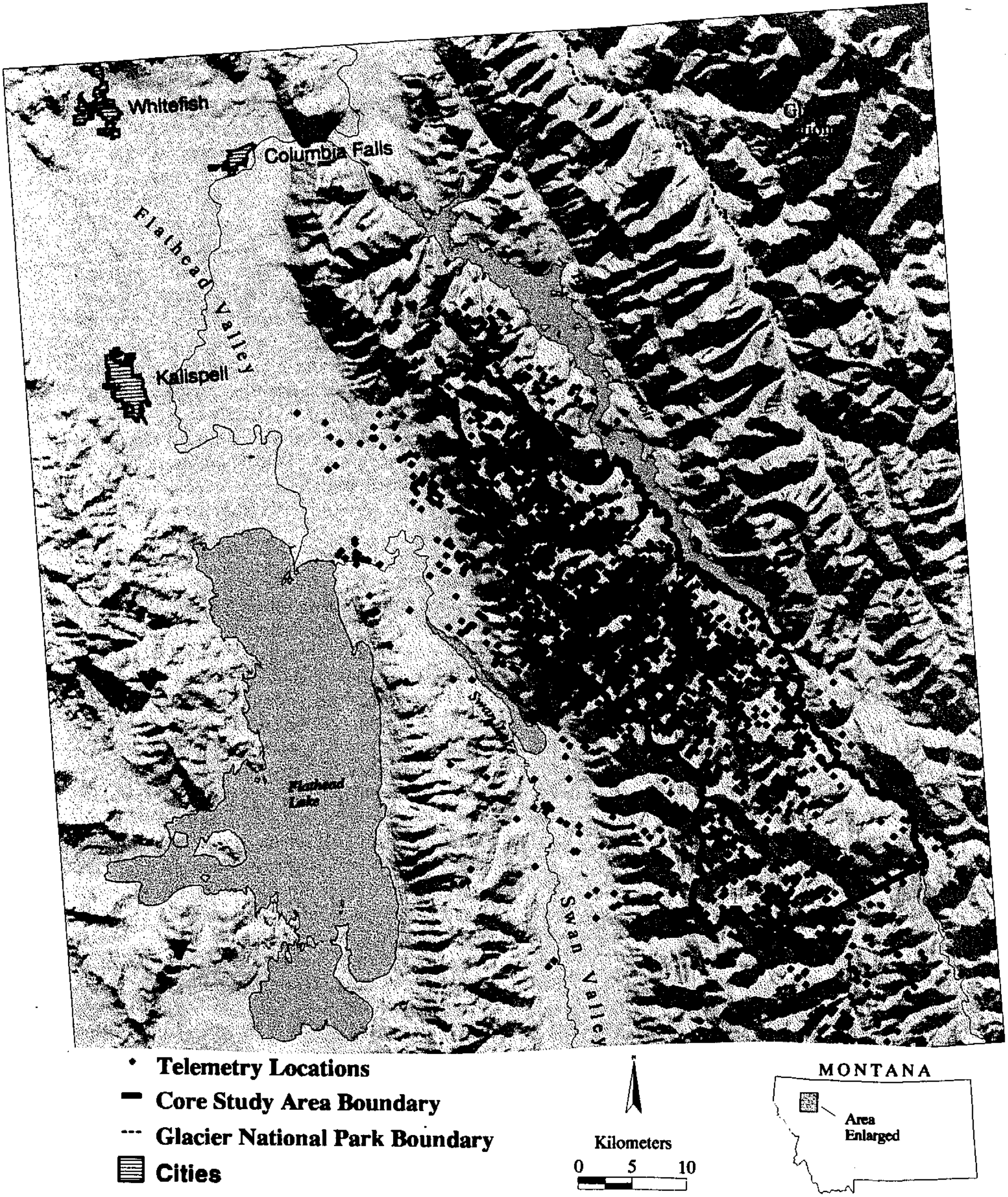

Figure 9.1. Location of the study area in western Montana showing the spatial relationship between habitat occupied by grizzly bears and the urbanized and rural valleys. The Study Area and inner Core Area are shown relative to 4,460 telemetry points obtained from 50 individual grizzly bears. 1988-1996.

on the west by the edge of contiguous forest cover in the Flathead River and Swan River valleys. The study area was bounded on 3 of 4 sides by likely geographic barriers. Grizzly bears are not tolerated by humans beyond much of the western boundary because of its agricultural and suburban nature. Human occupation in the Flathead Valley declined from > 39 humans/km^2 in the city of Kalispell, to < 10 humans/km^2 on private lands in more rural locations within or adjacent to the study area (U.S. Census data). Human density in the Swan Valley was approximately 0.4 humans/km^2. In 1995, the greater Kalispell area had 42,814 residents (Kalispell Bypass Feasibility Study, Boyer Consulting Services). Public lands in the study area were administered by the USDA Forest Service under a multiple-use management strategy, and had a history of hydroelectric development, roading, and timber harvest since the early 1950's. There were approximately 1,962 km of roads in the study area, 54% of which were legally open to vehicular traffic as of 1990. The remaining roads were either permanently or seasonally closed to public traffic (Mace et al. 1996).

The study area was divided into 2 areas. Grizzly bears were not equally distributed in the study area based on capture, telemetry, and photographic sighting data (Mace et al. 1994). Most radiocollared grizzly bears lived primarily in the 692 km^2 Core Area (Fig. 9.1). We were also interested in assessing the importance of a 305 km^2 area, termed the "Rural Zone", to grizzly bears. This zone was located on the western edge of the study area and was defined as the roaded areas within or adjacent to private lands.

METHODS

Capture and Telemetry

Grizzly bears were captured during spring from 1987 through 1996, although several short-term snaring sessions were conducted during other seasons. Effort to capture grizzly bears was expended in both the Core and non-core areas (Mace et al. 1994).

We designed capture sessions to mark as many bears as possible by modifying snaring methods and placement (Flowers, 1977, White et al. 1982). Two Aldrich foot snares (Aldrich Animal Trap Co., Clallam Bay, WA 98326) were placed at each site, baited with approximately 23 kg of meat, and checked daily. We used different combinations of wooden cubbies (Jonkel and Cowan 1971) and trail sets each year.

Grizzly bears were immobilized with "Telazol" and a premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966). Bears were divided into 6 classes: adult ($\geq$ 5 years old) males and females, subadult (2-4 years old) males and females, cubs (0.5 years old), and yearlings (1.5 years old). We fitted captured grizzly bears with motion-sensitive radiocollars, and to ensure that collars would not be worn permanently, we generally used 2.5 cm cotton spacers to close the collar belting, 2 for adults, and one spacer for subadults (Hellgren et al. 1988). We defined capture rate as the number of snare-nights/capture. A convex polygon was constructed from snare locations each year, from which the density of snares used each year (snares/100 km^2) was calculated. Grizzly bears were relocated from fixed-wing aircraft one to 2-3 times/week as weather permitted. Relocations were obtained throughout each bears' active season. We attempted to visually observe all bears from the aircraft when feasible.

Dispersal

We defined dispersal as the period between family breakup and sexual maturity. The dates of family breakup and subsequent subadult movements were determined from aerial telemetry, when either mother and off-spring or both were radio-collared. For each family, we used the last visual observation when the family was seen together, or the date when the mother was first seen without her off-spring. We could not verify the mother of subadults in all cases. In these instances we used weight of evidence, (location of bear at capture and reproductive status of other resident marked and unmarked females), to link a subadult with the probable mother. Early movement patterns relative to the natal home range were estimated from telemetry data. For the first 2 years of dispersal, we calculated the percentage of locations of subadults within natal ranges. Natal ranges were defined as the 100% minimum convex polygon (MCP) of the mother during the years prior to dispersal (Mohr 1947). Annual home ranges, using the MCP method were also constructed for other classes.

Mortality

Our most complete mortality records were from 1988 though 1996. Mortalities were categorized as man-caused or natural, and whether they were "reported" or "unreported."

Man-caused mortalities included those bears legally harvested, mistaken for black bears during a legal black bear hunting season, killed in defense of human life, removed from the study area for habituated or food-conditioned behavior (Herrero 1985), those maliciously killed, and those caused by research activities. Malicious killings were those cases where bears were shot and left, and did not occur during a hunting season. Mortalities were also classified as known or suspected. We defined suspected mortalities as those instances where no carcass was located but extenuating circumstances suggested that a mortality had occurred (e.g. a collar with the belting cut). Possible mortalities or emigrations of non-radioed but marked male bears were also included in the suspected category, . These bears were frequently observed during snaring and photographic sighting sessions for several years then not seen again.

Natural mortality was assessed using several criteria including the lack of evidence suggesting human intervention, season, and location. Cubs were assumed to have died naturally when they were not with their radiocollared mother. Natural yearling mortality was also assumed if they disappeared during spring (Hovey and McLellan 1996).

Unreported mortalities included natural and man-caused mortalities that would not have been known had the bear not been radiocollared. Such mortalities would not be present in official mortality records.

Mortalities were further classified by 3 jurisdictions; those occurring within the Bob Marshall Wilderness, on multiple-use lands, and in the Rural Zone.

Annual cause-specific mortality rates and 95% confidence intervals were estimated for radiocollared bears using censored telemetry data with the computer program MICROMORT (Heisey and Fuller 1985).

Population Size, Density, and Structure

Local population size, density, and structure was estimated from radiocollared grizzly bears between 1989-1995 when most bears were instrumented. Using the method of McLellan (1989a), radiocollared bears and attendant young were counted in proportion to the amount of time they spent in the study area each year. For example, an individual that never left the study area counted as 1.0 bear while an individual having only one half of its' locations in the study area counted as 0.50 bear. Percent time was then summed for all radiocollared individuals.

We used photographic sightings (Mace et al. 1994) of unmarked bears, and visual observations made by study personnel at other times, to estimate the number of unmarked bears present. We conservatively reduced duplication of unmarked bears by examining physical characteristics, family group size, time, and location data. Density estimates were also calculated for the Core Area and the Rural zone.

We constructed annual home ranges for all radioed bears each year using the 100% minimum convex polygon method (Mohr 1947). We used these home ranges to estimate the percent occupancy of the Core Area each year.

Population Trend and Vital Rates

Finite rate of increase ($\hat{\lambda}$) was calculated for the period 1987-1996 using Lotka's equation as revised by Eberhardt et al. (1994) and further refined by Hovey and McLellan (1996). This method employed only survival and reproductive data obtained from radiocollared female grizzly bears. For females, 4 parameters were estimated from demography data: 1) adult, subadult, yearling, and cub survival rates, 2) age at first parturition, 3) reproductive rate, and 4) maximum age of reproduction.

We used equation 1 (Hovey and McLellan 1996) which assumed a stable age distribution as follows:

$$0 = \hat{\lambda}^{a} - S_a \hat{\lambda}^{a-1} - S_c S_y S_s^{a-2} m[1-(S_a/\hat{\lambda})^{w-a+1}] ,$$

where S_a,S_s ,S_y, and S_c were adult subadult, yearling, and cub survival rates respectively. Annual survival rates of grizzly bears were estimated using censored telemetry data obtained throughout each bears' active season (White and Garrott 1990). Survival rate of each female class except cubs was calculated as $\hat{S} = 1$ - (recorded deaths/bear-years). Cub survival rates were estimated by 1 - (cub deaths/total number of cubs born).

The reproductive rate (m) per female was defined as number of female cubs/interbirth interval. The number of cubs produced was ascertained from visual observations during early spring aerial telemetry flights, while families were still near their dens. The interbirth interval was defined as the years of care given the litter plus any intervening period before the next birth (Hovey and McLellan 1996). We used only those females for which we had at least one complete interval. We omitted one interbirth interval as it may have been influenced by our research program. All vital rates, their SE's, and 95% CI's were estimated by bootstrapping (Efron and Gong 1983) data 5000 times using the computer program BOOTER 1.0© (F. Hovey). Survival rate estimates derived from bootstrapping differed slightly from those calculated using Heisey and Fullers (1985) method. Age of first parturition (a) was set at 6 years and maximum age of female reproduction (w) was set at 25 years. The sex ratio of cubs was assumed to be 50:50. We also calculated the average annual exponential rate of increase as $r = \log_e \lambda$ (Caughley 1977). The trend of the population was also estimated between 1989-95 using the ratio ($\lambda = N_{t+1}/N_t$) of solitary marked and unmarked grizzly bears between 2 successive years (Caughley 1977,page 51).

RESULTS

Capture

Fifty individual grizzly bears were captured in 108 capture episodes between 1987-1996 (Table 9.1). We accumulated 8,627 snare-nights during the study. Capture success ranged from 20-113 snare-nights/capture and averaged 80 snare-nights/capture.

No new adult females were captured after 1990 (Table 9.1). Most adult males were also captured early in the study. The one adult male captured in 1993 left the study area immediately after capture and was never relocated again. New subadult males and females continued to be captured throughout the period.

Our sample of 50 individual grizzly bears was 58% female and 42% male. Median age of females at capture was 3.5 years and varied from one to 19 years-old (Fig. 9.2). Thirty-eight percent of the female captures were adults, 38% were subadults, and 24% were one year-olds. Median age of males at capture was 4.5 years and varied from one to 11 years. Forty-three percent of the male captures were adults, 38% were subadults, and 19% were one year-olds.

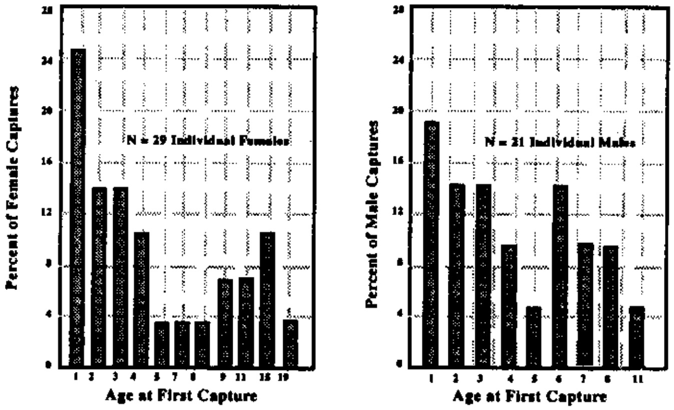

Figure 9.2. Age structure of 50 grizzly bears captured in the Swan Mountains between 1988 and 1995.

Table 9.1. Grizzly bear capture effort and success from 1987-1996. Swan Mountains, Montana.

Characteristic	Year										Total
	87	88	89	90	91	92	93	94	95	96	
Capture polygon size (km²)	101	866	866	518	560	999	559	425	37	30	
No. snares	14	61	60	44	42	44	32	23	4	8	
Snare-nights	142	2196	2100	1296	750	789	814	402	40	98	8627
Snares/100 km²	14	7	7	8	8	4	6	5	11	27	
No. grizzly captures	6	25	19	15	12	7	16	5	2	1	108
No. individuals	4	15	15	12	8	6	13	5	2	1	
Snare-nights/capture[a]	24	88	111	86	63	113	51	80	20	98	
No. new individuals[b]	4	13	5	8	5	3	6	4	1	1	50
No. new ad f	2	4	1	3	0	0	0	0	0	0	10
No. new ad m	0	6	1	0	0	0	1	0	0	0	8
No. new subad f	2	2	2	1	3	3	3	2	1	0	19
No. new subad m	0	1	1	4	2	0	2	2	0	1	13

[a] Snare-nights/No. individuals.

[b] New individuals are defined as those grizzly bears not previously captured.

Reproduction and Dispersal

Cub Production. Between 1989 and 1996, we documented the birth of 28 cubs from 17 litters of radiocollared female grizzly bears. Mean litter size was 1.64 cubs/litter ± 0.12 (SE). Most litters were of 2 cubs (65%), followed by litters of 1 cub (35%). On average, there were 4.0 ± 1.21 (SE)/ cubs born to radioed females each year. Of the 9 litters where gender of the cubs was known, the sex ratio was 64% female and 36% male. Using the age classification of Craighead et al. (1995), we observed no difference in litter size among 4 age classes of adult females ($X^2 = 2.19$, 6 df, $P = 0.90$) (Fig. 9.3).

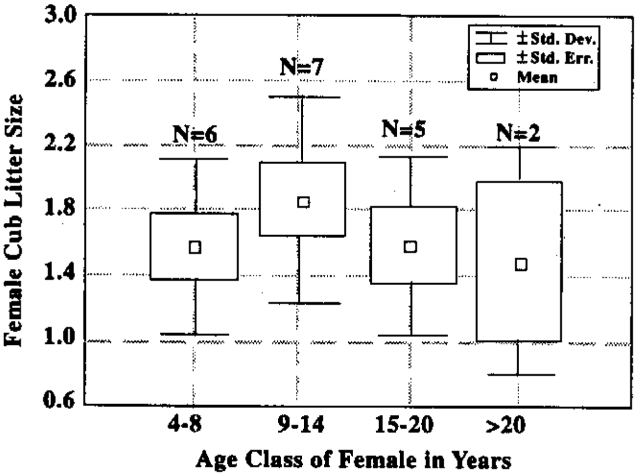

Figure 9.3. Litter size of female grizzly bears as a function of age. Swan Mountains, Montana.

Age of First Reproduction, Reproductive Longevity. Age of first reproduction was positively ascertained for 3 female grizzly bears that we radio-monitored from subadult to adult status. These 3 individuals successfully produced their first litters at ages 4, 5, and 8 years. Ancillary information from 3 other females, which had short mammae length and a pinkish mammae color when captured during the year prior to cub production, suggested that they could be included in this list. One of these bears was age 6 and the other 2 were 7-year olds. Pooling these bears resulted in a mean

Table 9.2. Summary of family breakup dates and early dispersal movements relative to natal home range for 18 radio-collared grizzly bears, 1987-1996. Swan Mountains, Montana.

Mother Id	Young Id	Gender	Age	Dispersal date[a]	Percent locations in Natal Range	
					Year 0	Year 1
1	3[b]	f	2	5/11/88	82 (28)	91 (23)
1	147[b]	f	2	5/11/88	74 (38)	87 (38)
147	32	f	2	5/07/92		
147	33	m	2	5/07/92		
5	17	f	2	6/28/93	69 (29)	94 (16)
94	94a	ukn	2	5/29/91		
94	94d	ukn	3[c]			
96	98	m	2	5/26/89	67 (15)	
96	18	f	2	5/26/89	5 (22)	10 (39)
96	137	f	2	5/26/89	69 (16)	51 (47)
96	50	m	3	5/24/94	0 (25)	13 (8)
96	21	f	3	5/24/94		
14	34	f	2	5/07/92	95 (37)	94 (12)
14	35	f	2	5/07/92	97 (36)	100 (16)
45	62	m	2	6/03/93	33 (18)	5 (21)
48	7	f	2	5/20/93	81 (27)	100 (4)
48	8	f	2	5/20/93	100 (20)	83 (18)
18	18a	ukn	3[c]			

[a] Dispersal date based on last visual observation of family group together or when mother first observed with breeding adult male.

[b] Bear numbers 3 and 147 dispersed following death of mother on 5/11/88.

[c] Bear did not disperse as 2 year-old at end of study. We assumed this bear would disperse as a 3 year-old.

age of first reproduction of 6 years and ranged from 4-8 years. Bears with engorged vulvae were considered to be at some stage of estrous. Mean age for those females in estrous (n = 19) was 9.65 ± 0.968 (SE), and 4.091 ± 0.908 (SE) years for the 22 bears not in estrous.

Six complete interbirth intervals were documented for 5 female grizzly bears. One of these intervals was compromised by loss of a complete litter. This female lost her single cub to natural causes during July 1989, bred the following year, and then produced another litter. The mean interbirth interval was 3.0 years and varied from 2 to 4 years.

We were unable to document the end of reproductive activity in older female grizzly bears. Our older females successfully produced litters at age 20, 22, and 23 years.

Dispersal Schedule and Movements. Date of family breakup was estimated for 16 young grizzly bears (n = 11 f, 4 m, and 1 unknown) (Table 9.2). All young grizzly bears dispersed during spring (median = 24 May, n = 16, range = 7 May - 28 June). We knew the age at breakup of 18 subadults, 14 of which (78%) dispersed as 2-year olds and the remainder dispersed as 3-year olds (Table 9.2).

Most movement pattern data were obtained for only the first 2 years subsequent to family breakup because collars were designed to fall off of young bears, and because some bears died early following family breakup. We were able to evaluate dispersal movement patterns of 12 radiocollared grizzly bears (n = 9 f, 3 m) relative to their natal home range (Table 9.2). The average percent of telemetry locations within natal ranges for dispersing females during year 0 (year of breakup) and 1 were 75% and 78% respectively. The average percent of telemetry locations within natal ranges for dispersing males during year 0 (year of breakup) and 1 were 33% and 9% respectively.

Two of 3 subadult males, for which we had movement data, had obtained human foods after moving into the Rural Zone. One of these bears is known to be dead, and we suspected that the other died as well. The third subadult male was not human-conditioned to our knowledge but was illegally killed after moving near or into the Rural Zone.

Mortality

Marked and Unmarked Grizzly Bear Mortality. Mortality records for unmarked bears were confined to the study area, although several marked or radiocollared bears died elsewhere. We documented 35 grizzly bear mortalities (Table 9.3), 25 of which were grizzly bears wearing functional ra-

Table 9.3. Cause-specific and class-specific mortality records for 35 grizzly bears. Numbers represent known and suspected mortality of marked and unmarked bears. Not all marked bears were radiocollared at time of death nor did they all die within the study area. Swan Mountains, Montana. 1988-1996.

Class	Cause of Mortality								Total (%)
	Natural	Mistaken id	Legal hunt	Self defense	Management removal	Malicious	Research	Unknown	
Adult									
M	1	0	0	3	0	0	0	2[a]	6 (17)
F	2	2	0-1[b]	0	1-1[b]	0	0	2	9 (26)
Subadult									
M	0	0	0	0	0	2	0	1[a]	3(9)
F	1	3	0	0	0	0-1	0	0	5 (14)
Cub	6	0	0	0	0	0	0	0	6 (17)
Yearling[c]	0	1	0	0	2-2[b]	0	1	0	6 (17)
Total (%)	10 (29)	6 (17)	1 (3)	3 (9)	6 (17)	3 (9)	1 (3)	5 (14)	35 (100)

[a] Suspected mortality of unknown cause.

[b] Where 2 numbers are presented, the first represents the number of marked bears and the second represents the number of unmarked bears.

[c] Yearlings include bears > 0.5 years old until year of dispersal.

dio collars, 6 were marked bears without radio collars, and 4 bears were unmarked. Thirty-two of these mortalities (91%) were known, and we suspected 3 additional deaths. The average number of mortalities each year from 1988-1996 using all 35 cases was 3.8 ± 0.97 (SE) bears (range = 0-10).

We could not determine the cause of death in 5 (14%) of 35 cases involving marked and unmarked bears (Table 9.4). Of the 30 cases where the cause was known, most (29%) deaths were natural. One bear out of 108 capture episodes (0.9%) was classified as a research mortality. This yearling male was killed by an adult male ≈ 12 hrs after being released from a snare.

Season of death was known for 32 cases; grizzly bears died during spring (41%), summer (13%), and autumn (47%). Natural mortality was prominent during spring and summer (Table 9.4), while management removal was the primary cause of loss during autumn. Two families (female with 2 cubs, female with 2 2-year olds) that had become habituated to humans and food-conditioned were removed. No mortality was observed while bears were in winter dens.

Mortality Records By Area. We were interested in documenting the location of death for those marked and unmarked grizzly bears killed by humans in relation to the Core Area and Rural Zone. We knew the location of death for 19 man-caused mortalities (excluding one research mortality), 5 of which died outside of the study area in the Bob Marshall Wilderness. Of the remaining 14 mortalities in the study area, 2 bears died in the Core Area (14%) (Table 9.5). Conversely, 12 of 14 (86%) bears

Table 9.4. Seasonal cause-specific mortality records for 32 of 35 grizzly bears where the season of death was known. Numbers represent known and suspected mortality of marked and unmarked bears. Not all marked bears were radiocollared at time of death. Swan Mountains, Montana. 1988-1996.

Season	Cause of Mortality (number and percent of season)							
	Natural	Mistaken id	Legal hunt	Self defense	Management removal	Malicious	Research	Unknown
Spring	5 (38)	3 (23)		1 (8)		1 (8)	1 (8)	2 (15)
Summer	4 (100)							
Autumn		3(20)	1 (7)	2 (13)	6 (40)	2 (13)		1 (7)

Table 9.5. Summary of 14 marked and unmarked grizzly bear mortalities that were man-caused, relative to the Core Area and Rural Zone. Swan Mountains, Montana. 1989-1996.

Bear Id	Date	Sex, age	Jurisdiction	Cause of mortality
363	1 Oct., 1988	F, 14	Core	Legal Hunt
7	20 May, 1994	F, 3	Core	Mistaken Id
147	17 Sep.,1993	F, 6	Rural	Management
32[a]	24 Sep., 1992	F, 2	Rural	Management
33[a]	14 May, 1992	M, 2	Rural	Management
Ukn42	4 May, 1992	F, 3	Rural	Malicious
1	May, 1988	F, 12	Rural	Mistaken Id
98	9 June, 1989	M, 2	Rural	Malicious
144	31 May, 1990	M, 13	Rural	Defense of Life
26	22 Sep., 1996	F, 4	Rural	Mistaken Id
50	18 Oct., 1995	M, 4	Rural	Malicious
11	9 June, 1995	F, Adult	Rural	Management
11a[b]	9 June, 1995	F, 0.5	Rural	Management
11b[b]	9 June, 1995	F, 0.5	Rural	Management

[a] Offspring of adult female No. 147. [b] Offspring of adult female No. 11.

Table 9.6. Cause-specific annual mortality rates of radiocollared grizzly bear classes based on censored telemetry data. Swan Mountains, Montana. 1987-1996.

Parameter	Class					
	Ad m	Ad f	Subd m	Subad f	Cub	Yrling[a]
Sample Size[b]	13/29	16/56	11/11	15/21	28/23	25/30
Survival	0.873 (0.764 - 0.997)	0.899 (0.826 - 0.979)	0.828 (0.638 - 1.00)	0.828 (0.688 - 0.996)	0.77 (0.626 -0.949)	0.90 (0.80 - 1.0)
Mortality cause:						
Natural		0.034 (0 - 0.079)		0.043 (0 - 0.125)	0.23 (0.05 - 0.37)	
Mistaken Id		0.017 (0 - 0.050)	0.086 (0 - 0.247)	0.129 (0 - 0.265)		
Self defense	0.095 (0 - 0.197)[c]					
Management		0.017 (0 - 0.050)				0.063 (0 - 0.148)
Malicious			0.086 (0 - 0.247)			
Research						0.032 (0 - 0.092)
Unknown	0.032 (0 - 0.093)	0.034 (0 - 0.079)				
Mortality category:						
Human-caused	0.095 (0 - 0.197)	0.033 (0 - .080)	0.171 (0 - 0.387)	0.129 (0 - 0.265)		0.095 (0 - 0.191)
Unreported	0.032 (0 - 0.093)	0.067 (0 - 0.131)	0.171 (0 - 0.387)	0.129 (0 - 0.265)	0.23 (0.05 - 0.37)	

[a] Yearlings include bears > 0.5 years old until year of dispersal .

[b] Number of bears/radio-years

[c] Annual mortality rate estimate (lower - upper 95% CI)

died or were removed in the Rural Zone. Most of the bear losses in the Rural Zone were due to management removals (Table 9.5). These 6 cases of management removal involved adult females with young that had become food-conditioned and habituated.

The 5 mortalities in the Bob Marshall Wilderness involved 3 cases of mistaken identification of marked grizzly bears. The remaining 2 adult males were killed in defense of human life.

Cause-specific Mortality Rates. Cause-specific mortality rates were estimated from censored radio telemetry data (170 bear/years) for adult males and females, subadult males and females, cubs, and yearlings (Table 9.6). Annual mortality rates were based on the deaths of 25 radiocollared grizzly bears and the unmarked attendant young of marked adult females.

Adult female mortality rates were highest for natural and unknown causes (3.40%). Two adult females died of natural causes; a 15 year old female was believed killed and fed upon by an adult male, and a female, accompanied by 2 cubs, probably died in an avalanche.

Mistaken identification mortality during black bear hunting seasons was the leading cause of subadult female mortality (12.90%). One subadult female (age 2) died during the spring breeding season of natural wounds believed inflicted by a radiocollared adult male. Cubs were most susceptible to natural mortalities (23.0%).

