

CAUSES AND CONSEQUENCES OF SEXUAL HABITAT  
SEGREGATION IN GRIZZLY BEARS

by

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**ABSTRACT**

I studied habitat use and population dynamics of 2 grizzly bear (*Ursus arctos*) populations to test 3 competing hypotheses of sexual habitat segregation (no avoidance, food competition, and sex competition) and 3 competing hypotheses on the effects of adult male mortality on female reproduction (additive, compensatory, depensatory). Twenty bears were radio-monitored from 1980 to 1984 in Kananaskis, Alberta and 28 bears were radio-monitored from 1985 to 1990 in the Selkirk Mountains of Idaho and British Columbia. The Kananaskis population had high mortality of older adult males and a corresponding influx of younger immigrant males. That population had a low reproductive rate and appeared to be declining. The Selkirk population had low mortality of older adult males and few younger immigrant males - that population had a high reproductive rate and appeared to be stable. Sexually mature adult females avoided food-rich, male-occupied habitat in Kananaskis where there were many potentially infanticidal, immigrant males; but not in the Selkirks where there were few such males. Sexually immature subadult females did not avoid food-rich, male-occupied habitat in either study area. Mean litter size of cubs was smaller in Kananaskis than in the Selkirks despite earlier age at first reproduction. Age of mothers, food supply, and population density did not explain the smaller litters but adult female avoidance of immigrant males and food-rich, male-occupied habitats appears to explain the smaller litters. My results reject the "no avoidance" and "food competition" models but support the "sex competition" model of habitat segregation. My results also reject the "additive" and "compensatory" models but support the "depensatory" model

of adult male mortality. Trophy hunting of adult males was not compensatory for reproduction and beneficial for population growth as commonly believed, but was actually depensatory for reproduction and contributed to population decline.

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## Chapter 1

### GENERAL INTRODUCTION

A controversy exists concerning the causes and consequences of sex and reproductive class habitat segregation in grizzly bears. Some researchers (Pearson 1975; Wielgus 1986; Mattson et al. 1987; McLellan and Shackleton 1988) reported that female grizzly bears, especially females with cubs, used habitats that were different from and less favourable than those used by males. They interpreted that as female avoidance of aggressive, cannibalistic males, but have not tested the hypothesis. An alternative explanation may be that females do not avoid males but simply have different habitats available to them or choose to use different habitats. I call that the "no avoidance" model of habitat segregation.

Hornocker (1962), Egbert and Stokes (1976), McCullough (1981), and Stringham (1983) suggested that female bears and other subdominants may avoid adult males because those males compete with and cannibalize subdominants for food. I subsume competition and cannibalism and call that the "food competition" model of habitat segregation.

Stringham (1980), Wielgus (1986) and LeCount (1987) speculated that females with cubs avoid immigrant, adult males because those males are unlikely to have sired cubs and will kill cubs to induce estrus and gain a breeding opportunity (Hrdy and Hausfater 1984). I call that the "sex competition" model of habitat segregation. None of the three competing hypotheses have been tested, to date.

A related controversy also exists on the effects of hunting adult males and whether female reproduction is independent of mortality and

density of adult males (Miller 1990). Bunnell and Tait (1981), Knight and Eberhardt (1985), and Rogers (1987) all suggested that reproduction is determined by food supply and independent of mortality and density of adult males. I call that the "additive" model of male mortality.

McCullough (1981) and Stringham (1983) suggested that reproduction is dependent on mortality and density of adult males. They hypothesized that adult males regulate reproduction directly by killing cubs or indirectly by denying resources to females. McCullough (1986) and McLellan (1989a) further suggested that mortality of adult males may increase female reproduction because of reduced density of competitive or cannibalistic adult males. I call that the "compensatory" model of male mortality.

Stringham (1980) and LeCount (1987) suggested that hunting of adult males encourages immigration of subadult males with subsequent increases in density of potentially infanticidal, non-sire males (Hrdy and Hausfater 1984). They suggested that adult male mortality could result in reduced reproduction because of increased sexually-motivated infanticide. I call that the "depensatory" model of male mortality. None of the three competing hypotheses have been tested, to date, but many bear managers assume the compensatory model (Miller 1990).

During my M.Sc. research I found sexually segregated habitat use in a hunted and sexually skewed (capture sex ratio = 3 males:1 female) grizzly bear population in Kananaskis, Alberta at the edge of the species' range (Wielgus 1986). I speculated that the skewed sex ratio was caused by numerous immigrant males and that the observed sexual habitat segregation was due to female avoidance of those immigrant males. I also speculated that females restricted themselves to poorer

quality habitats where males were rare and that their reproduction would suffer as a result. Those predictions correspond to the "sex competition" model of habitat segregation and the "depensatory" model of male mortality.

In this thesis I test the three models of habitat segregation and the three models of male mortality by reanalyzing my data from the hunted Kananaskis population (population dynamics, sex and reproductive class habitat segregation) and comparing that to new data I obtained in the Selkirk Mountains of Idaho and B.C. The Selkirk population was also at the edge of the species' range but was not hunted and the initial capture sex ratio was 1 male:1 female, suggesting few immigrant males. I predicted that the Selkirk population would show no sex and reproductive class habitat segregation. I also predicted that the Selkirk population would show higher reproduction than the Kananaskis population because of the absence of habitat segregation.

In Chapter 2, I estimate population parameters including density, sex and age composition, reproduction, survival, and population growth for the Kananaskis sample population. In Chapter 3, I estimate the same parameters for the Selkirk sample population. In Chapter 4, I test the 3 competing hypotheses on sex and reproductive class habitat segregation. In Chapter 5, I test the 3 competing hypotheses on effects of adult male mortality on female reproductive rate. In Chapter 6, I present general conclusions. I followed the recommendations of Romesburg (1981), Matter and Mannan (1989), and Keppie (1990) and concentrated on scientific tests of hypotheses. I excluded descriptive accounts of movements, home ranges, and food habits because such accounts were extraneous to my tests of hypotheses.

## Chapter 2

### POPULATION DYNAMICS OF KANANASKIS GRIZZLY BEARS

#### INTRODUCTION

Numbers of grizzly bears have declined from an estimated 100,000 in the 1850's to less than 900 currently in the 48 conterminous United States; major causes of population decline are human-induced mortality and low reproductive rate (Servheen 1990). The future of the species in North America can only be assured in Alaska and Canada (Servheen 1990).

There are an estimated 780 grizzly bears in Alberta and numbers are declining (Servheen 1990). Nagy and Gunson (1990) estimated 62 grizzly bears in southwestern Alberta, at the edge of the species' range. Sport hunting of grizzly bears was closed in southwestern Alberta in 1970 because bear numbers were believed to be declining. Increased sightings and complaints led the Alberta government to reopen the hunting season in the Bow Crow Forest or Bear Management Area 6 (BMA 6) in 1982. Sport hunting of grizzlies was also reopened in Kananaskis Provincial Park (BMA 5) in 1987 because the population was believed to be increasing (Carr 1989). Both seasons were closed again in 1988 because of public concern. Nagy and Gunson (1990) reviewed harvest statistics and recommended against sport hunting in Kananaskis but advocated limited hunting of males in the Bow Crow.

