EFFECTS OF RESOURCE EXTRACTION INDUSTRIES ON
BEHAVIOUR AND POPULATION DYNAMICS OF GRIZZLY BEARS IN
THE FLATHEAD DRAINAGE, BRITISH COLUMBIA AND MONTANA.

By

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We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
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Date August 24/1989
The range and numbers of grizzly bears (*Ursus arctos* L.) have been greatly reduced since Europeans settled North America and there is concern that various human activities threaten many of the remaining bears. In this thesis I examine relationships between resource extraction industries and grizzly bear ecology, behaviour, and population dynamics in an area undergoing timber harvest and gas exploration.

The major hypothesis investigated was that the industrial activities in the study area would be detrimental to the grizzly population and I predicted either a low density of bears compared to other interior populations, or at least a negative rate of increase. To determine specific causes for any observed population response, I monitored behavioural reactions of grizzly bears to industrial activities and habitats modified by these activities.

The selection of seasonal home ranges and use of habitat components, elevation, and aspects by grizzly bears from these ranges are presented. Based on 4872 relocations of 55 radio-collared bears over a 9 year period, grizzlies were found to generally follow 1 of 2 seasonal home range selection strategies. Mountain resident (MR) bears remained in mountainous terrain for the entire year while elevational migrating (EM) bears moved down to the Flathead Valley bottom twice each year. Habitats frequently used by bears were low elevation riparian areas, snowchutes, high elevation burns, and
low elevation timber and open timber. Cutting units were rarely used.

Most bears used habitats within 100 m of roads less than expected, resulting in an effective habitat loss of 8.7%. Avoidance of roads was independent of traffic volume, suggesting that only a small number of vehicles is sufficient to displace bears. However, roads and nearby areas avoided by bears during day were used at night. Yearlings and females with cubs used habitats near roads more than other bears. Five comparisons of bear use before, during, and after industrial activity indicated little displacement.

Because the estimated average density of grizzly bears was 6.4/100km², which was high for an interior population, and their estimated rate of increase was positive ($r_s = 0.081$), the major hypothesis was rejected. Resource extraction industries did contribute to grizzly bear mortality indirectly, however, by making roads which provide easy access to hunters, poachers and settlers. Of the 9 grizzlies which died when radio-collared, 2 were killed by legal hunting, 5 were illegally killed; 3 of these illegal kills occurred in 4% of the study area with permanent human settlement. Vehicular access planning and post-operational control are major recommendations of this study.
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CHAPTER 1: GENERAL OVERVIEW

Relatively recent reductions in grizzly bears (*Ursus arctos* L.) throughout most of western North America have resulted in bears being restricted to remote and mountainous locations with limited human intrusion. Their apparent need for seclusion from people (Hamer 1974, Craighead 1976, Knight 1980) may be incompatible with exploitation and development of natural resources such as forests, oil, gas, and minerals, over a large portion of their range. Although these industrial activities are generally considered to be harmful to the grizzly population (Mundy and Flook 1973, Pearson 1975, Schallenberger 1980, Horejsi 1986), developments are destined to occur because of the economic value of natural resources. Concurrent with resource extraction, most people desire the continued existence of remaining grizzly bear populations (Hamer and Herrero 1983). If we are to sustain both industry and grizzly bears, intensive management based on detailed biological information is required (Hamer and Herrero 1983).

Until recently, most grizzly bear research focussed on population dynamics, behaviour, food habits, and habitat use, without specifically addressing the influence of human industrial activity (see review in LeFranc et al. 1987). This focus changed in 1975 when the grizzly bear in the U.S.A. (excluding Alaska) was classified as threatened under the U.S.A. Endangered and Threatened Species Act and it became
illegal to destroy or adversely modify critical grizzly bear habitat (Jacobsen 1980). The Act highlighted the detrimental influence that human activities have had on grizzly bears, and consequently, research began to focus on the relationship between people and bears (Zager et al. 1983, Aune et al. 1986, Simpson et al. 1985, Reynolds et al. 1986, Horejsi 1986, Ballard 1987, Mattson et al. 1987, Archibald et al. 1987). Although these studies were usually directed at behavioural responses of grizzly bears to humans, the variables of ultimate importance are those determining population dynamics (Shank 1979).

I investigated both behavioural and population responses of grizzly bears to timber harvest, gas exploration, and, to a lesser degree, to human settlement and hunting in the Flathead drainage between 1979 and 1987. Linking the two levels of responses, behavioural and demographic, allowed me to identify how the grizzly population was influenced by people. It also provided a focus for management prescriptions on the most important factors, while reducing emphasis on less critical ones.

This thesis consists of four chapters following this general introduction to the study, study area, and general methods used. The second chapter covers the selection of seasonal home ranges from the study area, and habitats, elevations and aspects from within these ranges by grizzly bears during a period of resource extraction.

The third chapter consists of modifications of two papers
(McLellan and Shackleton 1988 a, McLellan and Shackleton in press a) that address the behavioural responses of grizzly bears to roads, seismic exploration, timber harvest, and road maintenance. Chapter 4 treats the population dynamics of the grizzly population during the period of resource extraction. It combines 3 papers; one on density and age-sex composition of bears, one on mortality rates and causes of death, and the third on natality rates and rate of population increase (McLellan in press a, b, and c). The final chapter contains a summary, general discussion and conclusions.

STUDY AREA

The study area (Figure 1) was the 2900 km$^2$ composite home range of grizzly bears captured and radio-collared in the North Fork of the Flathead River drainage in south-eastern British Columbia and adjacent Montana ($114^\circ 85' W; 49^\circ 1' N$). This river flows through the area at an elevation ranging from 1310 to 1200 m. The 5 to 10 km wide, flat bottomed valley contains extensive riparian areas which support several key spring and autumn bear foods. Large portions of the area were burned during the late 1800's and early 1900's (Zager et al. 1983). Lodgepole pine (Pinus contorta) is the dominant tree species in the valley. In several locations, buffalo berry (Shepherdia canadensis), an important summer bear food, grows in abundance. During the mid 1970's, a mountain pine beetle (Dendroctonus ponderosae) epidemic killed many pines, and during the following decade a large proportion of the trees were harvested
Figure 1. Map of the study area.
by clear-cut logging.

On either side of the wide valley, subranges of the Rocky Mountains rise to >2800 m. In the side valleys, sub-alpine fir (Abies lasiocarpa), spruce (Picea engelmanni x P. glauca) and Douglas-fir (Pseudotsuga menziesii) are common. Many of these higher timbered sites suffered an infestation of spruce bark beetles (Dendroctonus pbesus) during the 1950’s and early 1960’s, and again during the early 1980’s, which killed trees, many of these were salvaged by clear-cut logging. Extensive forest fires burned some high elevation areas early in the century. Some of these areas currently produce huckleberries (Vaccinium spp.), another important grizzly bear food during late summer and autumn. Rock outcrops, alpine and subalpine meadows, and snowchutes are common in mountainous portions of the study area.

The intensity of industrial activity in the study area varied greatly within and between years. At least some timber harvest occurred each year of the study, with a maximum of about 200 forestry employees working at one time. Ongoing gas exploration began in 1980 and a maximum of approximately 300 employees worked in the study area at one time. The nearest settlement in Canada is 100 km from the study area, but settlement begins at the border in the U.S.A.

Many game animals, including grizzly bears, are hunted in the study area. Regulations for grizzly hunting have become increasingly restrictive since 1968 when the use of bait for attracting bears became illegal. Prior to 1971 when the autumn
season was closed, the average annual number of bears taken legally in the British Columbia Ministry of Environment Management Units in which the study area is located, 4-01 and 4-02, was 13.8. After 1975 when compulsory reporting of kills began, this number was reduced to 5.5.

METHODS

Capture and Radio-telemetry

Using foot snares at approximately 150 trap locations, 65 different grizzly bears were captured, ear-tagged, lip-tattooed, and had a vestigial premolar removed for aging by counting cementum annuli; 55 of these bears were radio-collared (Telonics Ltd; Mesa, Arizona; 164-166 MHz). When first captured, 3 grizzlies were cubs (0 to 1 years), 17 were yearlings (1 to 2 years), 11 were subadult males (2 to 5 years), 8 were subadult females, 16 were adult males (> 5 years) and 10 were adult females.

All radio-collared bears were relocated from fixed-wing aircraft approximately once each week. Because of the numerous roads in the study area, ground tracking was relatively efficient. Locations from the ground were usually obtained by recording a compass bearing from at least 3 separate map locations. In steep terrain where signal bounce created problems, numerous approximate bearings were taken while walking at least 180° around the animal. Radio locations used to determine an individual's home range were obtained at least one day apart.
CHAPTER 2: SEASONAL HOME RANGE AND HABITAT SELECTION DURING A PERIOD OF RESOURCE EXTRACTION

Most grizzly bears do not live in reserves or parks and many must co-exist with a variety of human activities. Many activities such as timber harvesting, mining, ranching, gas and oil developments, and hydro-electric reservoirs can eliminate or at least alter the physical and vegetative characteristics of the bears' habitat. Even in parks, where the environment has most protection, highways, railroads, and tourist facilities can affect habitats and animals which depend on them. Understanding the relationship between grizzly bears and their habitat is important if we are to plan developments in ways that reduce our impact on bears and minimize the probability of dangerous bear-human encounters.

Johnson (1980) suggested that resource selection by animals is hierarchical. He defined first order selection as that of a species' geographical range, from which an individual makes a second order selection by choosing the location of its home range. Higher orders of selection include the habitats used from within a home range, choice of feeding and bedding sites within a habitat, and the selection of foods within a feeding site.

The degree of selection possible and the way an animal selects probably depends upon the level considered. For example, an animal is less likely to be in a general geographic area due to choice than due to circumstances of birth.
Selection at this level is more a question of basic requirements of the species than of an active choice by individuals.

When selecting a seasonal home range from a geographical area, an animal usually chooses a mosaic of habitats. Some of these habitats the animal will require, others will be less important, while some may be of little or no value but be included within the range simply because they are interspersed among those habitats that the animal does require. For an animal with large ranges due to specific behaviour or to habitat requirements, a preponderance of low quality habitat may confuse an analysis of seasonal range selection.

Most grizzly bear habitat research has been focused at the order of selection of habitat components from an animal's range or study area (Zager et al. 1983, Servheen 1983, Almack 1986). At this level, the bears' ability to know the distribution of general habitats and rapidly move about the seasonal range is important in determining how we measure habitat selection (McLellan 1986). In this chapter I investigate 2 levels of selection by various age and sex classes of grizzly bears during a period of resource developments: (1) seasonal home ranges from a geographical area, and (2) habitat components, elevations, and aspects from within these seasonal ranges.

METHODS

MEASURING SELECTION

Many methods have been proposed to estimate selection at
the level of habitat from within a study area by comparing habitats used to those available. Availability has usually been assumed to equal the area a habitat covers (see reviews in Alldredge and Ratti 1986, McLellan 1986). A lack of selection is assumed if an animal uses habitats in the same proportion as their coverage (= availability).

The method of Neu et al. (1974), as modified by Marcum and Loftsgaarden (1980), has been used most often in grizzly bear habitat research (Servheen 1983, Zager et al. 1983, Almack 1986). McLellan (1986) identified shortcomings of this and other methods for measuring habitat selection. These shortcomings are particularly prevalent when some habitats cover more area than others and are therefore assumed to be more available. This problem is rooted in the ability of an animal to learn the distribution of resources, whether these be potential home ranges, habitat units or feeding sites. Generally, if an animal knows the location of all resources and if it can choose any with equal effort, then all resources are equally available. If the animal does not have this knowledge or if it cannot obtain any resource at an equal cost, as in the case of food selection by a generalist predator, then a measure of availability is important. The process of selection and how we measure it will vary among Johnson’s (1980) orders of selection because of differences in what an animal can learn and because of differences in costs required to obtain various resources.

For the selection order of habitat components from a
seasonal home range, McLellan (1986) proposed that: (1) if there is relatively little cost in moving among habitats, (2) if resources in the habitat are not depleted within the duration of the study, and (3) if an individual has learned the location of habitats within its range, then the availability of a habitat is not equal to the proportion of the area it covers, but all are equally available and selection equals use. An omniscient animal will always be at a site that it has selected at that particular time for a particular reason (McLellan 1986). It is recognized, however, that habitat selection does not necessarily equal habitat value and animals may "actively" select habitats for some activities such as feeding while "passively" using other habitats. For example, an animal may use a certain habitat to travel through only because it lies between feeding sites. To differentiate among degrees of active selection and passive or default use, higher orders of selection must be studied and reasons for selection ascertained.

Selection of Seasonal Ranges

Based on major changes in foods and habitats used by grizzly bears, I recognized 5 seasons: (1) Early spring - emergence from dens until green-up or approximately between early April and 10 May. This season was short or non-existent for bears which emerged late from dens. (2) Spring - from green-up until the ripening of berries or, approximately 10 May to 1 August. (3) Summer - when berries (Vaccinium spp.,
Shepherdia canadensis became the dominant food or between approximately 1 August and 20 September. (4) Autumn - from when berry use decreased until denning, or approximately 20 September to mid-November. (5) Winter - when bears hibernated. Seasonal home ranges were plotted using the minimum convex polygon method (Mohr 1947). This chapter contains data collected between April 1979 and December 1987.

To permit comparisons among studies, my study area was partitioned into 10 habitat components (Table 1) similar to those described by Servheen (1983), Zager et al. (1983), and Almack (1986), and by management agencies in Montana (Christensen and Madel 1982) and British Columbia (Harper 1988). Due to geology, vegetation, and disturbance history, habitat components were relatively homogeneous, yet large enough to encompass most radio location error polygons.

The study area was also divided into 6 elevation groups (1 was < 1400 m; 2 to 5 were at 200 m intervals between 1400 and 2200 m; 6 was > 2200 m), 4 aspects and flat (< 5% slope).

To determine the characteristics of the geographical area, 257 points were randomly located over the entire study area and at each point the habitat component, elevation and aspect were recorded (Marcum and Loftsgaarden 1980). The same information at an additional 1977 random points was recorded and those lying within the seasonal range (x = 168 points/range) of each bear were used to estimate the characteristics of this range. The habitat component, elevation and aspect characteristics of composite seasonal ranges of all bears were estimated by
Table 1. Habitat component descriptions for the Flathead study area after Servheen (1983) and Zager (1983).