Adult males were most (9.50%) prone to die during ungulate hunting season in defense-of-life by hunters in the Bob Marshall Wilderness after the bears confiscated harvested elk (*Cervus elaphus*). One adult male was killed on private land while breaking into a dog kennel for dog food. Subadult males were equally susceptible to malicious killing and mistaken identification (8.60%).

The annual mortality rate for all classes and causes was 13.6% (8.17 - 18.44%). The annual man-caused mortality rate for all classes was 7.0% (95% CI = 3.4 - 11.0%). The annual unreported mortality rate was estimated to be 8.70% (95% CI = 4.70% - 12.90%).

Local Population Size, Density, and Structure

Study Area. Annual estimates of grizzly bear population size and age structure were determined for the study area from 1989-95, when a larger portion of the population had been marked and instrumented. On average, there were 22.6 marked grizzly bears present in the study area each year (Table 9.7). Solitary adult females (x = 32.9%) and subadults (x = 27.2%) constituted a greater proportion of the population than adult males (x = 15.3%). There were more subadult females than subadult males each year. On average, 27.2% of the population was cubs or yearlings. Between 1989-1995, the annual density of marked bears averaged 1.6 ± 0.11 (SE) bears/100 km^2.

We documented additional unmarked bears in the study area each year through visual observation and during photographic sighting sessions. All unmarked bears were observed or photographed in the Core Area. The number of unmarked bears, including attendant young, varied from 2 to 14 individuals per year. Therefore, our study area density estimates were considered minimum values.

Core Area and Rural Zone. Density estimates were, on average, nearly twice as high for the Core Area

Table 9.7. Annual density estimates based on percent of time radiocollared bears spent in the 1457 km study area. The number of unmarked bears observed in the study area are also given.1989-1995.

	Cub	Yrling	Sub m	Sub f	Ad m	Ad f	Total Dep young	Total Subadult	Total Adult	Total Bears	# family groups
89	4	0	1.4	4.5	4.2	5.5	4	5.9	9.7	19.6	2
90	4.3	1	3.7	3.9	4.9	9.1	5.3	7.6	14	26.9	3.1
91	10	3.1	1.9	2	2.9	9.3	13.1	3.9	12.2	29.2	7.5
92	0	6	1.8	3.5	1.7	7.3	6	5.3	9	20.3	4
93	0	0	1.7	5.1	3.9	8	0	6.8	11.9	18.7	2
94	3.8	0	3.3	4	3.9	6.7	3.8	7.3	10.6	21.7	3.8
95	4.8	2	2	4	3.8	6.3	6.8	6	10.1	22.9	6.3
mean	3.84	1.72	2.25	3.85	3.61	7.45	5.57	6.11	11.07	22.75	4.1
% of total	16.9	7.6	11.3	17	16	33	24.5	26.85	48.65		18

a= The number of family groups is a subset of adult female class. For example, in 1988 there were.9 adult females , 1.9 of which had young.

b= Bear/ 100 km^2

c= Includes 1 2-year old of unknown gender from marked female relative to the entire study area (Table 9.8). Conversely, bears spent little time in the Rural Zone and density estimates were relatively low. On average, the density in the Core Area was 8 times greater than the Rural Zone. The additional unduplicated unmarked bears, observed in the Core Area, suggested that density estimates in this area were minimum values.

Spatial Arrangement of Home Ranges

The density of male grizzly bears in the study area was lower than females because of their tendency to move though a large portion of the NCDE (Fig. 9.4). The 100% MCP for all males during the study (7,852 km²) was 4.3 times that of the pooled sample of females (1,843 km²). The high affinity grizzly bears exhibited for the study area was the result of small female home ranges, which averaged 125 km² (Mace and Waller 1997a) and either geographic or psychological barriers on 3 of 4 sides of the study area. During the entire study, no radiocollared females crossed the Hungry Horse Reservoir on the eastern side of the study area (Mace and Waller, 1997a), nor crossed the highly urbanized and roaded Flathead Valley (Mace et al. 1996b). Further, we observed no movement from the study area along the northern boundary, where again urbanized areas separated the study area from Glacier National Park. Movement across the southern boundary into the Bob Marshall Wilderness was observed for males, and those female grizzly bears with home ranges along this boundary. This affinity for the study area by females was reflected in the age structure of the population (32-33% adult female).

Table 9.8. Comparative density estimates (bears/100 km²) in 3 divisions of the entire study area. Swan Mountains, Montana. 1989-95.

Year	Density of bears in 3 divisions[a] of the study area (bears/100 km²)		
	Study area	Core area	Rural zone
89	1.3	2.5	0.02
90	1.8	2.8	0.5
91	2.1	3.7	0.2
92	1.4	2.1	0.3
93	1.3	2.2	0.4
94	1.4	2.3	0.1
95	1.6	2.0	0.8
Mean (SE)	1.6 (0.1)	2.5 (0.2)	0.3 (0.1)

[a] Three divisions were: entire 1,475 km² Study Area, the 692 km² Core Area, and the 305 km² Rural/roaded area.

The large composite MCP range for males was partially due to several males captured on the southern periphery of the study area. Although these males spent most of their time elsewhere, they returned to the study area each spring during the breeding season. Two adult males were captured in the Core Area that left immediately after capture and never returned. We lost radio contact with one shortly after release, and the other lost it's radio collar on the RMEF.

Annual MCPs were used to estimate the amount of the Core Area occupied by grizzly bears each year. When classes were pooled, the average occupancy was 88% and varied from 45-100% (Table 9.9). For adult females, annual home range occupancy of the Core area averaged 57%, and varied from 31-74%. These measures of percent occupancy were minimum, because of the additional unmarked bears present each year (Table 9.7). Sixty percent of the Core area was > 0.5 km from a road.

Vital Rates and Population Trend

Between 1987-1996 we radiomonitored 16 adult and 15 subadult females, and followed the fate of 28 cubs and 25 yearlings by following their mothers (Table 9.10). Annual survival rates varied by class. Estimates for adult and subadult females were 0.899 ± 0.046 (SE) and 0.825 ± 0.089 (SE) respectively (Table 9.10). The reproductive rate estimate for female cubs using bootstrapping procedures was 0.389 ± 0.104 (SE).

Using the derivation of Lokta's equation, our estimate of $\hat{\lambda}$ was 0.977 (95% CI = 0.875 - 1.046) giving an annual exponential rate of $r = 0.009$ (-0.11 - 0.092). We used a cutoff point for $\hat{\lambda}$ of 0.995 to describe local population trend. Values ≥ 0.995 represented a stable to increasing population, those > 1.0 a growing population, and those < 0.995 indicated population decline. The distribution of 5000

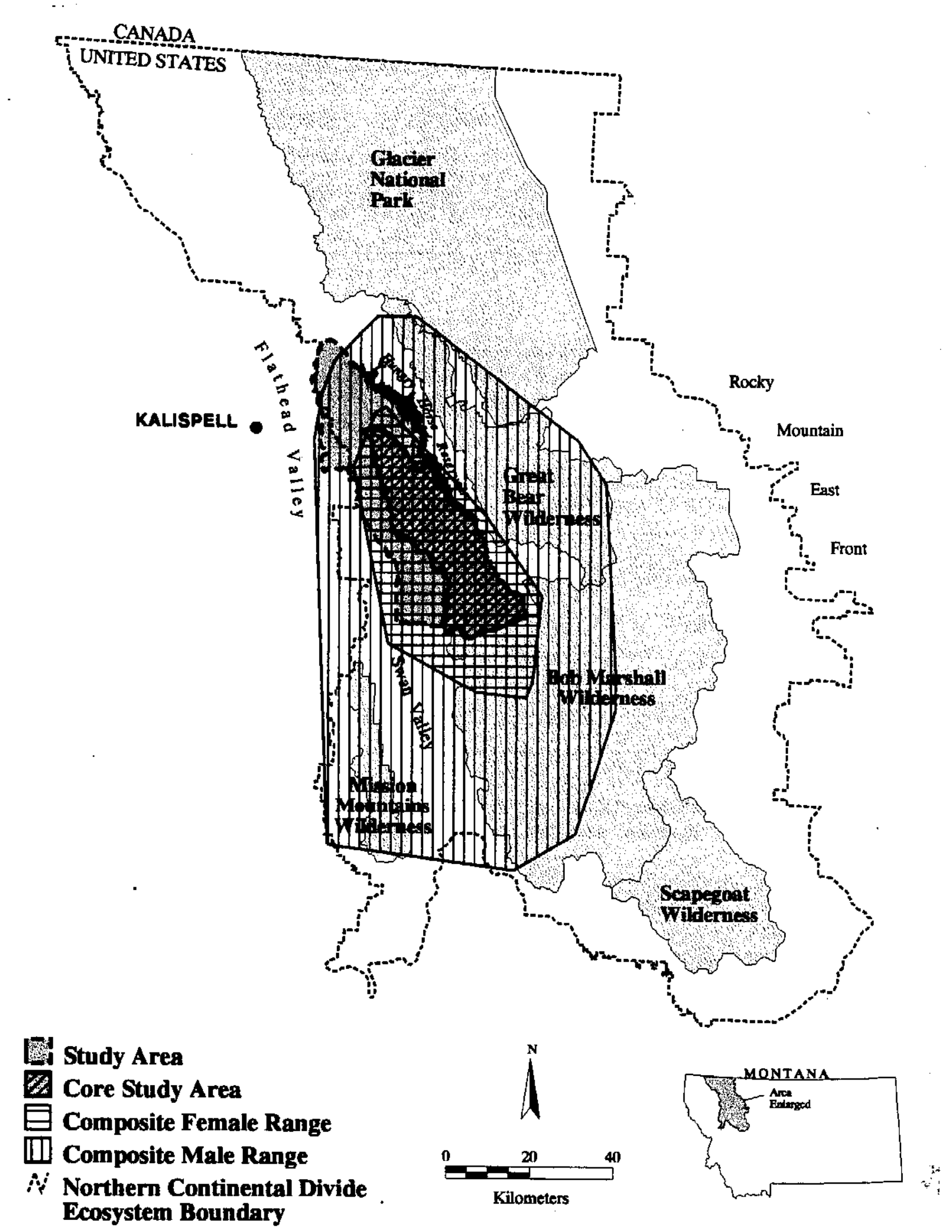

Figure 9.4. Composite minimum convex polygons for male and female grizzly bears relative to the Northern Continental Divide Ecosystem, 1987-1995.

Table 9.9. Grizzly bear occupancy of the Core Area based on home ranges. Swan Mountains, Montana.

Class	Percent occupancy of core area by year							Mean %
	89	90	91	92	93	94	95	
Ad f	56 (6)[a]	64 (8)	74 (9)	72 (7)	57 (9)	45 (7)	31 (7)	57
Ad m	92 (5)	83 (3)	47 (2)	67 (2)	82 (4)	85 (4)	18 (2)	68
Subad f	58 (5)	36 (3)	19 (2)	15 (4)	13 (4)	18 (4)	12 (3)	25
Subad m	17 (2)	49 (4)	46 (3)	24 (1)	1 (1)	31 (2)	8 (1)	25
All Classes	100 (18)	99 (18)	93 (16)	94 (14)	93 (18)	90 (17)	45 (13)	88

[a] Percent (Number of radiocollared individuals).

Table 9.10. Estimated annual survival rates by class, reproductive rate, and population trend of grizzly bears in the Swan Mountains, Montana. 1987-1996.

Parameter	Survival and Rate of Change Estimates					
	Sample size	Estimate[a]	Lower 95% CI	Upper 95% CI	SE of estimate	Variance proportion (%)[b]
Adult female survival (S_a)	16/56[c]	0.899	0.785	0.966	**0.046**	**37.25**
Subadult female survival (S_s)	15/21[c]	0.825	0.629	0.962	**0.089**	**56.07**
Yearling survival (S_y)	25/30[c]	0.906	0.906	1.000	**0.049**	**1.53**
Cub survival (S_c)	28	0.785	0.643	0.928	**0.076**	**2.87**
Age first parturition (a)	fixed	6.0				
Reproductive rate (m)[d]	6	0.261	0.214	0.316	**0.026**	**2.88**
Maximum age (w)	fixed	25.0				
Lambda (λ)	5000	0.977	0.875	1.046	**0.043**	

estimates of $\hat{\lambda}$ (Fig. 9.5) revealed that 59% of the observations were ≥ 0.995, 55% of the estimates > 1.0, and 41% were < 0.995. Therefore, there was a 69%,probability that the population was declining, a31%.probability that the population was stable to increasing, and a27%. probability of an increasing population. The uncertainty in $\hat{\lambda}$, as indicated by the proportion of the variance explained (Table 9.10), was primarily due to sampling variation in subadult female survival (50.93%), followed by the variation in adult female survival (25.93%). The obtained value of $\hat{\lambda}$ changed slightly (0.909 < 1.025 > 1.11) when the sex ratio of female: male cubs was changed to 64:36%.

The trend of the population was also estimated between 1989-95 using the number of marked and unmarked grizzly bears that were ≥ 2 years of age (Fig. 9.6). The mean estimates of $\hat{\lambda}$ and r using this method were 1.020 and 0.019 respectively.

DISCUSSION

We believe that the local population dynamics of grizzly bears in the Swan Mountains was an example of source-sink demography. Areas or subpopulations where fecundity exceeds mortality are termed "sources", and demographically inviable areas or subpopulations are termed "sinks" (Pulliam 1988, Donovan et al. 1995). In the following 4 paragraphs, we encapsulate the evidence suggesting the Core Area was near carrying capacity for grizzly bears given the current landscape structure and function, and that the Rural Zone was a sink area. We then build upon source-sink and density dependence theory to place the observed fecundity, mortality, trend, density, dispersal, and occupancy data in perspective.

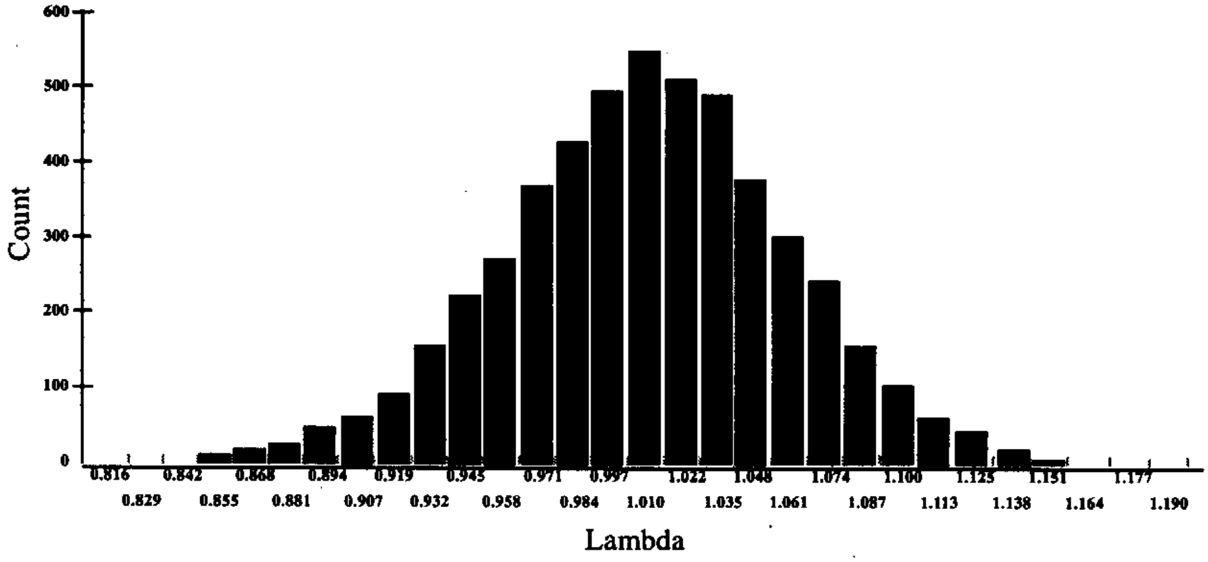

Figure 9.5. Distribution of 5000 bootstrap simulations on the value of lambda.

Twenty-eight cubs were born to radiocollared grizzly bears and we documented 25 deaths of radiocollared bears and their attendant young. Our estimate of the finite rate of increase (λ) (1.009 ± 0.050) supported these birth and death statistics, indicating exceedingly slow population growth. Our calculated exponential rate of increase (r) revealed that it would take approximately 77 years to observe a doubling of the local population given long-term stability of vital rates. Our annual density estimates also suggested the population was relatively stable, and therefore the lower and upper bounds of our 95% confidence intervals for λ were not observed.

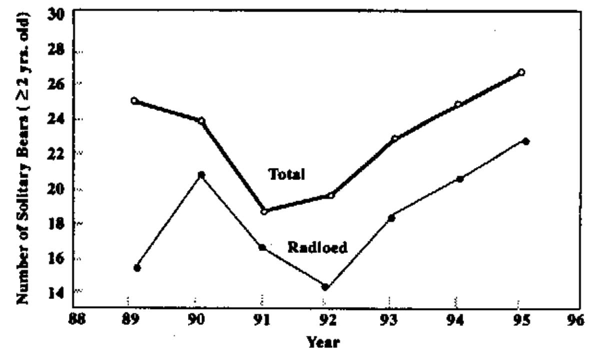

Figure 9.6. Trend of the grizzly bear population based on percent of time radiocollared solitary bears (≥2 years old) spend in the study area each year. The total number of bears observed was derived by summing the radiocollared bears and the count of unmarked solitary bears observed each year from Table 9.7 Swan Mountains, Montana. 1985-1995.

The mean annual density estimate for the Core Area of 2.5 bears/100 km^2, with a maximum of 3.7 bears/100 km^2, was greater than that observed by K. A. Aune and W. F. Kasworm (unpubl. data) of ≈ 0.15 - 1.3 bears/100 km^2 on the RMEF portion of the NCDE, and the estimate of 1.2 bears/100 km^2 for the Greater Yellowstone Ecosystem (Eberhardt and Knight 1996). These density estimates exceeded most other published estimates from northern and interior areas (Pearson 1975, Russell et al. 1979, IGBC 1987, Clarkson and Liepins 1994, Miller et al. 1987, Wielgus et al. 1994, Wielgus and Bunnell 1994a). We further demonstrated that the annual density of grizzly bears in the Core Area was 8 times greater than in the Rural Zone. Source-sink models generally assume that when the finite rate of increase is > 1, net movement will be out of the source habitat (Doak 1995). However, if sink habitats are attractive to bears for any reason, they can attract individuals in a density-independent fashion. We believe our Rural Zone (sink habitat) was attractive because of the availability of high quality forage during spring and autumn, the availability of ungulate carcasses on winter ranges, and the presence of human foods (e.g. domestic fruit orchards, garbage).

During dispersal, all 3 subadult males made movements within the natal range, which for each included portions of the Rural Zone where they ultimately died or we suspected they died. Conversely, subadult females did not venture into the rural zone after family breakup.

The high level of occupancy (x = 88%) in conjunction with low fecundity, high mortality, high density, and stable trend suggested that the carrying capacity in this area may have been closely met given the current distribution of natural resources and the levels of habitat degradation and human use (Mace et al. 1996).

Density dependence theory suggests that vital rates will be suppressed as population density increases. It is generally believed that unexploited brown bear populations will stabilize in a density-dependent fashion although the form of this dependence is unclear and possibly derived from multiple causes (Harris 1984). At higher densities all reproductive parameters may be suppressed, or in some cases mortality rates only may increase (Bunnell and Tait 1980). The observed litter size in the Swan Mountains (1.64 cubs/litter) was among the lowest reported in the literature (IGBC 1987). Interbirth intervals may also be affected in a density dependent fashion: intervals may increase at higher population densities. Unfortunately, our observed interbirth intervals were difficult to compare to other studies because of variable methods. Three of our 17 litters (18%) were retained until year three.

High densities of adult males may serve to increase mortality of subadult males and cubs (McCullough 1981, Young and Ruff 1982, Stringham 1983). Our evidence for intraspecific mortality in cubs-of-the-year was poor. Of the 6 natural cub mortalities, 2 siblings were believed to have died in an avalanche. The cause of death for the remaining 4 cubs could not be determined as they simply disappeared between telemetry flights. However, we believe that 2 adult males did kill other grizzly bears. In one case a 10 year-old male was implicated in the death of a 2 year old female. The second case involved an 11 year-old male killing and eating a 15 year-old female.

Local population density and trend estimates are rare in the brown bear literature, but are available from several areas. Studies in the North Fork of the Flathead River, in the extreme southern portion of British Columbia, Canada (adjacent to the NCDE) are reported by McLellan (1989a, 1989b, 1989c). In this area, the local population was increasing at an annual exponential rate of 0.07 given a density of 6 bears/100 km^2. McLellan's work was based on a smaller area than our study area: an area that was approximately the size of a Swan Mountain females' annual home range (125 km^2). Grizzly bears were not equally distributed within our study area, and we too were able to obtain annual density estimates of between 5-6 bears/100 km^2 for 125 km^2 portions of our Core Area (Mace unpubl. data). The ability to manipulate densities based on the size and location of areas used in the estimate suggested that population densities of bears should be compared with caution (Caughley 1977, White and Garrott 1990).

Unfortunately, no estimate of λ was provided by K. A. Aune and W. F. Kasworm (unpubl. data) for the only other intensively studied portion of the NCDE. However, they reported maximum annual survival rates for adult female, subadult female, and cub/yearling of 0.967, 0.918, and 0.852 respectively. These higher survival rates coupled with a larger estimated litter size (Aune et al. 1994) and shorter interbirth interval (2.6 years), suggested that the local RMEF grizzly bear population was more likely to be stable or increasing than the Swan Mountains.

The annual mortality rate for grizzly bears in the Swan Mountains was higher than other brown bear populations in North America (Craighead et al. 1974, Sidorowicz and Gilbert 1981, Harris 1984, Mclellan 1989b, K. A. Aune and W. F. Kasworm unpubl. data, Eberhardt et al. 1994). Bunnell and Tait (1980) recommended that total annual mortality not exceed 12.5%. The observed total mortality rate in this study was 13.6% (95% CI of 8.52-18.44%). Annual survival rates for females must equal or surpass 90% to support population growth as indicated by the positive trends for Yellowstone National Park (Eberhardt et al. 1994) and in southern British Columbia (Hovey and McLellan 1996). It was clear that our population under study, even though skewed towards females, was at the probable maximum sustainable mortality, beyond which a decline would be certain.

Habitat degradation and urbanization were the primary factors limiting population growth. Habitat managers will be challenged to increase bear numbers and improve long-term local population trend in source-sink landscapes such as the Swan Mountains. The projected human growth for the Flathead Valley area was estimated to be 17% by the year 2000, thus managers should brace themselves for an increasing number of humans using and living in grizzly bear habitat in this area.

Managers should be aware that even small incremental levels of habitat degradation can lead to declines in precariously stable populations (Doak 1995) such as those in the Swan Mountains.

MANAGEMENT RECOMMENDATIONS

The Swan Mountain region of the NCDE is a mosaic of mixed ownership and stewardship philosophies. The region is variously administered as public multiple-use and wilderness lands, state, private, corporate, and Native American lands. Long-term grizzly bear management success in this region requires flexible management and monitoring strategies that involve all effected agencies and publics. This strategy must be adaptive (Lancia et al. 1996, Mattson et al. 1996), with clear objectives and expectations for grizzly bear population size and trend. To succeed, this adaptive strategy will require that agencies be able to adequately monitor and integrate scientific information on grizzly bears into planning efforts (Mattson et al. 1996). Effective management must incorporate several key elements: 1) The Swan Mountain region must be placed in a population and habitat perspective relative to the NCDE, 2) population objectives for grizzly bears based on the current perspective, and 3) a detailed local management plan that is adaptable to the NCDE perspective within limits, and to new information.

NCDE Perspective

The Swan Mountain study area constituted approximately 6% of the NCDE, and grizzly bears inhabiting this region were a part of a larger population estimated by the state of Montana to exceed 500 individuals (Dood et al. 1986). However, the population trend and habitat condition of the greater NCDE was unknown. In this context, status and trend of Swan Mountain grizzly bears becomes much more important. Although significant progress has been made in monitoring habitat potential and effectiveness in the western portion of the NCDE (Mace et al. 1997), there is no on-going population monitoring system to determine population status, size, and trend in the entire NCDE. Regardless of perspective, a clear definition of population objectives and a management strategy to implement those objectives is essential for the Swan Mountains.

Population Objectives

Population management can have one of 3 objectives: conservation, sustained yield, and control (Caughley 1977, Miller 1990). The goal of a conservation management strategy is to raise densities of small or declining populations. For populations sufficiently large, and with stable to increasing trend, sustained yield management methods can maintain densities and avert crisis situations through removal (via hunting or other methods). When a population is considered too dense, or has too high a rate of increase, control measures are used to stabilize or reduce densities.

Current management of grizzly bears in the NCDE includes elements of all 3 objectives. Conservation is the primary objective, however in regions of the NCDE where either social or biological capacity has been met, population size is regulated through agency "control actions." Existing control programs that remove or translocate bears from contentious grizzly bear/human interfaces may be sufficient to accomplish control, sustained yield, and conservation goals. Aside from natural mortality, management removal was the second highest source of mortality in the Swan Mountains, and often involved females. Thus in the absence of regulated hunting, control programs may continue indefinitely as de facto sustained yield management programs, and not be inconsistent with conservation objectives.

Until a landscape scale perspective is obtained, we recommend a conservation management strategy for the Swan Mountains because 1) our estimates of local population size, trend, survival, and reproductive rate were not without error, and there was a non-trivial probability of population decline, 2) mortality rates for adult and subadult females were high relative to other locals, and may represent the maximum beyond which a decline in the local population would be certain, 3) this local population was semi-isolated because of human development including hydroelectric development.

Local Management Plan and Monitoring

As stated, a local management plan should be adopted that is responsive to feedback from the continuing collection of information from both the entire NCDE and the Swan Mountain region. This information includes: 1) mortality levels, 2) habitat effectiveness, and 3) public acceptance of the program.

Mortality Assessment. Population monitoring programs are a fundamental part of wildlife management. Without such a monitoring program, managers will find it difficult to choose the correct management strategy, and the consequences of error are great (Miller 1990). History has shown that grizzly bears are extirpated primarily because humans kill them, and human-caused mortality was the leading cause of the observed trend in the Swan Mountains as well. In this context, mortality is an exceedingly important but difficult parameter to measure. It is difficult because not all mortalities are reported. Our estimated annual rate of unreported natural and man-caused mortality was 8.70% (4.70 - 12.90%), which was higher than the previous 2.9% annual rate estimated for the NCDE (Brannon et al. 1988). Therefore, a simple annual tally of reported mortalities will not be effective in judging level and consequence of mortality. Because female grizzly bears factor heavily in population trend, we recommend that local management plan include a continuing monitoring program for a radiocollared sample of approximately 5 female (adult and subadults) grizzly bears distributed throughout the Swan Mountains. The goal of this monitoring program is to estimate female survival and reproductive rates. Observed deviations from the survival and reproductive rate estimates presented herein would serve as a valuable index to population trend and would assist managers in selecting the most appropriate population objective (Eberhardt 1990).

Mistaken identification during the black bear hunting season was the primary cause of death for subadult females. The low annual survival rate for subadult females contributed most (50.93%) to the trend in the local population. We propose that a bear identification course be a prerequisite for obtaining a black bear hunting license. Continuing restriction of black bear hunting opportunity in other western states will increase the numbers of inexperienced non-resident hunters.

Habitat Conservation and Assessment. The local management plan must include provisions for habitat conservation and a long-term program to monitor habitat effectiveness. Habitat conservation efforts in all jurisdictions must include provisions to minimize unnatural attractants, minimize displacement and mortality, and an easement or acquisition program directed towards private lands frequented by grizzly bears.

Programs that control human access in grizzly bear habitat are necessary for recovery efforts (U.S. Dep. Agric., Fish and Wildlife Serv., 1993) and will become even more important as human populations grow. Although the effects of roads and human access on grizzly bear displacement and mortality are well understood (Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996), restrictive road access programs have been shown to polarize and antagonize certain publics (Kellert et al. 1996, Mace et al. 1996, Mattson et al. 1996). However, based on the location of our observed mortalities, strict road access programs on national forest lands will not be sufficient to significantly improve the population trajectory as long as mortality and habituation of bears on private lands is not reduced. Yet, until effective management programs are developed on private lands, federal lands should be considered invaluable source areas and managed to reduce man-caused mortality. This would be accomplished by establishing effective areas of high security that transcend seasonal habitats, and where access is regulated.