Wielgus (1986) found sexually segregated habitat use by grizzly bears in Kananaskis and the Bow Crow from 1980 to 1984. In this chapter I estimate population parameters of grizzly bears in Kananaskis and the Bow-Crow from data collected during that habitat study. Population

parameters include density and numbers, sex and age composition, reproductive rate, survival rate, and population growth rate. My objectives are to estimate the status of the grizzly population in Kananaskis and the Bow Crow and to examine potential relations among harvest of male bears and population dynamics.

## METHODS

### *Study area*

The study area covered 9000 km<sup>2</sup> in the Kananaskis Provincial Park and Bow Crow Forest of southwestern Alberta (50-51° N, 115-116° W). Elevation ranged from 1300 m to 2700 m in rugged mountainous terrain. Climate was continental with long, cold winters and short, cool summers. Vegetation is in the subalpine fir-Engelmann spruce (Abies lasiocarpa-Picea engelmanni) forest region (Rowe 1972). Forests were comprised of lodgepole pine (Pinus contorta), Engelmann spruce, and alpine fir.

### *Trapping and monitoring*

Grizzly bears were trapped using Aldrich leg snares and immobilized with Ketamine hydrochloride and Xylazine hydrochloride. Immobilized bears were weighed, ear-tagged, had a premolar tooth extracted for ageing (Stoneburg and Jonkel 1966), and were fitted with activity-sensing radio-collars.

Trapping and radio-collaring of bears was done in 2 areas, the Highwood and Sheep trapping zones. The 254 km<sup>2</sup> Highwood trapping zone (HTZ) covered a 50-year-old burn in the mountains (1800 m) of Kananaskis

and was dominated by soapberry (Shepherdia canadensis) shrubfields and forbfields. Immediate surrounding areas were largely unburnt and appeared to have comparatively little food production. Trapping in the HTZ took place from 1980 to 1984.

The Sheep trapping zone (STZ) was a 225 km<sup>2</sup> area about 20 km to the east in the foothills (1400 m) and was chosen primarily for capture of black bears (Ursus americanus). It was not centered on a burned-over area. Trapping in the STZ took place from 1980 to 1983.

Fixed-wing radio-telemetry was conducted weekly during the non-denning period (early April to early December) from 1981 to 1984 to monitor the bears.

*Density, numbers, and sex and age composition*

I estimated density by determining the mean annual number of bears present in the female 97.5% multi-annual composite home range (Ackerman et al. 1990). Most bear researchers use similar methods (LeFranc et al. 1987: 52-53), allowing direct comparisons. I believe that all bears, especially highly visible and easily identifiable females with offspring (LeFranc et al. 1987: 106), were accounted for in that 868 km<sup>2</sup> range because intensive field work in that range from 1980 to 1985 revealed no additional individuals (Wielgus 1986; Carr 1989). I rejected the female 100% and male 97.5% composite ranges because I could not account for all bears in the larger areas (e.g., 1033 and 5000 km<sup>2</sup>).

If female bears were captured after 1980 (the first year of study) but restricted their movements to the composite range for at least 2 consecutive years, their presence was extrapolated back to 1980 because

females tend to remain in the same area throughout their lives; males were not extrapolated back to 1980 because they may be immigrants (Glenn and Miller 1980). Cubs were extrapolated back to year of birth. This method provides a minimum density estimate because it assumes all bears present in the composite range were captured.

I estimated numbers of bears for Kananaskis (BMA 5) and the Bow Crow Forest (northern half of BMA 6) by applying my density estimates to the 2315 km<sup>2</sup> mountainous region of the study area. That area was believed to be inhabited by both females and males based on observed habitat use by bears (Wielgus 1986). Foothills were little used by males and no use by females was observed.

I estimated sex and age composition by calculating the mean annual percentage of male and female adults ( $\geq 6.5$  years), male and female subadults (2.5 to 5.5 years), and cubs (0.5 to 1.5 years) in the monitored population.

#### *Reproductive rate*

Reproductive rate was determined from visual aerial and ground observations of females and their cubs. I calculated reproductive rate as the mean number of new cubs per litter divided by the mean birth or breeding interval (Craighead et al. 1974). This method yields a maximum estimate because it incorporates breeding as well as birth intervals, and females could breed but fail to produce cubs. The rate does not include cubs that died in the den or shortly after leaving the den.

### *Survival rates*

I estimated seasonal and annual survival rates for adult males and females ( $\geq 6.5$  years), subadult males and females (2.5 to 5.5 years), and cubs (0.5 to 1.5 years) using the techniques of Heisey and Fuller (1985), which calculate the number of deaths recorded during the number of radio-days monitored. Sex was determined during capture and age was determined from known birth year or estimated by counting cementum annuli (Stoneburg and Jonkel 1966). Birth dates of bears were assigned at February 1. Seasons were defined as spring (April-June, includes grizzly bear hunting season), summer (July-August), fall (September-November, includes general hunting season), and winter (December-March, includes denning season).

Date and cause of death were determined by compulsory reporting of sport-hunting kills and reports from conservation officers. This method yields a maximum estimate of survival because only reported kills were tallied - animals that disappeared were assumed not to have died.

I also estimated survival rates for adult females and cubs by extending the sampling period to include deaths occurring just after radio-monitoring ceased. One adult female with yearling cubs was shot in the fall of 1985. She was included in the survival calculations and her accompanying cubs were assumed to have died by January 1, 1985. To prevent biasing survival downwards, I assumed that all other adult females survived through 1985 and that all other unmonitored cubs survived to weaning at 2.5 years of age.

### *Population growth*

I estimated the exponential rate of increase by iterating the Lotka equation (Caughley 1977). Sex- and age-specific survival and reproductive rates were those estimated from radio-collared bears and dependent offspring.

## **RESULTS**

### *Trapping and monitoring*

A total of 24 grizzly bears (18 males, 6 females) were captured from 1980 to 1983. Fourteen males and 6 females were captured in the Highwood trapping zone (HTZ) and 3 males were captured in the Sheep zone (STZ), 1 additional male was captured in nearby Peter Lougheed Park.