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<th>Component Name</th>
<th>Description</th>
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<td>cutting unit</td>
<td>Open or partially timbered site where timber harvest has disturbed natural vegetation.</td>
</tr>
<tr>
<td>meadow</td>
<td>Naturally open sites with relatively flat topography.</td>
</tr>
<tr>
<td>riparian</td>
<td>Hydrologically active with moving water that may be ephemeral. Generally timbered with dense understory.</td>
</tr>
<tr>
<td>road</td>
<td>Open, disturbed areas, cleared or graded.</td>
</tr>
<tr>
<td>rocky</td>
<td>Loose rock or solid bedrock with various plant communities intermixed.</td>
</tr>
<tr>
<td>burns</td>
<td>Areas with conifers less than 10 m in height due to early succession after a wildfire. These sites were often dominated by shrubs.</td>
</tr>
<tr>
<td>Component Name</td>
<td>Description</td>
</tr>
<tr>
<td>----------------</td>
<td>-------------</td>
</tr>
<tr>
<td>snowchutes</td>
<td>Steep open areas where periodic avalanches limits vegetation to forbs, graminoids, shrubs and stunted trees.</td>
</tr>
<tr>
<td>open timber</td>
<td>Sparsely timbered, relatively flat areas generally above 1800 m in elevation where sedge and forb fields are common.</td>
</tr>
<tr>
<td>sub-alpine</td>
<td>All other areas except above with between 5 and 30% canopy cover.</td>
</tr>
<tr>
<td>timbered</td>
<td>All other areas except above with greater than 30% canopy cover.</td>
</tr>
</tbody>
</table>
including all points from each individual's seasonal range. Because one point could be located in the range of several bears, the sample size of points representing the composite range was reduced to the number of different points used, but each point was weighted by how frequently it was used.

At the level of seasonal range selection from the study area, I chose the method of Neu et al. (1974), as modified by Marcum and Loftsgaarden (1980), for 2 reasons. First, although a few bears may have learned the location of all potential seasonal ranges in the study area, this is unlikely to be true for most, and so they cannot freely choose from all. Secondly, by their extensive nature, seasonal ranges would contain many habitat components, elevations or aspects, not because the bear desired them, but by default and so confuse analyses.

To test if the seasonal ranges had an equal proportion of random points in each habitat category as the entire area, the G test was used (Sokal and Rohlf 1981). If significantly different (P < 0.05), the Bonferroni z statistic (Marcum and Loftsgaarden 1980) was utilized to determine which categories covered different proportions of the 2 areas. I used 90% simultaneous confidence intervals for habitat components (k=10), and 95% intervals for elevation (k=6) and aspect (k=5).

Selection from within Seasonal Ranges

Unlike selection of seasonal ranges from the study area, bears on established ranges probably know the location of most habitat units within a seasonal range at the component level.
and are free to choose any, independent of the area they cover. Therefore, bear selection of habitat components, elevations, and aspects from within seasonal ranges will equal their use. However, because of the possibility of selection by default, the area covered by various habitat components, elevations and aspects in seasonal ranges will be mentioned. I will address higher orders of selection in the future and this should reveal the purposes various habitats are used for.

Comparisons among Age-sex Classes and Reproductive Status of Adult Females

To compare habitat components, elevations and aspects used by different age-sex classes and three reproductive states of adult females (with cubs, with yearlings or older offspring, and alone), the G test was used (Sokal and Rohlf 1981). If significantly different (P < 0.05), the Bonferroni z statistic was used to determine which categories the bears used differently with the same simultaneous confidence intervals that were used for seasonal range selection.

RESULTS

Selection of Seasonal Ranges from the Study Area

Grizzly bears followed 1 of 2 general strategies of seasonal range selection. Some lived in the mountains on either side of the Flathead Valley and rarely, if ever, descended to the valley floor. I called this group mountain resident (MR) bears. A second group, elevational migrating
(EM) bears, moved to the valley soon after emerging from their dens and generally remained at lower elevations until berries became ripe in high elevation burned-off areas. Members of both groups of bears usually moved to these burns, but most EM bears returned to the valley during the autumn. To reduce variance caused by these 2 strategies, data from each group are analyzed separately in this chapter, and are only combined to investigate areas that both strategists use. Seasonal range selection was determined by comparing the ranges of each group to the entire study area.

During early spring, spring, and autumn, EM bears chose seasonal ranges that had different proportions of habitat components, elevations, and aspects than occurred over the entire study area (all $P < 0.001$). In these three seasons, EM bears selected ranges with characteristics typical of the valley bottom, with significantly more low elevations and flat terrain than the entire study area and less burns and open timbered subalpine habitat. The summer ranges of EM bears did not have significantly different proportions of habitat components or elevations than the study area but did have more west facing aspects (Figures 2, 3, 4, and 5).

Insufficient data were collected to determine the selection of early spring ranges or habitats from these ranges by MR bears. The spring, summer, and autumn ranges of MR bears, however, had significantly different proportions of habitat components, elevations, and aspects (all $P < 0.001$) than the entire study area. All three seasonal ranges of MR
Figure 2. The proportion of random points (coverage) located in various habitat components (top), elevations (middle), and aspects (bottom) over the entire study area and early spring ranges of Elevational Migrant (EM; n=13) bears. Also shown is the proportion of early spring radio-locations (use) of EM bears in the habitat components, elevations, and aspects.
Figure 3. The proportion of random points (coverage) located in various habitat components (top), elevations (middle), and aspects (bottom) over the entire study area and spring ranges of Elevational Migrant (EM; n=29) and Mountain Resident (MR; n=8) bears. Also shown is the proportion of spring radio-locations (use) of EM and MR bears in the habitat components, elevations, and aspects.
Figure 4. The proportion of random points (coverage) located in various habitat components (top), elevations (middle), and aspects (bottom) over the entire study area and summer ranges of Elevational Migrant (EM; n=21) and Mountain Resident (MR; n=8) bears. Also shown is the proportion of summer radio-locations (use) of EM and MR bears in the habitat components, elevations, and aspects.
Figure 5. The proportion of random points (coverage) located in various habitat components (top), elevations (middle), and aspects (bottom) over the entire study area and autumn ranges of Elevational Migrant (EM; n=24) and a Mountain Resident (MR; n=8) bears. Also shown is the proportion of autumn radio-locations (use) of EM and MR bears in the habitat components, elevations, and aspects.
bears had significantly less flat terrain, but more elevations above 1800 m, burns and rocky habitats than the entire study area (Figures 3, 4, and 5).

Habitat Selection Within Seasonal Ranges

**Early Spring** - During the early spring, EM bears were located most often in timber (45% use, n = 204; 50% coverage of EM bears’ early spring ranges n = 778), followed by riparian (21% use, 12% coverage) and open timber (12% use, 5% coverage; Figure 2). These bears used elevations below 1400 m (68% use, 56% coverage) and flat terrain (66% use, 43% coverage) most often. EM bears were located 4% of the time in cutting units (13% coverage) during the early spring.

Of the 300 possible cells combining habitat components, elevations and aspects, two were used much more than others. Riparian below 1400 m and on flat terrain covered 5.3% (n = 2234 total random points) of the study area but received 18.7% of the use during early spring. Timber below 1400 m and on flat terrain consisted of 11% of the study area but EM bears were relocated in it 28.6% of the time. A cluster of cells of open timber on south and east aspects above 1800 m, received 9.3% of the use but covered only 1.5% of the area.

**Spring** - Riparian was the most frequently used habitat component (55% use, n = 1863; 11% coverage, n = 1371) by EM bears during spring and timber was second (24% use, 52% coverage; Figure 3). EM bears were located most often on flat (80% use, 40% coverage) and low (74% use, 49% coverage < 1400 m).
m) terrain. The single cell of riparian, below 1400 m and flat received 51.3% of the EM bears’ spring use while covering only 5.3% of the study area. Although this cell type dominated EM bear use, the flat, timber cell below 1400 m was also used frequently (14.1% use, 11.7% coverage). Cutting units were used rarely (3% use, 10% coverage) during spring.

MR bears used snowchutes (32% use, 4% coverage) most often followed by timber (16% use, 24% coverage), burns (14% use, 27% coverage), and riparian (13% use, 1% coverage; Figure 3). Elevations most often used by MR bears during spring were between 1600 and 2000 m (62% use, 56% coverage) on east and south aspects (66% use, 46% coverage). Combined information on snowchute use by EM and MR bears (n = 173 locations) indicated all aspects between 1400 m and 1600 m were used, but most use was of east and south aspects (65% use, 39% coverage of snowchutes). Cutting units (3% use, 12% coverage) and elevations above 2200 m (2% use, 10% coverage) were rarely used by MR bears.

**Summer** - EM bears used burns (52% use, n = 1391; 23% coverage, n = 946) most often during the summer (Figure 4). These bears were relocated between 1600 and 2000 m (57% use, 41% coverage) most often but also used low elevations (22% use, 26% coverage < 1400 m) during summer. South and west aspects were commonly used (23% and 33% use, 18% and 28% coverage respectively) as was flat terrain (27% use, 23% coverage).

MR bears were also located most often in burns (69% use, n = 184; 38% coverage, n = 403; Figure 4), and with information
from both MR and EM bears combined, heavily used cell clusters during summer were south and west facing burns between 1600 and 2200 m (37% use, 7% coverage). Of the burns in the study area, 40% were open timbered (5 to 30% canopy cover), and they received 60% of the total use of burns (n = 855) which is significantly more use ($G = 3.96$, df = 1, $P = 0.047$) relative to their coverage than open burns received. Although burns dominated bear use during summer, other cell clusters receiving heavy use were open timber below 1600 m and on flat terrain (5% use, 1% coverage), and open timber on south and west facing slopes just below the burns at 1400 to 1800 m (3% use, 0.5% coverage). Cutting units were rarely used by EM (1% use, 8% coverage) or MR bears (0.5% use, 4% coverage) during the summer.

**Autumn** - Timber was the most frequently used habitat component (52% n = 825, 51% coverage, n = 984) by EM bears during this season, followed by riparian (21% use, 12% coverage; Figure 5). Elevations below 1400 m (57% use, 55% coverage) and flat terrain (59% use, 45% coverage) were most often used.

MR bears were located most often in rocky habitats (31% use, 25% coverage), followed by timber (24% use, 21% coverage) and burns (18% use, 37% coverage; Figure 5). Elevations between 1800 and 2200 m (60% use, 54% coverage) were used most frequently. West was the least used aspect (11% use, 27% coverage) by MR bears during the autumn. Cutting units were also infrequently used by EM (2% use, 10% coverage) and MR (0% use, 1% coverage) bears during autumn.
Variation Among Age-Sex Classes and Reproductive Status of Adult Females

**Early Spring** - Only data collected on use by EM adult males, adult females and subadult females was sufficient to permit comparisons during early spring. These 3 classes used habitat components, elevations and aspects differently (all $P < 0.001$). EM adult males were located more often on flat terrain (89% $n = 92$), below 1400 m (93%) and in riparian areas (33%) than either adult females (49%, 50%, 10%; respectively, $n = 69$) or subadult females (49%, 44%, 11% $n = 44$).

Adult females with cubs used open timber (54%, $n = 24$), elevations between 1800 and 2200 m (91%), and south aspects (74%) significantly more than when alone (0%, 12%, 0%, $n = 17$) or with older offspring (11%, 14%, 14%, $n = 28$).

**Spring** - The 5 age-sex classes of EM bears used habitat components, elevations, and aspects differently during spring. Use by adult and subadult males was similar to each other as was use by adult and subadult females, but there were differences between sexes. EM males used elevations above 1600 m and snowchutes more than EM females (15% vs 9% & 8% vs 2% for adults and subadults respectively). Compared to the other EM age-sex classes, independent yearlings used meadows (0% vs $x = 3$%), riparian (27% vs $x = 55$%), and elevations below 1400 m (36% vs $x = 73$%) less, and timber (45% vs $x = 23$%), cutting units (13% vs $x = 3$%) and elevations between 1400 and 1600 (52% vs $x = 15$%) more than the other age and sex classes.

There was a difference in the use of habitat components,
elevations, and aspects (all $P < 0.001$) among EM females at different stages of reproduction. Females with yearlings made the greatest use of riparian (72%, $n = 194$), followed by when they were alone (57%, $n = 281$), and least when with cubs (47%, $n = 170$). The inverse was found for the frequency of use of timber; females with cubs were located there 32% of the time, females alone 24%, and those with yearlings only 14%. EM females with cubs were also relocated below 1400 m (63%) and on flat terrain (70%) less than when alone (78% and 85% respectively) or with yearlings (91% and 93% respectively).

MR adult male and female grizzly bears also used habitat components, elevations, and aspects in different proportions (all $P < 0.05$) during spring. Males were found more than MR females at elevations below 1400 m (11% vs 0.5%) and on flat terrain (23 vs 11%). Although there was a significant difference between how MR adult males and females used habitat components, simultaneous confidence limits did not reveal any one to differ. There were no significant differences in use by MR females of different reproductive status in this season.

Summer - There was a difference in use of habitat components, elevations and aspects (all $P < 0.001$) by the 5 classes of EM bears during summer. Adult females were relocated more frequently in open timber (17%, $n = 587$) than the other age-sex classes ($x = 6$%). Independent yearlings were found below 1400 m (49%, $n = 118$, vs $x = 19$%), on flat terrain (62% vs $x = 27$%) and in riparian habitats (20% vs $x = 7$%) more often during the summer than other bears. No significant
differences were noticed between summer use by adult male and female MR bears.

EM adult females used open timber less frequently when with yearlings (9% n = 148) than when with cubs (16% n = 171) or alone (23% n = 257). When with cubs, females were located more often below 1400 m (31% vs 9% and 16%) and on flat terrain (40% vs 16% and 22%) than when with yearlings or alone respectively.

Autumn - The only significant difference noticed between the classes of EM bears during autumn was greater use of timber (61% n = 287) by males of both ages than adult and subadult females (45% n = 508). There were too few relocations of independent yearlings during autumn for comparisons. MR adult males were relocated more often in timber (36% n = 43 vs 14% n = 50) and below 1400 m (21% vs 2%) than were adult females.

DISCUSSION

The two strategies of seasonal home range selection found by grizzly bears in the Flathead Drainage are similar to those reported on Admiralty Island, Alaska, by Schoen et al. (1986). On Admiralty Island, most bears migrate down to low elevations and feed on salmon (Onchorynchus spp.) during the summer, but some bears remain at higher elevations throughout the year and forgo this rich food source.