Private lands, and areas of concentrated human use on public lands, are attractive to grizzly bears due to the presence of human or livestock foods, domestic fruits, and garbage. Efforts to minimize food conditioning and habituation through county planning efforts and increased enforcement will also be necessary to reduce mortality. Managers should seek legal means to encourage sanitary conditions on public and private lands.

Local Public Acceptance. At a broad scale, all planning efforts will ultimately fail without local public participation, ownership, and acceptance. Successfully maintaining or increasing capacity for grizzly bears in the Swan Mountains will require a new strategy for grizzly bear management in rural settings; one that includes local citizens, elected officials, and agency personnel, (Mattson et al. 1995). These citizens and officials must be identified and participate in planning and monitoring efforts. It is our contention that deriving a successful management program for grizzly bears in an ever increasing urban environment may well prove the most difficult challenge yet presented to managers.

CHAPTER 10

CONCLUSIONS AND RECOMMENDATIONS

CHAPTER 10

CONCLUSIONS AND RECOMMENDATIONS

Antropogenic Influences

We documented how grizzly bears behaved in a landscape dominated by humans. Our analyses were conducted at several landscape scales and hierarchies of resource selection. At the broadest scale, selection against private lands (chapter 7.1) with high densities of humans (Chapter 7.3) were observed, especially by female grizzly bears. Selection against private land was manifested by both spatial avoidance and in relatively high mortalities rates for those bears that were unwary, food-conditioned, or habituated (Chapter 9).

On public lands, we demonstrated the negative relationships among grizzly bears, roads, and trails (Chapters 3.2, 3.4 and 7.2). Avoidance of roads increased as road densities and traffic volumes increased (Chapters 3.2, 7.1 and 7.3). At all landscape scales, bear density declined as road densities and traffic volume increased (Chapter 3.4). Under certain habitat conditions and seasons, the positive attraction to specific cover types were stronger than the negative impacts of roads. Thus, in highly preferred seasonal habitats that tended to be open-canopied, grizzly bears would tolerate low levels of disturbance and would not abandon the habitat. This inverse relationship had both positive and negative management implications: bears tolerated low levels of disturbance, but their vulnerability to humans increased. Thus management efforts should focus on minimizing road density and road-use, and protecting seasonally preferred habitats.

Timber harvest units were a prominent feature of the study area landscape. Our study population survived and reproduced successfully within this landscape. We found that cutting units can provide preferred habitat during summer, however no comprehensive food studies or comparisons in adjacent wilderness areas were conducted. In the Swan Mountains, the negative effects of cutting units were related more to open roads than to reduction of habitat to earlier seres.

Status of the Population

The local population of grizzly bears was tenuously stable during the period of study. Our estimated annual mortality rate was higher than most other brown bear populations in North America. Further, the local population of grizzly bears in the Swan Mountains was at or near carrying capacity given current landscape structure and function. The population under study, though skewed towards females, was experiencing the probable maximum sustainable mortality rate, beyond which a decline would be certain. We have therefore recommended that a conservation strategy (local plan, Chapter 9) be pursued because our study population could not be placed into an ecosystem perspective. A conservation strategy for the Swan Mountains entails increasing bear numbers. Accomplishing this goal will require an aggressive private land habitat protection program. Such a program would include easements on, and acquisition of, private lands frequented by grizzly bears. Local planning efforts should be used to direct development away from crucial habitat. To be successful, local planning efforts will require public acceptance. A continuing public education program would help foster positive attitudes towards grizzly bears. Such a program would also help limit food-conditioning and habituation of grizzly bears. To maintain public support, conservation goals must be clearly stated and defined.

Habitat Effectiveness and Population Status

The establishment of management thresholds for human activities in the Swan Mountains and adjacent private lands is an important and necessary element of grizzly bear conservation. In this report we presented an analysis of habitat effectiveness in the study area and an extrapolation area (Chapter 7.3). However, there were no easily derived thresholds that could be used to set management standards. Difficulties arise because threshold values are those values beyond which long-term viability of the local population would be compromised. Viability is diminished by excessive mortality, restricted movement, or incremental habitat loss.

In the absence of known biological thresholds, standards should be considered relative to risk. There are two components of risk: risk of direct mortality, and risk of indirect mortality through displacement, habitat degradation, and diminished reproductive potential.

In the absence of population viability analyses for the Swan Mountains or similar areas, risk assessment can be best evaluated by comparing results of our habitat effectiveness studies employing resource selection functions (Chapter 7.3) to mortality levels, vital rates, and trend estimates from our population studies (Chapter 9).

Table 10.1 presents seasonal potential and realized habitat effectiveness values and the adjusted change (weighted % degradation) that resulted in a tenuously stable local population (lambda = 1.009). Our 1457 km^2 Swan Mountains study area was approximately 9% private land and man-caused mortality was approximately 7 times higher in the rural portion of the study area (predominantly private land) than in the core (public land). These figures can be used to establish acceptable levels of change (risk) within similar areas. It is important to remember that the interplay of each human and habitat feature affected probability of grizzly bear use incrementally. Thus the influence of each feature can be assessed individually. The required assumption is that similar types and levels of degradation in the Swan Mountains would result in similar demographic responses elsewhere. It is unfortunate that there are no similar studies of grizzly bears from which results could be compared. We strongly urge other scientists studying grizzly bears to begin linking cumulative habitat impacts with population parameters.

Specific Recommendations

- Provide Habitat Security by Protecting Core Areas: Habitat management emphasis in the NCDE is placed on protection of female grizzly bears (Dood et al. 1985 , U.S. Dep. Agri. Fish and Wildl. Serv. 1993), and therefore identification of those areas required by females to survive should receive high priority for habitat conservation. Based on the location of our observed mortalities, strict road access programs on national forest lands will not be sufficient to significantly improve the population trajectory if mortality and habituation of bears on private lands is not reduced. Until effective management programs are developed for private lands, federal lands should be considered invaluable source areas and managed to reduce man-caused mortality. This would be accomplished by establishing high-security core areas that include seasonal habitats and where vehicle access is restricted. Core areas can be identified using seasonal habitat preference maps (Chapter 7.3). The process used to delineate core areas may vary by location.

Programs that control human access to grizzly bear habitat are necessary for recovery efforts (U.S. Fish and Wildlife Serv., 1993) and will become even more important as human populations grow. The effects of roads and human access on grizzly bear displacement and mortality are well understood (Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996a). Therefore, access management should be a strategy within core areas to minimize disturbance and illegal mortality. Motorized restrictions should be most pronounced during spring, and could be relaxed somewhat in non-core areas during other seasons. Approximately 60% of core areas having superior seasonal habitat should be at least 0.5 km from the nearest road.

Limiting subadult female mortality will have the greatest conservation benefit for this population. The 2 biggest sources of human caused mortality were mistaken identification during the spring black bear season and management removal (Chapter 9). We strongly urge that a mandatory black bear hunter education program be implemented to ensure that black bear hunters be able to differentiate grizzly bears from black bears. Our data suggests that the study area black bear population is over-harvested (Appendix G). Having non-resident licenses on a permit system, rather than over-the-counter, would accomplish 2 purposes; limit harvest of black bears, and limit the number of inexperienced non-resident hunters. Continuing restrictions on black bear hunting opportunity in other states has resulted in an increase in non-resident black bear hunters in our study area.

- Encourage Proper Sanitation Practices: Private lands, and areas of concentrated human use on public lands, are attractive to grizzly bears due to the presence of human or livestock foods, domestic fruits, and garbage. Efforts to minimize food conditioning and habituation through county planning efforts and increased enforcement will also be necessary to reduce mortality. Managers should seek legal means to encourage sanitary conditions on public and private lands.

- Develop a Local Management Plan: At a broad scale, all planning efforts will ultimately fail without local public participation, ownership, and acceptance. Successfully maintaining or increasing capacity for grizzly bears in the Swan Mountains will require a new strategy for grizzly bear management in rural settings; one that includes local citizens, elected officials, and agency personnel, (Mattson et al. 1995). These citizens and officials must be identified and participate in the development and monitoring of a localized management plan. Along with a provision for on-going public education, the local management plan must include provisions for habitat conservation and a long-term program to monitor habitat effectiveness on private lands. Habitat conservation efforts in all jurisdictions must include provisions to minimize unnatural attractants, minimize displacement and mortality, and an easement or acquisition program directed towards private lands frequented by grizzly bears.

- Monitor Mortality and Habitat Effectiveness: Population monitoring programs are a fundamental part of wildlife management. Without a monitoring program, managers will find it difficult to choose the correct management strategy and the consequences of error are great (Miller 1990). History has shown that grizzly bears are extirpated primarily because humans kill them. Human-caused mortality was the leading cause of the observed trend in the Swan Mountains, and in this context mortality is an exceedingly important parameter to measure, especially survival of female grizzly bears. We recommend that a local management plan include a continuing monitoring program for a radio-collared sample of about 5 female (adult and subadult) grizzly bears distributed throughout the Swan Mountains. The goal of this monitoring program is to estimate female survival and reproductive rates. Observed deviations from the survival and reproductive rate estimates presented in Chapter 9 would serve as a valuable index to population trend and would assist managers in selecting the most appropriate population objective (Eberhardt 1990). We strongly urge that public representatives participate in the monitoring program.

Assessment of female grizzly bear mortality should be accompanied by an ongoing program that measures changes in habitat effectiveness on private and public lands. Ongoing small, incremental losses of habitat can result in population decline (Doak 1995). We suggest a habitat monitoring program be conducted at two scales: 1) the program should evaluate habitat effectiveness at a large landscape scale using methods such as those described in Chapter 7.3. 2) we suggest a finer scale monitoring program for private lands, through cooperation with county planning offices and the public. This program would monitor inconspicuous changes in land use practices that would not be evident at landscape scales.

Table 10.1. Seasonal habitat effectiveness values in two portions of the Swan Mountain study area: private lands, and the public, state, and corporate lands administered for multiple-use. These habitat effectiveness indices were derived from a tenuously stable local population of grizzly bears with a high rate of mortality on private lands.

Season	Primary land Use					
	Multiple-use			Private		
	Potential[a]	Realized	Change	Potential	Realized	Change
Spring	81	61	16	81	41	48
Summer	70	53	11	63	19	28
Autumn	79	64	12	82	43	31

[a] Values represent mean % habitat potential in the absence of anthropogenic influences, mean % realized habitat value considering anthropogenic influences, and mean % adjusted change from potential (see Chapter 7.3).

Figure 10.1. Each year wildlife managers in the NCDE are involved with grizzly bear-human conflicts on private lands. In nearly all cases, these are bears who have become conditioned to human foods, garbage, livestock foods, bird feeders, or fruit orchards. In 1996 for example, MFWP personnel responded to over 90 public requests for assistance with grizzly bear problems on the western side of the NCDE alone. Sanitation on private lands with increasing numbers of humans will be an ongoing management challenge.

APPENDICES

APPENDIX A

ESTIMATING GRIZZLY BEAR POPULATION SIZE USING CAMERA SIGHTINGS[1]

R. D. Mace, S. C. Minta, T. L. Manley, and K. E. Aune

INTRODUCTION

Estimating population size of grizzly bears (*Ursus arctos horribilis*) is hampered by certain characteristics (Harris 1986, IGBC 1987, Miller et al. 1987, Miller 1990a): grizzly bears are secretive, aggressive, and difficult to observe; populations often inhabit mountainous, densely vegetated, and remote habitats; individual bears often have different probabilities of capture or observation that violate the assumption of equal catchability; age and gender are difficult to determine without handling; sampling opportunities are limited because bears spend 6-7 months in dens; and sample sizes are typically small. These factors impose logistical and financial constraints on researchers obtaining point estimates and confidence intervals (CI's) for the population. The most reliable estimator for grizzly bears is the Petersen capture-recapture design (Miller et al. 1987); it accommodates small samples and requires only a single sighting period after the initial marking period (Seber 1982). The few published estimates of grizzly bear populations have wide CI's (Harris 1986, IGBC 1987, Miller et al. 1987). Model biases are more serious than small-sample bias because important assumptions are violated (White et al. 1982).

Most advances in estimating population size for grizzly bears have been made using aerial surveys in areas where bears are highly visible (Miller et al. 1987, Miller 1990b). Bears are captured and marked, and subsequently both marked and unmarked bears are "recaptured" or sighted from aircraft in a series of independent searches. This design can produce several types of Petersen estimators that better meet model assumptions and produce larger sample sizes than do standard recapture methods (Minta and Mangel 1989, White and Garrott 1990, Arnason et al. 1991).

In forested habitats where bears are difficult to observe, density estimates are typically converted from combinations of capture data and either telemetry data (DeMaster et al. 1980, Miller and Ballard 1982, McLellan 1989a) or observation data (Troyer and Hensel 1964, Martinka 1974, Dean 1976). These methods frequently violate assumptions and usually have no estimate of precision (Harris 1986). The Petersen method has been largely unsuccessful with bears because animals initially are captured using bait and then recaptured using the same technique. For grizzly bears, this procedure violates the model assumption of equal catchability (Seber 1982). In addition, trapping sessions are costly, yet rarely produce adequate sample sizes or reliable data (Harris 1986, IGBC 1987, Miller et al. 1987).

We evaluated a self-activating camera for detecting grizzly bears in habitats with limited opportunity for visual sighting. To assess the camera technique as a sighting tool, we describe and evaluate sampling procedures and assumptions, and compare 2 estimators of population size and CI's with the goal of identifying model biases. Our camera technique is compared with other methods used in forested habitats.

METHODS

Using preliminary results on the distribution of marked bears, we delineated a 516-km^2 core area where radiocollared grizzly bears spent more time, and a 301-km^2 peripheral area (Fig. A.1). We emphasized population sampling in the Core Area, and sampled the peripheral area less to assess geographic closure

Initial Capture Method: Snaring

Grizzly bears were opportunistically captured during May and June of 1988-1990. We superimposed a 3.2-km capture grid over the core area and

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[1] Mace, R. D. S. C. Minta, T. L. Manley, K. E. Aune. 1994. Estimating grizzly bear population size using camera sightings. Wildl. Soc. Bull. 22:74-83.

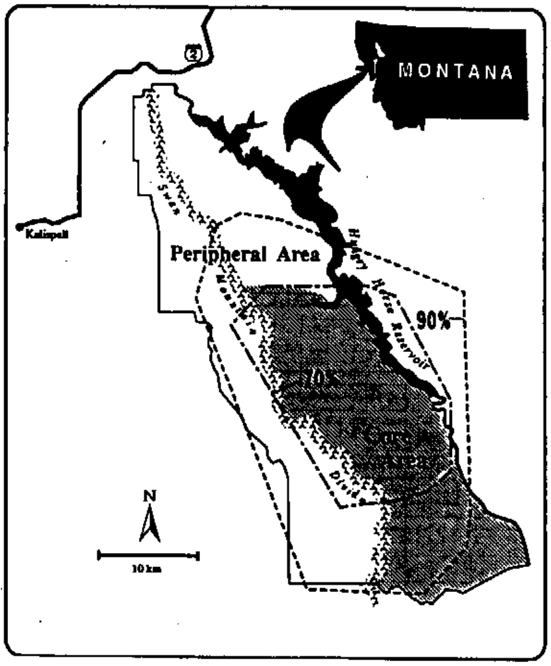

Figure A.1. Convex polygons (70 and 90%) constructed from 770 aerial telemetry locations obtained from 21 grizzly bears showing their relationship to the core and peripheral areas, Swan Mountain Range, Montana, 1989-1990 (data pooled).

portions of the peripheral area to identify accessible snare sites. Potential sites above snow-line were eliminated, and all sites were within 70 m of the nearest road.

We designed initial capture sessions to mark as many bears as possible within and surrounding the core area by modifying snaring methods and placement (White et al. 1982). Two Aldrich foot snares (Aldrich Animal Trap Co., Clallam Bay, WA 98326) were placed at each site and checked daily for 30-35 days. About 23 kg of wild ungulate bait was maintained at all sites, and sites were prebaited for 3-5 days before snares were set. Although the same 61 snare sites were used in 1988 and 1989, snare placement was changed. We used different combinations of wooden cubbies (Jonkel and Cowan 1971) and trail sets each year. In 1990 we stopped snaring in the peripheral area because of lack of captures, and sampled 37 sites in the core area. Several short-term snaring sessions were conducted at other times to recapture bears that lost radio collars.

We marked each bear with an ear tag and a 16.5- x 5-cm Armortite (Cooley Inc., Pawtucket, RI 02862) ear streamer with a unique symbol in each ear. Ear streamers were color-coded for gender. A premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966), and individuals ≥5 years old were classified as adults. Grizzly bears ≥2 years old were fitted with radiocollars. We defined capture rate as the number of snare-nights/capture.

Sighting Method: Cameras

The camera system consisted of a 35-mm fully automatic camera with flash, a passive infrared sensor that would differentiate between animal heat and background field, and a 12-volt battery. Bears were photographed approximately every 3 seconds while within the field, and the date of exposure was automatically recorded on each photograph. We placed cameras systematically in the core and peripheral areas in 1989 and 1990 using 2 1.6-km grids that were alternated among sessions. Each grid was superimposed on a map of the study area and every third grid cell was selected for sampling. Cameras were placed as central to the grid cell as possible. We used 27-42 cameras/session in the Core Area.

We conducted 3 camera sessions annually in 1989 and 1990 (Table A.1). Cameras were used during the same 3 periods each year to coincide with seasonal changes in food selection (Mace and Jonkel 1986): Session 1 in late spring when grizzly bears consumed herbaceous vegetation, Session 2 in summer when bears ate globe huckleberries (*Vaccinium globulare*) and serviceberries (*Amelanchier alnifolia*), and Session 3 in autumn when bears ate herbaceous vegetation, roots, and large ungulates.

Equal masses of raw meat (wild ungulate or domestic livestock) and 4 L of livestock blood were placed as bait at each camera station. We used about 40 kg bait/station during the first 2 sessions and about 15 kg bait/station thereafter. Supplementary lures varied among sessions and included canned blueberries, anise or vanilla extract, and commercial skunk scent. Each station was arranged around 3 trees. The bait and lure were suspended on a steel cable between 2 trees about 6 m above the ground to disperse scent without providing a reward to bears. We secured the camera 3-3.5 m up a third tree and aimed it at the ground below the bait. To minimize human scent, stations were checked only 2-3 times during a session, and baits were removed at the end of each session.

We defined sampling effort/session (camera-nights) as the sum of all nights that cameras functioned. Sessions did not begin until all cameras were deployed.

Population Size and Density Estimation Methods

We defined the sampling unit as a bear independent of its mother (≥2 yrs old, except 1 orphaned yearling). To be counted as a sighting, photographs of the same individual at the same camera station had to be separated by an interval of >24 hours; however, the same bear could be photographed at ≥2 stations and be counted as separate sightings within the same 24-hour period.

We defined the sighting rate as the number of camera-nights/sighting. Photographs of marked grizzly bears were scrutinized to determine the number of sightings/individual for each session. We also determined which photographs of unmarked bears constituted valid sightings. Within each session, we often were able to distinguish individual unmarked bears by date and location. When several photographs of unmarked bears occurred at the same station on the same day, we used body size, color, and unique markings to differentiate individuals.

We calculated population size for each of the 6 sessions using 2 estimators of the Petersen 2-sample model (Seber 1982:59). During each session, n_1 marked bears were in the core area. A second sample of n_2 bears were sighted by camera, m_2 of which were marked. We first used Bailey's binomial model (Seber 1982:61) employing a bias correction factor to compensate for small sample size (Eberhardt 1990: eq 13). Estimates from this model use aggregated sightings and assume sightings are binomially distributed. The 95% confidence intervals (CI's) for this estimator ($\hat{N}_b$) were derived from the exact binomial values of the 95% CI of the sighting probability ($\hat{p} = m_2/n_2$) (Overton 1969, Seber 1982). The coefficient of variation (CV) of $\hat{N}_b$ was approximated by $1/m_2^{-.5}$ (Seber 1982:60-61). We calculated a second population estimate using the Monte Carlo simulation method (Minta and Mangel 1989), which simulates the sighting distribution of unmarked animals from the exact sighting frequencies of marked animals. Using 10,000 simulations/session, we derived a probability distribution and computed a maximum likelihood estimate ($\hat{N}_s$) and a 95% likelihood interval (abbreviated CI for consistency).

Testing Assumptions of the Petersen Model

The first assumption of the Petersen model is that the target population is geographically and demographically closed during sessions. Because marking was not done during a session, we could not statistically test for closure (Otis et al. 1978, White et al. 1982). Therefore, we used telemetry and cameras to assess closure during sessions using location and survival data obtained from marked grizzly bears. We located marked grizzly bears ≥3 times during each session; those individuals located in the core area ≥2 times and known to be alive throughout a session were considered the marked (n_1) sample.

We also assessed geographic closure during the entire 2-year study by constructing a composite home range and comparing capture and sighting rates obtained in the core and peripheral areas. We pooled the location data from 1989 and 1990 to construct 70% and 90% convex polygons (Ackerman et al. 1989). We used 770 aerial locations from individuals composing the n_1 sample during any of the 6 sessions. Polygons were constructed using 1 location/bear/week from den emergence to den entry.

When using the Petersen model, we assumed that marked bears did not lose their marks between the 2 sample periods, and that all marks were reported in the second sample. We used visual observation during telemetry flights and photographs to assess loss of marks.

We hypothesized that individual bears were not equally susceptible to baited camera stations. To evaluate sighting heterogeneity, we compared the distribution of empirical sightings with expected sightings derived from the parameters of the empirical distribution (Minta and Mangel 1989). Thus, expected sightings were generated by the binomial distribution function with $n = m_2$, $p = n_1^{-1}$, and $q = 1 - n_1^{-1}$. For each session, we also calculated the variance of the observed sightings (σ^2) and the expected binomial variance, $\sigma_b^2 = npq = m_2 n_1^{-1}(1 - n_1^{-1})$. Sample size permitting, we calculated a chi-square goodness-of-fit test for paired distributions. Cells with expected frequency classes <1 were grouped. Because of low frequencies, goodness-of-fit results and inferences should be interpreted as indicating trend only (Minta and Mangel 1989).

We compared density estimates (bears/100 km^2) of independent marked grizzly bears in the core area during each session to those derived from the binomial and simulation methods. We did not use the boundary strip method (Otis et al. 1978) because densities reflected only marked bears present in the core area each session.

RESULTS

Demography of Marked Grizzly Bears During Sessions

Twenty-seven grizzly bears were captured 52 times in the study area between 1988 and 1990. Three additional bears were captured in the core area at other times. We captured male and female grizzly bears of all age and gender classes except adult females with young. Adult females and their 2-year-olds were captured only after breakup of family groups. The number and demography of marked grizzly bears differed among sessions and between years because of mortality, egress, and additional captures in 1990. Between 12 and 17 marked bears were in the core area each session (Table A.1).

Assessment of Demographic and Geographic Closure

Several individuals living along the edge of the core area could readily enter or exit the photogrid. However, daily movements of grizzly bears during the 6 sessions averaged 1,569 m (SE = 197 m) (R. D. Mace, unpubl. data), suggesting that individuals moving outside the grid could reenter within 24 hours. There were no birth pulses during the sessions because grizzly bears gave birth during winter. No marked grizzly bears died within the core area during any session, and no human-caused mortalities of unmarked bears were recorded. For the purposes of this study, we considered the core area closed during the 9-18 days each session was conducted.

Geographic closure of the core area was further demonstrated by comparing snaring and sighting rates with the peripheral area. Twenty-six grizzly bears were captured 51 times in 3,711 snare-nights in the core area (1 capture/72.8 snare-nights). Conversely, only 1 grizzly bear was snared in the peripheral area in 1,563 snare-nights. We obtained 66 sightings in the core area in 2,334 camera-nights for a sighting rate of 1 sighting/35.4 camera-nights. Only 1 unmarked grizzly bear was photographed in the peripheral area in 1,249 camera-nights.

Telemetry information also indicated that the core area was important to marked animals throughout the 2-year study.

The 70% and 90% convex polygons showed that the marked population had a strong affinity for the core area during the 2-year period (Fig. A.1). Movements from the Core Area were primarily by males captured on the extreme edge of the area.

Photographic Sighting Rates

We obtained 729 photographs of marked (86%) and unmarked (14%) grizzly bears during the 6 sessions. Sixty-six (9%) photographs met our criteria

Table A.1. Sampling periods, sampling effort, population demography, and sighting rates of marked grizzly bears during 6 photographic sighting sessions in the Swan Mountains, Montana, 1989-1990.

Characteristics	1989 Sessions			1990 Sessions		
	1	2	3	1	2	3
Sampling period	9-17 Jul	22 Aug-4 Sep	6-17 Oct	11-22 Jul	17-30 Aug	27 Sep-14 Oct
Camera-nights	201	347	465	397	356	468
Cameras/100 km²	5.2	5.4	8.1	5.2	5.4	5.2
No. marked bears in core area						
Ad m	3	3	3	4	4	4
Ad f	2	3	3	7	7	7
Subad m	5	4	4	2	2	2
Subad f	1	0	0	1	2	2
Family group	3	2	2	2	2	2
Marked bears/100 km²	2.7	2.3	2.3	3.1	3.2	3.2
Bears sighted[a]	11 (6)	14 (8)	12 (4)	8 (4)	2 (1)	3 (2)
Sighting rate[b]	18.3	24.8	38.8	49.6	178.0	156.0

[a] Number of sightings of marked bears (no. individuals contributing to sighting).

[b] Camera-nights/marked bear sighting.

for a valid sighting. Sighting rates of marked bears varied among sessions from 178 during Session 2, 1990 to 18.3 during Session 1, 1989 (Table A.1). Marked adult males were sighted most frequently, and most marked adult males and subadult females were sighted (Table A.2).

Table A.2. Sighting rates of marked grizzly bear age and gender classes during photographic sessions in the Swan Mountain Range, Montana, 1989-1990.

	Year					
Age and Gender	1989		1990		Pooled	
Ad m	12.6[a]	4/4[b]	305.2	2/3	20.7	4/5
Ad f	101.3	2/3	407.0	1/7	139.6	2/7
Subad f	28.1	4/5	407.0	1/2	45.5	4/5
Subad m	506.5	1/1	1,221.0	1/2	558.5	2/4
Family group	1,013.0	1/3		0/2	2,234.0	1/4

[a] Camera-nights/marked bear sighting.

[b] Number of marked bears contributing to sighting rate/number of marked bears present in core area.

Estimation of Population Size and Density

Individual marked bears responded differently to camera stations, resulting in heterogeneous sightability (Table A.3). By comparing the 2 models we identified the heterogeneity and gauged its influence on population estimators.

During Session 1, 1989, the observed sighting distribution was similar to the expected distribution based on random binomial sightings ($X^2 = 3.39$, 3 df, $P = 0.34$). However, the variance ratio (observed sighting variance to binomial sighting variance; Table A.3) of 1.41 indicated a deviation from random sightability; some bears avoided the stations more than expected whereas others were attracted more than expected. The sighting distribution of Session 2, 1989 showed little deviation from expected values with the exception of 1 bear photographed 5 times. That bear contributed to the inflated variance (1.81) and accounted for 92% of the chi-square value ($X^2 = 19.22$, 5 df, $P = 0.002$). However, the small sample makes the test result suspect. Session 3, 1989 was similar to Session 1 except that 2 bears were strongly attracted to the stations, producing the highest variance ratio (3.09) of the study. As an indicator, those 2 bears accounted for 86% of the chi-square value ($X^2 = 54$, 5 df, $P < 0.001$).