Captures of new, young males increased after the hunting season was opened in 1982. Numbers of new males captured per year in the HTZ and STZ was 4 in 1980 (ages = 4.5, 9.5, 12.5, and 14.5 years); 3 in 1981 (ages = 4.5, 5.5, and 15.5 years); 2 in 1982 (ages = 3.5, and 5.5 years); and 8 in 1983 (ages = 3.5, 3.5, 3.5, 3.5, 5.5, 6.5, 7.5, and 15.5 years). Mean age of captured males was 9.5 years for 1980 to 1981 ( $n = 7$ ,  $SD = 4.8$ ) and 5.8 years for 1982 to 1983 ( $n = 10$ ,  $SD = 3.7$ ). No new males were captured in 1984 but trapping effort was greatly reduced that year. Fifteen of 18 male bears were collared and radio-monitored, 3 went uncollared in 1980.

One 6.5 year-old without offspring was captured in 1980. One 14.5 year-old with yearlings was captured in 1981, prior to the opening of the grizzly bear hunting season; her two female offspring (2.5 years)

and one new estrus adult (6.5 years) were captured in 1982 after the hunting season began. Another new estrus adult (10.5 years) was captured in 1983. No new females were captured in 1984. Five of 6 female bears were collared and radio-monitored, 1 died at capture in 1980.

Trapping effort was 1806, 2074, 2124, 1868, and 118 trap-nights annually from 1980 to 1984. Trapping success was much greater in the HTZ than in the STZ despite similar trapping effort. Twenty different bears were captured over 5 years (3916 trap nights) in the HTZ. Only 3 males (2 subadults, 1 adult) were captured over 4 years (3309 trap nights) in the STZ and no bears were ever radio-located there.

*Density, numbers, and sex and age composition*

Ten to 20 different bears were known to reside in the 868 km<sup>2</sup> female 97.5% composite range from 1980 to 1984 (Table 1). Numbers of subadult and young, adult male bears appeared to increase after the hunting season was opened in 1982. Numbers of females appeared relatively stable from 1980 to 1984, assuming females were present in their composite range prior to their capture. No unaccounted females with offspring were observed in the female composite range during the period of study. Numbers of cubs may have been underestimated from 1980 to 1982 because the reproductive status of 1 adult female was unknown for those years.

Mean annual density was 1.62 bears/100 km<sup>2</sup> (61.72 km<sup>2</sup>/bear) for an estimated population size of 38 bears (Table 1). Mean sex and age composition was 30% adult males, 22% adult females, 22% subadult males,

Table 1. Annual number of bears in the 97.5% female composite home range, percent composition (%), estimated density (bears/100 km<sup>2</sup>), and estimated population size for different sex and age classes of grizzly bears in Kananaskis Park and the Bow Crow Forest of southwestern Alberta, 1980 to 1984.

Year	Cubs	Subadult males	Subadult females	Adult males	Adult females	Total
1980	2 (20)	1 (10)	1 (10)	3 (30)	3 (30)	10
1981	2 (20)	2 (20)	1 (10)	3 (30)	2 (20)	10
1982	0 (0)	3 (27)	2 (19)	3 (27)	3 (27)	11
1983	2 (10)	6 (30)	2 (10)	7 (35)	3 (15)	20
1984	5 (26)	4 (21)	1 (5)	5 (26)	4 (21)	19
Annual Mean	2.2 (15)	3.2 (22)	1.4 (11)	4.2 (30)	3.0 (22)	14.0
Density <sup>1</sup>	0.25	0.39	0.16	0.48	0.34	1.62
Pop. <sup>2</sup>	5.78	9.02	3.70	11.11	7.87	37.50

<sup>1</sup> Density estimate based on mean annual number of bears in the 97.5% female multi-annual composite home range (868 km<sup>2</sup>).

<sup>2</sup> Population estimate based on application of density estimate to grizzly-occupied portion (2315 km<sup>2</sup>) of Kananaskis and the Bow Crow Forest.

11% subadult females, and 15% cubs (Table 1). That gives approximate sex ratios of 1.5 males:1 female for adults and 2 males:1 female for subadults.

#### *Reproductive rate*

Mean litter size for cubs of the year was 1.40 ( $n = 5$ ,  $SD = 0.54$ , sizes = 1, 1, 1, 2, 2) and mean birth or breeding interval was 3.00 years ( $n = 3$ ,  $SD = 0$ ). Combined, these values yield an estimated reproductive rate of 0.46 cubs/adult female/year or 0.23 female cubs/adult female/year. One female bred at 3.5 years of age and gave birth at 4.5 years; her sister bred at 3.5 and 4.5 years and was assumed to give birth at 5.5 years. Another female was lactating when captured at 6.5 years. This small sample yields a mean age at first parturition of 5.5 years.

#### *Survival rates*

Sex and age-specific seasonal and annual survival rates are summarized in Table 2. Three of 9 adult males were legally shot during 8.29 bear-years for an annual survival rate of 0.70. One bear was shot during the spring season in Alberta and 2 bears were shot during the spring hunting season in adjacent British Columbia (B.C.).

One of 9 subadult males was shot during 6.80 bear-years for an annual rate of 0.89. That male was shot in self defense by a sport hunter in Alberta during the fall general season. Of 18 male bears

Table 2. Seasonal and annual survival rates, number of bear-years monitored, and number of bear deaths/number of radioed bears for different sex and age classes of grizzly bears in Kananaskis, Alberta, 1980 to 1984.

Sex/Age Class	Survival Rate					Annual (95% CL)	Bear Years	Deaths /Bears
	Spring	Summer	Fall	Winter				
Adult Males	0.70	1.00	1.00	1.00	0.70	(0.46-1.00)	8.29	3/9
Subadult Males	1.00	1.00	0.89	1.00	0.89	(0.72-1.00)	6.80	1/9
Adult Females	1.00	1.00	1.00	1.00	1.00	(1.00)	8.75	0/5
Subadult Females	1.00	1.00	1.00	1.00	1.00	(1.00)	2.40	0/2
Cubs	1.00	1.00	1.00	1.00	1.00	(1.00)	2.47	0/5
Adult Females <sup>1</sup>	1.00	1.00	0.93	1.00	0.93	(0.83-1.00)	14.92	1/5
Cubs <sup>1</sup>	1.00	1.00	0.78	1.00	0.78	(0.56-1.00)	7.02	2/5

<sup>1</sup> includes deaths occurring 1 year after radio-monitoring ceased.

captured from 1980 to 1984, 8 were reported shot by 1987 and 7 simply disappeared by 1984. Of the 8 known deaths, 3 were legally harvested in Alberta, 3 were legally harvested in B.C., and 2 were legally shot in self defense in Alberta. All these deaths were reported by hunters. Mean age of killed males was 11.12 years ( $n = 8$ ,  $SD = 4.98$ , ages = 5.5, 6.5, 7.5, 9.5, 10.5, 13.5, 16.5, and 19.5 years). Chronology of male deaths and disappearances were: two males (ages = 4.5 and 14.5 years) disappeared in 1980 and one 5.5 year-old was shot in 1981. One 16.5 year-old was shot in 1982. One 3.5 year-old and one 15.5 year-old disappeared in 1983. Three males (ages = 6.5, 10.5, and 13.5 years) were shot and three males (ages = 4.5, 4.5, and 8.5 years) disappeared in 1984. An additional three males (ages = 7.5, 9.5, and 19.5 years) were shot from 1986 to 1987.