In the Flathead study area, EM bears selected early spring and spring ranges centered in the wide Flathead Valley. Before green up, these bears chose timbered sites and riparian
habitats most often from their ranges. Major foods appear to have been roots of *Hedysarum sulphurescense* and winter weakened or dead ungulates (McLellan, unpublished data). Although this early season has not been distinguished in the Rocky Mountains, Servheen (1983) did report movements to low elevations early in the year.

Once green-up occurred, EM bears used riparian habitats, where several major bear foods grow abundantly, more often than all other habitat components combined. Servheen (1983) and Zager et al. (1983) also found grizzlies to use riparian areas more than expected, but not to the extent reported here. The hydro-electric impoundment and human settlement in their study areas, as elsewhere, have probably reduced the viability of the EM strategy in many grizzly populations.

In spring, MR bears chose ranges in the mountains on either side of the wide Flathead valley. Habitat use by MR bears during spring was similar to that described by Zager et al. (1983), with snowchutes being the most frequently used component followed by timber and riparian.

In summer, both EM and MR bears were located in high elevation burns where huckleberries were abundant, more than in all other habitat components combined. Although Zager et al. (1983) recorded high use of shrubfields during the summer of 1979, the use was much less than found in my study area. Zager (1980) suggested that dry conditions and a poor huckleberry crop in 1979 may have caused varied habitat selection during that summer (Zager 1980).
In autumn, EM bears again chose ranges in the valley while MR used ranges in the mountains. Preliminary analysis indicates that EM bears forage mainly on *Hedysarum sulphureum* and hunter crippled ungulates, while MR bears feed on *Hedysarum sulphureum* and a variety of berries (McLellan unpubl. data).

Although they were not completely isolated, either geographically or reproductively, limited information indicates that the two strategies may have different consequences on the bears' movement patterns, body size and fitness (McLellan unpubl. data). It remains unclear if the strategies result from intraspecific competition at high densities causing displacement to suboptimal habitats, or caused by displacement in the past which has been maintained by learning.

Some authors (Pearson 1975, Russell et al. 1979) have reported segregation between adult males and female grizzlies with cubs, and postulated that it was because adult males were aggressive towards and sometimes kill cubs, yearlings and even adult bears (Glenn et al. 1976, Mundy and Flook 1973, Pearson 1975, Reynolds and Hechtel 1979, Troyer and Hensel 1962). Similar patterns of differential use of habitats were recorded in this study, especially in early spring when EM adult females with cubs remained near their dens at high elevations while the other EM bears descended to the valley.

Although differential habitat use by the sexes was apparent during the rest of the year, it was not as pronounced as in other areas (Pearson 1975, Russell et al. 1979). In both
spring and summer, females with cubs were not located in the population's most highly selected habitats, elevations and aspects as frequently as when they were alone or with yearlings. Segregation between independent yearlings and other grizzly bears was more distinct, with yearlings using timber and cutting more often and elevations slightly higher than other EM bears but lower than MR bears during spring. In summer, yearlings often used areas at lower elevations than other bears. These habitat use patterns, combined with use of habitats near roads (see Chapter 3) may offer both young bears and adult females with cubs, security from adult males.

Some differences in use by the different age-sex classes that can be interpreted as segregation, such as more use of high elevation habitats by EM males than by EM females, or more use of low habitats by MR males than by MR females, may simply be due to males having larger home ranges than females and therefore encompassing a greater variety of habitats, rather than one class avoiding the other.

**MANAGEMENT IMPLICATIONS**

At the habitat component, elevation and aspect levels of selection that I investigated here, some general management guidelines can be generated. Between mid-May and late July, grizzly bears were found >50% of the time either in riparian or snowchute habitats that cover only 7% and 2% of the study area. Between late July and late September, burns also received over half the use but covered only 16% of the area. Proper
management of these 3 habitat components is critical for the long term conservation of the species in the Flathead Valley and other areas with similar habitats.

For riparian and snowchutes, proper management may simply be limited to protection from development and settlement, however, active management should be investigated. For example, snow may rarely slide when conditions are optimum for large avalanches to generate bear habitat. The use of explosives to start avalanches when conditions are optimal could maintain avalanche chutes in their most productive state for bear foods.

Because burns are an early successional component, protection of this habitat can only be a temporary management action. Prescribed fires and/or a "let burn" policy in appropriate high elevation sites will be required to maintain and improve the distribution of this habitat.

Because timber was frequently used by bears in the spring and autumn, and because cutting units were rarely used in any seasons by either MR or EM bears, it could be interpreted that timber harvest had a negative effect on grizzly bear habitat. However, some bears chose to forage in portions of some cutting units for brief periods, and, although timber is often used by bears, it is not clear how much timber is required by bears to maintain their current population density. When the selection process is studied at more detailed levels, reasons for the use of some cuts and not others may be better understood.
CHAPTER 3: THE BEHAVIOURAL RESPONSE OF GRIZZLY BEARS TO RESOURCE EXTRACTION INDUSTRIES

There are many kinds of bear-industry interactions, but the most immediate concern is the extensive network of roads that industries depend on for access. Roads also increase access for hunters and poachers, the probability of vehicle-bear collisions, and the frequency of energy costly flight responses by the bears. Also, indirect population constraints could result if long term displacement of bears from areas adjacent to roads occurs. Roads often follow valley bottoms and pass through riparian areas which are frequently used by grizzly bears. If roads do displace bears, this should lead to increased pressure on similar habitats in undisturbed regions and the "loss" of these essential but limited habitats. Some variation in bears' responses to roads has be predicted; adult females with young cubs may avoid areas near roads more than other bears (Zager 1980); darkness may acts as cover for bears (Servheen 1981) and their use of areas adjacent to roads should occur mostly at night.

Although the interaction between grizzly bears and the extensive road networks that resource extraction industries depend on has been of concern to land managers, the influence that the actual industrial operations has had on these bears is also important.

This chapter first presents data on displacement of grizzly bears by roads developed for resource-extraction
industries. I tested the null hypothesis that grizzly bears use areas adjacent to roads as often as they use areas away from them. I also explored the effects of age-sex class and reproductive status of bears, habitat type, amount of vehicular traffic, and time of day on this pattern of use, and on demographic implications. Finally, I present data on a series of natural experiments in which I was able to compare locations of individual bears before, during, and after periods of industrial activity.

Unlike Chapters 2 and 4, which use data collected between 1979 and 1987, this Chapter is based only on information obtained before December 1985.

METHODS

EFFECTS OF ROADS

Five distance-from-road categories (DRC) were delineated: 1) 0 to 100 m; 2) 101 to 250 m; 3) 251 to 500 m; 4) 501 to 1000 m; and 5) >1000 m. Category widths increased with distance from roads because radio relocations are "probability areas" not points, so their precision is a function of the bear-observer distance. Most ground locations were made from roads, so narrower distance categories were acceptable for locations near roads.

Roads were separated into 3 classes: primary roads (main roads leading into the valley), secondary roads (first-order branches off primary roads), and tertiary roads (all other roads accessible by 2 wheel-drive vehicles). Traffic frequency
was sampled opportunistically by counting vehicles (primary roads: n = 241, 205.4 hours; secondary roads: n = 145, 97.9 hours). Vehicles were classed as small (passenger car or pickup truck) or large (> pick-up truck).

Home ranges of all bears contained roads. Using the Marcum and Loftsgaarden (1980) method to estimate resource availability, 1928 random points were located over a map of the study area. For each point, the habitat component (Servheen 1983, Zager 1980), elevation, and DRC of the nearest of each class of road were determined. All random points (x = 228 per seasonal range) occurring within the minimum convex polygon of each bear's seasonal range were used to determine the proportion in each DRC.

The observed frequency of radio locations within each DRC was compared with the expected (available) using the G-test (Sokal and Rohlf 1981: 704-721). If significantly different (P < 0.05), confidence intervals were calculated for each DRC using the Bonferroni approach with 90% simultaneous confidence limits (Marcum & Loftsgaarden 1980). Radio locations separated by at least 10 h were considered independent because a bear could travel between all DRC's in this time; most relocations (96%) were separated by at least 1 day. For many analyses, radio locations for more than 1 bear were grouped and compared to the sum of random points from each of these bear's seasonal home ranges. Because ranges overlapped, the same point could occur within the seasonal range of several bears and be used more than once. Therefore, total sample sizes of random points
were reduced to the number of different points used.

Locating bears during the day often included walking through densely vegetated habitats lacking trails, while night locations could only be made from roads. Consequently, bears located at night were usually individuals that had been located earlier in the day in parts of the study area with high road densities. It was inappropriate to compare all day and night locations, so samples were paired within a 24 h period, and Wilcoxon's matched-pairs signed-ranks test was used. Day-night pairs were also grouped by DRC to enable comparisons at different distances from roads. If the paired locations fell in different DRC's, the closer category was used for analysis.

Bear locations at or near den sites were omitted because they were strongly affected by factors other than roads. For the same reason, locations of bears foraging for huckleberries in high elevation burns during the summer were not used. Good huckleberry production is limited to these burns but, because of a lack of harvestable timber, these areas were 1.5 to 7 km away from roads, so both their use and availability data all fall in the >1000 m DRC.

Due to the short duration of the early spring season, both early spring and spring as described in Chapter 2 were combined and called spring for this chapter. Similarly, because most relocations during the summer were in high elevation burns and therefore not used in this analysis, locations during summer in other habitats were combined with autumn locations for this chapter. Minimum sample sizes for comparisons among individual
bears were defined as 15 relocations per season per bear. Data from both EM and MR bears were grouped in this chapter.

EFFECTS OF INDUSTRIAL ACTIVITIES

Most data presented in this Chapter were obtained in a 12 km$^2$ portion of the study area consisting of 8 minor side-drainages, each perpendicular to a major, steep mountain ridge. Each drainage had been burned by wildfire in the 1920’s (Zager et al. 1983), and is now in various seral stages. Generally, lodgepole pine forest occurs at lower sites (<1525 m), but with increasing elevations these trees, plus some subalpine fir and spruce, become more sparsely distributed up to treeline around 1975 m. Globe huckleberry (Vaccinium globulare) grows abundantly in the 12 km$^2$ area, and their berries dominate the grizzly bears’ diet from early August to late September.

The basic experimental design used to examine bear responses to industrial treatments involved a comparison of radio locations of the same grizzly bears recorded before, during, and after an industrial activity took place. Specific locations were determined either from fixed wing aircraft, or by ground triangulation using at least three compass bearings from a separate known map locations with error polygons less than 10 ha. Occasionally, in steep terrain or remote areas, it was impossible to use triangulation. In these cases, specific locations (accurate to <10 ha) were determined by walking a semi-circle and often completely around the bears while taking numerous bearings. General locations (accurate to <50 ha) were
often obtained in unroaded areas by triangulation from the nearest road. In the case of the intensively studied 12 km² berry area, the road was 2 to 3 km distant.

Treatments

There were 2 periods; 1 was the summer berry season when bears limit their movements and generally restrict themselves to 1 or 2 berry patches. This period is important because most of the fat reserves required for hibernation are laid down at this time. The second period was spring when bears normally are much more mobile throughout their home ranges in search of more widely dispersed foods or mates. Both periods provided contrasting conditions with potentially different implications for bear-industry interactions. Displacement in the summer berry season could have more significant negative effects on bears than during other seasons when more alternative foods were available and survival during hibernation was not at risk.

Seismic Activity in the Vaccinium Area:

The seismic activity involved hand-cut seismic lines for gas exploration. These lines were established across the 12 km² berry area during the period when huckleberries were ripe in 1981, 1984, and 1985 (Figure 6). For each of the lines, 3 zones of industrial activity were defined:

Zone 1 was the seismic line itself, or was the major helicopter flight path servicing the line, together with a 500 m strip on each side. Most helicopter activity, all
Figure 6. The paths of the 4 seismic lines (broken, straight lines) across the 12 km$^2$ Vaccinium spp. berry area and the dates they were cut are shown. Also illustrated are the 8 minor drainages.
drilling, setting charges, stringing and collecting sensing cable, and blasting occurred along the line. Drilling could require 5 days to cross the berry area, and each of the 5 portable drills, compressors, and equipment baskets were transported by either Bell 205 or 212 helicopters. These machines made up to 20 return trips/day from a staging area to the line, and spent up to 260 min/day actively moving equipment along a portion of the line. Difficult drilling, poor weather, and mechanical problems occasionally reduced the intensity of activities.

During the drilling period, smaller helicopters made up to 15 additional trips/day along the line. The smaller helicopters were used to string sensing cables, but these were more active than the large machines, traversing the line up to 30 times/day, and frequently landing or hovering to drop and pick up loads.

Zone 2 was 501 to 2000 m from the seismic line or major flight path, and without a mountain ridge between. I could hear and observe all helicopter traffic in Zone 1 from Zone 2. Helicopters crossed Zone 2 up to 15 times/day.

Zone 3 consisted of areas >2000 m from the seismic line or major flight path, or areas within this distance but with mountains between. Helicopter overpasses occurred less frequently in this zone.

I tested the null hypothesis that the proportion of the bears' radio-locations in the 3 zones were equal before, during and after the seismic program. Radio-locations for each
collared bear using the area when huckleberries were ripe during a year of seismic activity were used. All zones contained portions of the Vaccinium patch (Figure 6), but local berry production and consequent bear use can change significantly between years, so only within-year location data were used. I believe that any confounding due to within-year differences in berry availability resulting from variable ripening dates and bear consumption was minimal in this area largely because the seismic lines were independent of terrain, running straight across all aspects and elevations.

The activities of the grizzlies were scan-sampled (Altmann 1974) at 15 s intervals. Sampling began when I first observed a bear and ended either when it moved out of sight or darkness fell.

The "G" test (Sokal and Rohlf 1981), with a level of significance of $P < 0.05$, was used to compare use between periods. Within the huckleberry area, radio locations separated by 10 h were classified as independent. Grizzly bears could easily traverse the burn in much less time than this. Most locations were separated by at least 1 day.

**Bear-Industry Interactions during Spring:**

Four bear-industry interactions during the spring period studied in sufficient detail, involved the following:

1. A crew of 6 people using 3 pick-up trucks was stringing sensing cable along a seismic line. They were active in this area for 6 h.
2. A seismic sensing cable had been strung along a section of line crossing another riparian area the previous day and more cable was being transported along the line by a small helicopter. This machine made 6 trips along the line at an estimated height of 150 m above ground level over 4 h. A recording truck carrying a small, operating generator, was stationed in the riparian area, and charges were detonated along this portion of the line.

3. On the first day of activity, a D7 Caterpillar tractor was piling slash and building skid roads. On the second day the D7, 4 skidders, 1 loader, 3 power saws, and 14 loggers were actively harvesting timber for 10 h.