Sighting rates were generally lower for 1990 sessions than for those during 1989. The lower number of sightings contributed to wider CI's compared with 1989 sessions. The variance ratio of 2.13 for Session 1, 1990 reflected the disproportionate attraction to, and avoidance of, stations. Two bears explained 84% of the chi-square value ($X^2 = 23.1$, 3 df, $P < 0.001$). Although estimates for Sessions 2 and 3, 1990 are displayed for comparison (Fig. A.2), sightings

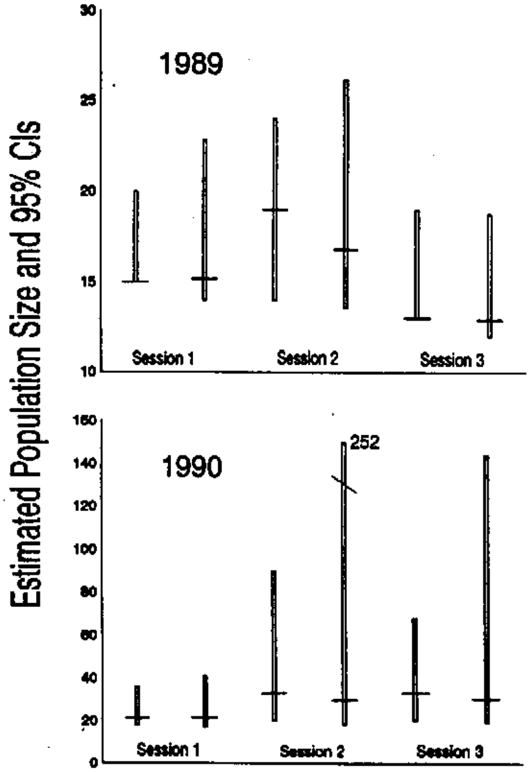

Figure A.2. Population estimate (horizontal bars) and 95% confidence intervals (vertical bars) of total grizzly bears in the core area using the Monte Carlo simulation (left bar) and Bailey's binomial (right bar) methods for each sighting session of 1989 and 1990, Swan Mountain Range, Montana.

Table A.3. Marking and sighting data and derived variables used in estimating confidence intervals, and degree of sighting heterogeneity for grizzly bears in the Swan Mountain Range, Montana, 1989-1990.

Year Session	Marked core area n_1	Number sightings n_2	Number sightings marked m_2	Sighting probability $\hat{p} = m_2/n_2$	CV of N[a]	Observed sighting variance[b]	Binomial sighting variance[c]	Sighting distribution of n_1 bears[d]					
								0	1	2	3	4	5
1989													
1	14	12	11	0.92	0.30	1.03	0.73	8	2	3	1		
								6.2	5.2	2.0	0.5	0.1	0.0
2	12	20	14	0.70	1.07	1.81	1.07	4	5	2			1
								3.5	4.5	2.7	1.0	0.2	0.0
3	12	13	12	0.92	0.92	2.83	0.92	8	1	1		1	1
								4.2	4.6	2.3	0.7	0.1	0.0
1990													
1	16	11	8	0.73	0.47	1.00	0.47	12	2		2		
								9.5	5.1	1.2	0.2	0.0	
2	17	4	2	0.50	0.11	0.22	0.11	16		1			
								15.	1.9	0.1	0.0		
3	17	6	3	0.50	0.17	0.26	0.17	15	1	1			
								14.	2.7	0.2	0.0		

[a] Approximate coefficient of variation of Bailey's binomial estimator.

[b] Calculated from sighting distribution of the n_1 marked bears.

[c] Calculated as npq = $m_2 n_1^{-1} (1-n_1^{-1})$.

[d] Shows how many times marked bears were sighted. For example, during Session 1 of 1989, 8 different marked bears were never sighted (0 category), 2 were sighted once, 3 were sighted twice, and 1 was sighted 3 times. If those 14 bears had been sighted randomly, their sightings would be binomially partitioned, as shown beneath the observed distribution.

were too infrequent for valid population estimates.

We conclude that the simulation method produced inherently less biased population estimates and CI's compared with the binomial model because it simulates the exact form of the sighting heterogeneity.

The density of marked grizzly bears in the core area during most sessions (Table A1) were comparable to those derived from the simulation method. The minimum densities derived from marked bears during 1989 sessions varied from 2.3-2.7 bears/100 km^2 (Table A.1). Using the simulation results and associated 95% CI, density estimates for the 3 sessions in 1989 were: Session 1 ($2.9 \leq 2.9 \leq 3.9$), Session 2 ($2.7 \leq 3.7 \leq 4.6$), Session 3 ($2.5 \leq 2.5 \leq 3.7$). The same comparison for Session 1 of 1990 showed a minimum known estimate of 3.1-3.2 marked bears/100 km^2, and simulation results of $3.5 \leq 4.1 \leq 7.0$.

DISCUSSION

We used 4 criteria to judge the utility of cameras for sighting grizzly bears in forested habitats: how severely were model assumptions violated? were adequate photographic sample sizes obtained and estimators credible? was the camera method logistically and financially practical? was our design an improvement over other methods?

Assessment of Model Assumptions

Natural barriers surrounding the study area helped confine grizzly bear movement during sessions. Snaring, camera, telemetry, and survival data provided compelling evidence of demographic and geographic closure during camera sampling.

For closed population models, we assumed that: all animals have the same probability of being caught in the first sample, initial capture does not affect future catchability, and the second sample is a simple random sample. The Petersen model is robust to departures from these assumptions when a systematic rather than a random second sample is taken, and by assuming the catchabilities in the 2 samples are independent (Seber 1982, Minta and Mangel 1989, Arnason et al. 1991). Our use of systematically deployed snares and cameras reduced violations of these assumptions.

Our fundamental sampling problem was unequal catchability during capture and sighting sessions. Any population is likely to contain an uncatchable portion and an unequal probability of capture for different cohorts in the first capture. In our study, family groups were the least catchable and sightable class of bear. However, because the initial captures were conducted for 3 years, members of family groups that were uncatchable during 1 year were eventually caught as independent animals. Initial snaring may have affected subsequent sightability with cameras; although both relied on baits, the lures and the amount of human scent present differed, and only snares involved physical restraint. To some degree, these subtle variations in design reduced bias from unequal catchability and sightability (Seber 1982:86).

Sighting rates varied among sessions and between years. We believe the attractiveness of baits to grizzly bears was correlated with seasonal availability of preferred foods. Marked bears moved less during the globe huckleberry season (Session 2) than other seasons. This berry crop was judged to be poor in 1989 and grizzly bears were photographed easily. Conversely, an especially good huckleberry crop occurred during 1990; bears moved less, and the sighting rate was low. We obtained low sighting rates during Session 3 of both years because some bears were preparing winter dens, and freezing temperatures and snow reduced the effectiveness of baits.

By using photographs and visual observation during telemetry flights, we verified that bears did not lose their marks between marking and sighting. The assumption that all marks are reported on sighting in the second sample was subject to error. Although some sightings may have been missed if bears quickly moved beyond the photographic zone before the camera fired, we had no difficulties determining whether an individual was marked, and we identified all individuals by unique ear streamers.

Photographic Sample Sizes and Estimators

Seber (1982:564-565) concluded that the Petersen model seems to be the most useful method, provided assumptions are satisfied and sufficient recaptures in the second sample are obtained. The binomial model uses only the total number of marked and unmarked bear sightings. Conversely, the simulation method uses the sighting frequencies of marked individuals, thereby accommodating small sample sizes and sighting heterogeneity. Sighting probabilities were high (0.50-0.92), and the estimates derived from the simulation method were based on adequate sample sizes and produced credible estimates.

Comparisons with Other Approaches

We did not compare the camera method with other sighting methods and we did not know the actual bear density. We know of no method to derive an estimator of precision for population estimates based on capture intensity or telemetry. In forested habitats, few grizzly bear studies have reported point estimates with associated measures of statistical confidence (Harris 1986, IGBC 1987). More commonly reported are density estimates without error terms, derived from the number of known grizzly bears in a given area (Martinka 1974, McLellan 1989a). We know of only 1 capture-recapture study using physical recaptures (Hornocker 1962) and the small study area, small sample sizes, and selective capture methods were likely problematic (IGBC 1987). Using observation data from 6 garbage dumps in Yellowstone National Park, Craighead et al. (1973) reported that estimates derived from both Petersen and Schnabel methods were comparable to their estimate from direct counts. Unfortunately, computations or results were not documented, details were lacking, and assumptions were ignored (Harris 1986, IGBC 1987). Open population models require large samples and multiple capture periods. We know of none that has been successfully applied to grizzly bears in forested areas. Roop (1980) violated open model requirements that trapping effort be evenly distributed in space and time.

MANAGEMENT RECOMMENDATIONS

Eighty-six percent of 729 photographs were of marked animals. Without this marked sample, we could not have differentiated individuals with enough certainty to meet the assumptions of mark loss and mark reporting. Radiotelemetry also was necessary to evaluate closure. Consequently, there was no evidence suggesting that the technique could be used for grizzly bears without a marked sample.

Because independent methods of initial capture and sighting are desirable, initial capture should use the most effective means for maximizing the marked sample. For grizzly bears in forested habitats, we recommend placing at least 2 snares at each site and varying capture and baiting methods among years. At least 25% of the population (subjective estimate) should be captured, and >50% is preferred. Capture and marking should be done for 3 years to attain a representative sample of adult females and 2-year olds. We recommend 1 camera session be conducted each year and that stations be placed systematically or randomly each session. The session should be conducted when attractants are not in competition with highly preferred foods. We recommend inverse sampling (Seber 1982:118) where a session is continued until a prescribed number of marked bears are sighted. At some point the assumption of closure would likely be violated and cost may become prohibitive. For our study, annual labor and logistical support cost about $20,000 and $14,000/snaring and camera session respectively.

Our camera method offers several advantages over existing sighting techniques. A large study area can be systematically sampled in a relatively brief period, all bears in the population are simultaneously and continuously detectable, and physical capture is unnecessary. These conditions allow better conformance to model assumptions, and are likely to produce larger samples.

Behavioral characteristics of grizzly bears in forested habitats make estimating population size inherently problematic despite improvements in models and field methods. Techniques such as our camera method combined with telemetry may increase sample size and reduce some model biases, but unequal catchability and sightability remain intractable. Use of different capture methods over several years will reduce intrinsic capture heterogeneity.

A completely independent sighting method would eliminate behavioral "trap" response and relax other model assumptions. This cannot be achieved if attractants are used for both marking and sighting. Detecting grizzly bears either randomly or systematically in forested habitats without attractants is very difficult, although an alternative is to tag bears with radioisotopes and then collect scats (this has not been applied to grizzly bears). Other advances in marking and sighting models (e.g. Arnason et al. 1991) may prove helpful.

SUMMARY

Grizzly bear population size in forested habitats is difficult to estimate, and few studies report point estimates with associated measures of statistical confidence. Experimental designs suffer from logistical problems, model biases, and small sample sizes. We describe a capture-sighting design applicable to forested areas where direct observation of bears is difficult. We reduced bias and increased sample size by using snares for the initial marking period and automatic cameras for the second sample. Capture heterogeneity during the initial marking period was reduced by snaring 27 grizzly bears during 3 years in the same study area in western Montana. Cameras recorded adequate sightings (11-20) in 4 of 6 sessions. Monte Carlo simulation adjusted for severe sighting heterogeneity among marked bears, producing 6 seasonal density estimates and 95% confidence intervals (CI's) ranging from $2.5 \leq 2.5 \leq 3.7$ to $3.5 \leq 4.1 \leq 6.7$ bears/100 km^2. Sighting rates varied considerably (18-178 camera-nights/sighting), but were generally highest during spring when attractants were more effective. Advantages of our camera method over existing sighting techniques included the ability to sample a large area in a brief period, all individuals are simultaneously detectable, and physical capture is unnecessary. These conditions allowed better conformance to model assumptions.

APPENDIX B

FACTORS AFFECTING THE PHOTOGRAPHIC DETECTION RATE OF GRIZZLY BEARS IN THE SWAN MOUNTAINS, MONTANA[1]

R. D. Mace, T. L. Manley, and K. E. Aune

ABSTRACT: Seven seasonal population estimates were derived from 1989 to 1991 for grizzly bears (*Ursus arctos horribilis*) in the Swan Mountains of western Montana using a capture/recapture model for closed populations. Mace et al. (1994) discussed in detail the study design and population modeling procedures which used systematic snaring for initial capture and self-activating cameras for recapture. Twenty-one marked grizzly bears within the camera grids formed the foundation for recapture analysis. We generated 27 photographic records of detections and 71 non-detections in 7 photo sessions. On average, the marked population we sampled was dominated by adult female (29.5%) and adult male (22.6%) grizzly bears. Nearly an equal number of male and female bears were detected on film, but the non-detection sample was skewed towards females (73.3%). Adult males were more frequently detected than adult females or females with young. Most detections (66.6%) were of bears with a prior history of detection. Adult males moved greater distances and consequently encountered more camera stations than other age/gender classes. Generally, movements for all age/gender classes were greatest during the spring and decreased thereafter. When the 7 photo sessions were pooled, it was shown that grizzly bears were not exposed to many camera stations (x = 1.6, SD = 1.8) and bears we successfully detected were confronted with significantly more stations (x = 2.30, SD = 2.3) than those we failed to detect (x = 1.30, SD = 1.44). Logistic regression showed that detections decreased over time. We concluded that differential movement patterns among age/gender classes played an exceedingly important role in photographic detection. The precision of population estimates could be improved by grid densities >5-8 camera station/100 km^2 for grizzly bear populations with similar age/gender structure. Recommendations to increase and sustain precision of population estimates using cameras are provided.

INTRODUCTION

Grizzly bear population size is notoriously difficult to enumerate for biological and logistical reasons (Harris 1986). However, recent advances using portable, self-activating cameras (Mace et al. 1994) to resight (recapture) grizzly bears demonstrated that meaningful population estimates can be derived in mountainous habitats. Systematic grid snaring was used for initial capture and systematically deployed cameras were used for resightings. Mace et al. (1994) evaluated accuracy and bias of several closed population models using resighting data from 6 camera sessions and concluded that Monte Carlo procedures provided an accurate measure of population size.

In this paper, we evaluate the effects of several biological factors on photographic detection. Specifically we evaluate detection in terms of each bears' gender, age-class, reproductive status, history of photographic resighting, average distance moved during photo sessions, and the number of cameras available per individual.

METHODS

Capture, Recapture, and Telemetry Procedures

Grizzly bears were initially captured during the spring of 1988-91 using leg-hold snares placed in a systematic grid (Mace at al. 1994). Captured bears were immobilized with either titelamine with zolazepam or ketamine with xylazine. Each bear was fitted with ear-tags and 2 unique 16.5 cm by 5 cm Armortite ear streamers for recognition in photographs. Ages were determined by cementum analysis (Stoneberg and Jonkel 1966). Individual grizzly bears >1 year old were fitted with tempo-

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[1] Mace, R. D., T. L. Manley, and K. E. Aune. 1994. Factors affecting the photographic detection rate of grizzly bears in the Swan Mountains, Montana. Int. Conf. Bear Res. and Manage. 245-251.

rary radio collars (Telonics, Mesa AZ) utilizing a cotton spacer for long-term bear safety (Hellgren et al. 1988). One independent yearling was instrumented as well.

Grizzly bears were photographically detected using self-activating camera units (Mace et al. 1994). Each unit consisted of a 35 mm camera with flash, a passive infrared sensor, and a 12-volt battery. Thirty-six exposure print film was used.

We conducted 7 sampling periods between 1989 and 1991 using a systematic design at grid densities of between 5 and 8 cameras/100 km^2. Three photo sessions per year were conducted in 1989 and 1990, and one spring session was conducted in 1991. The spring session each year occurred when grizzly bears were generally consuming herbaceous vegetation and carrion. We again deployed cameras during the height of the berry season when grizzly bears were foraging on the fruit of globe huckleberry (*Vaccinium globulare*) and serviceberry (*Amelanchier alnifolia*). Cameras were again deployed in the autumn after most berry foraging had ceased and bears were again consuming vegetation and some large mammals. Naive population density estimates for marked bears varied between 2.3 - 3.29 independent grizzly bears/100 km^2 during each sampling period.

The grizzly bear population was photographically sampled at similar times each year (Table B.1). Attractant baits were weighed to ensure consistency among photo stations. Additional lures were used at each photo station and varied among sessions and years (Table B.1). Sampling effort per photo station, termed "station grid-nights" was defined as the sum of all portions of a 24-hour day that a photo station was functional during the period when all other stations were deployed. Station grid-nights were then summed to give a total for the entire photo session.

Each photo station was composed of 3 trees forming a triangular pattern. The attractant bait was hung between 2 trees and the camera unit was secured approximately 3.5 m up the third tree and aimed at the ground below the bait. Cameras were deployed and monitored by foot, all-terrain vehicle, truck, and a Hughes 500 helicopter; visits to stations were minimized.

As weather permitted, we obtained a minimum of 3 aerial telemetry locations on each bear during each session using a Cessna 180 or 182. Bear location and photo station UTM coordinates were entered into the computer-aided graphics program SURFER (Golden Software Inc.) for spacial analyses.

Analysis Procedures

Twenty-one marked grizzly bears provided photographic information for all or a portion of 7 photo sessions. Each individual was classified as either being photographically detected or not during each session. An individual was termed "detected" if it was photographed at least once during a photo session. Grizzly bears were considered to be within a grid and available for detection if >50% of each bears' locations during a photo session was within the boundary of the grid area. Photographic detections were evaluated for each bear and session. Bears were classified by gender and age-class. Adults were those reproductively mature animals ≥ 5 years old with the exception of one 3

Table B.1. Camera deployment dates and lures used to detect grizzly bears in the Swan Mountains, Montana, 1989-91.

Session number	Session dates	Number cameras	Grid nights	Weight of bait kg[a]	Lure[b]
1	9 Jul-17 Jul, 1989	27	201	43	1
2	22 Aug-4 Sept, 1989	28	347	41	1
3	6 Oct-17 Oct, 1989	40	465	15	2
4	11 Jul-22 Jul,1990	27	397	15	3
5	17 Aug-30 Aug,1990	28	356	15	4
6	27 Sep-14 Oct,1990	27	468	15	5
7	19 Jun-21 Jul,1991	29	725	15	2

[a] domestic or wild ungulate meat

[b] 1: blueberries and 3.7 liters of livestock blood
2: blood only
3: blood and anise extract
4: blood and vanilla extract
5: blood and "Canine Call" (commercial skunk scent)

year old female. Subadults were independent animals 2-4 years old but included one weaned yearling. Bears were classified as moving through the environment either alone or as a family group. Family groups were classified as a single unit in terms of photo detection as offspring did not move independently of their mother.

Prior history of photographic resighting was used to separate those individuals who had been detected during previous sessions from those who had not. This variable was not applied to multiple resightings within a photo session. The first photo session (1-1989) was deleted from this analysis as there were no prior sessions.

Some grizzly bears learned to chew the rope suspending the attractant bait and were consequently rewarded. For each photo session we classified each bear as having been rewarded during previous sessions or not.

The number of photo stations potentially available to each grizzly bear during a session was estimated. Convex polygons were constructed from aerial telemetry locations and from photo station coordinates where bears were successfully photographed. To increase the number of location points per bear, and to more accurately evaluate the spacial relationship between bear and photo grid, we included telemetry locations ± 10 days from the inclusive grid dates. When possible, we developed convex polygons for marked grizzly bears not wearing functional radio transmitters if they visited at least 3 photo stations. For those non-radioed bears photographed at <3 stations, we used the number of stations where they were detected.

The number of cameras available to each bear also depended on the performance of cameras. Performance problems occurred because of mechanical failure, harsh site conditions, inclimate weather, and interference by other species of wildlife. Therefore it was possible that grizzly bears visited some baited stations when cameras were not functioning or all frames were exposed from other causes. As a correction factor, we eliminated 12 of 207 (5.7%) photo stations that functioned <50% of the time.

Average daily movements (ADM) in meters were generated for each bear and session using distance measurements derived from consecutive aerial telemetry data. Average ADM's were then derived for each age/gender class for each photo session.

Contingency data were evaluated using Pearsons X^2 with the Yates correction for small samples (Sokal and Rohlf 1969). The variables ADM and number of cameras available were compared among 5 age/gender classes using Mann-Whitney (MW), Kruskal-Wallis (KW), and KW one-way analysis of variance procedures. Logistic regression was used to evaluate the frequency of detection through time. We selected a maximum likelihood probit estimation procedure (Agresti 1990) using the software package SYSTAT (Systat Inc. 1988).

RESULTS

The grizzly bear population we sampled 7 times with cameras was dominated by adults (x = 71.4%) (Table B.2). Adult females (x = 29.5%) and

Table B.2. Summary of population characteristics for marked grizzly bears sampled through photography, Swan Mountains, Montana.

Age/gender class	Number of marked grizzly bears in each of 7 photo sessions							Av.	Av. %
	1	2	3	4	5	6	7		
Adult	9	10	8	11	11	11	10	10.0	74.1
Subadult	5	2	2	5	6	6	2	4.0	28.6
Male	4	4	3	5	6	6	4	4.6	33.0
Female	10	8	7	11	11	11	8	9.4	67.0
Adult male	3	4	3	3	3	3	3	3.1	22.6
Adult female	3	4	3	6	6	6	1	4.1	29.5
Family group	3	2	2	2	2	2	6	2.7	19.4
Subadult male 1	0	0	2	3	3	1	1.4	10.1	
Subadult female	4	2	2	3	3	3	1	2.6	18.7

adult males (x = 22.6%) were the most prevalent age/gender classes. Relatively few subadult males were present in the population and an average of 19.4% of the population was family groups.

The 21 individual grizzly bears generated 27 (27.5%) records of photographic detection and 71 (72.5%) records of non-detection from the 7 photo sessions. Fifty-seven percent of the original marked population (from session 1) was still alive or within the core study area by Session 7.

Seventy percent and 72% of the detections and non-detections, respectively, were of adult animals (Table B.3). Therefore, we rejected the null hypothesis that photographic detection was independent of the frequency of adult and subadults in the population (X^2 = 0.00, 1 df, P = 1.0). Male and female grizzly bears were almost equally represented in the sample of photographic detections (Table B.3), although most (73.2%) of the non-detections were female bears. The null hypothesis that frequency of detection was independent of gender was not significant (X^2 = 3.15, 1 df, P = 0.076).

We rejected the null hypothesis that frequency of detection was independent of the 5 age/gender classes (X^2 = 9.601, 4 df, P = 0.048). However, only one of 10 age/gender subsets was significantly different (Table B.3). The frequencies of detection between adult males and adult females were significant (X^2 = 3.607, 1 df, P = 0.058) and frequency differences between adult males and family groups were significant (X^2 = 5.627, 1 df, P = 0.002).

Eighty-one percent of the 98 photographs were of solitary animals, and these independent individuals comprised the majority (92.6%) of the detection sample. In only 2 of 19 (10.5%) cases were family groups detected. The hypothesis that frequency of resighting was independent of unit status was not rejected (X^2 = 2.446, 1 df, P = 0.118).

We assessed the relationship between prior history of detection and its effect on detection during later sessions (omitting session 1-1989). Most of the 21 detections (66.6%) were of bears who had been photographed before. However, previous detection did not ensure that grizzly bears would continue to be detected, as 47.6% of the records showed that bears with prior detections were not photographed (X^2 = 1.591, 1 df, P = 0.207). In most instances, grizzly bears were unsuccessful in actually obtaining the hanging bait (85 of 98 cases, 86.7%). However, those bears with a history of reward were more likely to be detected during a later session than not (69.2%).

Adult males moved greater distances (n = 17, x = 2,092 m, SD = 1,347 m) during the photo sessions than other age/gender classes (Table B.4). Family groups moved the least (n = 18, x = 942 m, SD = 346 m). The KW-ANOVA suggested that variation in the distance moved varied among the 5 age/gender classes (F-ratio = 5.941, 4 df, P = 0.000). Adult males moved farther than solitary adult females (MW-U = 376.0, 1 df , P = 0.001), subadult females (MW-U = 236.0, 1 df, P = 0.006), and family groups (MW-U = 272.0, 1 df, P = 0.001). With the exception of sub-

Table B.3. Summary of contingency data regarding the age/gender of marked grizzly bears and frequency of photographic detection (n=27 detections and 71 non-detections). Swan Mountains, Montana.

Age/gender class	Number of cases		%detected	Significant x^2 test[a]
	Detected	Not detected		
Adult	19	51	27.1	
Subadult	8	20	28.6	
Male	13	19	40.6	
Female	14	52	21.2	
Adult male	11	11	50.0	a b
Adult female	6	23	20.7	a
Family group	2	17	10.5	a b
Subadult male	2	8	20.0	a
Subadult female	6	12	33.3	a

[a] Those age/gender classes with the same letter were significantly different in frequency of detection and non-detection using the x^2 test with $p< 0.05$.

Table B.4. Seasonal average daily movements (m) of marked grizzly bear during photo sessions (n, mean, SD) in the Swan Mountains, Montana.

Season	Average daily movement by age/gender class				
	Adult male	Adult female	Subadult male	Subadult female	Family group
Spring	8	10	4	8	10
	2352	1157	1188	1354	1003
	1960	334	613	475	283
Summer	5	10	3	5	4
	1920	741	1840	1352	964
	294	548	1335	670	560
Autumn	4	8	3	5	4
	1786.	736	1007	653	769
	502.	717	385	308	269
Total	17	28	10	18	18
	2092	1042	1329	1159	942
	1347	665	827	570	346

adult males which showed a slight increase in ADM between spring and summer, other age/gender class decreased their movements as the active season progressed. ADM's for spring, summer, and autumn using all bears were 1,537 m (SD = 1,020 m), 1228 m (SD = 775 m), and 894 m (SD = 615 m) respectively. When age/gender classes were pooled for each season, seasonal movements were significantly different (KW = 9.153, 2 df, P = 0.01).

The five age/gender classes were exposed to variable number of photo stations (Table B.5) and the null hypothesis that numbers of cameras available to each class were equal was rejected (KW = 11.55, 4 df, P = 0.021). Adult males were exposed to more cameras than adult females (MW-U = 358.0, 1 df, P = 0.029), than family groups (MW-U = 342.0, 1 df, P = 0.000), and subadult females (MW-U = 317.0, 1 df, P = 0.001).

Table B.5. The number of camera stations within grizzly bear convex polygons in the Swan Mountains, Montana.

Number cameras per polygon	Age/gender class				
	Adult male	Adult female	Subadult male	Subadult female	Family group
n	18	28	10	19	19
minimum	0	0	0	0	0
maximum	9	10	6	2	3
mean	2.7	1.4	1.9	1.0	0.9
SD	2.4	2.0	1.9	0.7	0.8
Signficant[a]	a	a	a	a	a
	b	b			
	c			c	
	d				d

[a] Those age/gender classes with the same letter were significantly different using the MW-U test with $p < 0.05$.

Male grizzly bears were exposed to more (n = 28, x = 2.4, SD = 2.3) camera stations than females (n = 66, x = 1.2, SD = 1.40) and differences were significant (MW-U = 560.0, 1 df, P = 0.002). Adults were not exposed to more stations (n = 65, x = 1.6, SD = 1.9) than subadults (n = 29, x = 1.4, SD = 1.28)(MW-U = 877.0, 1 df, P = 0.767). Solitary bears also were not exposed to more stations (n = 75, x = 1.6, SD = 1.7) than family groups (n = 19, x = 1.3, SD = 1.9) (MW-U = 540.0, 1 df , P = 0.10). Overall, grizzly bears in our study were not exposed to many camera stations (n = 93, x = 1.60, SD = 1.80) and in 21.5% of the cases had no cameras within their polygons. In 94% of the cases, bears had <4 cameras within their polygon.

Grizzly bears detected by camera were confronted with more camera stations (n = 27, x = 2.30, SD = 2.3) than bears we failed to detect (n = 71, x = 1.27, SD = 1.44) and these differences were significant (MW-U = 588.0, 1 df, P = 0.007).

The proportion of the marked grizzly bear population successfully detected decreased over time (photo sessions) even though new bears were added to the marked sample each year. Although there were some changes in the demographics of the focal population, bears were exposed to similar number of cameras each session (KW = 4.389, 6 df, P = 0.624). The MLE logistic regression showed a loss function of -0.250 for detections of marked grizzly bears. The estimated proportion of marked bears detected per session decreased from approximately 54% during photo session one, to 8% during session 7 (Fig. B.1).