None of the 5 adult females died during 8.75 bear-years for an annual survival rate of 1.00 (Table 2). One adult female, however, was shot in self defense by a hunter in the HTZ in the fall of 1979 - 1 year before trapping and monitoring began. Another radio-collared adult female with yearling cubs was shot in self defense by a sport hunter in 1985, 1 year after radio-monitoring ceased. If we include the latter death and assume that all other adult females survived through 1985 we get 1 death in 14.92 bear-years for an annual survival rate of 0.93 (Table 2). Neither subadult female died during 2.40 bear-years for a survival rate of 1.00 (Table 2).

None of the 5 cubs died during 2.4 bear-years for a survival rate of 1.00 (Table 2). If I assume that the cubs of the killed adult female died by Jan 1 1985, however, and assume that all other cubs survived to

weaning at 2.5 years of age, the estimated survival rate is 0.78 during 7.02 bear-years (Table 2).

#### *Population growth*

Age-specific reproductive rates used in the Lotka equation were 0.23 female cubs/adult female/year, based on an assumed 1 male:1 female sex ratio of cubs (e.g., LeFranc et al. 1987). Reproduction started at 5.5 years of age.

Age-specific survival rates for adult females (0.93) and cubs (0.78) included deaths occurring just after radio-monitoring ceased. Survival rates excluding those deaths were unrealistic for adult females (1.00) and cubs (1.00). I substituted the estimated rates of subadult males (0.89) and adult females (0.93) for subadult females because the estimated rate (1.00) was unrealistically high and based on a small sample (Table 2). Maximum age was set at 21.5 years because mean maximum age was 21.36 years (SD = 3.94) for 22 different populations (LeFranc et al. 1987: Table 10).

The Lotka equation was solved for both subadult female survival rates. The exponential rate of increase was -0.01 for the subadult female survival rate of 0.89 and +0.01 for the subadult female survival rate of 0.93.

## DISCUSSION

### *Density, numbers, and sex and age composition*

The very high trapping intensity and lack of unaccounted females in the composite range suggests that all bears, especially females, were trapped and accounted for in that composite range. The estimated density (61.72 km<sup>2</sup>/bear) was similar to the Selkirks (42.7 to 70.9 km<sup>2</sup>/bear; Chapter 3) and other interior grizzly populations (LeFranc et al. 1987: 52-53), but considerably lower than in the Flathead Valley of B.C. (16.47 km<sup>2</sup>/bear; McLellan 1989b). McLellan (1989b) calculated density for his trapping zone only and cautioned against direct comparisons. I do not use his method to estimate density because the Highwood trapping zone was comprised of burned-over habitat and was not representative of the larger unburned study area. Applying McLellan's method would weight densities towards adult males, subadult males, and subadult females, but away from adult females and offspring because of sex and reproductive class habitat segregation in that zone (Chapter 4). I encountered similar problems with McLellan's method in the Idaho trapping zone in the Selkirk Mountains study area (Chapter 3).

Percentages of females were lower and percentages of males were higher than in most other grizzly populations (LeFranc et al. 1987: 47-49; McLellan 1989b; Chapter 3). The sex ratios of 1.5 males:1 female for adults and 2 males:1 female for subadults contrasts with ratios of approximately 1 male:2 females for adults and 1 male:1 female for subadults in the Selkirks (Chapter 3).

The observed sex and age composition may be atypical but there are compelling reasons to accept it as accurate. The very high annual

mortality (30%) of older (mean age = 11.12 years) adult males may have allowed high rates of immigration by subadult and young, adult males. It appears that 10 new, younger males (mean age = 5.8 years) entered the composite range after the hunting season was opened in 1982. That immigration corresponded with increased deaths of older adult males - only one collared male was reported shot from 1977 to 1981 in Kananaskis and the Bow Crow but 4 collared males and 3 uncollared males (Nagy and Gunson 1990) were reported shot there from 1982 to 1987. Three other collared males were reported shot in adjacent B.C. between 1982 to 1986. An additional 5 collared males simply disappeared from 1982 to 1984. All those data suggest that a large number of older, resident males were being removed after 1981 upon opening of the hunting season.

Kemp (1976) and Young and Ruff (1982) documented a 3-fold increase in subadult males after removing 30% of adult male black bears. LeCount (1987) also suggested that high mortality of adult male black bears resulted in a preponderance of immigrant subadult males in his study area. An alternate explanation for the apparent increase in young males is that trapping for males became more effective after 1982; but trapping effort remained similar from 1980 to 1983.

Few bears ( $n = 3$  males) were trapped in the STZ and no bears were ever radio-located there. Care should be taken to ensure that my density estimates for the Kananaskis and Bow Crow are not extrapolated to such areas. My density estimates are higher than those of Carr (1989) (1.62 vs 1.22 bears/100 km<sup>2</sup>) but my population estimates are considerably lower (38 vs 77), especially for females (12 vs 28). Carr (1989) used the Chapman-Robson mark/recapture technique to estimate number of males and then assumed an approximate 1:1 sex ratio to estimate number of

females. He also assumed population closure (no immigration) of males. I observed a sex ratio skewed towards males and evidence of immigration by males. I suggest the present population estimates are more accurate and that the estimated number of female bears for Kananaskis and the Bow Crow is alarmingly low.

#### *Reproductive rate*

The estimated reproductive rate of 0.46 appears considerably lower than that in the Flathead (0.85; McLellan 1989a) and in the Selkirks (0.74; Chapter 3). The mean birth or breeding interval (3.00 years) is a minimum but is similar to that of the Flathead (2.67 years; McLellan 1989a) and the Selkirks (3.00 years; Chapter 3) and is the accepted average for grizzly populations in North America (LeFranc et al. 1987: 54). The mean age at first parturition (5.5 years) is also a minimum and appears younger than for most other populations ( $\geq 6$  years; Lefranc et al. 1987: 54; McLellan 1989a; Chapter 3). Longer birth intervals and later ages at first parturition would lower the reproductive rate and population growth rate even further than that reported here.

Mean cub litter size (1.40) appears smaller than in the Flathead (2.26; McLellan 1989a) and the Selkirks (2.22; Chapter 3) and is among the smallest reported in North America (LeFranc et al. 1987: 54). The small litter size is in surprising contrast to the early estimated age at first parturition. Bunnell and Tait (1981) suggest that litter size and age at first parturition are positively related since both parameters are influenced by nutrition. Perhaps the small litter size is related to the abundance of immigrant males. LeCount (1987) found high

rates of infanticide in a heavily hunted black bear population with many immigrant males. Hrdy and Hausfater (1984) reviewed infanticide in many species and found that most killing of young is by immigrant males. I did not observe any instances of infanticide but it may have occurred prior to first observation of cubs. Wielgus (1986) did observe that female bears appeared to avoid males and used poorer quality habitats than males; perhaps their nutrition and cub litter sizes suffered as a result.