4. A small Caterpillar tractor and a grader operated almost continuously for 8 h to improve an old access road for timber extraction.

The working hypothesis used in these 4 interactions, was that bears within 250, 251 to 500, and 501 to 1000 m of an industrial activity would move away immediately. For these tests, it was imperative that the bear be located prior to the onset of the human activity and be monitored constantly at the onset of the activity. It could then be sampled at decreasing frequencies. A potential difficulty of this hypothesis is that grizzlies normally are extremely mobile at this time of year in the absence of human stimuli and so a bear which moves away from a human activity may have done so anyway. By continuously monitoring the bears and the human activity, I can have more confidence deciding if they are displaced by activity.
RESULTS

EFFECTS OF ROADS

Of the 624 aerial relocations, 32% were >1 km from roads compared to 15% of the 2196 made on the ground. This significant difference (P < 0.01) was a result of the radio receiver's limitations rather than a measure of bear use. After omitting data from the most distant DRC, there was no difference between the 422 aerial and 1857 ground relocations of the remaining four DRC's (P > 0.10).

Grizzly bear use of the five DRC's over both seasons combined, using aerial relocations, differed from that expected under the null hypothesis (P < 0.01). They used the 0 - 100 and 101 - 250 m DRC's significantly less than expected, but none more than expected. Ground locations were biased only when >1 km from a road and, because displacement from roads occurred only in the closest DRC's, aerial and ground relocations were combined for subsequent analyses, omitting data from the most distant DRC.

Use of the 4 DRC's differed significantly from what was expected in spring (P < 0.01), summer-fall (P < 0.01), and for both seasons combined (P < 0.01; Figure 7). In spring, habitats within 100 m of roads were used significantly less than expected and the lesser used area extended to 250 m during summer-autumn.
Figure 7. Observed versus expected use by 23 grizzly bears of the 4 Distance-to-Road-Categories (m; DRC) in the Flathead Valley, B.C. Data are combined for all road types, both seasons, ground and aerial radio-locations, and all age-sex classes, between 1979 and 1985. Use differing significantly (P < 0.05) from expected is indicated by + or -. For differences in n values, and Distance-to-Road-Categories see Methods in this Chapter.
Individual Variation

Of the 23 grizzlies for which I had adequate spring information, 14 (61%) used the closest DRC (0 - 100 m) significantly less and 1 used it significantly more than expected. The remaining bears' use of this DRC was not significantly different from expected. No bears used the 101 - 250 m differently than expected, while 6 used either the 251 - 500 or 501 - 1000 m significantly more and 2 less, in spring.

The 0 - 100 DRC was used less than expected in summer-autumn by 7 of 14 bears, while 3 also used the 101 - 250 m DRC also significantly less. Greater use was recorded by 7 bears; each in 1 of the DRC's between 101 and 1000 m.

Variation Among Age-Sex Classes

Independent yearlings used areas within 250 m of roads significantly more, and DRC's between 500 and 1000 m significantly less than all other classes of bears (Figure 8). Two of the 3 yearlings were offspring of radio-collared females and they used the closest DRC significantly more when alone than when they were cubs with their mothers. Contrary to what was predicted by Zager (1980), adult males used the closest DRC significantly less than did either adult or subadult females (Figure 8).
Figure 8. Relative use (proportion of radio-relocations) by 5 age-sex classes of grizzly bears of the 4 Distance to Road Categories (DRC; m) in the Flathead Valley, between spring and fall (1979 to 1985). Significant (P < 0.05) differences among classes in their use of each DRC are indicated by different letters. The number of radio locations = n; number of bears in parenthesis. For Distance-to-Road-Categories see Methods in this Chapter.
**Variation Within Age-sex Classes**

There was less variation within than among some age-sex classes' use of areas near roads. All 3 independent yearlings used areas within 100 m of a road more than expected, the difference being significant for 1 yearling. Two of these yearlings used the 501 - 1000 m DRC significantly less. All 6 adult and 3 subadult males used the closest DRC significantly less, and 1 individual in each of these age-classes also used the 101 - 250 m DRC less than expected. Four of 5 subadult and 4 of 6 adult females used areas in the closest DRC less than expected.

**Female Reproductive Status and Responses**

In spring, females with cubs, with yearlings, or alone, used the 4 DRC's differently from each other ($P < 0.05$). When with cubs, they used the closest DRC significantly more than when with older offspring or when alone (Figure 9). In summer-autumn, the 3 groups of females used all DRC's similarly ($P > 0.10$; Figure 9).

**Influence of Traffic Volume**

Primary roads were used on average by 1.3 large and 3.5 small vehicles per h; 0.4 large and 1.5 small vehicles per h used secondary roads. For most of the year, tertiary roads were used almost exclusively by ourselves and a group studying wolves. Forestry and gas exploration personnel used them for short periods, and hunters used them frequently in the autumn.
Figure 9. Relative use of the 4 Distance to Road Categories (DRC; m) by female grizzly bears of different reproductive status during spring (top; n=5) and summer-fall (bottom n=2). Where use of a DRC differed significantly (P < 0.05) among females of different status, this is indicated by different letters. The number of relocations = n.
I predicted bears would use areas adjacent to primary roads less than to roads with less traffic, but they did not. For both seasons combined, bears significantly reduced their use only of the 0 - 100 m DRC in all road classes, and, in general, used the 2 most distant DRC’s more than expected (Figure 10).

**Nocturnal Behaviour**

Overall, bears used areas near roads significantly more at night than during daylight (Wilcoxon’s Z = 1.71; n = 121). When data were subdivided and re-analyzed for each DRC separately, the probabilities of the 2 distributions being the same were 0.054, 0.066, 0.052, and 0.405 for DRC’s 1 to 4 respectively. With the smaller sample sizes, none were significant, although night use of the 3 closest DRC’s was greatest. For the paired locations, bears were located on roads 12 times; 10 during the night. If roads were used equally during day and night, the probability of such an occurrence is only 0.012. I also noted many more fresh bear tracks in mud and snow on roads early in the morning than later in the day.

**Influence of Habitat Type**

Habitat components were not randomly distributed relative to the DRC’s (P < 0.01). For example, most roads were built to remove timber, and cutting units comprised 33% of the habitats within 100 m of roads, but only 4% in the >1000 m DRC. Conversely, riparian areas made up only 5% of habitats in the 0
Figure 10. Observed versus expected use by 23 grizzly bears of each Distance to Road Category (m) with different levels of traffic (Primary - top; Primary and Secondary - middle; Tertiary - bottom) in the Flathead Valley, B.C. Data represent all spring and summer-fall seasons between 1979 and 1985. Use differing significantly (P < 0.05) from expected is indicated by + or -. For differences in n values see Methods in this Chapter.
- 100 m DRC, and 17% by the 251 - 500m DRC. To overcome the lack of independence between habitats and roads, and to distinguish which feature the bears were responding to, I compared the use of each habitat component with the use expected within each DRC. If roads caused bears to reduce their use of a given habitat component, use of such a habitat should have decreased the closer it was to a road. But, if bears responded primarily to habitats rather than to roads, I should find no difference in their use of a given habitat among the DRC's.

When the habitat components were examined separately, there were adequate data only to analyze use of timber and riparian types, which together comprised 72% of all data used. These habitats provided the densest cover, and I expected grizzlies to be displaced least while using them. However, they used timber and riparian within 100 m of roads significantly less than expected in spring, and used timber in this closest DRC significantly less in summer-autumn. These results support the hypothesis that bears were displaced by roads and not simply avoiding the types of habitat found near roads.

EFFECTS OF INDUSTRIAL ACTIVITIES

Seismic Activity in the Vaccinium Area

When the 226 specific radio locations of 2 adult females, 1 subadult female and 1 subadult male were combined over the 3 years, I found no difference (P > 0.20) in these bears' use of the 3 zones before, during or after the seismic activity
(Figure 11). When the 373 general radio locations were also included, again I found no difference (P > 0.15) in the bears' use of the 3 zones.

Individual comparisons using both specific and general relocations for each bear each year that seismic work occurred, showed only 2 significant differences in zone use in 11 cases; an adult female with 2 cubs in 1984, and a subadult female in 1985 (Table 2).

The adult female was not located in Zone 1 during the seismic activity but was in Zone 2 in 11 of 15 locations. On one occasion she and her cubs were observed for 1.5 h on an open hillside overlooking the seismic activities which were 1400 m from them. During this period, 10 helicopter flights were made along the line and 4 charges detonated. When helicopters flew approximately 1400 m from her, the female raised her head for 3 to 15 s before resuming her previous behaviour. On 2 of the 10 occasions she did not even raise her head from feeding. When the underground charges were detonated they were heard as faint rumblings by humans about 2000 m away, but the bears gave no visible response. Scan-sampling her behaviour revealed she fed 81% of the time (n = 168), compared to 85% (n = 416) in 2 samples in the 1984 berry season when seismic work was not in progress (P > 0.20). This same bear was not displaced from Zone 1 by seismic activity when she was on her own in 1985 (Table 2).

During the seismic work, the subadult female changed (P < 0.01) her locations, using Zone 2 less and Zone 3 more, than
Figure 11. Proportions of combined radio locations of 2 adult females (23, 35), and 2 subadults (1 male 47, 1 female 36) grizzly bears over a 3-year period, in each of the 3 Distance Zones, before, during, and after seismic exploration.
Table 2. Proportions of all relocations of 4 radio collared grizzly bears in each of 3 distance zones from active seismic operations in a 12 km$^2$ *Vaccinium* habitat. Proportions are shown for before, during and after the seismic operations. The levels of probability of equal distributions among the zones ($P$) and sample sizes ($n$) are shown.

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Dates with $^a$ and $^b$ represent separate incidents.
either before or after the activity took place (Table 2). However, she used Zone 1 at a similar frequency during all 3 periods. The relocations indicated that she used Zone 1 almost exclusively during the seismic activity, even when helicopters passed only about 100 m above her. The bear was bedded when the intensive drilling and a Bell 205 transporting equipment gradually approached her. After 7 min of almost constant helicopter work within 100 m of her, she became active and 150 min later had travelled approximately 2400 m and out of the drainage. The following morning she was located about 10 km away in a habitat rarely used by grizzly bears during this season. She remained there 6 days before returning to the berry producing area and the seismic line. This was the only case where the seismic activity appeared to cause a temporary range abandonment.

One other adult female grizzly bear was known to have left this berry area for brief periods when seismic work was in operation, but the intensity and location of the seismic work was such that it is doubtful she was aware of it immediately prior to her leaving. Similar limited movements in time and distance from the berry area occurred when seismic work was not in progress. Both adult females moved to another berry area shortly after the 1984 seismic line was completed. Although the activity may have influenced their movements, the changes were not immediately initiated by human activity. The poor berry crop in 1984 also may have had influenced their movements.
Bear-industry Interactions during Spring

1. An adult female and a subadult male were located together 500 m south of the line when the seismic crew began stringing sensing cable across the riparian area occupied by the bears. When the workers crossed the stream 4 h later, the 2 bears had moved to within 100 m of the line. When the crew finished work 2 h later, the bears were about 350 m away from the line and 1 h later 400 m away. The bears crossed the line during the night and by daybreak had moved 5 km away. The bears clearly were not displaced from the 250-500 m areas around the activity, and although the bears moved to <100 m from the activity, it is unclear that they responded to it. If they did move away from the line because of the seismic activity, they were not displaced by >400 m.

2. A subadult male was found prior to the start of the day’s seismic activities in a riparian area 80 m from a seismic road and a recording truck. The bear remained for 8 h <100 m from the line until at least 2 h after work ceased, and 6 h later he had moved. The riparian area was investigated the following day and signs of feeding and a bed were found 90 m from the line. Again the bear was not displaced from any of the distance categories by the industrial activity.

3. An adult male was first located on an snowchute approximately 1000 m from an inactive logging site. The following day he was found 400 m from this inactive site, but about 600 m from an operating D7 Caterpillar tractor. The third day, the logging crew began working and he remained in a
snowchute approximately 400 m away for at least 2 h. The following 4 days, he was located 320, 520, 500, and 2000 m from the logging operation. This bear was not displaced from the 250-500 and 501-1000 m distance classes.

4. An adult female and 2 cubs had occupied a small basin for 10 days when a small Caterpillar tractor and a grader began work on a road into the basin. Immediately prior to this activity, the bears were located on an open ridge about 800 m from the road and remained there throughout the day despite the activity. They left the basin several days later after road maintenance had finished. These bears were not displaced from the 501-1000 m distance category.

Long-term Effects on the Bears

None of the bears studied, and which were potentially disturbed by the various industrial activities, died during the study. However, it is possible that the seismic activity had an effect on 1 bear. One of the adult females who did not appear to respond immediately to the seismic work in the 12 km² berry area, gave birth to at least 2 cubs. I saw her with one in the early spring 1 km from her den and found the remains of another small cub in a scat collected at her den site. Three weeks later she was alone. She had raised cubs successfully before, and though possible, it is unlikely that her eating her cub and the loss of the other were related to the 1981 seismic activity several months prior. She had 2 cubs after the 1984 seismic program and both survived through the 1985 seismic
activity period.

Another adult female which used the 12 km$^2$ area had 3 cubs with her during the 1981 seismic season, another 2 in 1984 and then 3 in 1986; she successfully weaned all 8 offspring. A subadult female which also used this area had her first litter of 2 cubs in 1986 at 5 years of age, the year after she was displaced from the area by the seismic work; she successfully weaned both of these.

DISCUSSION

Loss of Habitats Near Roads

Most grizzly bears used areas near open roads significantly less than expected. This was equivalent to a habitat loss of 58% in the 0 - 100 m DRC and 7% in the 101 - 250 m DRC. For the whole Flathead study area, it represents a loss of 8.7% of the area available to the bears. Further, the types of habitat often associated with roads (25% of riparian habitat is within 250 m of a road) are especially valuable to bears, because they contain high quality foods in spring and autumn.

The bears' reduced use of areas within 100 m of primary, secondary or tertiary roads did not differ, suggesting that even a little traffic is sufficient to displace them. No bear's home range lacked roads or other human activities, so all should have had some opportunity to habituate or adapt to predictable road-related stimuli. Certain aspects of their behaviour may have reduced the degree of habitat loss bears experienced. The first is their use of roads and adjacent areas at night, which supports Servheen's (1981) prediction
that darkness offers cover to bears. Obviously, bears cannot use all areas all the time, but by altering their use of areas near roads from daylight to darkness, they may continue to use a large portion of valuable habitats located near roads. Although darkness probably provided security cover, traffic volume also would be reduced at night.