DISCUSSION

Several, often compounding sources of bias are common to all capture/recapture experiments with wildlife. These include behavioral responses, heterogeneity in the response of individuals to capture/recapture methods, and the effect of time (White et al. 1982). These biases are especially acute and difficult to measure for grizzly bears because of inherently low capture and recapture sample sizes. Coupled with the difficult terrain this species inhabits, it is no surprise that population estimates and measures of bias for grizzly bear populations are rarely obtained. We attempted to learn, as quickly as possible, the effectiveness of self-activating cameras for recapturing grizzly bears and sampled the same population 7 times in 3 years. Using cameras to recapture grizzly bears had several advantages over other recapture techniques such

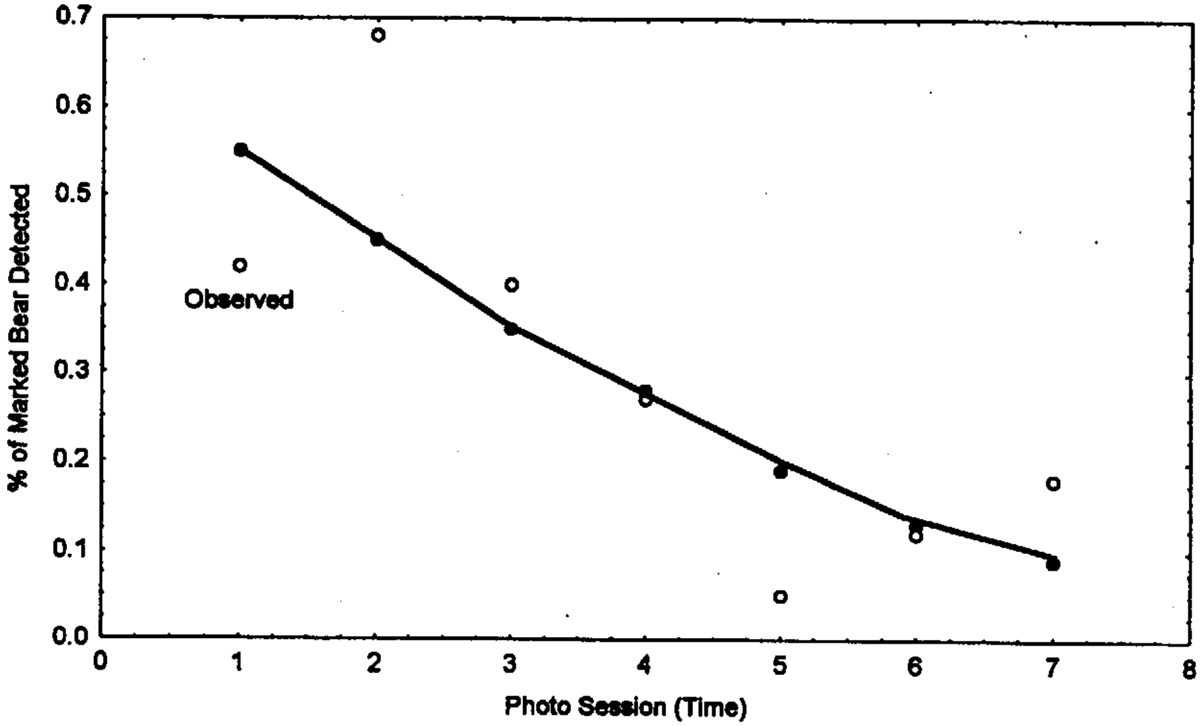

Figure B.1. Results of logistic regression showing decline in frequency of photographic detection of grizzly bears over 7 photo sessions, Swan Mountains, Montana.

as snares (Mace et al. 1994). First, the assumptions of closed population modeling can be more easily met by maximizing coverage of an area with cameras over a short period when population demographics are stable (e.g. no death, immigration). The shorter duration a sampling session is conducted, the more likely critical assumptions will be met. Second, bias due to catchability can be reduced through the use of an alternative recapture technique (Seber 1982), in this case cameras. Third, bias due to human odor and presence is minimized. Fourth, no physical restraint of bears is necessary, eliminating possible injury or death to bears from handling.

It was our intent to isolate those factors affecting photographic detection. Perhaps the greatest surprise to us was the low number ($x = 1.60$) of cameras available to individual grizzly bears given an ADM of over 1000 m for all age/gender classes. In 21.5% of the cases grizzly bears moved within either the synusia or along the periphery of photo grids and were unavailable for detection. These estimates of camera numbers within polygons were optimistic because we included locations ± 10 days surrounding the grid deployment dates. Our use of camera grid densities of between 5 and 8 cameras/ 100 km^2 obviously did not maximize the opportunity for grizzly bears to locate the baited photo stations. We believe that much of the variation in photographic detection among age/gender classes was explained by relationships between ADM and camera grid densities. Increasing the density of cameras within the sampling area would probably increase detection rates.

Male and female grizzly bears were nearly equally represented in the photographic detection sample, but far more of the non-detections were of female bears because females on average moved less and consequently encountered fewer photo stations. The frequency of detection varied significantly among age/gender classes. Adult males were resighted more often than adult females and females with young. Subadult females and males appeared to be detected in proportion to their presence in the population. We believe that detection frequencies would differ among populations with different demographics, densities, and movement patterns.

Mace et al. (1994) discussed several other factors which appear to influence photographic detection. During the summer, better detection of grizzly bears occurred when the globe huckleberry crop was poor and bear movements increased. The author's also cautioned that late autumn sampling was negatively influenced by snow, freezing temperatures, or pre-hibernation lethargy (Nelson et al. 1983).

We believe that both marked and unmarked grizzly bears were confronted with a novel technique during the early photo sessions and that interest in the baited sites decreased as more sessions were conducted. To date, we relied on olfactory cues to attract bears to the photo stations. However, there are other alternatives such as auditory stimuli (e.g. predator or fawn calls) that may prove equally effective. We believe that a long-term program to estimate population size would benefit by presenting bears with a variety of attractants. If the chosen capture/recapture model allows for unequal recapture probabilities, rewarding bears with some bait may help retain adequate photo detection rates over time. Furthermore, we believe that population monitoring programs would benefit by deploying cameras less frequently than described here (e.g. once per year).

APPENDIX C

COMPARISON OF TWO CAPTURE-RESIGHTING METHODS TO ESTIMATE GRIZZLY BEAR POPULATION SIZE USING CAMERAS

R. D. Mace and J. S. Waller

INTRODUCTION

Cameras have been used to monitor aspects of wildlife ecology and behavior for many years (e.g. Shiras 1913, Dodge and Snyder 1960, Cowardin and Ashe 1965, Temple 1972, Montalbano et al. 1985). However, few efforts have used cameras as a resighting tool for formal estimates of wildlife population size. For grizzly bears (*Ursus arctos h.*), estimates of population size with confidence limits are rare because of behavioral, logistical, and financial constraints (Miller 1990, Mace et al. 1994). Estimating population size in heavily forested and mountainous habitats has proven problematic (Mattson et al. 1996).

One objective of our research on grizzly bears in the Swan Mountains was to evaluate self-activating cameras as a resighting tool to estimate annual population size. Our capture, resighting, analysis, and an early critique of the technique were described by Mace et al. 1994a, 1994b. Our purpose here is to further evaluate the capture-resighting program with an additional 5 years of data, and to compare several population estimates to the minimum number of individuals known to be present each year.

METHODS

Grizzly bears were systematically and opportunistically captured from 1987 through 1995. Effort to capture grizzly bears was expended in both the Core and Peripheral Areas. In 1988 and 1989 we superimposed a 3.2-km capture grid over the entire study area to identify snare sites (Mace et al. 1994). From 1990 to 1995, most capture effort was concentrated in the Core Area.

Population Size Estimators

General Procedures. Capture and resight (or recapture, sighting) methods were used to estimate population size each year. Estimates were based on the photographic sighting of marked and unmarked grizzly bears during annual photographic sessions. Population estimates were obtained during late spring based on recommended sampling procedures by Mace et al. (1994) (Table C.1).

We placed cameras systematically in the Core and Peripheral areas in 1989 and 1990, and in the Core Area only after 1990 using a 1.6-km grid that changed each year. Details of the camera system, use of attractants, and other sampling protocols were given by Mace et al. (1994).

We defined sampling effort/session (camera-nights) as the sum of all nights that cameras functioned. Sessions did not begin until all cameras were deployed.

We defined the sampling unit as a bear independent of its mother (>2 yrs old, except 2 lone yearlings). Photographs of the same individual at the same camera station had to be separated by an interval of >24 hours. We defined the sighting rate as the number of camera-nights/sighting. Photographs of marked and unmarked grizzly bears were scrutinized to determine the number of sightings/individual for each session.

We delineated the area sampled with cameras each year by constructing 100% convex polygons from camera UTM coordinates each year. We then applied a buffer strip to each polygon representing the average daily movement (m) of grizzly bears during the sampling period. We used the average daily distance moved during July as derived from telemetry data. These movement data varied by class. Adult males averaged 6,577 m/day (n = 120, sd = 22,362) and subadult females averaged 1,066 m/day (n 109, sd = 1,081) during July. Subadult males (n = 77, x = 1,322, sd = 1,332), lone adult females (n = 130, x = 1,193, sd = 1,183) and family groups (n = 130, x = 1,131, sd = 1,129) were intermediate. For the buffer, we excluded adult male data and obtained an average daily movement buffer of 1,167 m. We used telemetry and cameras to assess closure during sessions using location and survival data obtained from marked grizzly bears. We located marked and radioed grizzly bears during each session; those individuals located in the buffered camera polygon at least half the time and known to be alive throughout a session were considered the marked (n_1) sample. Geographic closure was further assumed using composite home range data reported by Mace et al. (1994). We used visual observation during telemetry flights and photographs to assess loss of marks.

Analysis Procedures. We calculated population size each year using 2 estimators of the Petersen 2-sample model (Seber 1982:59). During each session, n_1 marked bears were in the buffered camera polygon. A second sample of n_2 bears were sighted by camera, m_2 of which were marked. We calculated population estimate using the Monte Carlo simulation method (Minta and Mangel 1989) using the NOREMARK software (White 1996), which simulated the sighting distribution of unmarked animals from the exact sighting frequencies of marked animals. Using 10,000 simulations/session, we derived a probability distribution and computed a maximum likelihood estimate (s) and a 95% likelihood interval (CI).

A second estimate of population size each year was obtained using the simple "Petersen Estimate." Rather than using the number of camera sightings, as was done in the Monte Carlo estimates, we determined the number of marked and unmarked individuals photographed. Population estimates (N^*)and their variances (v^*) were obtained using the following formulas from (Seber 1982:60):

$$N^* = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

$$v^* = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)}$$

RESULTS

Estimates of Local Population Size and Density

Sighting effort each year varied from 287-725 camera-nights ($\bar{x}$ = 555, sd = 143.2) within buffered camera station polygons (Table C.1). We sampled greater than 600 km² of habitat each year, and the density of marked grizzly bears present also varied among years ($\bar{x}$ = 1.7 bears/100 km², SD = 0.30). No marked bears died, and no human-caused mortalities of unmarked bears were recorded during camera sessions.

Monte Carlo Estimates. Camera sighting rates of marked grizzly bears varied by class and year (Table C.2). Adult males exhibited the highest sighting rate ($\bar{x}$ = 194 camera-nights/sight) and family groups the lowest ($\bar{x}$ = 1,944 camera-nights/sighting) of all classes. Sighting rates were

Table C.1. Sampling periods, sampling effort, population demography,and sighting rates of marked grizzly bears during 7 annual sighting sessions in the Swan Mountain Range, Montana.

Characteristics	Year						
	89	90	91	92	93	94	95
Sampling Period	9-17 Jul	12-28 Jul	19 Jun-19 Jul	2-19 Jul	10-30 Jul	7-14 Jul	29 Jun-25 Jul
Camera grid polygon size (km²)	845	845	722	719	658	768	628
Camera-nights	287	653	725	464	571	569	619
Cameras/100 km²	4.1	5.2	3.9	4.0	4.9	4.7	4.8
No. marked bears in grid Polygon:							
Adult male	3	3	1	2	2	3	3
Adult female	3	4	1	1	5	3	0
Subadult male	2	4	1	1	1	0	0
Subadult female	4	2	2	3	4	3	3
Family group	2	3	5	3	2	3	3
Marked bears/100 km ²	1.7	1.9	1.4	1.4	2.1	1.6	2.1

Table C.2. Sighting rates of marked grizzly bear age and gender classes during annual photographic sessions in the Swan Mountain Range, Montana, 19889-95.

Class	Sighting Rates per Year							
	89	90	91	92	93	94	95	Mean Rate
Adult male	72[a] (1/3)[b]	131 (2/3)	361 (1/1)	93 (1/2)	0 (0/2)	569 (1/3)	206 (2/3)	194
Adult female	144 (1/3)	218 (1/4)	0 (0/1)	0 (0/1)	0 (0/5)	190 (2/3)	na[c]	409
Subadult male	96 (1/2)	0 (0/4)	0 (0/1)	0 (0/1)	286 (1/1)	na	na	540
Subadult female	144 (3/4)	653 (1/2)	0 (0/2)	155 (2/3)	571 (1/4)	0 (0/3)	0 (0/3)	555
Family group	0 (0/2)	0 (0/3)	0 (0/5)	0 (0/3)	0 (0/2)	0 (0/3)	310 (1/3)	1944
Total:								
Bears sighted[d]	13 (6)	9 (4)	2 (1)	8 (3)	3 (2)	4 (3)	5 (3)	
Sighting rate[a]	22.1	72.5	362.5	58.0	190.3	142.2	123.8	

[a] Camera-nights/marked bear sighting.

[b] Number of marked bears contributing to resighting rate/number of marked bears present in grid.

[c] Age and gender class not present in grid.

[d] Number resightings of marked bears (no. individuals contributing to sightings).

low in 1991 and 1993 relative to other years and estimates were considered suspect based on criteria reported by Mace et al. (1994). Data for these 2 years were included for comparative purposes but were not deemed reliable estimates of population size.

Annual resighting rates suggested that marked grizzly bears may have exhibited a time series response to camera stations (Fig. C.1). Annual rates varied from 22.1 camera-nights/resight (1989) to 363.5 camera-nights/sighting 1991 (Table C.2).

Point estimates for solitary bears using monte carlo simulation methods varied from 15-25 with wider 95% CI's during years of lower sighting rates (e.g. 1992) (Table C.3). Annual density estimates averaged 2.48 ± 0.343 (SE) solitary bears/100 km^2.

Petersen Estimates. As was observed in Monte Carlo simulations, sighting rates of marked bears during 1991 and 1993 cameras sessions were insufficient for population estimates ($v^* = 185$ and 140 respectively) (Table C.4). Population estimates are presented for these 2 years for comparative purposes only. An average of 23% (range = 10-43%) of the radioed bear sample was resighted at least once with cameras each year.

Annual density from point estimates for solitary grizzly bears averaged 3.32 ± 0.45 (SE) bears/100 km^2.

Comparison of Estimates to Known Minimum Bears. During photo sessions each year, we documented the minimum number of marked and unmarked solitary bears present within the camera grid polygon. These minimum counts varied from 13 to 19 solitary grizzly bears (Table C.5). Monte Carlo estimates were highly suspect during years 1991 and 1993 when sighting probabilities using cameras were ≤ 33%. Petersen estimates were similarly suspect during these years as evidenced by relatively high variances.

Population estimates were obtained during 5 annual sessions. During these years, Monte Carlo point estimates were generally closer to the simple count of marked and unmarked bears than were Petersen estimates. Aside from Monte Carlo estimates during 1989 and 1994, we do not believe the upper 95% estimates were reasonable.

DISCUSSION

Annual estimates of population size were made using a capture-resight (recapture) design employing self-activating cameras. The capture-resight design allowed us to make formal Monte Carlo and Petersen estimates. Capture-resight studies not involving visual observations (e.g. Miller et al. 1987) are rare for brown bears (Miller 1990b). We chose to use self-activating cameras deployed within a systematic grid each year out of necessity; bears could not be reliably observed from the ground or from aircraft, and no seasonal concentration areas such as berry fields, human refuse dumps, or fish spawning areas existed for detailed observations. Our capture-resight periods were confined to a 2-3 week period during July in an attempt to reduce influences of immigration, emigration, and death. The

Table C.3. Marking and sighting data used in estimating point estimates and confidence intervals for solitary grizzly bears in the Swan Mountain Range, Montana, 1989-1995.

Year	Marked bears n_1	Number sightings n_2	Number sightings marked m_2	Sighting probability $p = m_2/n_2$	Monte Carlo Estimates[a]	Sighting distribution of n_1 bears[c]					
						0	1	2	3	4	5
1989	14	14	13	.93	15-15-21	8	2	2	1	1	0
1990	16	12	9	.75	17-17-38	12	2	0	1	1	0
1991[d]	10	6	2	.33	22-42-96	11	0	1	0	0	0
1992	10	21	8	.38	16-24-47	7	1	1	0	0	1
1993[d]	14	11	3	.27	28-45-89	12	1	1	0	0	0
1994	12	6	4	.67	13-14-21	9	2	1	0	0	0
1995	13	9	5	.56	15-19-38	10	1	2	0	0	0

[a] Lower 95% CI - point estimate - upper 95% CI.

[b] Solitary bears/100 km^2 (based on buffer camera polygon area).

[c] Shows how many times marked bears were sighted. For example, during Session 1 of 1989, 8 different marked bears were never sighted (0 category), 2 were resighted once, 3 were resighted twice, 1 was resighted 3 times, and 1 was resighted 4 times.

[d] 1991 and 1993 estimates are provided for comparison to other years but sighting rates of marked bears were too low for valid estimates.

Table C.4. Peterson estimates obtained from number of marked and unmarked grizzly bears present and photographically sighted in camera grids from 1989-95. Swan Mountains, Montana.

Year	Marked bears present (n_1)	Number individuals sighted (n_2)	Number marked bear sightings (m_2)	Petersen estimate (N^*)	Variance (v^*)
1989	14	7	6 (43)[a]	16	2
1990	16	7	4 (25)	26	51
1991[c]	10	4	1 (10)	27	186
1992	10	8	3 (30)	24	43
1993[c]	14	6	2 (14)	34	140
1994	12	4	2 (17)	21	36
1995	13	6	3 (23)	24	37

[a] Number in parenthesis is percent of marked individuals photographically sighted.

confined sampling period, use of buffer strips (Otis et al. 1978), and presence of geographic barriers (Mace et al. 1994, Mace and Waller, 1997) allowed us more freedom to explore estimates based on closed populations (Seber 1982). However, given the high mobility of grizzly bears, especially males, movement from the study area occurred during sampling periods. As elsewhere (Miller et al. 1987), we used telemetry to assess presence of marked bears and the degree of closure each period.

Our use of cameras in an area with radio-collared individuals offered an opportunity to assess sighting bias relative to each grizzly bear class over time. These biases, pervasive in wildlife studies (White et al. 1982), were identified early in the research and caused by heterogeneity among individuals and classes, small sample sizes (Mace et al. 1994), and because of the relationship between sighting probability and the density of cameras within grids (Mace et al. 1994). Our local population was too small to estimate size of sex and age classes separately. Between 1989 and 1995, sighting rates appeared to decline. We believe that declining rates occurred after bears became progressively less interested in a technique that offered little to no food reward. Although we attempted to prevent food reward, and altered supplemental lures each year, the most consistent sightings using cameras were from those individuals that did receive an unintentional food reward. However, it was clear that sighting rates were poorest for family groups and best for highly mobile adult males.

Both capture and camera survey data suggested that a high proportion of the local population was marked, which in our study reduced the need for a formal capture/recapture design. Each year, marked and radioed bears made up the majority of individuals resighted (77-93%). An additional one to 3 unmarked solitary bears were photographed each year. Therefore, point estimates using both Monte Carlo and Petersen estimates were generally close to the known minimum number of marked and unmarked bears present each year. Yet the 95% confidence limits surrounding the annual estimates were generally wide, except those years with high sighting probabilities and rates.

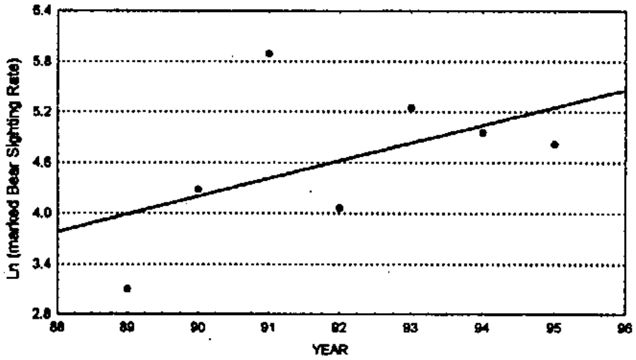

Fig. C.1. Camera sighting rates for marked grizzly bears in the Swan Mountains, Montana during 7 spring sampling periods.

Table C.5. Summary of estimates of population size and density of grizzly bears in the Swan Mountains, Montana.

Population Estimator	Number of Solitary Grizzly Bears per Year Lower 95% CI - point - upper 95% CI. (density)						
	89	90	91	92	93	94	95
Count (marked + unmarked)	15 (1.8)[a]	19 (2.2)	13 (1.80)	15 (2.1)	18 (2.7)	14 (1.8)	16 (2.5)
Monte Carlo	15-15-21 (1.8-1.8-2.5)	17-17-38 (2.0-2.0-4.5)	NA[b]	16-24-47 (2.2-3.3-6.5)	NA	13-14-21 (1.7-1.8-2.7)	15-19-38 2.4-3.0-6.1)
Petersen	6-16-38[c] (0.7 - 1.9 - 4.5)	8-26-83 (1.0 - 3.1 - 9.8)	NA	6-24-98 (0.71 - 3.3 - 13.6)	NA	4-21-135 (0.52 - 2.7 - 17.5)	6-24-96 0.71 - 3.8 - 15.2)

[a] Solitary bears/100 km^2 (based on buffer camera polygon area).

[b] Sighting rates of marked bears were during 1991 and 1993 were too low for reliable population estimates.

[c] 95% CI for Petersen estimates constructed from the poisson distribution using m_2 as entering variable in Appendix A1 (Seber 1982:63).

APPENDIX D

VEGETATION MAPPING USING SATELLITE IMAGERY

The vegetation map created from LANDSAT TM imagery was an important component in 4 of our research endeavors (Mace and Waller 1996, Mace et al. 1996, Mace and Waller 1997, Waller and Mace 1997a). The vegetation map was derived from a 30 class map created early in the project. The following excerpt from Manley et al. (1992) describes the creation of this 30 class map:

"An August 28, 1988 Landsat TM satellite image was purchased. The image was cloud free, haze(smoke) free, and free of seasonal snow cover for the area of interest. All computer image processing was completed using ERDAS Inc. software on a PC. Due to computer space limitations, classification was performed on quarter scenes of the image. An unsupervised classification method was used. The image was checked for bad data and corrections were made using the BADLIN program. The first step involved a histogram adjustment to account for atmospheric scattering (Jensen 1986). The procedure shifted each band downward so that the data file values all started at 1. The adjusted image was then transformed into 3 bands, using the tasseled cap coefficients developed by Crist and Cicone (1984). The 3 bands represented brightness, greenness, and wetness respectively. The transformed data were sampled into 30 clusters using ISODATA to create a signature file. ISODATA did not weight the classes with pixels from the top of the image. Using MAXCLAS, the transformed image was converted into a 30 class GIS file using the minimum distance to the mean. The GIS file was rectified to +/- 1.0 pixel using topographic maps and UTM coordinates. A detailed outline of the spectral classification procedure is provided in Appendix A."

We constructed a matrix using the 30 spectral classes and 9 classes of aspect (9x30=270 cells). Each cell of the matrix was classified into 1 of 15 cover types based upon aerial photo interpretation of 1600 random Universal Transverse Mercator (UTM) coordinates (6 points/cell). The matrix cell was classified by the majority of points that occurred therein. If ties occurred, assignments were made based upon a priori knowledge of the study area. The 15 classes were:

1 water
2 shadow (unclassified)
3 nonvegetated (rock)
4 wet meadow
5 mesic grass/forb
6 xeric grass/forb
7 hydric shrub
8 mesic shrub
9 xeric shrub
10 low temperate, low radiation forest
11 low temperate, high radiation forest
12 temperate, low radiation forest
13 temperate, high radiation forest
14 subalpine low radiation forest
15 subalpine high radiation forest

We used Polaroid photographs of aerial bear telemetry locations to assess the accuracy of the final map, and refine areas where error was observed. After 4 iterations, minimum accuracy of 80% was obtained. The 15 classes were further combined into 5 classes to allow testing for selection with our limited telemetry sample sizes. The 5 classes were:

1 shadow (unclassified)
2 water
3 nonvegetated/grass-forb land
4 shrub land
5 forest

After further inspection and experience, we felt that several physiographic features not identified by satellite imagery should be included. These features were timber harvest units, avalanche chutes, and slabrock areas.

Digital maps of timber harvest units were obtained from the U.S.D.A. Forest Service. We then hand mapped and digitized avalanche chutes and slabrock complexes identified from aerial photographs. These 3 features were then overlaid upon the 5 class cover type map. Thus our final map consisted of 8 cover types:

1 water
2 shadow (unclassified)
3 nonvegetated/grass-forb land
4 shrub land
5 forest
6 slabrock
7 avalanche chute
8 timber harvest unit

This map provided resolution sufficient to detect selection by grizzly bears, yet was general enough to provide complete matrices for selection tests. In practice, water and unclassified areas were often excluded from analysis. Dominant plant taxa stratified by cover type and elevation zone are presented in Table D.1.

Table D. 1. Relative dominance of taxa in low temperate, temperate, and subalpine elevation zones and 7 cover types within the Swan Mountains, MT study area. Only the 5 most dominant species in at least one cover type/zone combination are listed.

Species by Life Form	Cover type Unclassified	Grass Land / Non-vegetated	Shrub land	Forest	Chute	Slabrock	Cut
Trees:							
Abies lasiocarpa	69 55 59	** 21 92	24 76 92	15 71 86	25 73 82	* 88 89	26 67 *
Larix occidentalis	0 t 0	** 0 0	13 t t	4 t t	5 t 0	* 0 0	33 3 *
Picea engelmannii	17 22 8	** t t	13 14 2	11 14 1	20 12 t	* 2 .2	25 28 *
Pinus albicaulus	0 3 26	** 6 7	0 3 6	t 3 13	0 1 17	* 10 11	t t *
Pinus contortus	0 t 0	** 1 t	6 t t	2 1 t	t t 0	* 0 t	2 t *
Populus trichocarpa	0 0 0	** 0 0	0 0 0	t t 0	t t 0	* 0 0	4 1 *
Pseudotsuga mensiesii	14 17 0	** 72 t	43 6 t	67 10 t	48 13 t	* t 0	9 t *
Shrubs:							
Acer glabrum	7 2 0	11 t 0	40 2 t	23 2 t	30 10 t	* t 0	21 2 *
Alnus sinuata	t 4 t	0 t t	1 10 t	1 3 t	3 14 1	* t t	7 7 *
Amelanchier alnifolia	1 1 t	43 31 2	3 1 t	7 1 t	13 5 t	* t t	4 t *
Berberis repens	0 t 0	11 t 0	t t t	t t t	t t 0	* 0 0	t 0 *
Ceanothus velutinus	0 t 0	11 t 0	2 t 0	t t 0	t t 0	* 0 0	t t *
Menziesia ferruginea	0 28 16	0 0 9	t 23 7	1 29 13	t 3 2	* 20 6	2 35 *
Pachistima myrsinites	23 6 1	0 26 2	15 5 4	16 4 t	4 8 18	* t t	19 3 *
†Prunus virginiana	t t 0	11 t 0	t t 0	t t 0	2 t 0	* 0 0	t 0 *
Rubus parviflorus	2 4 0	0 1 0	8 5 t	11 3 t	15 14 5	* 0 0	15 15 *
Sambucus racemosa	0 t t	0 t t	t t t	t t t	t 2 t	* t t	t 4 *
†Sorbus scopulina	1 4 t	0 5 2	6 12 5	2 7 1	6 20 6	* 3 t	2 t *
Spirea betulafolia	t 1 t	2 5 t	5 t t	3 t t	1 t t	* 3 0	1 t *
Spirea densiflora	t t t	0 2 4	0 3 2	t 1 t	t 4 t	* 2 2	1 t *
Symphoricarpus albus	15 t 0	0 t 0	t t 0	7 t t	13 1 0	* 0 0	5 t *
†Vaccinium globulare	32 45 36	0 24 26	11 32 39	19 41 43	5 17 36	* 53 46	11 25 *
Vaccinium scoparium	0 t 44	0 2 53	t 3 41	t 4 40	t t 29	* 18 44	t t *
Forbs:							
Achillea millefolium	t 1 t	4 6 t	1 t t	t t t	t t t	* t t	t t *
†Angelica arguta	0 0 t	0 0 0	0 t 0	t 0 0	0 t 0	* 0 t	0 0 *
Apocynum androsaemifolium	2 t 0	71 t 0	t t t	t 1 0	t t 0	* 0 0	0 0 *
Arnica latifolia	2 15 9	0 t 90 t	3 4 5	8 9 16	4 t 2	* 7 17	4 10 *
Athyrium filix-femina	2 1 0	0	t 2 0	0 2 0	4 6 0	* 0 0	4 4 *
Balsamorhiza sagittata	0 t 0	0 6 t	0 t t	t t 0	0 0 0	* 0 0	0 0 *
†Claytonia lanceolata	0 0 0	0 t t	0 t t	0 0 t	0 0 0	* t 0	0 0 *
Clintonia uniflora	35 t 0	0 0 0	3 1 t	12 2 0	4 2 0	* 0 0	8 5 *
Disporum hookeri	t t 0	0 t 0	4 t 0	1 1 0	1 t 0	* 0 0	t 0 *
Epilobium angustifolium	t 4 t	4 9 1	23 12 6	6 4 2	19 14 5	* t 1	47 46 *
†Equisetem arvense	0 0 0	0 0 t	0t 0	0 t 0	0 0 0	* 0 t	t t *
Eriogonum flavum	0 t 1	0 20 5	0 t t	0 t t	t t t	* 1 t	0 0 *
†Erythronium grandiflorum	0 2 4	0 7 23	0 t 9	t t 9	t t 4	*8 13	t t *
†Heracleum lanatum	0 t 0	0 t t	3 t t	t t t	1 1 0	* 0 t	t t *
Heucheria cylindrica	t 1 t	18 3 1	t t t	t t t	t t t	* 1 t	0 0 *
†Ligusticum species	0 t 0	0 0 0	0 t 0	0 t 0	0 0 0	* 0 0	t 0 *
†Lomatium coues	0 t t	0 t t	t t t	t 0 t	0 t t	* t t	0 0 *
Mitella breweri	0 3 3	0 t t	0 2 t	t 2 t	t 1 t	* t t	0 1 *
†Osmorhiza species	0 t 0	0 0 t	0 0 0	0 0 t	t 0 0	* 0 0	0 0 *
Penstemon species	0 t 0	0 t t	0 t t	t 0 t	0 0 t	* 4 1	0 0 *
Pteridium aquilinum	0 0 0	0 0 0	t t t	t t 0	7 t 0	* 0 0	2 t *
Senecio triangularis	0 4 2	0 0 9	1 11 7	2 9 7	t 9 1	* t 8	t 5 *
Smilacina stellata	9 t 0	0 t 0	2 1 t	14 t 0	4 3 t	* 0 0	11 3 *
†Taraxacum species	0 0 0	0 0 t	0 0 0	0 0 0	0 0 0	* 0 0	t 0 *
Thalictrum occidentale	5 3 t	0 t 2	1 8 1	9 5 t	4 13 3	* 0 t	2 6 *
Urtica dioica	0 t 0	0 0 0	3 0 0	t 0 0	5 1 0	* 0 0	t t *
Veratrum viride	0 1 3	0 t 2	t 4 2	t 2 1	1 5 1	* t 4	t t *
Viola glabella	t 1 t	0 t 0	3 3 t	1 2 t	2 9 t	* 0 t	3 4 *
Xerophylum tenax	26 53 67	4 31 27	45 46 60	33 56 55	37 29 78	* 72 47	11 6 *

†Bear food species included for comparison

* Cover type not present in elevation zone

** Only one plot in this cover type, zone combination. No trees were present.

t = Relative dominance<1

APPENDIX E

SUMMARY STATISTICS OF GRIZZLY BEAR HABITAT USE AND MOVEMENT RATES IN THE SWAN MOUNTAINS, MONTANA.