#### *Survival rates*

The estimated annual survival rate for adult males (0.70) indicates a very heavily hunted population and is among the lowest survival recorded in North America (Bunnell and Tait 1980, 1981, 1985). The survival rate appears considerably lower than that recorded in the Flathead (0.92; McLellan 1989c) and the Selkirks (0.81; Chapter 3).

The rate of 0.89 for subadult males is similar to that recorded in the Flathead (0.92; McLellan 1989c) and the Selkirks (0.90; Chapter 3) and is consistent with hunter's disdain for smaller, subadult animals (Bunnell and Tait 1980, 1981, 1985). Both adult and subadult male survival rates may have been overestimates because 2 marked and 5 collared males simply disappeared and could have been killed.

The estimated rate of 1.00 for adult females is unrealistic and may simply have been due to chance. One collared adult female was shot just after monitoring ceased in 1985 and 6 other uncollared females were reported shot in the study area from 1974 to 1981 (Nagy and Gunson 1990). The alternative estimate of 0.93 is more realistic and similar to

rates obtained in the Flathead (0.94; McLellan 1989c) and the Selkirks (0.96; Chapter 3). The substituted rates of 0.89 to 0.93 for subadult females are also more realistic than the estimated rate of 1.00 and closer to that obtained in the Flathead (0.94; McLellan 1989c) and the Selkirks (0.78 to 0.84; Chapter 3). Even these estimates for survival of females may be optimistic because they apply only to animals that resided in Kananaskis, which was protected from hunting during the period of study. Bears in the Bow Crow were subjected to sport hunting so females there may have experienced survival rates closer to those of the males.

The estimated rate of 1.00 for cubs is unrealistic (Bunnell and Tait 1985) and may be due to the small sample size (2.47 bear-years). It seems likely that the cubs of the killed female would have died by Jan 1 1985 after she was shot. She failed to provide a den for them and there were many immigrant, possibly infanticidal males in the area. The alternative estimate of 0.78 is more realistic and similar to that observed in the Flathead (0.82; McLellan 1989c) and the Selkirks (0.84; Chapter 3).

My estimates of male survival contrast with those of Carr (1989). He estimated mean annual survival rates of 0.90 for males and 0.96 for females by calculating the percentage of bears marked and present on January 1 and reported killed by December 31 of that year. He counted only bears that were subject to at least 1 full year of mortality - one male bear was not included in his analysis because that bear died only 2.5 months after capture. I believe the mortality estimates in Table 2 are more realistic.

*Population growth*

The estimated rates of growth for the female segment of the population ( $r = -0.01$  to  $+0.01$ ) are lower than those in the Flathead ( $r = +0.07$  to  $+0.08$ ; McLellan 1989a) and the Selkirks ( $r = 0.00$  to  $+0.02$ ; Chapter 3). The estimated growth rates are probably maxima because the survival rates and reproductive rates are maxima, so the population is more likely to be declining. My estimates again contrast with Carr (1989). He back-dated the population age structure to 1980 and concluded that many bears were being born into the population. Carr's assumed recruitment was largely comprised of immigrant subadult males rather than production by the resident females. None of the 10 captured subadult males were observed as offspring of resident females and all were  $\geq 3.5$  years of age at capture, suggesting that they were probably immigrants (Glenn and Miller 1980).

Differences in survival of females contributes more to variation in population growth than do differences in reproduction (Knight and Eberhardt 1985; McLellan 1989a). My estimates of adult female (0.93), subadult female (0.89 to 0.93), and cub survival (0.78) are very similar to the rates in the Flathead (adult females 0.94, subadult females 0.94, cubs 0.82; McLellan 1989c) yet that population showed a high rate of population growth ( $+0.08$ ). The low reproductive rate accounts for the low value of  $r$  in this population. Because mean age at first parturition is early and mean interbirth interval is the expected average, the small litter size must cause the low growth rate. The findings of my study suggest that female grizzly bears were few in number and probably declining because of low reproductive rate. Numerous younger, male bears

were interpreted as a healthy, growing population (Carr 1989), but probably reflected increasing numbers of immigrant males due to high mortality of older adult males.

### Chapter 3

## POPULATION DYNAMICS OF SELKIRK GRIZZLY BEARS

### INTRODUCTION

Grizzly bears within the U.S. portion of the Selkirk Mountains Grizzly Bear Ecosystem (SMGBE) are classified as threatened by the U.S. Fish and Wildlife Service. This same population extends into British Columbia where the bears are classified as vulnerable by the Committee on the Status of Endangered Wildlife in Canada.

The population parameters, movements, and habitat use of grizzly bears in the SMGBE were studied from 1983 through 1990 to assist in recovery from threatened status. Research began when one female was collared and radio-monitored from 1983 to 1985 (Almack 1985) and was extended when additional bears were captured and monitored from 1985 to 1987 (Knick 1988). Starting in 1988, research was extended from the U.S. into Canada because the population was believed to be decreasing (Knick and Kasworm 1989) and bears were using both American and Canadian portions of the SMGBE (Servheen and Young 1989; Compton et al. 1990). In this chapter, I estimate population parameters including density, sex and age composition, reproductive rates, survival rates, and population growth rates. My objectives are to determine the status of the SMGBE grizzly population and to examine potential relations among harvest of male bears and population dynamics.

## METHODS

### *Study area*

The SMGBE study area covers approximately 5700 km<sup>2</sup>; 3000 km<sup>2</sup> in northern Idaho and northeastern Washington and 2700 km<sup>2</sup> in southern B.C. (48-49° N, 116-117° W). Physiography is mountainous and climate is Pacific maritime/Continental with long winters and cool summers. Vegetation is classified as the Engelmann spruce-subalpine fir and interior cedar-western hemlock (Thuja plicata-Tsuga heterophylla) bigeoclimatic zones (B.C. Min. For. 1988).

Legal hunting of grizzly bears was not allowed in the American portion of the SMGBE under the Endangered Species Act; legal hunting in the B.C. portion was prohibited during research (1985 to 1990). Big game hunting for other species was allowed in both U.S. and B.C. jurisdictions during the fall general season and spring black bear season. Vehicle access was partially restricted in both jurisdictions, with road closures for U.S. National forests and some private forest lands in B.C.