Variation among age-sex classes in the use of areas near roads also may have had an ameliorating effect. Adult males used habitats near roads less than other classes, while independent yearlings and some adult females with cubs used these areas more than any other class, contrary to Zager’s (1980) prediction. This differential response was also found for grizzlies in Yellowstone National Park (Mattson et al. 1987) and for black bears (*U. americanus*) in Alberta (Tietje and Ruff 1983). Adult males sometimes kill cubs and yearlings (Glenn *et al.* 1976; Mundy & Flook 1973; Pearson 1975; Reynolds & Hechtel 1979; Troyer & Hensel 1962), so habitats near roads may have been relatively safe for these vulnerable classes of grizzlies. Females with cubs generally avoid adult grizzly males (Pearson 1975; Russell *et al.* 1979), and an experimental manipulation suggested adult male black bears regulated population density in northern Alberta (Kemp 1972, 1976).

A different response to roads was found only 150 km south of my study area. There, 2 female grizzlies used habitats within 199 m of open roads less and 2 males used such areas more frequently than expected (Zager 1980). The reason for the difference between these studies could be due to the small
sample of only 4 bears, but also to differences in habitat availability. Highly productive, low elevation habitats in Zager's (1980) study area were eliminated by water impoundment behind the Hungry Horse Dam, restricting bears to steeper mountain habitats and narrow side drainages where there were roads. Perhaps, as in Jasper National Park, Alberta (Russell et al. 1979), males frequently used the productive areas at low elevations in the narrow side valleys where roads are usually located, while females used higher elevations.

Most data on the displacement by roads in my study area, were collected on EM bears during spring and autumn, when all age-sex classes used the wide valley bottom and differential habitat use patterns was not affected by elevation to the degree it was in Jasper (Russell et al. 1979). In the Flathead, as in Tietje's and Ruff's (1983) flat study area, human-use areas probably had a more direct effect on age-sex class segregation of grizzlies than did elevation. When adequate information is obtained on MR bears, perhaps results similar to those of Zager (1980) will be found.

Demographic Consequences of Roads

To be of major concern to wildlife managers, behavioural responses to disturbance must have demographic consequences (Shank 1979). The population was at a relatively high density during my study, and the survival-fecundity rate of increase (Caughley 1977:55), was positive (see Chapter 4) indicating roads were not having a severe impact during my study.
Three characteristics of the study area may have reduced the potential impact of roads on the grizzly bear population. First, bear survival and reproduction depends greatly on fat reserves obtained primarily in late summer by foraging on huckleberries. In my study area, these grow best in high elevation, post-fire shrubfields that do not contain roads and are therefore totally available to the bear population. Second, in the B.C. portion of the study area, resource-industry employees make up most of the resident human population. Potential road-related impacts on the bears were probably lessened because of some industries' policies (e.g. Shell Canada: no firearms, restricted use of private vehicles, daily garbage incineration). Third, hunting regulations have generally become more restrictive in the study area, and the annual legal harvest of grizzlies is closely monitored.

Roads did increase the bears' vulnerability to legal hunters and to poachers by providing ready access. All but 1 known and suspected adult and subadult grizzly deaths (n = 28) since 1979 have been caused by people, either legally or illegally; most shot from roads (see Chapter 4). Although the Flathead grizzly population seems to have withstood the effects of human access during my short study, the roads' potential as a significant negative demographic factor remains high. Once roads are developed in any grizzly habitat, the population is placed in a more precarious position and management of bears must be changed accordingly.
Displacement of Bears by Resource Industry Activities

From the analysis of the pooled samples from the 4 bears over the 3 years of intensive study I cannot reject the null hypothesis that the bears were not displaced from an important habitat associated with seismic operation activities. When the behaviour of individual bears were examined year by year, in only 2 of 11 cases were there significant differences.

Results of bears' reactions to various types of industrial activity during spring, when the animals normally move throughout their ranges, also suggested minimal displacement from industrial activities. These results are similar to those described by Simpson et al. (1985), who studied the effects of geological exploration on the movements of grizzly bears in the Selkirk Mountains north of my study area.

Unlike bear responses in this and Simpson et al.'s (1985) study, Mace and Jonkel (1980) inferred significant displacement of bears because they never found 3 collared grizzly bears in a small drainage where active logging occurred, but relocated them frequently in adjacent drainages. The differences in bear responses in these studies may be partially a function of bear density relative to carrying capacity. Most bear populations appear to be limited by human predation (Cowan 1972, Bunnell and Tait 1985), but when not, other factors must eventually be limiting. Though habitat quality appears to be the ultimate factor limiting bear density, there is evidence that it is proximately regulated by socially induced-dispersal (Kemp 1972, 1976, Knight and Eberhardt 1985).
A bear subjected to a disturbance can choose to remain or move away from it, both choices have their costs. By staying, its metabolic costs can rise due to stress and it may even be killed if it comes across a human, whereas if it moves, it expends energy in travelling and searching for an alternative, perhaps less productive area. In a population at carrying capacity, a bear’s cost of moving (displaced) may be high due to social intolerance of other bears, or due to competition for some limiting resource. In my study area, there is a high density of grizzly bears (see Chapter 4), so here, the best strategy may have been be for a bear to remain unless the population was below carrying capacity, in which case socially available habitats would be relatively abundant and moving from the disturbance would incur less cost.

Overt versus Covert Responses

Although the 12 instances I observed of bears’ reactions to the use of helicopters for seismic exploration is a small sample, the results are consistent with those reported in other studies (McCourt et al. 1974, Quimbey 1974, McLellan and Shackleton in press b). In general, it appears that a movement response from a single helicopter overflight is most likely when the bear is in the open. Whether the aircraft is merely flying at a tangent to the bear or directly towards it, will also be important in open habitats.

In timbered habitats, I found that an overt avoidance or displacement response required high intensity helicopter
activity such as carrying equipment within 200 m of the bear. This does not mean that bears are not stressed by these activities. MacArthur et al. (1982) found that although mountain sheep (*Ovis canadensis*) showed no overt behavioural response to disturbance, their heart rate increased significantly, and Stemp (1983) found that the duration of elevated heart rate can last several hours. As increased heart rate is a typical first level response of mammals to stress, there is no reason to suspect grizzly bears to be different. Heart rate telemetry studies should be the next step in investigating the full potential effects of industrial activity on bears in cover. However, I found that most of grizzly bears in cover remained in the general location for several hours or even days after a bout of intensive helicopter activity. The few which were displaced, moved off slowly, indicating a low level response.

The generally moderate response of collared grizzly bears to industrial activity in the study area may be a function of habituation. Not only have these bears been exposed to some machinery and similar human activities throughout their lives, but they have been often radio-located from aircraft as well. Mech (1966) found that wolves (*Canis lupus*) habituated to aircraft after 1 day of monitoring, and similar behaviour may be expected with bears.
MANAGEMENT IMPLICATIONS

Grizzly bear food species vary greatly among seasons and it appears that quality and abundance of foods do as well (McLellan unpublished). Consequently, some seasonal habitats may be very restricted and others abundant, so even at carrying capacity, displacement may have relatively little cost for bears during seasons of food abundance (e.g., spring). If economically and logistically possible, industrial activities should be conducted during this season.

The moderate to low response of collared bears to industrial activity does not necessarily suggest that this activity has no detrimental effects. Quantitatively or qualitatively different industrial activities may show greater or longer lasting displacement of bears.

Even at the level of industrial activity in my study, potential problems remain. There is always a risk of confrontations between seismic company employees and bears because constructing seismic lines often did not displace the bears. In addition, the seismic line increases the ease of human access to remote areas, including those where bears are particularly visible and vulnerable. It is therefore important to make old seismic lines impassable to all-terrain vehicles, particularly those lines passing through berry patches to which bears show high annual fidelity.
CHAPTER 4. DYNAMICS OF A GRIZZLY BEAR POPULATION DURING A PERIOD OF INDUSTRIAL RESOURCE EXTRACTION

The behavioural responses of grizzly bears to industrial activities and the resulting habitat alterations, indicate where significant overt conflicts likely occurred, but the response variables of ultimate importance are those measuring the dynamics of the population (Shank 1979). By combining information about the bears' behavioural, habitat use, and population responses to industrial activity, I expected to gain a more complete understanding of the relationship between industry and grizzlies than if I limited my research to only one or two of these aspects.

I hypothesized that the industrial activity in the study area would be harmful to grizzly bears, and predicted that it would result in a low density of bears compared to other interior areas without industrial activity, and/or that their survival-fecundity (Caughley 1977:54) exponential rate of population increase would be negative. To test this hypothesis, I first present data on grizzly bear density and age-sex structure of the population during a period of resource extraction. Then mortality rates, causes of death, and estimates of reproductive variables are reported. Finally, I estimate the rate of increase of the population, and investigate the sensitivity of this estimated rate of increase to changes in parameter values.
METHODS

**Density Estimation**

Estimating grizzly bear density is difficult in a heavily timbered area without the presence of seasonal concentration sites such as garbage dumps or salmon spawning streams (Knight and Eberhardt 1985), particularly where the system is open to immigration and emigration. Standard capture-recapture methods were thought to be inappropriate for this study because: 1) the assumption of equal catchability could not be met because some individuals were clearly more difficult to capture than others, and almost all were much more difficult to recapture, and 2) the study area was not a closed system and so I was sampling bears from a much larger area than the trapping areas alone, which would lead to an inflated density estimate. Adding one home range radius around the study area (Caughley 1977:140) may decrease this bias, but variation in home range size and shape reduces confidence with small samples.

A commonly used density estimation technique for grizzly bears is to record all bears seen or trapped in a study area of known size, and then derive the density by simple division (Mundy and Flook 1973, Martinka 1974, Pearson 1975, Russell et al. 1979, Servheen 1983). Using saturation trapping, observations, or both, partially alleviates the problem of unequal catchability because bears only have to be captured once, or not at all if only observation is required. Capturing or observing all of the grizzlies in a study area is unlikely, so this estimate is usually regarded as a minimum or a
conservative estimate (Mundy and Flook 1973, Russell et al. 1979). However, if all bears trapped or seen in a study area are included in the density estimate, we are faced with problem (2) mentioned above, and the "minimum" estimate may be actually higher than the true density.

I devised two methods to estimate density. The first is based on home range information determined by radio tracking. First, I decided on a core study area (trapping Area A; Figure 12) where I would estimate the density of grizzly bears and concentrated almost all trapping there. However, with a maximum field crew of 3 available, even this area was too large to trap efficiently, so I delineated a more intensive trapping area (trapping area B; Figure 12) within area A where most timber harvest and gas exploration occurred (Table 3). After the trapping was completed, trapping areas A and B were plotted as minimum convex polygons by enclosing all successful trap locations for the entire study period. Trapping area A covered 264 km2 and B 130 km2.

Each bear's 97.5 percent multi-year, minimum home range convex polygon (Harestad 1981) was then plotted using ground and aerial relocations. Each bear's contribution to the density estimate was the proportion of this home range that fell within the trapping area boundaries (Figure 13). Thus, only bears with a 97.5% multi-annual home range located entirely within a trapping area were counted as a "whole" bear.

In Chapter 2, I compared random points from within entire
Figure 12. The study area. Almost all trapping occurred in the larger Area A, while the most intensive trapping effort was confined to a portion of Area A called Area B.
Figure 13. Radio location points and 97.5\% multi-annual home range of a subadult female grizzly bear. The proportion of this range which overlapped a trapping area is the bear’s contribution to the population density estimate.
Table 3. Extent of Resource Extraction Industries and residences in the Flathead study area as of 1986.

<table>
<thead>
<tr>
<th>Human Activity</th>
<th>Area A</th>
<th>Area B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (km$^2$)</td>
<td>264</td>
<td>130</td>
</tr>
<tr>
<td>Open roads (km/100 km$^2$)</td>
<td>69</td>
<td>93</td>
</tr>
<tr>
<td>Cutting units (km$^2$/100 km$^2$)</td>
<td>16</td>
<td>18</td>
</tr>
<tr>
<td>Seismic lines (km/100 km$^2$)</td>
<td>63</td>
<td>86</td>
</tr>
<tr>
<td>Drill rigs (per 100 km$^2$)</td>
<td>0.04</td>
<td>0</td>
</tr>
<tr>
<td>Industrial camps (per 100 km$^2$)</td>
<td>1.1</td>
<td>0.8</td>
</tr>
<tr>
<td>Permanent residences (per 100 km$^2$)</td>
<td>2.3</td>
<td>4.6</td>
</tr>
</tbody>
</table>
seasonal ranges to points overlaid on the entire study area because I was interested in selection of entire seasonal ranges. In this chapter, however, extreme outlier locations (2.5%) from multi-year home ranges were omitted because they could lead to a small underestimate of density due to the nature of bears' ranges. Typically, ranges included several clusters of locations representing high-use areas, with a few scattered locations in between and some extreme outliers. After examining each range, an average of 2.5% of the locations were estimated to be outliers. Excluding these outlying locations of bears whose high-use areas were within the trapping areas, reduced the bias of not catching, and therefore of not counting bears whose high-use areas were elsewhere and only entered the trapping area occasionally.

This first density estimate is based on the assumption that I captured all, but only, those bears which had at least part of their 97.5% home range within the trapping area. If 100% home ranges had been used, I would have had to assume that I had trapped every bear that even just entered the trapping area during the study period. The first assumption may be false, and therefore the density estimate is conservative, but the second assumption is known to be wrong because several unmarked grizzlies were seen in the study area.

The second method I used resembles the first, but instead of using the proportion of each bear's range that fell in the trapping areas as their contribution to the density estimate, the proportion of time each bear spent in the trapping area was
used as their contribution to the estimate. This proportion was assumed to equal the proportion of each bear's radio locations, obtained from aircraft, that was in the trapping area. Aerial relocation eliminates any bias due to differential road access used for ground tracking.

Both methods rely exclusively on functioning radio collars, but batteries fail and collars are pulled off, so not all bears carried functioning collars for the entire study period. Consequently, I was forced to extrapolate information from when individuals were collared to when they were not. When an adult bear's collar ceased functioning, but the individual was later recaptured or harvested in the study area, I assumed it had remained in the same multi-annual home range it had occupied when radio tracked (average uncollared interval = 1.7 years). In this case, its contribution to the population estimate was the same each year whether it was collared or not. Unlike adults, which have relatively stable range locations between years, subadults were not included in the density estimate after their radios ceased unless they were recaptured and their new range determined. Bears which either shed their collars or were shot before they were relocated 20 times, were not included in the density estimate. The census date was in early May, which was when all bears had emerged from their dens, but was prior to when they were hunted.
Age and Sex Composition

Some characteristics of a grizzly bear population's age and sex composition are likely biased, if based on hunter harvest or trapped animals (Troyer and Hensel 1964, Bunnell and Tait 1980). However, when deriving one estimate of bear density, I assumed that every bear whose 97.5% home range overlapped the trapping area was captured. If this assumption is acceptable, then the population's age-sex structure can be estimated based on each individual bear's contribution, as was done to estimate the density.