R. D. Mace and J. S. Waller

In Chapters 3-5, we described habitat selection of Swan Mountain grizzly bears at the home range scale of selection. Individual grizzly bears were usually assessed separately because habitat and physiographic features varied across the study area and therefore by individual.

In this Appendix we report seasonal habitat use (and not availability) from our aerial telemetry database. Our goal here is to simply tabulate the telemetry data base relative to several habitat variables.

METHODS

We summarized our telemetry data base for 6 classes of bears over 4 seasons. Seasons were defined as early spring (den emergence - 7 May), spring (8 May - 15 July), summer (16 July - 15 September), and autumn (16 September - den entry). Individuals were classified as adult males, solitary adult females ($\geq$ 5 years old), subadult males or females (>1 and < 5 years old), adult females with cubs-of-the-year, and an adult females with young > 0.5 years of age. Only those bears with at least 10 telemetry points per season were included, except for early spring where we used the entire sample.

Various habitat variables were recorded while circling over each bear during aerial telemetry flights. Bears were classified as being present in one of 4 broad cover types. Cover types used were: coniferous forest (CF), shrub land (SH), grass-forb land (GF), and nonvegetated (NV). The CF cover type was defined as habitats with $\geq$ 40% overstory of conifers. The SH cover type was defined as those habitats with < 40% coniferous overstory and $\geq$ 15% deciduous shrub overstory. Habitats having $\leq$ 10% conifer overstory and $\geq$10% herbaceous cover were termed grass-forb lands.

Nonvegetated habitats were those with < 10% rooted vegetation.

Each grizzly bear was also categorized as occurring in one of 7 physiographic feature: forested creek bottom (FC), cutting unit (CT), road (RD), avalanche chute (AC), small rock out-crop (RO), slabrock (SR), or montane (mountain-side, MO).

Photographs were taken of each relocation while in the fixed-wing aircraft. After plotting relocations on 1:24,000 orthophotographic quadrangles, we determined elevation (m), percent slope, and degree aspect. For categorical analyses, aspect was generalized as either north (N) 315° - 44°, east (E) 45° - 134°, south (S) 135° - 224°, west (W) 225° - 314°, and flat.

For most variables, we first assessed whether individual grizzly bears differed in use patterns. For elevation and percent slope variables bears were compared using one-way analysis of variance (ANOVA). Categorical variables were assessed using the chi^2 statistic. Significant results from ANOVA ($P \leq 0.05$) were further assess using Tukey's post-hoc test. Results of these post-hoc tests were used to document the extent to which individuals differed. For example, when 7 grizzly bears were being compared, there were 21 possible comparisons.

RESULTS

Elevation

Grizzly bears in the Swan Mountains varied by season and class in their use of elevation (Fig. E.1). Bears generally used lower elevation in early spring, and moved to higher elevations as the seasons progressed. Females with cubs were the obvious exception during early spring, and stayed at higher elevations than the other classes throughout the year. Adult males utilized habitats at the lowest elevations of all classes during early spring and autumn.

Summary statistics for each season (Table E.1) highlights how individuals of each class differed from one another in regard to elevation during each season. During spring, subadult females were more similar in their use of elevation than other classes; 8% of all possible pairs differed significantly during this season.

Aspect

Individual grizzly bears of most classes differed significantly ($P \leq 0.05$) from one another in their use of aspect during each season (Table E.2). Adult males were the exception, using the 5 aspect categories similarly ($P > 0.05$) during each season (Table E.2). Relatively high use of the flat category was a result of several adult males venturing onto ungulate winter ranges in either the Flathead or Swan valleys during early spring. Seasonal use of aspect by the pooled sample of grizzly bears (Fig. E.2) showed the use of southern aspects declining as the season progressed. Conversely, use of the eastern aspect increased.

Slope

Grizzly bears exhibited the greatest variation in percent slope during early spring (Fig. E.3), and this variation could be explained by differential use of elevation by the different classes of bears (see Fig. E.1). In general, individuals of each class used percent slope significantly different ($P \leq 0.05$) from one another each season (Table E.3), with the exception of solitary adult females.

Overstory canopy

Grizzly bears in the Swan Mountains selected habitats relative to overstory canopy differently each season (Fig. E.4). When telemetry data from all bears were pooled, use of closed timbered habitats was greatest during early spring and declined during spring and summer. Summary statistics for each season and class (Table E.4), revealed substantial variation.

Distance moved

Classes of grizzly bears differed from one another relative to average daily movement (ADM) for each season ($P \leq 0.05$). Except for early spring, adult males exhibited the greatest ADM of all classes (Fig. E.5, Table E.5). The largest ADM estimate was 9,886 m for an adult male during spring. This bear moved 59.3 km over a 6 day period.

During early spring the ADM rate of subadult males and females with cubs differed significantly ($P \leq 0.05$). During spring adult males exhibited the greatest ADM and differed significantly from all other classes of bears. During spring subadult males differed significantly from females with cubs and subadult females. During summer, adult and subadult males moved at an equal rate, and both were significantly different than the adult and subadult female classes. Adult males again exhibited the greatest ADM during autumn, and differed significantly from adult and subadult females (Fig. E.5).

Cover type and physiographic feature

During early spring, most classes of bears were relocated most frequently in either montane forest of shrub lands (Table E.6). However, females with cubs appeared to be an exception and were relocated most often in either forested creek bottoms or avalanche chutes.

During spring, montane coniferous forests and avalanche chute shrub lands were utilized most often by most classes of bears (Table E.7). Use of rock outcrops or slabrock habitats was relatively infrequent.

Most classed of grizzly bears were relocated most often in shrub lands during summer (Table E.8). Most shrub land use occurred in openings in the montane forest. Use of shrub-dominated cutting units by grizzly bears generally increased over early spring and spring. Females with cubs used coniferous forest habitats within the slabrock physiographic feature more than other classes during summer.

Use of cover types and physiographic features by grizzly bears in the Swan Mountains during autumn was similar to that observed during early spring. Generally, grizzly bears were most often relocated in montane shrub lands (Table E.9).

Distance to cover types

Grizzly bears were relocated at variable distances to each cover type each season (Table E.10). During early spring, classes of grizzly bears differed only in the distance to the avalanche chute type. Adult females with cubs tended to be closer than other classes during this season.

During spring, distance to cover type varied by class of grizzly bear for the Avalanche chute and slabrock cover types. During summer, differences in distance to cover types was observed for the slabrock and cutting unit types. Adult males tended to be located closer to cutting units than other classes (Table E.10). Differential use of distance to cover types during autumn was observed for all by the slabrock type.

Table E.1. Summary statistics for grizzly bear use of elevation during 4 seasons. Swan Mountains, Montana.

Class	N. Bears	Anova and Tukey's Post-hoc test results[1]			Summary elevation statistics (m)			
		P-value	N different pairs	% different	Mean	lower 95% CI	Upper 95% CI	SE
Ad m								
es					1376	1317	1435	30
sp	10	0.00	6	13	1604	1568	1640	19
su	8	0.00	1	4	1623	1590	1656	17
fa	5	0.00	4	40	1495	1419	1572	39
Sub ma								
es					1546	1376	1715	78
sp	6	0.00	2	13	1609	1554	1665	28
su	6	0.00	7	47	1707	1653	1751	25
fa	5	na			1643	1569	1717	37
Subad f								
es					1563	1481	1645	40
sp	11	0.00	6	11	1614	1576	1653	19
su	8	0.00	1	4	1726	1691	1761	18
fa	5	0.00	4	40	1704	1639	1771	33
Ad f								
es					1516	1453	1578	30
sp	9	0.00	3	8	1656	1623	1688	16
su	9	0.00	7	19	1757	1727	1787	15
fa	6	0.00	2	13	1841	1798	1884	21
Ad f with cubs								
es					1712	1624	1801	41
sp	9	0.00	16	44	1699	1656	1741	22
su	7	0.00	5	24	1771	1738	1803	16
fa	6	0.02	2	22	1799	1751	1849	25
Ad f with 1-2 yr. olds								
es					1480	1412	1547	34
sp	8	0.00	7	25	1533	1490	1577	22
su	8	0.00	2	7	1746	1704	1788	21
fa	7	0.00	2	20	1690	1634	1746	28

[1] Individual bears of each class were tested among themselves relative to elevation using ANOVA. Significant P-values indicate individuals differed, the number of individuals that were significantly different from one another is also provided as is the percent of all possible combinations that differed.

Table E.2. Summary statistics for grizzly bear use of aspect classes during 4 seasons. Swan Mountains, Montana.

Class	N bears	Test of Individual Bear Differences			Percent of Aspect Class				
		chi^2	df	P	N	S	E	W	Flat
Ad m									
es					10	31	19	26	15
sp	10	17	20	0.62	12	37	28	18	4
sp	8	33	28	0.23	22	19	35	20	4
fa	5	15	20	0.80	18	18	33	22	9
Subad m									
es					8	38	8	38	8
sp	6	30	20	0.04	13	36	22	22	6
su	6	30	20	0.07	17	29	24	26	4
fa	5	72	16	0.00	23	22	35	11	9
Subad f									
es					12	62	12	12	4
sp	11	60	40	0.02	20	32	26	18	4
su	8	43	28	0.03	25	19	31	21	4
fa	5	54	16	0.00	33	15	40	6	7
Sol. Ad f									
es					0	63	13	25	0
sp	9	46	28	0.02	20	28	21	19	3
su	9	47	32	0.04	22	25	33	17	4
fa	6	23	20	0.29	23	22	38	16	2
Ad f with cubs									
es					15	38	15	31	0
sp	9	49	32	0.02	22	33	25	17	4
su	7	25	24	0.39	16	28	37	16	4
fa	6	11	15	0.75	33	12	45	10	0
Ad f with 1-2 yr. olds									
es					9	42	27	6	16
sp	8	65	28	0.00	12	23	28	26	10
su	8	29	28	0.39	15	23	40	20	4
fa	7	21	24	0.65	33	21	27	14	4

Table E.3. Summary statistics for grizzly bear use of percent slope during 4 seasons. Swan Mountains, Montana.

Class	No. Bears	Anova and Tukey's Post-hoc test results[1]			% Slope characteristics			
		P-value	N different pairs	% different	Mean	Lower 95% CI	Upper 95% CI	SE
Ad m								
es					33	27	39	3.0
sp	10	0.02	0	0	38	35	41	1.6
su	8	0.23	0	0	40	37	43	1.5
au	5	0.00	1	17	34	29	38	2.2
Subad m								
es					45	30	60	7.0
sp	6	0.00	1	7	38	33	43	2.4
su	6	0.02	2	13	38	35	42	1.8
au	5	0.00	1	20	35	30	41	3.0
Subad f								
es					50	44	57	3.0
sp	11	0.00	2	4	46	42	49	1.6
su	8	0.01	1	4	42	39	45	1.6
au	5	0.00	3	30	36	32	41	2.4
Sol Ad f								
es					50	41	59	4.0
sp	9	0.65	0	0	44	41	47	1.6
su	9	0.54	0	0	41	38	44	1.6
au	6	0.73	0	0	48	44	52	2.0
Ad f with cubs								
es					60	52	66	4.0
sp	9	0.00	4	11	47	43	52	2.0
su	7	0.00	2	29	44	40	47	1.9
au	6	0.14	0	0	42	38	46	2.0
Ad f with 1-2 yr. olds								
es					48	41	55	4.0
sp	8	0.00	6	21	41	37	45	1.9
su	8	0.01	4	4	36	33	39	1.7
au	7	0.04	0	0	41	37	46	204

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[1] Individual bears of each class were tested among themselves relative to percent slope using ANOVA. Significant P-values indicate individuals differed, the number of individuals that were significantly different from one another is also provided as is the percent of all possible combinations that differed.

Table E.4. Summary statistics for grizzly bear use of overstory canopy classes during 4 seasons. Swan Mountains, Montana.

Class	N bears	Test of Individual Bear Differences			% of Class in each overstory canopy class		
		chi^2	df	P	Timbered	Open Timbered	Open
Ad m							
es					68	23	10
sp	6	16	10	0.11	30	31	39
su	8	24	14	0.05	23	31	46
au	5	13	10	0.21	53	25	22
Subad m							
es					46	23	31
sp	6	6	10	0.77	31	31	38
su	6	29	10	0.00	16	48	36
au	5	25	8	0.00	29	37	34
Subad f							
es					35	38	27
sp	11	26	20	0.16	27	25	48
su	8	13	14	0.49	18	46	37
au	5	36	8	0.00	31	43	26
Sol ad f							
es					50	29	21
sp	9	15	16	0.51	31	30	39
su	9	19	16	0.28	19	46	34
au	6	11	10	0.36	23	15	26
Ad f with cubs							
es					69	15	15
sp	9	19	16	0.25	32	33	36
su	7	25	18	0.11	13	46	41
au	6	18	10	0.06	29	36	36
Ad f with 1-2 yr. olds							
es					50	31	19
sp	8	31	14	0.00	35	25	40
su	8	32	14	0.00	14	43	33
au	7	19	12	0.09	40	37	23

Table E.5. Seasonal daily movement rates of grizzly bears in the Swan Mountains, Montana.

Class	Distance moved per day (m)			
	Mean	Lower 95% CI	Upper 95% CI	SE
Ad m				
es	862	504	1219	178
sp	2162	1874	2451	146
su	1424	1212	1637	108
au	1143	900	1386	123
Subad m				
es	1554	724	2384	381
sp	1441	1159	1723	143
su	1474	1255	1692	111
au	967	760	1174	104
Subad f				
es	500	250	751	121
sp	899	772	1026	64
su	1062	925	1200	69
au	712	581	844	66
Ad f				
es	478	254	702	108
sp	1057	881	1233	89
su	836	705	966	66
au	600	458	742	72
Ad f with cubs				
es	60	0	150	41
sp	819	642	996	89
su	1101	940	1262	81
au	856	709	1003	74
Ad f with 1-2 yr. olds				
es	722	399	1044	157
sp	1076	885	1267	96
su	1141	975	1307	84
au	910	777	1042	67

Table E.6. Summary statistics for grizzly bear use cover types and physiographic features during the early spring. Swan Mountains, Montana.

Class[1]	Cover Type[2]	Physiographic Feature[3]						
		FC	MO	CT	RD	AC	R0	SR
Ad m	CF	29	39	2	3	0	2	0
	SH	3	6	3	0	2	0	0
	NV	0	0	0	2	2	2	0
	GF	0	2	0	2	2	2	0
Subad m	CF	8	38	0	0	0	0	0
	SH	0	23	8	0	0	0	0
	NV	0	0	0	0	0	8	0
	GF	0	15	0	0	0	0	0
Subad f	CF	0	50	0	0	4	0	0
	SH	0	21	0	0	4	4	0
	GF	0	13	0	0	4	0	0
Sol ad f	CF	4	35	0	0	4	0	0
	SH	0	15	12	0	12	4	0
	GF	0	8	0	0	8	0	0
Ad f with cubs	CF	46	0	0	0	23	8	0
	SH	0	0	0	0	0	8	0
	NV	0	0	0	0	0	8	0
	GF	0	0	0	0	0	8	0
Ad f with 1-2 yr olds	CF	11	36	2	0	2	2	0
	SH	0	20	0	0	5	0	0
	NV	0	0	0	0	5	3	0
	GF	0	6	0	0	0	5	0
All	CF	13	39	1	1	2	2	0
	SH	1	14	3	0	4	1	0
	NV	0	0	0	2	1	2	0
	GF	0	6	0	1	3	2	0

[1] Adult male (AM), subadult male (SM), subadult female (SF), solitary adult female (AF), female with cubs (FC), female with 1-2 year-olds (FY).

[2] Coniferous forest (CF), shrub land (SH), Nonvegetated (NV), grass/forb land (GF).

[3] Forested creek bottom (FC), Montane (MO), cutting unit (CT), Road (RD), avalanche chute (AC), rock outcrop (RO), slabrock (SR)

Table E.7. Summary statistics for grizzly bear use cover types and physiographic features during the spring. Swan Mountains, Montana.

Class[1]	Cover Type[2]	Physiographic Feature[3]						
		FC	MO	CT	RD	AC	R0	SR
Ad m	CF	9	23	0	1	1	1	
	SH	2	15	3	0	24	0	1
	NV	0	0	0	6	1	1	1
	GF	0	5	1	1	6	1	1
Subad m	CF	13	18	1	0	0	0	1
	SH	9	14	6	1	16	1	1
	NV	0	0	0	2	0	1	1
	GF	3	4	0	0	3	3	1
Subad f	CF	5	22	0	0	0	1	1
	SH	3	15	7	0	27	0	2
	NV	0	0	0	2	0	0	0
	GF	0	5	0	0	7	3	1
Sol ad f	CF	5	23	0	1	1	0	1
	SH	3	17	2	0	31	0	0
	GF	1	5	1	1	6	1	1
Ad f with cubs	CF	2	30	0	0	1	1	0
	SH	3	23	4	0	15	2	2
	NV	0	1	0	2	1	4	0
	GF	1	2	0	0	2	3	1
Ad f with 1-2 yr olds	CF	11	22	1	0	1	0	0
	SH	5	14	4	0	23	1	1
	NV	0	0	0	2	0	0	2
	GF	1	7	1	0	2	1	1
ALL	CF	7	23	0.2	0.3	0.5	0.4	0.3
	SH	4	16	4	0.1	23	1	1
	NV	0	0.2	0	3	0.2	1	1
	GF	1	5	1	0.3	5	2	1

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[1] Adult male (AM), subadult male (SM), subadult female (SF), solitary adult female (AF), female with cubs (FC), female with 1-2 year-olds (FY).

[2] Coniferous forest (CF), shrub land (SH), Nonvegetated (NV), grass/forb land (GF).

[3] Forested creek bottom (FC), Montane (MO), cutting unit (CT), Road (RD), avalanche chute (AC), rock outcrop (RO), slabrock (SR)

Table E.8. Summary statistics for grizzly bear use cover types and physiographic features during summer. Swan Mountains, Montana.

Class[1]	Cover Type[2]	Physiographic Feature[3]						
		FC	MO	CT	RD	AC	R0	SR
Ad m	CF	6	16	1	0	1	1	0
	SH	5	27	21	0	8	0	4
	NV	0	1	0	3	0	1	0
	GF	0	6	0	0	0	1	0
Subad m	CF	5	11	1	0	0	0	0
	SH	7	41	13	1	8	1	4
	NV	0	1	0	0	0	0	1
	GF	1	2	1	0	0	0	3
Subad f	CF	4	10	1	0	1	1	2
	SH	8	37	10	1	16	1	3
	NV	0	1	0	0	0	1	0
	GF	1	1	0	0	2	1	0
Sol ad f	CF	2	16	0	0	0	1	0
	SH	5	38	14	0	10	2	3
	NV	0	0	0	1	0	0	0
	GF	1	5	0	0	1	1	1
Ad f with cubs	CF	2	11	0	0	0	0	13
	SH	7	45	10	0	12	2	3
	GF	1	6	0	0	0	0	1
Ad f with 1-2 yr olds	CF	3	21	0	0	0	1	1
	SH	4	37	4	0	10	5	9
	NV	0	0	0	1	0	0	1
	GF	0	1	0	0	0	0	1
All	CF	4	14	1	0	0.4	1	1
	SH	6	37	13	0.2	10	2	4
	NV	0	0.3	0	1	0	0.3	0.3
	GF	1	3	0.1	0	0.5	0.4	1

[1] Adult male (AM), subadult male (SM), subadult female (SF), solitary adult female (AF), female with cubs (FC), female with 1-2 year-olds (FY).

[2] Coniferous forest (CF), shrub land (SH), Nonvegetated (NV), grass/forb land (GF).

[3] Forested creek bottom (FC), Montane (MO), cutting unit (CT), Road (RD), avalanche chute (AC), rock outcrop (RO), slabrock (SR)

Table E.9. Summary statistics for grizzly bear use cover types and physiographic features during the autumn. Swan Mountains, Montana.

Class[1]	Cover Type[2]	Physiographic Feature[3]						
		FC	MO	CT	RD	AC	RO	SR
Ad m	CF	14	36	2	1	0	0	0
	SH	1	23	13	1	7	0	0
	NV	0	0	0	1	0	1	0
Subad m	CF	13	14	0	0	0	0	3
	SH	5	29	14	0	6	4	4
	NV	0	0	0	1	0	1	0
	GF	1	1	0	3	0	0	1
Subad f	CF	17	14	0	0	0	0	0
	SH	2	35	2	0	11	3	2
	NV	0	1	0	0	1	1	1
	GF	0	8	0	0	1	1	1
Sol ad f	CF	4	17	0	0	1	1	0
	SH	7	44	2	0	12	1	1
	NV	0	1	0	0	1	1	0
	GF	1	6	0	0	0	1	0
Ad f with cubs	CF	1	26	0	1	0	0	0
	SH	0	41	4	0	6	0	4
	NV	0	0	0	1	0	1	0
	GF	1	5	0	0	3	0	1
Ad f with 1-2 yr olds	CF	16	24	0	0	0	0	1
	SH	3	33	4	0	6	0	3
	GF	0	4	0	0	2	0	2
All	CF	10	23	1	0.3	0.2	0.2	0.4
	SH	3	34	7	0.2	8	1	2
	NV	0	0.4	0	0.4	0.2	1	0
	GF	1	4	0.3	0.3	1	0.3	1

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[1] Adult male (AM), subadult male (SM), subadult female (SF), solitary adult female (AF), female with cubs (FC), female with 1-2 year-olds (FY).

[2] Coniferous forest (CF), shrub land (SH), Nonvegetated (NV), grass/forb land (GF).

[3] Forested creek bottom (FC), Montane (MO), cutting unit (CT), Road (RD), avalanche chute (AC), rock outcrop (RO), slabrock (SR)

Table E.10. Seasonal distance to cover types for each class of bear, Swan Mountains, Montana.

Season and Cover Type[1]	Anova P-value[2]	Distance to cover type by class (m) (mean, SE)					
		Ad m	Subad m	Ad f	Subad f	F cub	F with 1-2 yr. olds
Early Spring							
NV	0.91	593,52	330,110	440,63	300,58	322,91	381,42
SH	0.33	84,9	94,17	78,16	70,11	82,14	107,13
CF	0.60	21,7	4,4	28,8	37,13	19,9	31,8
AC	0.00	734,54	619,152	272,89	266,79	180,89	498,61
SR	0.17	993,15	885,67	1010,10	959,41	1020,0	985,18
CU	0.30	636,62	630,139	585,97	557,89	578,91	448,47
Spring							
NV	0.10	472,30	4,64,35	457,26	452,26	373,27	400,27
SH	0.07	90,8	139,20	97,7	109,12	104,10	100,8
CF	0.71	50,6	51,11	53,6	52,7	38,5	48,7
AC	0.00	382,35	497,48	289,32	348,33	463,41	536,38
SR	0.02	920,21	792,39	881,22	921,21	879,27	922,23
CU	0.70	498,34	544,45	548,30	516,32	508,34	479,33
Summer							
NV	0.39	368,21	346,27	364,22	353,21	363,24	302,21
SH	0.06	93,8	95,12	74,7	73,7	67,6	71,7
CF	0.09	50,5	38,6	42,5	50,5	45,6	30,4
AC	0.07	597,30	623,37	530,28	530,31	527,33	617,34
SR	0.00	897,21	720,34	817,26	790,28	850,29	752,35
CU	0.00	438,52	625,39	629,31	599,32	647,35	751,33
Autumn							
NV	0.04	534,36	456,40	416,31	468,32	423,37	390,36
SH	0.01	71,8	90,14	68,9	115,13	72,9	84,10
CF	0.00	33,5	32,5	39,5	67,11	33,6	31,7
AC	0.02	577,44	556,46	409,36	447,38	515,38	505,39
SR	0.24	873,31	773,43	861,27	834,32	855,36	887,31
CU	0.04	490,47	520,48	655,34	610,39	552,44	623,41

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[1] Non-vegetated/grass forb land (NV), Shrub land (SH) ,Coniferous forest (CF), avalanche chute (AC), slabrock (SR), cutting unit (CU).

[2] The distance to cover types for classes of bears were compared using ANOVA. Significant P-values ($P \leq 0.05$) indicated classes differed during that season.

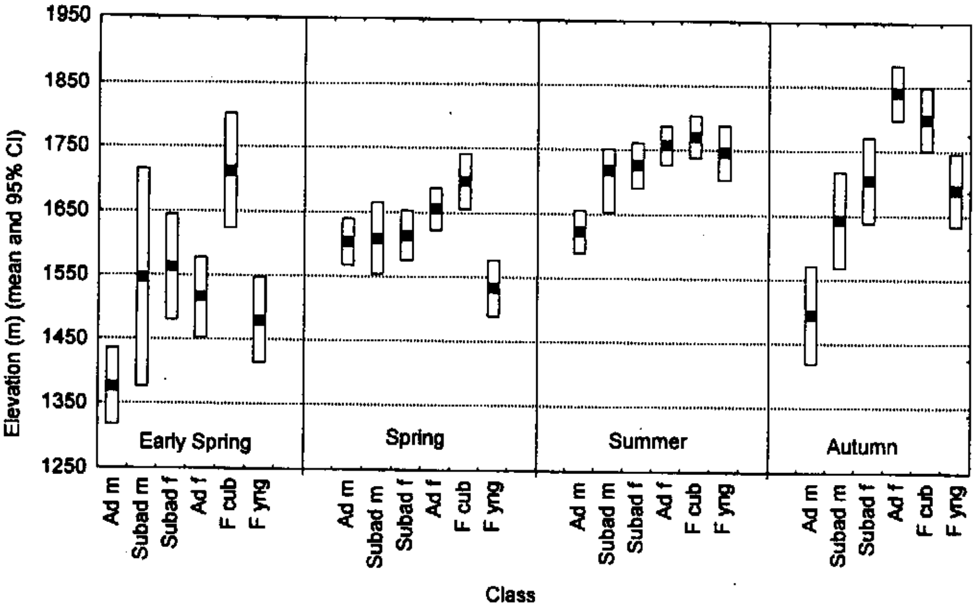


Figure E.1. Seasonal use of elevation by classes of grizzly bears in the Swan Mountains, Montana.