### *Trapping and monitoring*

Grizzly bears were trapped and radio-collared in 2 areas - a 100 km<sup>2</sup> trapping zone in Idaho and a 235 km<sup>2</sup> zone approximately 20 km north in B.C. Trapping in Idaho took place in spring (May 1 to June 30) from 1985 to 1987 and in fall (August 8 to 25) 1989. Trapping in B.C. took place in spring (May 25 to July 26) during 1988 and 1989. Bears were trapped using Aldrich leg snares and immobilized with 4.5 mg Ketamine

hydrochloride and 2.3 mg Xylazine hydrochloride per kg body weight. Immobilized bears were lip-tattooed, ear-tagged, and had a pre-molar tooth extracted for ageing (Stoneburg and Jonkel 1966). All bears were fitted with activity-sensing or mortality-sensing "drop-off" radio-collars (Hellgren et al. 1988).

Bears were monitored by fixed-wing radiotelemetry (Whitehouse and Steven 1977), conducted weekly during the non-denning period (early April to early November) from 1985 to 1990.

#### *Density and sex and age composition*

I estimated density by dividing the total number of bears captured and observed by the size of the area they occupied. Most other bear researchers use similar methods, allowing direct comparisons (LeFranc et al. 1987: 52-53). I calculated mean annual number of bears in the female 97.5% multi-annual composite home ranges (Ackerman et al. 1990). I calculated densities separately for the U.S. and B.C. portions because the female composite ranges were distinct in each portion. I believe all bears, but especially highly visible and easily identifiable females with offspring (LeFranc et al. 1987: 106), were accounted for in the U.S. composite range because of intensive field work in that range from 1985 to 1990 (Almack 1985; Knick 1988; Servheen and Young 1989; Compton et al. 1990). I am less confident in accounting for all bears in the B.C. composite range because field work extended for only 3 years there. I rejected the 100% home range because the 2.5% outermost locations greatly expanded the ranges (e.g, from 815 to 1848 km<sup>2</sup>) and I could not account for all bears in the larger areas. I used the female and not

male composite home range for the same reason - the male 97.5% ranges were too large (1691 to 1767 km<sup>2</sup>) to account for all bears. This method provides a minimum estimate because all bears residing within the composite home ranges are assumed captured.

I estimated sex and age composition by calculating the mean annual percentage of male and female cubs (0.5-1.5 years), male and female subadults (2.5 to 5.5 years), and male and female adults ( $\geq 6.5$  years) in the monitored population.

#### *Reproductive rate*

Reproductive parameters (number of cubs per litter, birth or breeding interval, age at first parturition, and age at reproductive senescence) were determined from visual aerial and ground observations of females and their cubs. I estimated reproductive rate by dividing mean litter size of new cubs by mean birth or breeding interval (Craighead et al. 1974). Because cubs were not observed in the den, the reproductive rates reported here are minimum rates; they do not incorporate cubs that died in the den or shortly after leaving the den.

#### *Survival rates and population growth*

Seasonal and annual survival rates were estimated using the techniques of Heisey and Fuller (1985), which calculates the number of deaths recorded during the number of radio-days monitored. I estimated seasonal and annual rates for adult males and females ( $\geq 6.5$  years), subadult males and females (2.5 to 5.5 years), and cubs (0.5 to 1.5

years). Sex was determined during capture and age was determined from known birth date or estimated by counting cementum annuli. All bears aged  $\geq 20.5$  years were placed into 1 age category because exact age could not be determined accurately past 20.5 years. Birth dates of bears were assigned at February 1. Seasons were defined as spring (April-June, includes black bear hunting season), summer (July-August), fall (September-November, includes general hunting season), and winter (December-March, includes denning season).

Date of death was determined by monitoring mortality-sensing radio-collars or by reports from hunters and investigating conservation officers. Cause of death was determined by examination of the carcass at the death site or by reports from hunters and conservation officers.

Survival rate for subadult females was also estimated by including 2 censored animals (e.g., those that dropped their collars) in the calculation. One subadult female lost her collar about April 15, 1990 and was reported shot on September 16, 1990. I assumed the other censored subadult female survived through to adulthood to prevent biasing survival downwards.

I estimated the exponential rate of increase by iterating the Lotka equation (Caughley 1977). Sex- and age-specific survival and reproductive rates used in the equation were those estimated from radio-collared bears and dependent offspring.

## RESULTS

### *Trapping and monitoring*

A total of 28 grizzly bears (15 females, 13 males) were captured, collared, and radio-monitored from 1985 to 1990. Eight females and 6 males were captured in the Idaho trapping zone and an additional 2 subadult males were captured outside that zone in Washington. Seven females and 5 males were captured in the B.C. zone.

Trapping intensity was higher in the U.S. than in B.C. - 1258 trap nights in the 100 km<sup>2</sup> U.S. zone (12.6 trap nights/km<sup>2</sup>) compared to 384 trap nights in the 235 km<sup>2</sup> B.C. zone (1.6 trap nights/km<sup>2</sup>). Trapping was conducted for 4 years in the U.S. and for 2 years in B.C. No new adult bears were captured during the final year of trapping in the U.S., all new bears that year were offspring of previously collared females. Three new adults were captured during the final year of trapping in B.C.

### *Density and sex and age composition*

Ten to 15 different bears were known to reside within the U.S. 97.5% composite range from 1985 to 1990 (Table 3). The 97.5% multi-annual (1985 to 1990) composite home range for females was 873 km<sup>2</sup> ( $n$  bears = 5,  $n$  locations = 273). No unaccounted bears were observed in that female composite range during the study. I estimated a mean annual density of 1.4 grizzly bears/100 km<sup>2</sup> (70.9 km<sup>2</sup>/bear) in that composite range (Table 3). The mean annual sex and age composition in the U.S. was 31% cubs (1:1 sex ratio), 16% subadult males, 12% subadult females, 10% adult males, and 31% adult females (Table 3).

Table 3. Annual number of known bears, percent composition (%), and estimated density<sup>1</sup> (bears/100 km<sup>2</sup>) for different sex/age classes of grizzly bears within the U.S. SMGBE, 1985 to 1990.

Year	Cubs	Subadult males	Subadult females	Adult males	Adult females	Total
1985	4 (33)	3 (25)	1 (8)	1 (8)	3 (25)	12
1986	3 (30)	2 (20)	0 (0)	1 (10)	4 (40)	10
1987	4 (31)	1 (8)	2 (15)	2 (15)	4 (31)	13
1988	4 (36)	0 (0)	2 (18)	1 (9)	4 (36)	11
1989	3 (23)	3 (23)	2 (15)	1 (8)	4 (31)	13
1990	5 (33)	3 (20)	2 (13)	1 (7)	4 (27)	15
Annual Mean	3.83 (31)	2.00 (16)	1.50 (12)	1.17 (10)	3.83 (31)	12.33
Density <sup>1</sup>	0.44	0.23	0.17	0.13	0.44	1.41

<sup>1</sup> Density estimate based on number of bears within the 97.5% female multi-annual composite home range (873 km<sup>2</sup>), see text.