Survival Rates and Causes of Death

Bear mortality was divided into: 1) natural and not directly due to people, 2) legal harvest, 3) illegal harvest, 4) legal control losses (the agency responsible either killed or removed a bear causing a problem to people), 5) illegal nuisance (a citizen illegally killed a bear causing a problem), and 6) research losses. All recorded mortalities were classified either as known when the carcass was examined, or suspect when the carcass was not recovered but there was sufficient circumstantial evidence to indicate a death had occurred (e.g. finding a collar cut off, rumors of a bear being killed after the radio signal of one that was frequently located near human settlement stopped being received, or when a cub was no longer seen with its mother).

Shooting radio-collared grizzlies is legal in British Columbia, Alberta, and Montana, though British Columbia hunting
regulations have requested hunters to avoid shooting collared wildlife since 1985. The bias against killing collared bears is unknown, but probably minimal. Between 12 and 20 hunters were permitted to hunt grizzly bears in the study area each spring, and when I encountered hunters in the field they were informed that they were allowed to shoot a collared bear if they desired. Also, collars were black and difficult for a hunter or poacher to see in most field conditions. I was not aware of any hunter who refrained from shooting a bear because it was collared.

Hunters in British Columbia, Alberta, and Montana must report grizzly bears they kill, so information on legal kills is readily available for both radio-collared and unmarked bears. Accurately documenting illegal and natural mortalities was more difficult. All collared bears were relocated from aircraft approximately once each week as well as from the ground, and the motion-sensitive radio transmitters used alerted us to the death of the animal or removal of a collar. When this happened, the location was inspected and the cause of signal change determined. To find unmarked bears killed for reasons other than legal hunting, I relied on information from people reporting the incident.

Seasonal and annual survival rates of radio-collared bears were estimated using the number of days that animals were tracked and by the number of deaths (Heisey and Fuller 1985). The method assumes equal mortality rates within seasons, so in this chapter, seasons were selected differently than in
Chapters 2 and 3. For estimating mortality rates, seasons were: 1) spring - May and June and included the grizzly bear hunting season in British Columbia; 2) summer - July and August; 3) autumn - September to November, and included the general, big game hunting season; and 4) winter - December to April when most bears were hibernating. Deaths related to research were not included in calculating survival rates.

Survival rates for cubs and yearlings of collared females were calculated from the number of days between my first observation of them to when they were last seen. If a cub disappeared, it was assumed to be dead. Similarly, missing yearlings were also assumed dead unless the entire litter separated from the mother during the mating season (May and June), which is the most common time of family break-up. However, some cubs can survive if separated from their mother (Russell et al. 1979), and separation is common for yearlings; thus survival estimates for these two classes may be low.

The time of family break-up could be a time of high mortality for young bears because of aggressive male suitors. A potential bias results if survival rates of uncollared young approaching this period are included in the calculations. I was able to record survival information on only 10 bears during this separation period, 9 of which were known to have survived, but the fate of the other is unknown. To reduce possible bias, the number of days between the last observation of a young bear when it was still with its radio-collared mother and when it was first captured after family break-up, were not counted as
days survived.

Complete annual survival rates of cubs were not determined because I did not enter maternal dens to count cubs at birth! Assuming a 1 February birthdate, their average age when first observed was 145 days, and cub survival was calculated only for the following 220 days (365-145).

**Natality and Rate of Increase**

Information on reproductive rates, including the age of first parturition, interval between litters and the number of cubs per litter, was collected by radio-tracking individual female bears over several years. Additional data on litter size were recorded from unmarked females observed in, or adjacent to, the study area. Calculating the annual survival rate of cubs for only the last 220 days of the year eliminates the bias of first observing litters when the cubs were an average of 145 days old. If one cub died before I observed the litter, the recorded litter size would be one less than the true value, but the recorded survival rate would be higher. Similarly, if a whole litter was lost prior to observation, these mortalities again would go unrecorded, but the breeding interval estimate would be extended, or if the litter was the female's first, her recorded age of first parturition would be inflated.

I used 3 methods of estimating reproductive rates. The first and second included only information from female bears that were radio-tracked through at least one interbirth
interval. For method 1, the reproductive rate was the total number of cubs observed, divided by the total number of bear-years required to produce them. This method gives more weight to individuals that were tracked for more than one interbirth interval and had more litters recorded. For method 2, the reproductive rate was the average of each individual’s rate. Method 2 gives equal weight to each bear regardless of how many of her litters were recorded. For method 3, the reproductive rate was the average litter size divided by the average interbirth interval. More information was available for estimating the reproductive rate using method 3 because all litter size data could be used.

Of the several distinct measures of rate of increase described by Caughley (1977:53), I chose to use the survival-fecundity rate, \( r_s \), which is the exponential rate at which a population would change if it had a stable age distribution appropriate to its current schedules of age-specific survival and fecundity. Caughley called this measure of increase "demographic vigour", because it measures how well populations contend with their current situations. I estimated this rate of increase by iterating the Lotka equation (Caughley 1977:110). The sensitivity of \( r_s \) to changes in parameter values was tested by altering the value of each parameter alone, while leaving the others at the best estimate from the available data, until the rate of increase equalled 0.0. I also changed all survival rates equally until a zero rate of increase was obtained.
RESULTS

Densities

Of the 65 different grizzly bears that I captured, 54 were caught in the trapping areas and of these, 47 were equipped with radios. The multi-annual (x = 2.1 years, range = 0.9 to 5.0) home range information used for the density estimates was based on 4482 radio locations of 13 male and 14 female collared individuals (x = 166 relocations/individual, range = 21 to 551). Five collared bears travelled with their collared mothers, so their telemetry data were redundant. Fifteen other bears were captured in the trapping areas but were not used in the density estimates. These included 3 males and 2 females caught at the extremity of their home ranges and on the periphery of the trapping area, leaving no overlap, 2 males which died shortly after capture, 4 males and 1 female that shed their collars within 1 month of capture and were never recaptured or harvested and therefore the location of their range was unknown, and 1 female cub and 2 adult males that were captured and radio-collared in the autumn of 1986 and whose home range locations were also unknown. The average range of the 27 bears used in estimating density had 42% overlap with trapping area A and 28% overlap with trapping area B. On average, 41% of these bears' aerial locations were in trapping area A and 28% in area B.

The estimated average minimum density of bears in the larger trapping area A was 4.5/100 km² using both methods.
This is known to be a low estimate because unmarked bears were often observed in the west side of this area, but it was too large to trap intensively. In area B, average densities of 6.0 and 6.1/100 km$^2$ were recorded over 8 years using the home range and aerial location methods respectively (Tables 4 and 5). The densities calculated for 1979 and 1980 may be low because few of the subadults captured then were radio-collared, thus violating the assumption that all bears were counted. The average density of grizzly bears estimate for the last 6 years of study was 6.4/100 km$^2$, and the highest annual estimate was 8/100 km$^2$.

Age-sex Composition

Of the 65 grizzly bears captured, only 3 were cubs and all of these were female. Seven females and 10 males were yearlings when first caught, for a 50:50 sex ratio in the first 2 age classes. Of the bears which were subadults when first captured, 11 were male and 8 female, which is not significantly different from an equal ratio ($P = 0.64$). Similarly, the ratio of captured adult bears, 16 male to 10 female, was not significantly different from equality ($P = 0.32$).

Based on the density of bears in the study area, I estimated that 21.5% of the population were cubs, 17.5% were yearlings, 26.5% were subadults and 34.5% were adults (Tables 4 and 5). Though there were more adult males captured than adult females, the density estimates indicate that there are more adult females than males in the trapping areas.
Table 4. Numbers and densities (bears/100 km$^2$) of bears in Trapping Area B each year determined by the proportion of 97.5% multi-annual home ranges which overlapped this area.

<table>
<thead>
<tr>
<th>Year</th>
<th>Cubs</th>
<th>Subadults</th>
<th>Adults</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>2.45</td>
<td>0.31</td>
<td>0.40</td>
<td>1.12</td>
<td>2.00</td>
<td>6.28</td>
<td>4.83</td>
</tr>
<tr>
<td>1980</td>
<td>0.0</td>
<td>2.45</td>
<td>0.34</td>
<td>1.19</td>
<td>2.00</td>
<td>5.98</td>
<td>4.60</td>
</tr>
<tr>
<td>1981</td>
<td>1.94</td>
<td>0.25</td>
<td>2.28</td>
<td>1.12</td>
<td>1.69</td>
<td>7.28</td>
<td>5.60</td>
</tr>
<tr>
<td>1982</td>
<td>1.33</td>
<td>2.19</td>
<td>1.10</td>
<td>0.98</td>
<td>1.69</td>
<td>7.29</td>
<td>5.61</td>
</tr>
<tr>
<td>1983</td>
<td>1.28</td>
<td>1.15</td>
<td>2.50</td>
<td>0.98</td>
<td>1.69</td>
<td>7.60</td>
<td>5.85</td>
</tr>
<tr>
<td>1984</td>
<td>1.33</td>
<td>0.61</td>
<td>2.27</td>
<td>1.08</td>
<td>1.69</td>
<td>6.98</td>
<td>5.37</td>
</tr>
<tr>
<td>1985</td>
<td>2.40</td>
<td>2.00</td>
<td>3.25</td>
<td>1.08</td>
<td>1.69</td>
<td>10.42</td>
<td>8.02</td>
</tr>
<tr>
<td>1986</td>
<td>2.20</td>
<td>2.54</td>
<td>1.99</td>
<td>1.29</td>
<td>2.18</td>
<td>10.20</td>
<td>7.85</td>
</tr>
</tbody>
</table>

Overall

Mean  1.62  1.44  1.77  1.11  1.83  7.75  5.96
%     23    18    22    14    23    100   ----

1981-86

Mean  1.75  1.46  2.23  1.09  1.77  8.30  6.38
%     21    18    27    13    21    100   ----
Table 5. Number and densities (bears/100 km²) of bears in Trapping area B determined by the proportion of their multi-annual aerial relocations (= time) which occurred in this area.

<table>
<thead>
<tr>
<th>Year</th>
<th>Cubs</th>
<th>Sub-</th>
<th>Adult Males</th>
<th>Adult Females</th>
<th>Total</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>2.20</td>
<td>0.67</td>
<td>0.27</td>
<td>1.04</td>
<td>2.33</td>
<td>6.51</td>
</tr>
<tr>
<td>1980</td>
<td>0.0</td>
<td>2.20</td>
<td>0.78</td>
<td>1.16</td>
<td>2.33</td>
<td>6.47</td>
</tr>
<tr>
<td>1981</td>
<td>2.07</td>
<td>0.25</td>
<td>2.56</td>
<td>1.04</td>
<td>1.70</td>
<td>7.62</td>
</tr>
<tr>
<td>1982</td>
<td>0.99</td>
<td>2.24</td>
<td>0.95</td>
<td>0.97</td>
<td>1.70</td>
<td>6.85</td>
</tr>
<tr>
<td>1983</td>
<td>1.36</td>
<td>0.99</td>
<td>2.42</td>
<td>0.97</td>
<td>1.70</td>
<td>7.44</td>
</tr>
<tr>
<td>1984</td>
<td>1.38</td>
<td>0.59</td>
<td>2.77</td>
<td>0.97</td>
<td>1.70</td>
<td>7.41</td>
</tr>
<tr>
<td>1985</td>
<td>2.20</td>
<td>2.00</td>
<td>3.27</td>
<td>0.97</td>
<td>1.70</td>
<td>10.14</td>
</tr>
<tr>
<td>1986</td>
<td>3.16</td>
<td>2.34</td>
<td>1.31</td>
<td>1.33</td>
<td>2.56</td>
<td>10.70</td>
</tr>
</tbody>
</table>

Overall

Mean 1.67 1.41 1.79 1.06 1.97 7.89 6.07

% 21 18 23 13 25 100 ----

1981-86

Mean 1.86 1.40 2.21 1.04 1.84 8.36 6.43

% 22 17 26 13 22 100 ----
Survival Rates

Sampling intensity of the 55 radio-collared bears was similar among seasons with an average of 7.3, 7.3, 7.4 and 7.5 bear-years of functioning collars per month for spring to winter respectively. Radio-collared bears and their dependent offspring were monitored for a total of 110 bear-years. Excluding the 2 deaths related to trapping, 7 mortalities were known or suspected to have occurred to bears with active collars, plus 4 deaths of their dependent offspring (Table 6).

Adult bears were tracked for 57.6 bear-years, during which 4 known or suspected deaths occurred for an average survival rate of 0.93. Of these deaths, 2 were females and 2 were males, for estimated sex-specific survival rates of 0.94 and 0.92 respectively (Table 6). Radio contact was lost prior to the life expectancy of the collar on one 9-year-old male and his fate remains unknown. This bear was last located during the mating season when other collars have failed because they were damaged by mates. It is also possible that he dispersed out of the study area, but if this male was illegally killed and the collars destroyed or removed, the annual survival rate of adult males would have been 0.88.

A decrease in survival of older bears was indicated. Both adult female mortalities, 1 natural and 1 illegal killing, were of bears 18 years of age and older.

Subadult females had an annual survival rate of 0.94 and
Table 6. The best estimates of annual survival rates of the radio-collared grizzly bears and their dependent offspring in the Flathead Valley, 1979 to 1987.

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>Bear-years of tracking</th>
<th>Mortalities</th>
<th>Survival rate (95% CL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Females</td>
<td>34.5</td>
<td>2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.94 (.87-1.0)</td>
</tr>
<tr>
<td>Adult Males</td>
<td>23.1</td>
<td>2</td>
<td>0.92 (.81-1.0)</td>
</tr>
<tr>
<td>Subadult Females</td>
<td>16.5</td>
<td>1</td>
<td>0.94 (.84-1.0)</td>
</tr>
<tr>
<td>Subadult Males</td>
<td>11.0</td>
<td>1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.91 (.76-1.0)</td>
</tr>
<tr>
<td>Yearlings</td>
<td>15.3</td>
<td>2</td>
<td>0.88 (.73-1.0)</td>
</tr>
<tr>
<td>Cubs</td>
<td>9.3</td>
<td>3</td>
<td>0.82 (.66-1.0)&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> does not include 1 illegally killed when recovering from drugging.