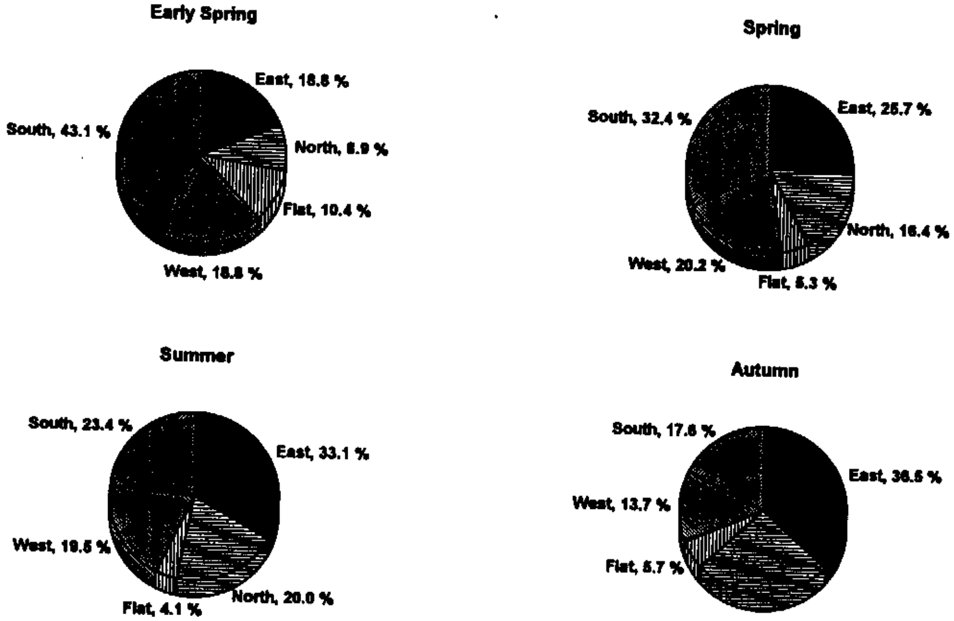


Figure E.2. Seasonal use of aspect by classes of grizzly bears in the Swan Mountains, Montana.

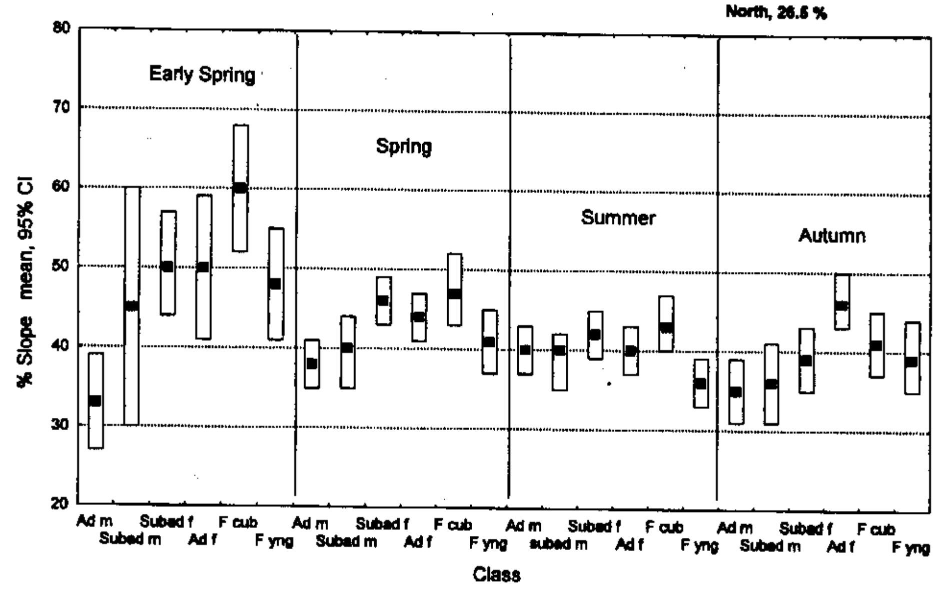


Figure E.3. Seasonal use of slope by classes of grizzly bears in the Swan Mountains, Montana.

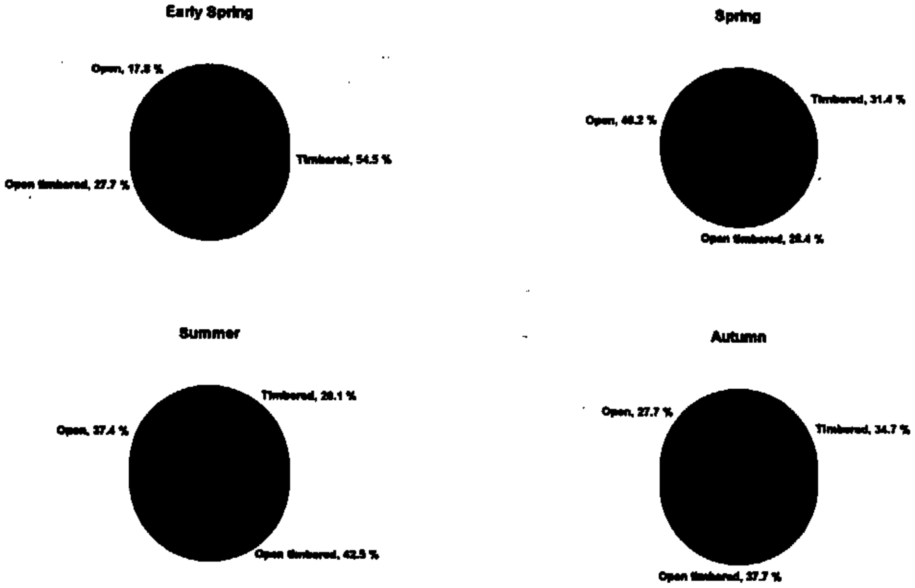


Figure E.4. Seasonal use of open, open-timbered, and timbered habitats by classes of grizzly bears in the Swan Mountains, Montana.

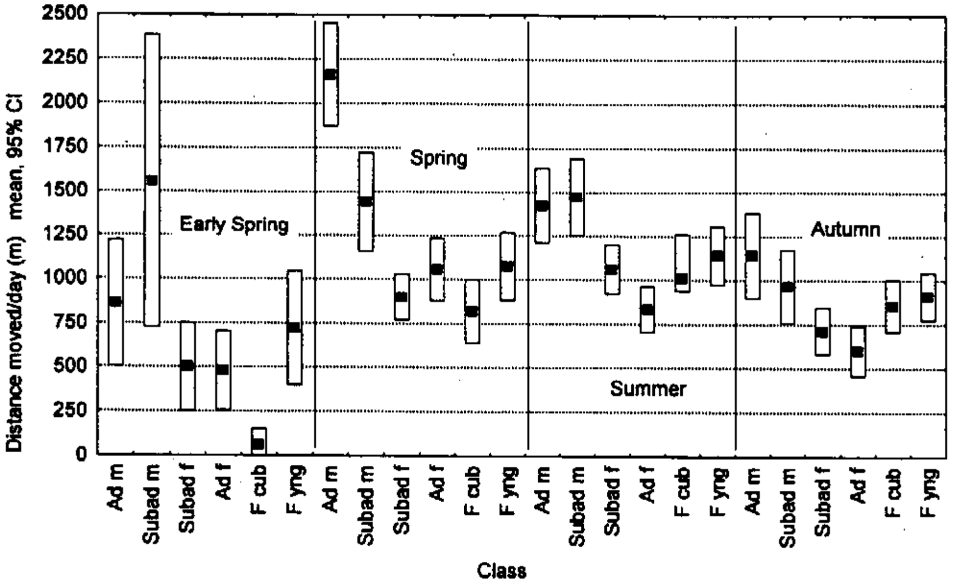


Figure E.5. Average daily movement distances (m) for each season by classes of grizzly bears in the Swan Mountains, Montana.

APPENDIX F

NOTES ON THE BREEDING SCHEDULE AND REPRODUCTIVE PAIRING OF GRIZZLY BEARS IN THE SWAN MOUNTAINS, MONTANA.

R. D. Mace and J. S. Waller

INTRODUCTION

During this study, we had the opportunity to collect information on the reproductive biology of grizzly bears in the Swan Mountains. We were particularly interested in breeding chronology, the duration of male/female pair bonds, and polygamy in Swan Mountain grizzly bears.

METHODS

The breeding season for grizzly bears was estimated using several sources of information. We recorded all instances where instrumented male and female pairs were observed together during fixed-wing aircraft flights during spring. We could not definitively determine the sex of unmarked adults in the company of marked adults. However, because male grizzly bears tend to be of a larger body size than females, differentiation was often possible. The locations of observed male/female pairs during spring were categorized by 2 habitat variables. Locations were classified as occurring in either the low temperate, temperate, or subalpine elevation zone or as occurring in either nonvegetated/grass lands, shrub lands, coniferous forest, avalanche chutes, slabrock, or cutting units (Mace et al. 1996). Comparisons of grizzly bear location to availability in the study areas were conducted using Bonferonni simultaneous confidence intervals (Byers et al. 1984). During May and June captures, each female was examined for evidence of estrous by inspection of external genitalia. Those bears having enlarged vulva were considered to be at some stage of estrous (Craighead et. al. 1969, Pearson 1975).

RESULTS AND DISCUSSION

Breeding Schedule

The duration of aerial observations of male/female pairs during the breeding season were generally too short to observe actual copulatory behavior. In only several instances did we actually observed bears copulating. Our data on breeding chronology therefore encompassed the period of pre- and post-copulatory behavior. We were not able to ascertain the length of the estrous period for individual female grizzly bears because observations per individual were too few during spring.

The schedule of breeding, based on observations of male/female pairs of grizzly bears, varied among years (Fig. F.1). The median annual date when male/female pairs were observed varied from 20 May in 1992 to 22 June in 1988. When observations of observed pairs were pooled among years (Fig. F.2), the peak of the breeding season occurred during the week of 28 May through 3 June. In general, we considered the best estimate of breeding season length to be that period between 14 May and 3 June (28 days). This breeding season length of approximately 28 days during late May and early June, was quite similar to those observed elsewhere in North America (IGBC 1987, p. 42).

Almost all adult females exhibited evidence of estrous during the spring capture program (Fig. F.2), and we were most successful at capturing adult females during the peak of the breeding season.

Reproductive Male/female Pairs

We observed male grizzly bears with 14 radio-collared females during 25 individual female estrous periods between 1988-1995. In 68% of these 25 spring estrous periods the radio-collared female was observed in the company of 1 male. Radio-collared females were observed with 2 individual males in 24% of the periods, and with 3 males in 8% of the estrous periods. Adult females were observed in the company of both adult and subadult males. In only one case did we observe an individual radio-collared male (a subadult) revisit the

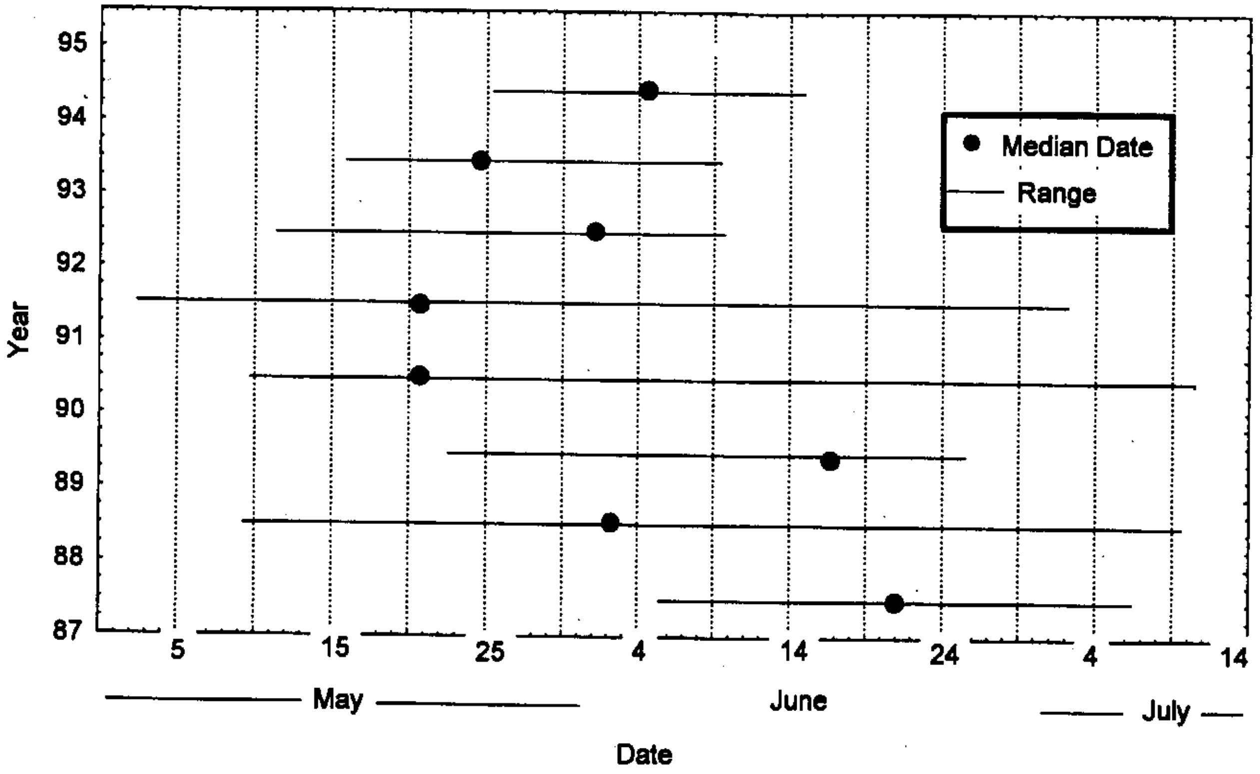


Figure F.1. Annual variability in the breeding schedule of grizzly bears as documented by visual observations of male and female pairs. Swan Mountains, Montana.

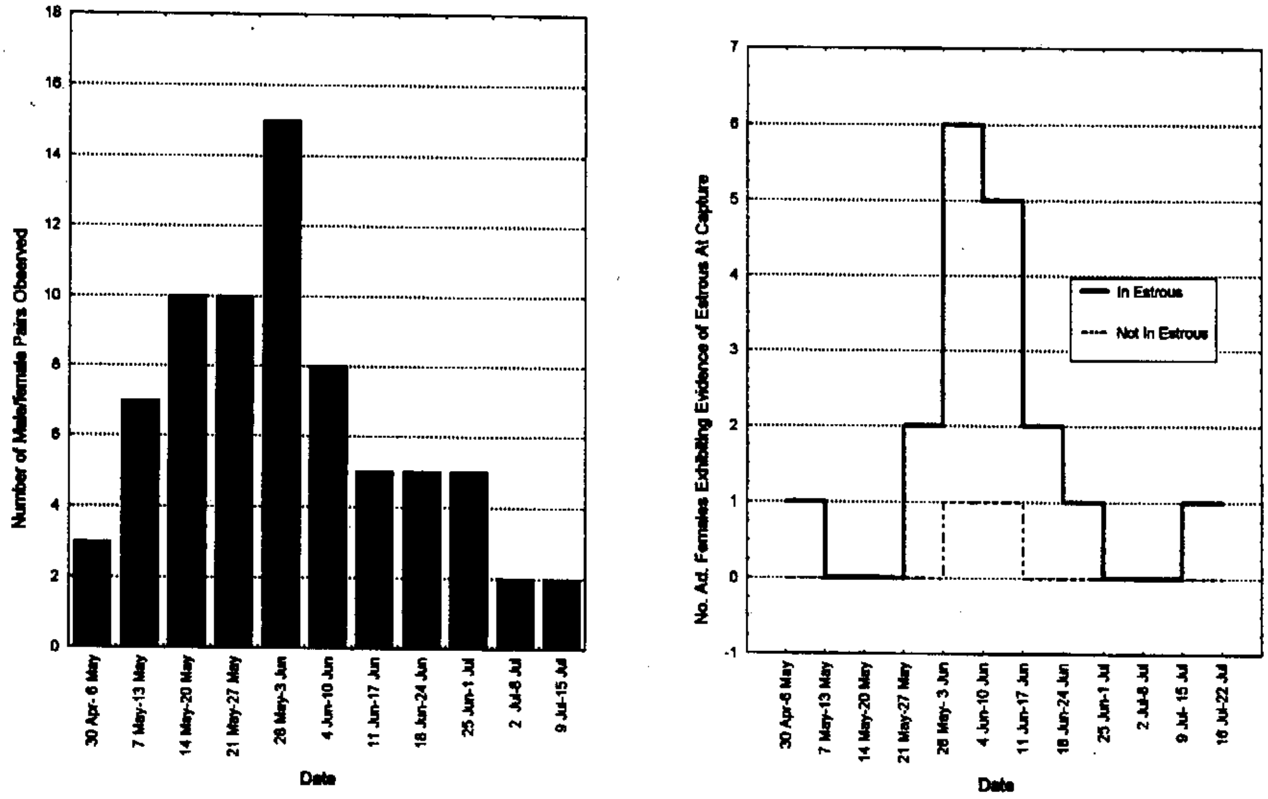


Figure F.2. The pooled sample of male and female pairs observed each week (left). Weekly tally of females exhibiting evidence of estrous during capture (right). Swan Mountains, Montana.

same radioed adult female more than once during a year. These data suggest that males generally spent < 1 week with each receptive female as found elsewhere (Murie 1981, Hornocker 1962, Modafferi 1984).

Twenty-four of 25 observed estrous periods occurred within the study area and in only 1 instance was a radio-collared female observed with an unmarked male. This suggested that most males were radio collared and that little immigration of males from elsewhere occurred during the breeding season. We observed radio-collared males with unmarked females in 16 instances between 1988 and 1995; 9 occurred in the study area and 7 occurred in other portions of the NCDE. Three radio-collared males moved extensively throughout the NCDE during spring and provided the 7 observations of unmarked females outside of the study area. Five of these 7 observations occurred in the Bob Marshall Wilderness, 1 in the Middle Fork Flathead River, and 1 along the Rocky Mountain East Front. Three of the 5 observations in the Bob Marshall Wilderness occurred during 1994 and may have been the same female.

We evaluated habitat selection from 57 observations of male/female pairs during the breeding season. No selection for elevation zone was observed ($P = 0.23$), therefore pairs were likely to be observed at all elevations. Selection of cover type was observed (Table F.1). Male/female pairs selected against the coniferous forest and cutting unit cover types relative to the availability of those types. Pairs exhibited positive selection for avalanche chutes during the breeding season.

Table F.1. Location of 57 male/female pairs during the reproductive period relative to habitat cover types. Swan Mountains Montana.

Cover type	Observed Proportion	Expected Proportion	Selection[a]
Nonvegetated/grass land	5.3	2.7	=
shrub land	15.8	13.4	=
Coniferous forest	38.6	61.6	-
Avalanche chute	33.3	5.2	+
Slabrock	3.5	1.4	=
Cutting unit	3.5	14.7	-

[a] Used less than expected (-), as expected (=), greater than expected (+) relative to availability.

APPENDIX G

CHARACTERISTICS OF A HUNTED BLACK BEAR POPULATION, SWAN MOUNTAINS, MONTANA

J. S. Waller and R. D. Mace

ABSTRACT Frequent incidental captures of black bear (*Ursus americanus*) occurred during a long-term study of grizzly bear (*Ursus arctos*) ecology in the Swan Mountains of northwestern Montana. These incidental captures provided an opportunity to compare harvest data to capture data, and examine some morphological characteristics of a hunted black bear population. Both spring and fall black bear hunting seasons were conducted within the study area. Hunter effort could not be quantified for the study area alone, but regionally remained constant during the study. Our capture effort varied across the study area and was stratified into 3 zones; north, core, and west. These zones also differed in the type of hunting that occurred within them, although known harvest levels did not differ. Median age of males and females was similar in the harvested and the trapped sample, and seemed to decline during the study. Observed median ages were consistent with that of a heavily hunted population. Sex ratio remained constant during the study and was consistent with that of a lightly exploited population. We concur with other authors that sex ratios are of limited value for estimating population trend and harvest rate. Marked bear returns suggested that current harvest rates were near or at the maximum sustainable within the study area. Some morphological characteristics of this population are presented and discussed, as well as trapping injury related to this study.

INTRODUCTION

In 1987 the Montana Department of Fish, Wildlife, and Parks (MFWP) initiated a 10-year study of grizzly bear ecology in the Swan Mountain range of northwestern Montana. During our effort to capture grizzly bears, frequent incidental captures of black bears occurred. This sample of marked black bears provided an opportunity to examine some demographic and morphological characteristics of a hunted black bear population. The objectives of this paper were to report trapping effort and hunter effort within the study area, then compare and contrast the observed age and sex structures of the capture and harvest samples and relate them to black bear management, and to discuss the implications to management of having varying hunter effort and grizzly bear density within bear management units. We further describe some physical characteristics of black bears within our study area.

STUDY AREA

The 927 km^2 study area was located in the Swan Mountains of northwestern Montana (Fig. G.1), and was bordered by the Flathead River and the town of Hungry Horse to the north, Hungry Horse Reservoir to the east, the Bob Marshall Wilderness to the south, and the crest of the Swan Mountains to the west. The study area was arbitrarily divided into 2 zones; the north zone and the core zone (Fig. G.1). In 1990 the study area was expanded westward to the edge of contiguous forest cover in the Swan and Flathead valleys finally encompassing 1,457 km^2. The area of expansion comprised a third portion termed the "west zone".

The study area lay within MFWP administrative Region 1 (northwest Montana), and comprised 30% of MFWP Bear Management Unit (BMU) 106. The study area included portions of 3 hunting districts (HD); HD130, HD132, and HD140.

METHODS

Black bears and grizzly bears were systematically captured in the study area within the 3 distinct zones (Fig. G.1). During the spring of 1988 and 1989, sixty traps were spaced as evenly as possible across the core and north zones; each trap site was approximately 2 miles equidistant. In the spring of 1990 we ceased trapping in the north zone because no grizzly bears had been captured there

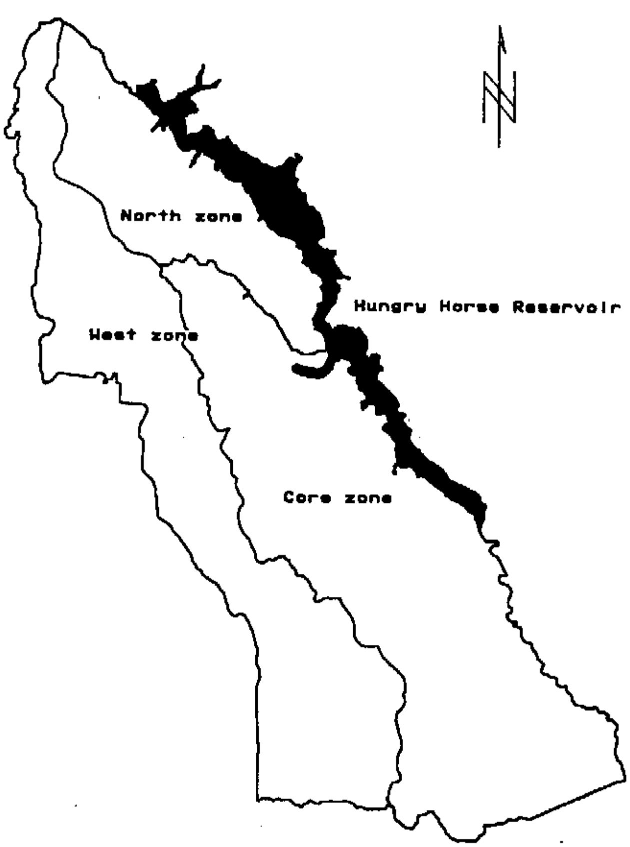


Figure G.1. Swan Mountains Montana, study area divided into 3 trapping zones.

(Mace and Manley 1990). Instead, the study area boundary was moved west to the edge of the Swan and Flathead valleys (west zone). Again, traps were placed equidistantly throughout this area. Trapping continued in the core zone as well. Bears were captured opportunistically during 1987, and 1991-1995 to meet other project objectives. We compared capture rates (nights/capture) between zones by age and sex using chi-square tests.

The majority of trapping was conducted during the spring between 1 May and 30 June each year. Trapping success declined dramatically during the summer months as alternative foods became available and bears were less attracted to bait. A variety of baits were used, but was primarily road killed deer and elk or livestock.

Bears were captured in log cubby sets and trail sets in the vicinity of the cubby. Snares were constructed of 6.3 mm galvanized steel aircraft cable with either cable clamp or compression sleeve fittings. Snare cables were anchored to live, healthy conifer trees of at least 20 cm diameter.

Captured black bears were immobilized with either Telazol® or a 2:1 mixture of ketamine hydrochloride (Ketaset®) and zylazine (Rompun®). Dosages were determined by visually estimating the bear's weight. Once immobilized, the captured bear was weighed on a scale, measured, and ear-tagged. The ear tag number was also tattooed on the upper lip. No radio collars were placed on any black bear. We estimated age from tooth eruption and wear patterns, then extracted a vestigial premolar for age verification. Measurements included zoological length, head circumference, neck circumference, shank length, chest girth (behind hump), fat level, breeding condition, nipple length and width, front and rear pad length and width, and claw length. Fat level was a subjective measure of overall condition, from 1 to 5, based on the amount of fat felt over the rib cage. T-tests were used to compare measurements between males and females.

To minimize the error associated with determining age, bears were grouped as sub-adults (1.5-5.5 years), and adults (>5.5 years). No cubs were captured during the study. Age of first reproduction varies considerably between studies, but 3-5 years is the most common (Reynolds and Beecham 1980, Yodzis and Kolenosky 1986, Rogers 1987, Hellgren and Vaughn 1989, Schwartz and Franzmann 1991). However, studies in our geographic region have found 5.5 years to be the age of first reproduction (Jonkel and Cowan 1971, Kasworm and Thier 1994).

During the study, MFWP administered both spring and fall black bear hunting seasons within the study area, and the use of dogs or bait was prohibited. The spring season was April 15-May 15 and the fall season was September 1-November 27. Successful hunters were required to present the skulls of harvested bears to MFWP personnel within 10 days of harvest so that a premolar could be extracted for age determination. We compiled data on black bears harvested within the study area from regional records. Hunter effort was estimated for the entire region from random telephone surveys of bear hunting license purchasers.

We assessed black bear population status by examining 4 criteria in the captured and harvested samples; 1) % females in adult age class, 2) % males in adult age class, 3) % females/males in sample (sex ratio), 4) median age by sex.

Bear movements were assessed by calculating the distance from the point of original capture to the point of recapture. Also, for those marked bears killed by hunters, kill drainage was compared to capture drainage.

RESULTS AND DISCUSSION

Demography

From 1987 to 1995, 191 individual black bears were captured during 8,529 trapnights (Fig. G.2). Thirty-nine individuals were recaptured 50 times. During this study we averaged 58 trap nights per black bear capture, and 40.5 trap nights per capture if 1994, (a year in which we targeted specific grizzly bears), is excluded (Table G.1). Other reported rates are; 23.7 nights/capture in Arizona (LeCount 1982), 34.8 nights/capture in Minnesota (Rogers 1987), 41.6 nights/capture in Alaska (Schwartz and Franzmann 1991), 32.8 nights/capture in Montana (Aune 1994), and 25.5 nights/capture in N.W. Montana (Kasworm and Thier 1994).

Capture rates were significantly different between the 3 study area zones ($X^2 = 63$, 6 df, $P = 0.00$) thus precluding analysis of a pooled sample. Adults of both sexes and subadult females were more likely to be caught in the west zone than the core or north zones. Adult males and females were less likely to be caught in the core zone than other zones. Subadult males were caught equally in all zones.