Sixteen to 21 different bears were known to live in the B.C. composite range from 1988 to 1990 (Table 4). The multi-annual (1988 to 1990) composite home range for females was  $815 \text{ km}^2$  ( $n$  bears = 8,  $n$  locations = 283). Some uncollared bears, including females with offspring, were observed near that composite range in 1989 and 1990 but they were not included in density calculations. I estimated a mean minimum annual density of 2.3 grizzly bears/100  $\text{km}^2$  ( $42.7 \text{ km}^2/\text{bear}$ ) in that composite range (Table 4). The mean sex and age composition in B.C. was 28% cubs (unknown sex ratio), 17% subadults (unknown sex ratio), 19% adult males, and 36% adult females (Table 4).

The B.C. composite range appeared to have higher densities of adult males, adult females, and cubs, than the U.S. range but densities of subadults were similar in the two areas. B.C. also appeared to have higher percentages of adult males but lower percentages of subadults than the U.S.

#### *Reproductive rate*

Mean litter size of new cubs was 2.22 ( $n = 10$ ,  $SD = 0.42$ ) and mean birth or breeding interval was 3.00 years ( $n = 6$ ,  $SD = 0.63$ ) for an estimated reproductive rate of 0.74 cubs/adult female/year or 0.37 female cubs/adult female/year (Table 5). Mean age at first parturition was 7.30 years ( $n = 5$ ,  $SD = 0.44$ ). Three females were observed to first give birth at 7.5 years; the remaining 2 females were estimated to first give birth at 6.5 and 7.5 years, based on the ages of their accompanying cubs (Table 5). Age of reproductive senescence was estimated at 21.5 years. Two of 4 older ( $\geq 20.5$  years) females were observed to be barren

Table 4. Annual number of known bears, percent composition (%), and estimated density<sup>1</sup> (bears/100 km<sup>2</sup>) for different sex/age classes of grizzly bears within the B.C. SMGBE, 1988 to 1990.

Year	Cubs	Subadults	Adult males	Adult females	Total
1988	4 (25)	2 (13)	3 (19)	7 (44)	16
1989	6 (29)	4 (19)	4 (19)	7 (33)	21
1990	6 (30)	4 (20)	4 (20)	6 (30)	20
Annual Mean	5.33 (28)	3.33 (17)	3.67 (19)	6.67 (36)	19.00
Density <sup>1</sup>	0.65	0.41	0.45	0.82	2.33

<sup>1</sup> Density estimate based on number of bears within the 97.5% female multi-annual composite home range (815 km<sup>2</sup>), see text.

Table 5. Reproductive parameters including cub litter size, birth interval (years), and age at first parturition (years) for individual adult female grizzly bears in the SMGBE, 1985 to 1990.

Bear #	New cubs	1 yr olds	2 yr olds	Birth Interval	Age at First Parturition
867	2, 2	2, 1	2	2, 3	7.5
1015	2, 2 <sup>*</sup>	2 <sup>*</sup>	2	3	7.5
1084 <sup>1</sup>	2 <sup>*</sup>	2 <sup>*</sup>	2	3 <sup>3</sup>	
1087	3				7.5
1047	2				
1045	2	2			6.5 <sup>*</sup>
1056	3 <sup>*</sup>	3	3	4 <sup>3</sup>	7.5 <sup>*</sup>
1076 <sup>2</sup>	2	2		3 <sup>3</sup>	
1044 <sup>1 2</sup>					
1048 <sup>1</sup>					
1075					
Mean	2.22	2.00	2.25	3.00	7.30

\* Extrapolated from presence and age of accompanying cubs, see text.

<sup>1</sup> Barren at old age ( $\geq 20.5$  years), see text.

<sup>2</sup> Died naturally at old age ( $\geq 20.5$  years), see text.

<sup>3</sup> Breeding interval.

for 2 and 3 consecutive years. Another older female may have been barren because she could not be observed for 3 consecutive years after reaching 19.5 years of age and females with cubs were typically highly visible. The remaining older female died of natural causes in 1991 after weaning her last litter in 1990. Another older female also died naturally from intraspecific predation (Table 5).

#### *Survival rates*

One of 11 adult females died naturally during 25.5 bear-years of monitoring for an annual survival rate of 0.96 (Table 6). That female was killed by an adult male during the 1989 summer season in B.C. Another adult female died naturally in the spring of 1991 but her death was not included in calculations because weekly radio-monitoring of bears ceased in the fall of 1990.

Two of 7 adult males died during 10.0 bear-years of monitoring for an annual rate of 0.81 (Table 6). Both were illegally shot during the 1987 spring black bear season in the U.S.

One of 9 subadult males died during 10.5 bear-years of monitoring for an annual survival rate of 0.90. That subadult male was illegally shot during the 1985 spring black bear hunting season in the U.S. Mean age of killed males was 6.16 years ( $n = 3$ ,  $SD = 2.51$ , range = 3.5, 6.5, and 8.5 years).

Two of 11 cubs died during 12.2 bear-years of monitoring for an estimated annual survival rate of 0.84 (Table 6). One new cub died of natural causes in the spring and its yearling sibling was illegally

Table 6. Seasonal and annual survival rates, number of bear years monitored, and number of bear deaths/number of radioed bears for different sex and age classes of grizzly bears in the SMGBE, 1983 to 1990.

Sex/Age Class	Survival Rate					Bear Years	Deaths /Bears
	Spring	Summer	Fall	Winter	Annual (95% CL)		
Cubs	0.91	1.00	0.93	1.00	0.84 (0.75-1.00)	12.2	2/11
Subadult Females	1.00	1.00	0.83	1.00	0.84 (0.57-1.00)	4.5	1/5
Subadult Females <sup>1</sup>	1.00	1.00	0.78	1.00	0.78 (0.56-1.00)	7.3	2/5
Adult Females	1.00	0.96	1.00	1.00	0.96 (0.91-1.00)	25.5	1/11
Subadult Males	0.90	1.00	1.00	1.00	0.90 (0.73-1.00)	10.5	1/9
Adult Males	0.81	1.00	1.00	1.00	0.81 (0.61-1.00)	10.0	2/7

<sup>1</sup> Estimate includes 2 censored animals, see text.

shot the next year during the fall hunting season (Knick and Kasworm 1989).

One of 5 subadult females died during 4.5 bear-years of monitoring for an annual survival rate of 0.84 (Table 6). She was illegally shot during the 1988 fall hunting season in the U.S. Another subadult female was illegally shot in B.C. during the 1990 fall hunting season, 4 months after she dropped her radio-collar. If I include the death of that censured female there were 2 deaths in 7.3 bear-years for an annual rate of 0.78.