<sup>b</sup> does not include 1 killed by another bear while trapped.

<sup>c</sup> calculated for 220 days.
subadult males 0.92 after a total 27.5 bear-years of active
collars. Yearlings were tracked for 3.0 bear-years by
collaring them and for 12.3 bear-years by tracking their
mothers. With one suspected illegal mortality of a collared
yearling, the estimate of the annual survival rate was 0.94. A
second yearling mortality may have occurred when a litter
changed from 3 to 2, however, a young grizzly was observed
shortly after in a location favoured by this family group. If
this young bear did die, yearling annual survival would be
0.88. Cubs had a 220 day survival rate of 0.82. If cub
survival rate was the same before they were first observed as
after, their annual rate would have been 0.73.

Three bears with operating collars died in the spring and 4
died in the autumn (Table 7). Although the mortalities were
seasonal, the average annual survival for all collared bears
was calculated to be 0.92 by both the product of the seasonal
rates and using a 1-year interval, reflecting the even sampling
intensity among seasons.

Causes of Mortality

Between 1979 and 1987, 30 grizzly bears are known to have
died or been removed from the study area, and there is evidence
that 8 additional mortalities probably occurred. These 38
instances included 9 bears with operating radio collars and 7
marked bears (Table 8).

Three mortalities were related to trapping. An uncollared
yearling was killed by its mother when both were captured at
Table 7. Seasonal survival rates of radio-collared grizzly bears in the Flathead Valley, 1979 to 1987.

<table>
<thead>
<tr>
<th>Season</th>
<th>Interval</th>
<th>N days in interval</th>
<th>N bear-years</th>
<th>Mortalities</th>
<th>Interval Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>May-Jun</td>
<td>61</td>
<td>14.7</td>
<td>3</td>
<td>0.966</td>
</tr>
<tr>
<td>Summer</td>
<td>Jul-Aug</td>
<td>62</td>
<td>14.5</td>
<td>0</td>
<td>1.000</td>
</tr>
<tr>
<td>Autumn</td>
<td>Sep-Nov</td>
<td>91</td>
<td>22.1</td>
<td>4^a</td>
<td>0.956</td>
</tr>
<tr>
<td>Winter</td>
<td>Dec-Apr</td>
<td>151</td>
<td>37.8</td>
<td>0</td>
<td>1.000</td>
</tr>
</tbody>
</table>

^a does not include 1 illegally killed when recovering from drugging or 1 killed by another bear while trapped.
Table 8. Known and suspected grizzly bear mortalities in the 2900 km² study area, Flathead Valley, 1979 to 1987.

<table>
<thead>
<tr>
<th>Source of mortality</th>
<th>Adult Male</th>
<th>Adult Female</th>
<th>Subadult Male</th>
<th>Subadult Female</th>
<th>Yearling</th>
<th>Cub</th>
<th>Unknown</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural death</td>
<td>0</td>
<td>1(1)</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>6(1)</td>
</tr>
<tr>
<td>Legal harvest</td>
<td>6(1)</td>
<td>5</td>
<td>7(1)</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>19(2)</td>
</tr>
<tr>
<td>Illegal harvest</td>
<td>0</td>
<td>2(2)</td>
<td>1</td>
<td>1(1)</td>
<td>2(1)</td>
<td>1</td>
<td>1</td>
<td>8(4)</td>
</tr>
<tr>
<td>Legal control</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Illegal nuisance</td>
<td>2(1)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2(1)</td>
</tr>
<tr>
<td>Research</td>
<td>0</td>
<td>0</td>
<td>1(1)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2(1)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>8(2)</strong></td>
<td><strong>8(3)</strong></td>
<td><strong>10(2)</strong></td>
<td><strong>2(1)</strong></td>
<td><strong>4(1)</strong></td>
<td><strong>5</strong></td>
<td><strong>1</strong></td>
<td><strong>38(9)</strong></td>
</tr>
</tbody>
</table>

a Numbers in parentheses represent mortalities of bears with active radio collars.

b includes 1 illegally killed when recovering from drugging.
the same location, and a radio-collared subadult male was killed by an unknown bear. In the third case, a radio-collared adult female was shot out of hunting season by a poacher before she had fully recovered from being immobilized. This mortality was classified as illegal harvest (Table 8), but, because she would not have been killed without the research, it was not included in calculating mortality rates (Tables 6 and 7).

Of all known mortalities, legal harvest was the most commonly recorded cause, accounting for 19 known deaths. Seven of 13 successful hunters whom I interviewed said that they had been on a road when they shot their bear.

Probably, I did not record all grizzly bears killed illegally in the study area. Of the 9 mortalities of bears wearing functioning radio collars, 2 were attributed to legal hunting while 5 were illegal (Table 8). Six of the 10 known or suspected illegal kills of marked and unmarked bears were in the 119 km² portion (4%) of the study area where the only permanent human settlement is concentrated. No known or suspected grizzly bear mortalities occurred at any industrial camps, though some black bears were killed and others trapped and removed.

One 18 year-old female died in the autumn of what I suspect was a natural cause, although it is possible that she was illegally shot.

Reproductive Parameters

A total of 27 female grizzly bears was captured and marked,
and 23 fitted with radio collars. The sample contained 11 radio-collared adults and 5 of these were radio-tracked for at least 1 complete breeding cycle.

Two bears had their first litter when known to be 5 and 6 years of age. Three others were estimated by cementum annuli to be 5, 6, and 8 years of age when they had their first litter. The average age of first parturition of these 5 females was 6.0 years.

Nine interbirth intervals were recorded for 5 females; 1 was 1 year, 2 were 2 years, 5 were 3 years, and 1 was 4 years, for an average of 2.67 years. All cubs in the litter of a 3-year and of the 1-year interbirth interval died.

At first observation, radio-collared females had 40 cubs in 17 litters for an average litter size of 2.35 cubs per female (Table 9). The average size of 21 litters of yearlings and 2 year-olds was 2.33. Adding litters of uncollared females reduces the average litter size of cubs to 2.26 and that comprised of 1 or 2-year-olds to 2.29.

Of the 40 cubs of radio-collared females, 21 were eventually captured and 11 were males and 10 were females. Most of these were captured as yearlings, and I do not know if behavioural differences between the sexes influenced the probability of capture.

Reproductive Rates

Five females were radio-tracked for at least one interbirth interval and produced 24 cubs in 21 bear-years for an estimated

<table>
<thead>
<tr>
<th>Litters from:</th>
<th>Frequencies of litter sizes</th>
<th>Number of litters of young</th>
<th>Total number</th>
<th>Average litter size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Collared Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cub(^a)</td>
<td>1</td>
<td>9</td>
<td>7</td>
<td>17</td>
</tr>
<tr>
<td>1 yr</td>
<td>1</td>
<td>7</td>
<td>6</td>
<td>14</td>
</tr>
<tr>
<td>2 yr</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>Uncollared Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cub</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>1-2</td>
<td>1</td>
<td>6</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>All Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cub</td>
<td>4</td>
<td>15</td>
<td>12</td>
<td>31</td>
</tr>
<tr>
<td>1-2</td>
<td>3</td>
<td>16</td>
<td>12</td>
<td>31</td>
</tr>
<tr>
<td>Totals</td>
<td>7</td>
<td>31</td>
<td>24</td>
<td>62</td>
</tr>
</tbody>
</table>

\(^a\) Cubs = litters of cubs; 1 yr = litters of yearlings; 2 yr = litters of 2 year olds; 1-2 = litters of both yearlings and 2 year olds.
reproductive rate of 0.875. These five females had individual reproductive rates of 0.67, 1.0, 0.83, 0.75, and 1.0 cubs per year for an average of 0.85. The third estimate of the reproductive rate is the average litter size divided by the average interbirth interval; 2.26/2.67 = 0.85.

**Survival-fecundity Rate of Increase**

For estimating the survival-fecundity rate of increase using the Lotka equation, the age of first parturition was 6 years, with one third of the females having an average sized litter at 5 years, one third at 6 years and one third at 7 years. By averaging the 3 estimates of reproductive rate and assuming a 50:50 sex ratio, females, 8 years and older, had reproductive rates, $m_x$, of 0.43. The values for survival rates were obtained from Table 6, except those for adults 15 years of age and older. The mortality rate for these older bears was set at 0.82, as was used by Knight and Eberhardt (1985), because an increased rate in older classes is expected (Caughley 1966) and my limited data suggested it. Using these data (Table 10), the population's rate of increase was estimated to be 0.081.

Although the samples represented almost the entire study population, actual numbers were small, and therefore I tested the sensitivity of the rate of change to errors in the estimates. To have a rate of increase of 0.0, the most sensitive parameter, prime adult survival rate, would have to be reduced from 0.94 to 0.76, while the subadult survival rate
Table 10. Values used to calculate of the rate of increase, $r_s$, using the Lotka equation for the grizzly bear population of the Flathead Valley, 1979 to 1987.

<table>
<thead>
<tr>
<th>Age</th>
<th>Reproductive Rate ($m_x$)</th>
<th>Proportion Surviving ($l_x$)</th>
<th>Annual survival rate</th>
<th>Stable age distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>cub</td>
<td>0</td>
<td>1.000</td>
<td>.82</td>
<td>.166</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>.820</td>
<td>.88</td>
<td>.126</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>.722</td>
<td>.94</td>
<td>.102</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>.678</td>
<td>.94</td>
<td>.088</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>.638</td>
<td>.94</td>
<td>.077</td>
</tr>
<tr>
<td>5</td>
<td>.38</td>
<td>.599</td>
<td>.94</td>
<td>.067</td>
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<tr>
<td>6</td>
<td>.38</td>
<td>.563</td>
<td>.94</td>
<td>.058</td>
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<td>7</td>
<td>.38</td>
<td>.530</td>
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<td>.050</td>
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<td>8</td>
<td>.43</td>
<td>.498</td>
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<td>.043</td>
</tr>
<tr>
<td>9</td>
<td>.43</td>
<td>.468</td>
<td>.94</td>
<td>.038</td>
</tr>
<tr>
<td>10</td>
<td>.43</td>
<td>.440</td>
<td>.94</td>
<td>.033</td>
</tr>
<tr>
<td>11</td>
<td>.43</td>
<td>.413</td>
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<td>.028</td>
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<td>12</td>
<td>.43</td>
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</tr>
<tr>
<td>13</td>
<td>.43</td>
<td>.365</td>
<td>.94</td>
<td>.021</td>
</tr>
<tr>
<td>14</td>
<td>.43</td>
<td>.343</td>
<td>.94</td>
<td>.018</td>
</tr>
<tr>
<td>15</td>
<td>.43</td>
<td>.323</td>
<td>.82</td>
<td>.016</td>
</tr>
<tr>
<td>16</td>
<td>.43</td>
<td>.265</td>
<td>.82</td>
<td>.012</td>
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<tr>
<td>17</td>
<td>.43</td>
<td>.217</td>
<td>.82</td>
<td>.009</td>
</tr>
<tr>
<td>18</td>
<td>.43</td>
<td>.178</td>
<td>.82</td>
<td>.007</td>
</tr>
<tr>
<td>19</td>
<td>.43</td>
<td>.146</td>
<td>.82</td>
<td>.005</td>
</tr>
</tbody>
</table>
Table 10. Continued.

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>.43</td>
<td>.120</td>
<td>.82</td>
<td>.004</td>
</tr>
<tr>
<td>21</td>
<td>.43</td>
<td>.099</td>
<td>.82</td>
<td>.003</td>
</tr>
<tr>
<td>22</td>
<td>.43</td>
<td>.080</td>
<td>.82</td>
<td>.002</td>
</tr>
<tr>
<td>23</td>
<td>.43</td>
<td>.066</td>
<td>.82</td>
<td>.002</td>
</tr>
</tbody>
</table>
of increase. A yearling survival rate of 0.35 or a cub survival of 0.33, would both decrease r to 0.0, if all the mortality occurred after the mating season. Greater mortality of these young bears could occur if deaths were prior to the mating season, because the mother’s interval length could shorten as a result. An 8% decrease in all survival rates would result in a zero rate of increase, as would a 7% decrease in all survival rates and in the reproduction rate.

Although my data concerning the age at first parturition are meager, females would have to be over 13 years old for r to stabilize at 0.0. Similarly, the other 2 reproduction parameters would require unrealistic values to obtain a zero rate of increase.

At the stable age distribution appropriate to the population parameter estimates, 44% of the females would be adults while only 40% of the live population’s were reported to be. It was also estimated that the live population of females consisted of 20% cubs, 16% yearlings and 24% subadults, while at a stable age distribution, the proportions would be 17%, 13%, and 27% respectively.

DISCUSSION

Methods for Estimating Density

Caution must be exercised when comparing my density estimates with those from other areas because of the different methods employed. For example, if I had used the method of recording all the different bears trapped and observed in the would have to be reduced from 0.94 to 0.69 to get a zero rate
study area as was done by others (Mundy and Flook 1973, Martinka 1974, Pearson 1975, Russell et al. 1979), the highest annual density would have been 20 bears/100 km^2, which is 2.5 times greater than the highest annual density estimated using my methods.

Similarly, Russell et al. (1979) estimated that they had captured all but 3 bears in their study area. From their home range data, I made an approximate density estimate using the proportion that each collared bear's home range overlapped their study area, and gave the 3 uncollared bears the average value. This resulted in a minimum density for the Jasper study area of 0.56 bears/100 km^2, which is less than half the 1.25/100 km^2 estimated when Russell et al. (1979) included the 3 unmarked bears. In making this re-analysis, I wish only to demonstrate potential differences between methods, not to give an alternative density estimate for Jasper National Park. The open system bias will decline as the size of the study areas increases and/or the ranges of the bears decrease.

**Population Density and Composition**

LeFranc et al. (1987:52-53) tabulated density estimates of grizzly bears from 20 interior study areas in North America. More than 1 estimate was presented in several of these locations, but the average of the highest estimate from each area was 1.68 bears/100 km^2. Glacier National Park, British Columbia, had the highest recorded densities of the 20 areas, with 3.6 to 5.6 bears/100 km^2. Even with the relatively
conservative methods I used, density estimates in my Flathead study area are higher than any of these. Higher densities of brown bears have been reported only in coastal Alaska (LeFranc et al. 1987; J. Schoen, pers. comm.) and in Eurasia (Zunino and Herrero 1972, Kistchinski 1972).