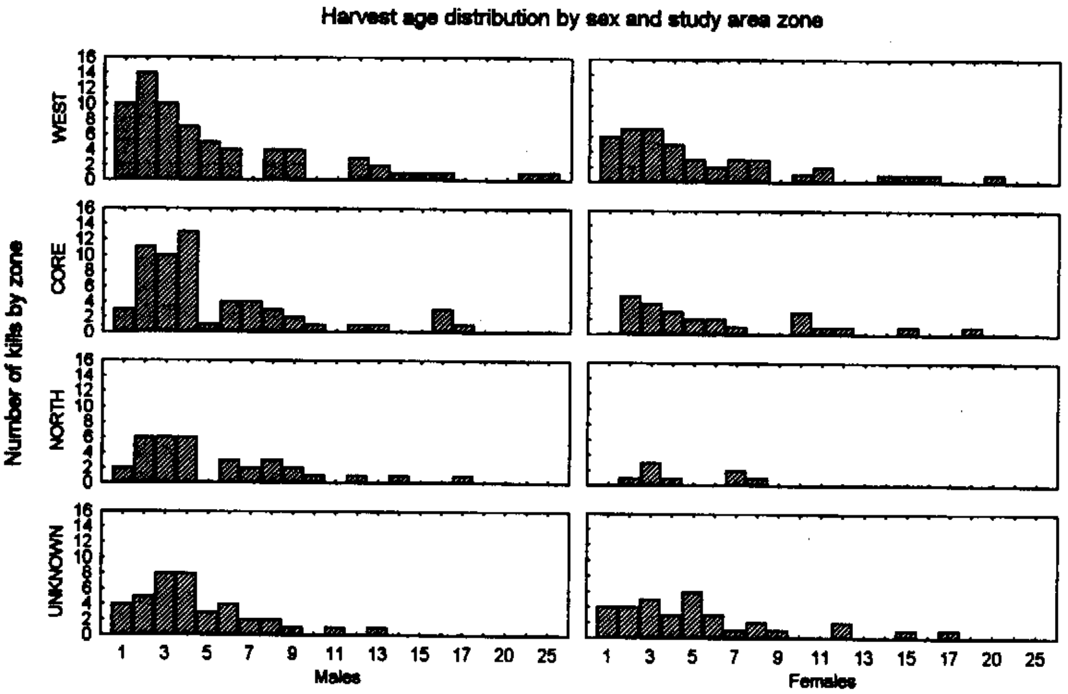
The 3 study area zones are distinct in several ways. The core area is hunted more heavily by nonresident and guided black bear hunters. The west zone is more accessible to the urban population of the Flathead and Swan valleys than the more remote core zone. The North zone is intermediate in accessibility, being further from the city of Kalispell (the largest local population center) than the west zone, but less remote than the core. Overall capture success (nights/capture), percent adults, and median age was highest in the west zone and lowest in the core (Table G.1). The west zone also had the most balanced sex ratio; the other zones being heavily skewed towards males (Table G.1). Further, grizzly bear densities in the core were high, and much higher than in the west zone (Mace and Waller In press). There is some evidence that high grizzly bear densities can reduce black bear densities (Aune 1994).

During the period 1987-1995, 4,437 black bears were harvested in MFWP Region 1. BMU 106, which contains the study area had 880 of these kills, or 20% of the regional harvest. We were able to place 224 of these kills within one of our study area zones. An additional 129 hunter kills within BMU 106 (37%) could not be classified as to zone, or if they were in the study area or not, and were placed in an unknown category. Thus the recorded study area bear harvest during 1987-1995 is 224-353, accounting for 25-40% of the kill in BMU 106 and 5-8% of the regional kill. On average, 25-40 bears are harvested each year in the study area. The total known harvest was equally distributed ($X^2 = 6.7$, 6 df, $P = 0.34$) among the 3 zones (Table G.2). Within each zone, 66-83% of the harvest occurred during spring, even though more hunters and hunter days occurred during fall. However, on a region wide basis, equal numbers of bears were taken in the spring and fall seasons. Regional numbers of hunters, estimated regional hunter days, and numbers of bears taken in the study area stayed relatively constant during the period of study (Table G.3). Spring hunter days ranged from 12,197 in 1988 (2,527 hunters) to 17,094 in 1987 (3,337 hunters). Fall hunter days ranged from 20,584 days in 1988 (2,867 hunters) to 26,655 days in 1992 (3,707 hunters).

The majority of the known non-guided harvest occurred within the west zone (52%), with 20% and 28% occurring in the north and core zones respectively. Guided hunters accounted for 16% of the harvest within the study area. The majority of the guided harvest (82%) occurred within the core zone, while 15% and 3% occurred in the west and north zones respectively. Bears harvested by guided hunters were not significantly older than those taken by

Table G.1. Capture rate (nights/black bear capture) % adults by sex, median age, and sex ratio of capture sample, Swan Mountains, Montana, 1987-1995.

	Capture Rate				%	%			Sex
	Subadults		Adults		Males	Females	Median age		Ratio
Zone	Males	Females	Males	Females	Adult	Adult	Males	Females	(M:F)
Core	87	243	178	257	33	49	4.5	5.5	68:32
North	60	239	72	179	45	57	4.5	6.5	76:24
West	63	147	74	63	46	70	5.5	8.5	56:44


Harvest age distribution by sex and study area zone

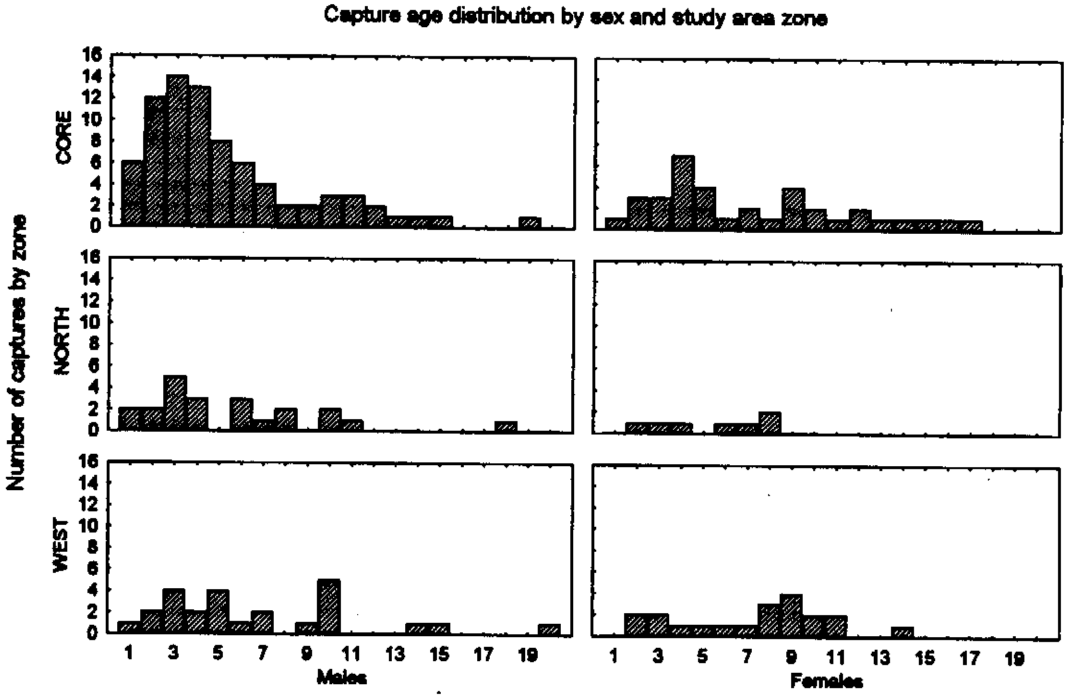

Capture age distribution by sex and study area zone

Figure G.2. Capture and harvest age distribution by sex and study area zone, Swan Mountains, Montana 1987-95.

Table G.2. Harvest by study area zone. Swan Mountains, Montana.

	Harvest				%	%			Percent of
	Subadults		Adults		Males	Females	Median age		Harvest
Zone	Males	Females	Males	Females	Adult	Adult	Males	Females	(M:F)
Core	38	14	20	10	34	42	4.0	4.5	23
North	20	4	12	3	37	43	4.0	4.0	11
West	43	26	20	14	32	35	3.0	4.0	29
Unknown	47	37	31	14	40	27	4.0	3.0	37
Total	148	81	83	41	36	34	4.0	4.0	100

unguided hunters (T = -1.18, 377 df, P = 0.24). Likewise, the proportion of males taken by unguided hunters was the same as that taken by guided hunters (65%).

Median age of males and females in the harvest was similar between zones but, for females, was lower than those in the capture sample. Median age of captured males was 4.5 years, the same as the median age of harvested males. Median age of captured females was 7.5 years, higher than the median age of harvested females (4.5 years). Percent adults was also slightly lower in the harvest sample than the capture sample, although the influence of the unknown zone may account for this difference. Several authors have cautioned that age ratios cannot detect changes in population size or trend (Caughley 1974, Bunnell and Tait 1980, Miller 1990), however the age structure of our capture and harvest samples seem indicative of a moderately to heavily exploited population. In the capture sample 49-70% of females were adults and 33-46% of males were adults (Table G.1), while in the harvest 32-40% of males and 27-42% of females were adult (Table G.2). Adults captured during studies of unexploited or lightly exploited populations comprised 51-64% of males and 65-90% of females (LeCount 1982, Young and Ruff 1982, Beecham 1983). Conversely, studies of moderately to heavily exploited populations have shown adults comprising 27-53% of males and 32-69% of females (Jonkel and Cowan 1971, Beecham 1983, Waddell and Brown 1984, Kolenosky 1986, Rogers 1987, Beck 1991, Schwartz and Franzmann 1991).

As in the capture sample, the harvest sex ratio is strongly skewed towards males in all 3 zones. Beecham (1983) states that long-term trapping ef-

Table G.3. Breakdown of black bear recaptures by age class*, sex, and year. Swan Mountains, Montana

	Males			Females			
Year	Yearling	Subadult	Adult	Yearling	Subadult	Adult	Total
1987	0	0	0	0	0	0	0
1988	1	2	1	0	0	1	5
1989	0	1	3	0	0	0	4
1990	0	6	9	0	2	7	24
1991	0	2	1	0	0	0	3
1992	0	1	7	0	0	2	10
1993	0	0	1	0	0	0	1
1994	0	1	1	0	0	0	2
1995	0	0	1	0	0	0	1
Total	1	13	24	0	2	10	50

* Yearlings = 1.5 years, Subadults = 2.5-5.5 years, Adults > 5.5 years.

forts should be expected to show an unbalanced sex ratio favoring males in unhunted populations and favoring females in heavily hunted populations. However a review of other published studies showed no relationship between sex ratio and hunting pressure (LeCount 1982, Young and Ruff 1982, Kolenosky 1986, Miller 1990, Schwartz and Franzmann 1991, Kasworm and Thier 1994). Indeed several authors caution against using sex ratio data (Caughley 1974, Downing 1981, Garshelis 1990) as ratios will stabilize regardless of population trend. Our data show age ratios indicative of a moderately to heavily exploited population and a sex ratio indicative of a lightly exploited population, further blurring the relationship between sex ratio and hunting pressure.

During this study, 61 marked black bears were taken by hunters, representing 17-27% of the total study area black bear harvest, or 5% of the standing marks, per year (Fig. G.3). Thus 5% is a minimum annual mortality estimate assuming no natural mortality and 100% tag return. Bunnell and Tait (1980) suggest that an absolute maximum sustainable harvest rate on black bears is 12%/year, assuming no natural mortality, equal mortality rate among age classes, 5 as the average age of first reproduction, and a natality rate of 0.5. Kasworm and Thier (1994) documented a non-hunting mortality rate of 7%, and a natality rate of 0.51 in their study area. A similar non-hunting mortality rate in our population would put the total mortality rate at the maximum sustainable level (12%). Any additional mortality, such as wounding loss, or significant tag loss, would result in a declining population. Specific tag loss probabilities could not be calculated from the available data, but was highly variable among individuals. One bear was harvested 7 years after tagging with both tags attached, while others had lost tags within 1 year of capture.

A 5% hunting mortality rate with an average kill of 25-40 bears/year would suggest a population of 500-800 bears. A 15% hunting mortality rate would indicate a population of 167-267 bears (Harris and Metzgar 1987). The true population is likely between these two figures. Recaptures could not be used to estimate population size or density for a variety of reasons; inconsistent and non-random trapping effort between zones and years, small sample sizes within zones and years, lack of home range data, unknown trapping heterogeneity and recapture probabilities, and closure violations between zones (White et al. 1982, Waddell and Brown 1984). Less than half (18 of 39) of our recaptured bears were caught in the same drainage in which they were originally marked. Five individuals (13%), all adult males, originally marked in the core, moved across the Swan crest and were recaptured in the west zone. Further, 9 of 61 marked bears (15%) harvested during the study were killed in a zone different from that of capture. All but 2 were adult males. Adult males, on average, ranged further than any other class (Table G.4).

Fraser et al. (1982) presented a method to estimate changes in harvest rate and population size from age-specific sex data. Unfortunately our sample sizes were insufficient to apply this method, a common problem with real bear data (Harris and Metzgar 1987, Miller 1990).

Morphology

Adult male black bears were significantly larger ($P \leq 0.02$) than adult females in all morphological measurements except fat level and rear claw length (Table G.5/G.6). We estimated the weights of 107 individual black bears then compared the estimates to scale weights. On average, we underestimated actual weight by 0.23 kg (SD = 14 kg), and estimates ranged from 62 kg low to 14 kg high. Males and females weighed, on average, 63.6 kg

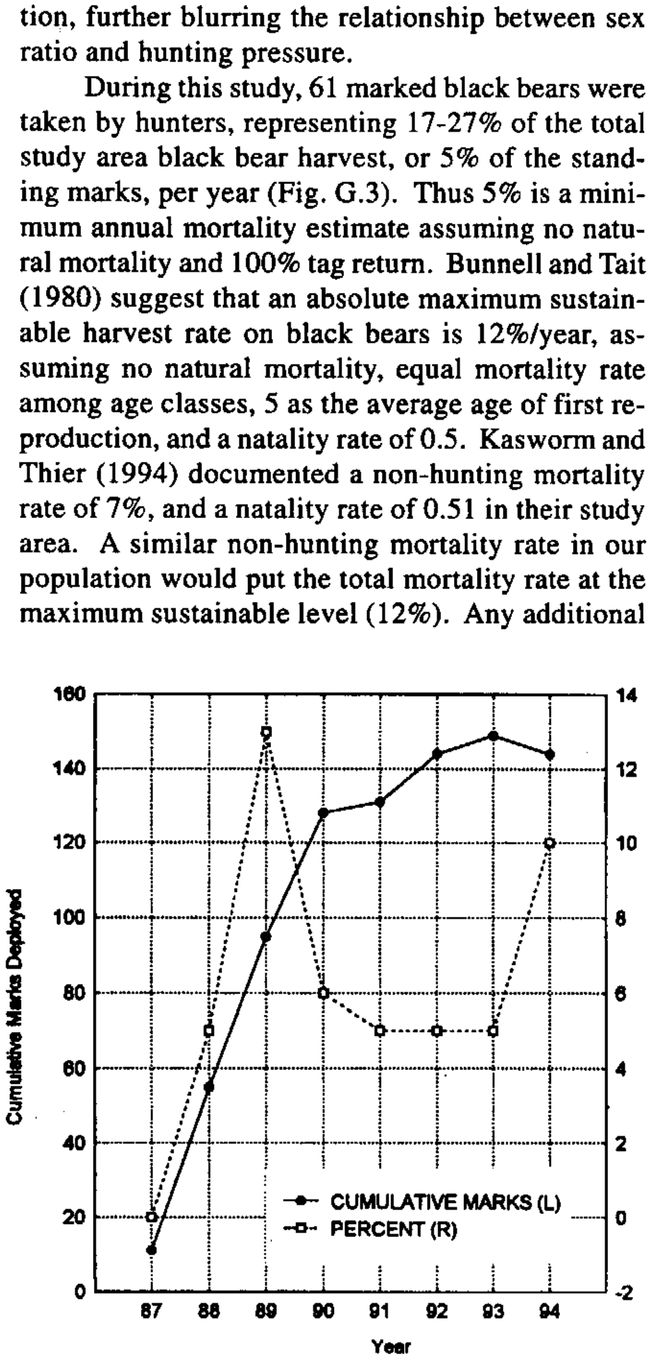


Figure G.3. Cumulative marks deployed and percent marks returned by year in Swan Mountains, Montana study area.

Table G.4. Average kilometers between point of intial capture and subsequent recapture of black bears by age class and sex, Swan Mountains, Montana

	Males		Females	
Age Class*	Average	n	Average	n
Yearling	0.0	1	0.0	0
Subadult	3.8	11	0.0	2
Adult	7.6	21	1.1	10

* Yearling = 1.5 years, Subadult = 2.5-5.5 years, Adult >5.5 years.

and 53.2 kg respectively (Table G.5). Weight was strongly correlated (r = 0.96) to chest girth using the log-log transformation by:

$$\text{Weight}_{(kg)} = 0.002*\text{Girth}_{(cm)}^{2.39}$$

Regression lines of males and females did not differ so sexes were pooled. Other authors have used power functions to obtain similar r values (Payne 1976, Nagy et al. 1984, Swenson et al. 1987). $\text{Log}_{10}\,\text{Weight}_{(kg)}$ was moderately correlated (r=0.89) to $\log_{10}$ front pad $\text{width}_{(cm)}$ for males, but significantly less for females (r = 0.75).

The ages of 120 individual bears were determined from cementum annuli (Matson's Lab 1995) and compared to visual estimates. On average we underestimated age by 0.8 years (SD = 2.9 years) and estimates ranged from 6 years low to 13 years high. Age was only weakly correlated to the various physical measurements we collected.

Of the 191 individuals captured, 156 were inspected for ectoparasites. Most (134) did not have any ectoparasites, 19 had ticks, 2 had mange, and 1 had mites.

Hide color was evenly split between black and brown color phases, 86 having black fur and 91 having brown fur. Only 4 of 181 individuals, for which color was recorded, had a blonde coat.

Breeding condition was recorded for 59 female bears. Nearly half (28) were in estrous at time of capture. Lactation was observed in only 4 of 54 cases in which mammary condition was recorded. Kasworm and Thier (1994) suggested that mammary gland nipple length was related to age and breeding history. We found that mean nipple length of females less than 6 years old was about half that of older females (t = -6.26, 54 df, P = 0.00), but the regression of nipple length on age is weakly correlated (r = 0.34).

Fat level was positively associated with age. No individual younger than 4 obtained a fat level greater than 3 and no bear younger than 9 obtained a fat level of 5. Breeding age adults seem to be attaining a higher nutritional level than subadults, possibly due to experience or preferential access to limited resources.

Few authors report injury rates associated with the capture and marking of bears which makes it difficult to suggest acceptable and unacceptable injury rates. Schwartz and Franzmann (1991) reported a 3% mortality rate, primarily associated with aerial darting, but did not report an injury rate. Beck (1991) reported a high injury rate (37%) during his study of Colorado black bears. We believe that this was due to the use of 4.8 mm diameter snare cable and the practice of using drag logs rather than healthy anchor trees. Cable diameters of less than 6.3 mm are likely to cause cuts, and drag logs encourage bears to continue fighting the snare. During our study, 14 (7%) individuals sustained moderate or severe injuries as a result of being snared. The most common injury was chewing of the capture foot. Eleven individuals (9 males, 2 females) sustained this type of injury, and we believe this was related more to the bears' psychological state than physical injury caused by the snare. Those bears that lost a foot due to chewing are presumed to have healed and survived, as did those individuals that were injured and later recaptured (n = 3). Frequent monitoring of trapsites via transmitter may help reduce this type of injury. Additionally, 1 individual suffered a wrist dislocation, 1 a broken forearm, and 1 suffered respiratory arrest (but survived). One trapping mortality occurred due to a heart problem, presumably exacerbated by the stress of being snared.

MANAGEMENT RECOMMENDATIONS

Montana's black bear management guidelines (MFWP 1994) specify 3 targets designed to maintain a conservative harvest of female bears; "a) no more than 40% of the annual harvest comprised of females, b) median age of harvested bears at least 6.5 years for females and 4.5 years for males, c) if harvest composition does not comply with a) and b) in any 3 consecutive years, all data from the management unit will be analyzed to determine what management changes are warranted". Similar criteria are used throughout the Pacific Northwest to manage bear harvests (Garshelis 1990). Our study area met requirement a. in both harvested and captured samples, but has not met requirement b. in either sample since 1990, and never met requirement b. for the female segment of the harvest. The same situation was observed within BMU 106; requirement a. was being met, but requirement b. was not, and has not since 1990 (MFWP, Unpublished data). We believe the word "and" in requirement c. should be changed to "or" until empirical testing of these criteria has been conducted. A top research priority should be to validate or discount the utility of these criteria.

Technology exists to manage populations at scales finer than that currently used. Hunter effort

Table G.5. Morphological characteristics of captured adult (>5 years old) black bears, Swan Mountains, MT 1988-95. All measurements except fat level are in cm unless otherwise noted.

Character	Mean	Minimum	Maximum	SD	n
Adult Males					
Weight (kg)	89.0	52.3	154.5	23.9	25
Age (yrs)	9.7	6.0	20.5	3.5	48
Length	158.4	133.3	180.3	9.2	44
Head	58.8	45.7	68.6	4.6	31
Neck	59.3	43.2	73.7	7.4	32
Shank	34.5	22.2	40.6	4.3	20
Chest girth	93.9	68.5	114.3	9.5	43
Fat level	3	1	5	1	43
Front pad width	11.4	10.2	12.7	0.7	28
Front pad length	6.8	5.7	8.9	0.8	24
Front foot length	11.5	10.2	13.3	1.0	24
Front claw length	3.3	2.5	5.7	0.8	23
Rear pad length	15.0	9.8	17.8	1.5	27
Rear pad width	10.7	8.9	15.2	1.2	27
Rear foot length	19.3	15.5	21.7	1.3	26
Rear claw length	2.1	1.0	4.4	0.6	24
Adult Females					
Weight (kg)	58.3	38.6	79.5	9.9	19
Age (yrs)	9.8	6.0	17.5	2.8	36
Length	142.2	120.6	158.7	8.9	33
Head	51.0	44.4	55.9	2.8	21
Neck	47.1	39.4	54.6	3.7	23
Shank	30.9	19.0	36.2	4.5	17
Chest girth	78.8	62.9	94.0	6.6	33
Fat level	2.3	1	4	0.6	34
Front pad width	9.5	8.2	10.5	0.6	26
Front pad length	5.8	4.4	7.0	0.6	21
Front foot length	10.2	7.6	12.1	0.9	21
Front claw length	2.9	2.2	3.8	0.4	21
Rear pad length	12.6	9.2	14.6	1.2	21
Rear pad width	9.4	7.6	19.0	2.4	22
Rear foot length	16.2	1.9	19.7	3.5	21
Rear claw length	2.0	1.6	2.5	0.26	20

and success can and should be recorded to levels that can be applied to population management. Current management could be described as being at a metapopulation level (BMU). However, the application of change-in-ratio techniques to monitor harvest rates are hindered by small sample sizes.

The black bear demographic data collected during this study was of limited utility due to the lack of radio telemetry and inconsistent trapping effort. Any future effort to validate these population management criteria must be conducted to a strict research protocol to ensure that trapping effort is consistent within a geographically defined study area. Trap bias can be minimized by marking a high percentage of the population in a high intensity, short term trapping effort. Radio collars

Table G.6. Morphological characteristics of captured subadult (<5.5 years old) black bears, Swan Mountains, MT 1988-95. All measurements except fat level are in cm unless otherwise noted.

Character	Mean	Minimum	Maximum	SD	n
Subadult Males					
Weight (kg)	48.0	13.6	164.5	28.7	42
Age (yrs)	3.1	1.0	5.0	1.2	78
Length	132.5	58.4	190.5	20.0	63
Head	47.7	33.3	69.2	6.5	46
Neck	43.6	24.8	83.8	10.0	51
Shank	31.4	18.7	41.9	4.8	40
Chest girth	70.2	40.9	118.1	12.7	63
Fat level	1.8	1	4	0.8	66
Front pad width	9.9	7.5	13.0	1.2	51
Front pad length	5.8	2.7	10.8	1.6	47
Front foot length	10.1	7.0	14.3	1.4	47
Front claw length	3.0	2.2	5.4	0.6	47
Rear pad length	13.2	7.3	17.1	1.9	47
Rear pad width	9.2	7.3	12.1	1.2	47
Rear foot length	17.6	12.1	22.9	2.1	47
Rear claw length	2.0	1.3	2.8	0.3	47
Subadult Females					
Weight (kg)	39.8	13.6	81.8	13.7	21
Age (yrs)	3.4	1.0	5.0	1.1	27
Length	127.5	80.0	150.0	14.1	26
Head	45.0	33.6	57.1	4.7	22
Neck	40.9	27.3	52.1	4.97	24
Shank	27.6	18.4	33.0	4.2	18
Chest girth	66.3	46.3	85.7	8.0	27
Fat level	1.9	1	3	0.5	26
Front pad width	9.0	7.0	10.2	0.8	22
Front pad length	3.7	2.7	4.5	0.4	22
Front foot length	3.7	2.7	4.5	0.4	22
Front claw length	2.5	1.9	3.2	0.3	21
Rear pad length	11.6	8.9	14.0	1.3	22
Rear pad width	8.9	6.6	16.5	1.9	21
Rear foot length	16.0	12.7	19.0	1.4	22
Rear claw length	1.9	1.3	2.5	0.3	21

are essential for estimates of survival, mortality, and reproduction. Hunter effort and distribution needs to be quantified for the study area through surveys and check stations. Regional personnel need to be trained to recognize bears that have been previously marked and to collect pertinent information. Utilizing new technologies may overcome some of the limitations inherent with current techniques; transponder tags may eliminate problems of tag loss and hunter bias, GPS collars can dramatically increase telemetry sample size, and DNA techniques could be used in place of marking. Proposed research activities should also use methods that minimize the risk of injury to study animals. Snares and culvert traps can be designed and used safely, provided certain guidelines are followed (Jonkel 1993).

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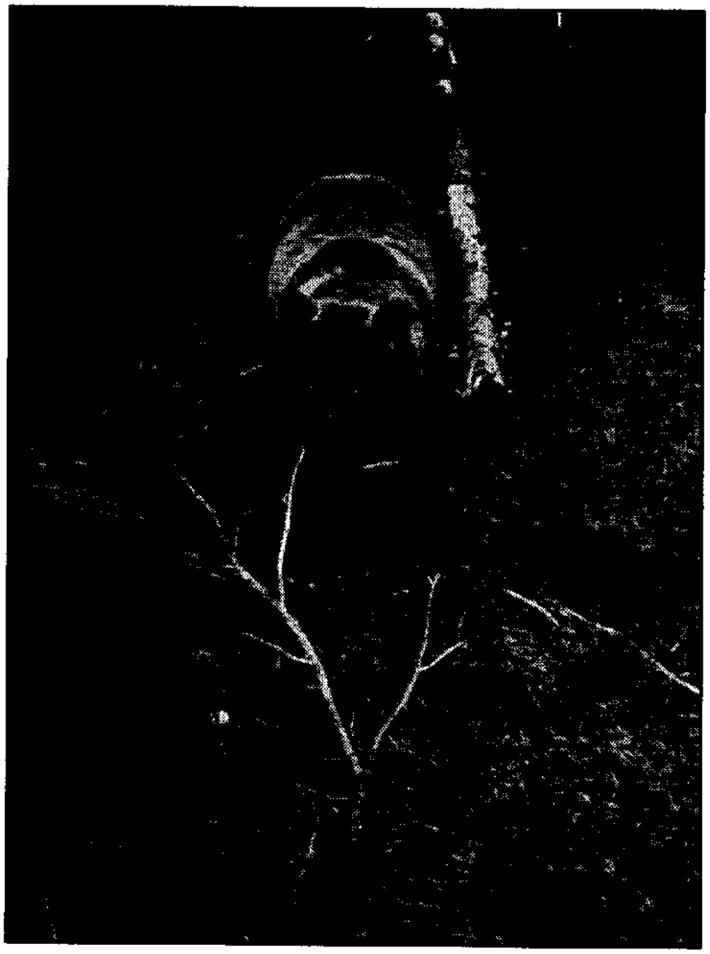

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