Annual variation in the density of bears in my study area appears due to 3 factors, 1) synchronous weaning of offspring among females, 2) my inability to capture and therefore include all weaned offspring, and 3) the enlarged ranges of those dispersing subadults I did capture. Consequently, years with high densities occurred were when most females were accompanied either by cubs or by yearlings, and low density years are when these same females were solitary. The difficulty of keeping track of independent subadult bears probably resulted in them being underestimated.

Because the large home ranges of adult males (Bunnell and Tait 1980) reduces the probability of capturing all whose 97.5% range overlapped the study area, this class is probably underestimated. Adult males also removed their collars more frequently than did other age/sex classes. Four adult males, known to have been near the center of trapping area B, were not included in the age/sex composition or the density estimate because I was not sure of their range locations. For these reasons, the actual density of bears in my study area is probably higher than estimated here.

The standing age distributions, derived by both my methods (Tables 4 and 5), are similar to those that Aune et al. (1986)
reported for a grizzly bear population on the eastern edge of the Rocky Mountains. Both populations appear to have slightly higher proportions of cubs and yearlings, and fewer adults than reported in Glacier and Yellowstone National Parks (Martinka 1974, Craighead et al. 1974).

Survival Rates

The estimated survival rates of adult grizzly bears (0.93) and cubs (0.82) in the Flathead are similar to those recorded for bears between 5 and 15 years of age (0.91 and 0.93) and for cubs (0.80 and 0.89) in Yellowstone National Park by Craighead et al. (1974) and by Knight and Eberhardt (1985) respectively. The survival rates of Flathead yearlings (0.94) and subadults (0.93) was higher than those reported in Yellowstone. Craighead et al. (1974) estimated survival rates of 0.95 for yearling females, 0.68 for yearling males, 0.80 for subadult females, and 0.73 for subadult males during the period when garbage dumps were in use in the Park. Knight and Eberhardt (1985) noted the difficulty in obtaining an accurate estimate of these values, but suggested survival rates of 0.73 for yearlings and 0.75 for subadults in Yellowstone after the dumps were closed.

Causes of Mortality

I suspected that only 1 recorded mortality was due to natural causes during 85 bear-years that adult and subadult grizzly bears were radio-tracked, and I found no evidence of
other unmarked adult or subadult bears dying from natural causes. Similarly, no natural mortalities were reported in approximately 27 bear-years of radio-tracking adult and subadult grizzly bears in other studies in the mid Rocky Mountains (Hamer et al. 1983, Hamer and Herrero 1983, Russell et al. 1979, Servheen 1981, Sizemore 1980). Instead, 6 known or suspected deaths of bears with functioning radio collars were caused by people in my study area, excluding the 2 research related losses. In the other studies mentioned above, another 7 bears with functioning radio collars were either killed by people, or were removed from the study area as part of bear-people management programs.

Although most recorded deaths of grizzly bears were due to legal hunting, the less biased sample of radio-collared bears indicated that illegal killing was perhaps even more common, particularly near human settlement.

No recorded or suspected grizzly bear deaths were directly related to the industrial activity in the study area. Shell Canada Ltd. does not permit firearms in its camps and discourages the use of private vehicles in the area. After 1980, garbage was incinerated at least once each day. Although grizzlies were occasionally reported near camps, they did not remain for long. The logging camps did not have incinerators, but the largest camp moved its garbage daily to a dump approximately 6 km away. Some smaller camps had poor garbage management, with dumps as close as 100 m from the cook-house. Black bears were known to have been shot in these
camps, but I was not aware if grizzlies were also killed.

There was no evidence that any adult or subadult grizzly bears died indirectly because of the industrial activity. If stress or displacement caused by the industries had impaired foraging efficiency, altered the animal's physiology, or caused an energetic drain to the extent that bears eventually died because of it, they would have been recorded as natural mortalities. Because the only natural mortality recorded was of an old bear who's range was in a portion of the study area with relatively little industrial activity, I conclude that the level of human activity experienced by the study bears was not sufficient to cause the death of these age classes of bears. One cub was eaten by its mother just prior to leaving the maternity den, 8 months after the female had seismic activity in her seasonal range, but it is doubtful that the 2 events were related (see Chapter 3).

Natality

Mean litter size is the parameter estimate based on the largest sample in this and other studies, and so is likely the most useful for comparisons. The average litter size of 2.26 in the Flathead is similar to 2.29 reported on the Rocky Mountain East Front (Aune and Brannon 1987), and 2.24 in Yellowstone National Park prior to the closing of the garbage dumps (Craighead et al. 1974). It is higher, however, than the average in other interior areas: 1.7 in both Glacier National Park, Montana (Martinka 1974, Kendall 1985) and
southern Yukon (Pearson 1975), 1.9 in Yellowstone Park after the dumps were closed (Knight and Eberhardt 1985); and 2.0 in Canadian Rocky Mountain National Parks (Mundy and Flook 1973).

Data on interbirth intervals are less numerous than those on litter size in the literature, and different studies have reported it in slightly different ways (Knight and Eberhardt, 1985). In Yellowstone Park, Knight and Eberhardt (1985) calculated an average of 3.0 years between litters, and suggested that 3.2 years would be a comparable frequency for pre-dump closure periods using Craighead et al.'s (1974) data. At McNeil River, Alaska, Glenn et al. (1976) recorded an average of 3.6 years for 12 interbirth intervals. All these estimates are longer than the 2.67 years estimated in the Flathead study area.

In their review, Bunnell and Tait (1981) suggested that the natality rate of bears was controlled by nutritional factors, generally in a density independent fashion. However, McCullough's (1981) and Stringham's (1983) analysis of grizzly bear data collected in Yellowstone National Park by Craighead et al. (1974), showed a negative correlation between recruitment and the number of adult males. They did not differentiate the cause of the apparent density dependence between changes in natality rate, cub mortality rate, nor examine the possible confounding (Stringham 1983) introduced by the availability of natural foods.

Grizzly bear litter sizes within the unhunted and unsettled Glacier National Park, Montana, are among the
smallest recorded on the continent (Martinka 1974, Kendall 1985). Immediately outside the park, grizzlies are hunted, and as about twice as many males as females were shot, this should have affected the sex ratio of living population of adult bears (McLellan and Shackleton 1988). In this unprotected area, both Aune and Brannon (1987) and I found grizzly bear litter sizes to be among the largest in North America. This information, combined with the rare occurrence of natural mortality of subadult and older bears in all telemetry studies made in the mid-Rocky Mountains, supports the hypothesis that density-dependent population regulation acts on both reproductive and mortality rates.

The density-dependent mechanism that affects cub production may not be a significant reduction in food at high bear densities, but rather a reduction in high quality habitats available to females accompanied by offspring and to subadults, due to the presence of adult males (Pearson 1975, Russell et al. 1979, this thesis Chapters 2 and 3). In unhunted areas such as parks and reserves, adult males should be relatively numerous and female displacement common (Pearson 1975, Russell et al. 1979), whereas hunted populations contain fewer males and segregation is not as pronounced. This could be more adequately investigated by a comparative population, habitat and behaviour study, focusing on age/sex class differences, between Glacier National Park, Montana, and adjacent study areas.
Rate of Increase

Although few rates of increase have been reported, the value of 0.081 I estimated appears high for grizzly bears, reflecting both high natality and low mortality rates. My samples on some reproductive parameters such as the age of first parturition are limited, but unrealistic values would be required to reduce the rate of increase to zero. This is not the case for survival rate values. If subadult female survival rates were as low as those given by Craighead et al. (1974) or by Knight and Eberhardt (1985), the rate of increase would decrease to 0.037 and 0.015 respectively. Although the rate of change is even more sensitive to changes in adult mortality, the larger sample of bear-years recorded for this age class, and the similarity of the rates reported between studies, increases confidence in my estimate.

Effects of Industry

If the level of activity of the resource extraction industries operating during my study had caused female grizzly bears to expend additional energy, reduce foraging efficiency, or use sub-optimal habitats to a degree that the population's demography was significantly affected, I expected to find some indication of impaired reproduction. One female lost her entire litter of 4 month old cubs approximately 8 months after a seismic line traversed her seasonal range (see Chapter 3). Although the 2 events were probably not related, it was the only reduction in reproduction remotely attributable to the
activities of resource industries. The litter sizes I recorded were as high or higher than most other grizzly bear populations with or without resource industries. Similarly, the survival-fecundity rate of increase or "demographic vigor" (Caughley 1977:55) of the grizzly bear population was high during the period of resource extraction, indicating a productive population.

Because I found both a high density of grizzly bears and a positive rate of increase during a period of industrial activity, I reject my main hypothesis.
CHAPTER 5: CONCLUSIONS

It is very difficult to conduct large scale experiments with a wide-ranging and long-lived species. This is particularly true when the species occurs at low densities typical of grizzly bears, without some confounding and consequent difficulties for interpretation. The design of my study does not allow me to conclude that the industrial activity in the study area had no effect on the demography of the grizzly bear population. Reducing the amount of legal kill by changes in hunting regulations between 1968 and 1982 confounds the influence of industry. The positive rate of increase may be the population’s response to relaxing a factor (hunting) which kept it below carrying capacity.

Although grizzly bears used cutting units less than expected, it is also possible that timber harvest improved the bear’s habitat over the short term by increasing ungulate numbers which are an important bear food. Unfortunately, there are no data on ungulate response to the logging, but my subjective estimates indicate that both white-tail deer (Odocoileus virginianus) and moose (Alces alces) populations increased during the study period, while elk (Cervus elaphus) decreased in numbers. This possible benefit may be only short term because ungulate numbers may decrease after second growth timber is established.

There was little evidence that the level and type of habitat alteration in the study area had a serious effect on
the grizzly population. Although there were striking exceptions, the integrity of the 2 most important spring habitats, riparian and snowchutes, was maintained in most locations. Similarly, burns were by far the most important summer habitat, and these had not been altered by development. If these important habitats had been carelessly modified by the various industries, it is probable that negative population responses would have been evident.

There was little evidence that the disturbance and displacement caused by the level and types of human activities that occurred in the study area had a significant impact on the grizzly population. The habitat loss equivalence due to the high road density was likely offset by increased nocturnal use of areas near roads and differential use of these areas by age-sex class. The dense cover in most of the study area and the ability of bears to habituate to human activities likely reduced the impact of potential human induced disturbances (McLellan and Shackleton in press b).

I had no evidence that industrial personnel killed any grizzly bears during the period of study. In a study such as this, there is a potential bias due to industrial personnel keeping their camps cleaner than normal because I was studying the bears in the area. However, I doubt that they did modify their behaviour because my base was 10 km away from the closest industrial camp and I never "inspected" a camp for proper garbage management. Nor did I notice differences between camps in my study area and one located outside of it.
The construction of roads was the most notable impact of the resource industries in the Flathead study area because roads permitted easy access for hunters, poachers and settlers. In my study area, 8 of the 9 deaths of bears with functioning radio collars were caused by people and 5 of these were illegal. Most of the recorded illegal killings of marked and unmarked bears occurred in 4% of the study area with human settlement. Most bears were shot, both legally and illegally, from roads. Fortunately, the high reproductive rate of the Flathead grizzly bears appears to have compensated thus far for this level of mortality.

On the East Front of the Rockies in Montana, cattle ranching, human settlement, and oil and gas exploration occur. There, 30 of 32 recorded grizzly bear mortalities were due to people; 10 by legal hunting and 20 for other reasons (Aune and Brannon 1987). As in my study area, the grizzlies on the East Front also have a very high reproductive rate (Aune et al. 1986), and the population trend may be stable (K. Aune, pers. comm.). In other areas, this may not be the case.

In 2 areas of western Alberta, where industrial roads provide easy access, the number of grizzly bears being killed by people appears to be causing population declines. Horejsi (1986) recorded 5 legal hunter kills and 3 illegal kills of 35 marked bears in 4 years, resulting in an annual mortality rate of 6%. Horejsi (1986) reported that 4 of 9 marked adult females were killed. Although he did not present any reproductive information, he suggested that the population was
declining. In the second well accessed study area in Alberta, 11 hunter kills, 5 research related deaths and 2 natural mortalities from a total of 38 marked bears in 5 years was thought to be causing a decrease in a grizzly bear population with a low reproductive rate (Nagy et al. 1988).

If wildlife managers consider the mortality rate of grizzlies to be excessive, and the user groups (hunters) can be convinced of this, it is relatively easy to reduce the number of legal kills. However, once an area is accessible and settled to the degree where illegal and control killing alone are excessive, reducing the number of human induced mortalities becomes extremely difficult and expensive. This is one of the problems facing the grizzly bears in Yellowstone National Park and adjacent areas (Knight and Eberhardt 1984).

The reduction in grizzly bear numbers and the eventual elimination of the species appears to follow a consistent pattern in the interior of North America, with industrial activity playing a very important role. Wilderness is first explored by hunters, trappers, foresters and geologists. Then industry builds roads to remove resources, and these roads, in turn, make it much easier for hunters and poachers. Grizzly numbers may begin to decline at this stage if hunting seasons are too liberal for the productivity of the area. Also, new access is often followed by ranchers and settlers, and soon the grizzlies are gone.

Stopping resource development to maintain grizzly populations (and other wilderness values) is a viable option
for some relatively small areas. However, due to the economic value and continued demand for natural resources, industries are destined to extract resources from most of the remaining, "unprotected" grizzly bear habitat. Alternatively, maintaining grizzlies requires having, 1) conservative hunting regulations based on the area’s productivity, 2) stringent regulations for habitat protection and for camp and personnel management, 3) access plans to ensure roads are closed after developments are complete, and 4) keeping human habitations from being scattered in many drainages. Regulations such as these will likely be unpopular with some administrators and citizens who want to continue to "settle the west". Land and wildlife managers, and user groups must co-operate with the resource industries to educate the public and advertise the value of long term co-ordinated land use plans. In this way it may be possible to extract natural resources from an area while sustaining viable grizzly bear populations, and maintain the option of regaining wilderness.

The Flathead study should be viewed as one, relatively short term, experimental unit. Until replicates of this study are conducted, testing both population and behavioural responses of grizzly bears to industrial activities in different regions, it is difficult to extrapolate results with confidence. The characteristics of the Flathead Drainage that made industry and grizzlies compatible during the short duration of my study may have limited distribution.

Research is continuing in my study area to further evaluate
long term impacts of resource industries. In addition, the research is being expanded to include the influence of ungulates discussed earlier, and potential interspecific competition between black and grizzly bears.
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