#### *Population growth*

Reproductive rates used in the Lotka equation were 0.37 female cubs/adult female/year beginning at 7.5 years of age. Age-specific survival rates were those estimated from collared bears. Maximum age was set at 21.5 years because of reproductive senescence and natural death. That maximum is supported by data from LeFranc et al. (1987: 51); of 22 different populations, mean maximum age was 21.36 years (SD = 3.94).

The Lotka equation was solved for both subadult female survival rates. The exponential rate of increase ranged from 0.00 for the survival rate of 0.78 and +0.02 for the rate of 0.83.

## DISCUSSION

### *Trapping and monitoring*

The high trapping intensity, lack of new captures during the last year of trapping, and lack of uncollared bears suggest that all bears in the U.S. composite range were trapped and monitored. The lower trapping intensity, 3 new captures during the final year of trapping, and observations of uncollared bears in the B.C. composite range suggest that all bears may not have been accounted for there. The density estimate for the U.S. may therefore be more accurate than the estimate for B.C., which may be an underestimate.

### *Density*

Density estimates for the B.C. and the U.S. composite ranges (42.7 and 70.9 km<sup>2</sup>/bear, respectively) are similar to Knick's (1988) previous estimate of 40.8 km<sup>2</sup>/bear, the Kananaskis population (61.72 km<sup>2</sup>/bear; Chapter 2), and to estimates from other interior grizzly populations (LeFranc et al. 1987: 52-53). They are considerably lower than those of McLellan (1989b) for the Flathead Valley of B.C. (6.0 bears/100 km<sup>2</sup> or 16.4 km<sup>2</sup>/bear), but he calculated density for his trapping zone and cautioned against direct comparisons. I did not use his method because the U.S. trapping zone encompassed a large (60 km<sup>2</sup>) burned-over berry field and was not representative of the larger study area. When I used McLellan's method densities were 3 times higher than reported here because bears concentrated in the burned-over area. That method could result in gross over-estimates of population density and size if applied

to the whole study area. Similar results were obtained using McLellan's method in the Highwood trapping zone of Kananaskis (Chapter 2). The method I used is sometimes believed to underestimate density because some bears may be present at the edge of the composite range without entering and being trapped in the trapping zone (McLellan 1989b). I suggest that such partial use of the composite range by uncaptured bears may be offset by partial use of the composite range by captured bears.

Estimated densities appeared higher in B.C. (2.3 vs 1.4 bears/km<sup>2</sup>) for all sex and age classes except subadults. That can be explained by the fact that only 1 adult female mortality occurred in the B.C. composite range. All other mortalities (2 cubs, 2 subadult females, 1 subadult male, 2 adult males) occurred in or near the U.S. composite range and those mortalities could have resulted in lower densities in the U.S.

#### *Sex and age composition*

The estimated sex and age composition was similar to other interior grizzly populations (LeFranc et al. 1987: 47-49; McLellan 1989b) but different from Kananaskis where there were fewer females and more males (Chapter 2). The percentages of adult females and cubs were similar (approximately 30% each) between the 2 areas but B.C. appeared to have a higher percentage of adult males (19 vs 10%) and a lower percentage of subadults (17 vs 28%) than the U.S. This difference reflects the trend in density. One explanation for the paucity of subadults in B.C. may be that the higher density and percentage of adult males in B.C. forced subadults, particularly subadult males, out of the

area - perhaps to the adjacent U.S. Three of the 5 subadult males observed in the U.S. ITZ were offspring of resident females but the other 2 may have been immigrants. Subadults may disperse to areas of lower adult male density (e.g., the U.S. composite range) and increase their representation in that area. I do not know if such a process is occurring in the SMGBE but it has been postulated for grizzly bears (Bunnell and Tait 1981; McCullough 1981; Stringham 1983; Chapter 2) and observed for black bears (Kemp 1976; Young and Ruff 1982)).

#### *Reproductive rate*

Mean cub litter size (2.22), interbirth interval (3.00 years), age at first parturition (7.30 years), and age at reproductive senescence (21.5 years) are similar to those observed in other populations (LeFranc et al. 1987: 51, 54-55). The estimated reproductive rate of 0.74 appears higher than that in Kananaskis (0.46) because of larger litter sizes (2.22 vs 1.40; Chapter 2). The rate is similar to those estimated by Craighead et al. (1974) and Knight and Eberhardt (1985) for the Yellowstone population. McLellan (1989a) estimated higher rates for Flathead grizzlies (0.85 to 0.87) but he observed shorter birth intervals (2.67 years) with similar litter sizes (2.26).

#### *Survival rates*

The estimated survival rates of 0.84 for cubs, 0.90 for subadult males, and 0.96 for adult females were similar to those in the Flathead Valley (0.82 for cubs, 0.91 for subadult males, 0.94 for adult females;

McLellan 1989c) and in Kananaskis (0.78 for cubs, 0.89 for subadult males, 0.93 for adult females; Chapter 2). Survival rates for adult males (0.81) and subadult females (0.78 to 0.84) appeared lower in the SMGBE than in the Flathead (adult males = 0.92, subadult females = 0.94; McLellan 1989c) but rates for adult males appeared higher than in Kananaskis (0.70; Chapter 2). Previous estimates for this population were 0.53 for males and 0.89 for females (Knick and Kasworm 1989) but sample sizes were considerably smaller (13.7 vs 65.5 bear-years). These new estimates suggest that male survival is not as low as previously estimated.

The subadult female estimate of 0.78 may be more accurate than the estimate of 0.84 because it incorporates both mortalities and is based on a sample size of 7.3 bear-years vs 4.5 bear-years. It is still a maximum rate of survival because another censured subadult female was assumed to live through to adulthood, adding 2.3 bear-years of assumed survival to the calculation.

Six of 8 deaths were illegal shootings and all of those occurred in or near the U.S. composite range. Two subadult females, 2 young adult males (6.5 and 8.5 years), 1 subadult male, and 1 cub were illegally shot in open-access areas (no road closure) during sport hunting seasons. Adult female survival was quite high (no shootings) possibly because collared adult females resided within areas that were protected by road closures. Survival rates for uncollared females outside protected areas may be lower, so the estimate given here is maximal. Higher mortality for adult males can be explained by their desirability to hunters and poachers and their larger home ranges (Compton et al. 1989) which impinged on unprotected areas. Bunnell and Tait (1980)

suggested that adult males experience higher mortality than adult females because of their trophy status and because their larger home ranges increase their probability of encountering human hunters or poachers. That appears to be the case in the SMGBE.

The lower survival for subadult females and the higher survival for subadult males is the reverse of that expected (Bunnell and Tait 1980). High mortality of subadult females may have resulted because they attempted to establish home ranges adjacent to but outside their maternal home ranges. That entailed leaving road-closure areas and residing in regions of open-road access, increasing their susceptibility to shooting. By contrast, subadult males had larger home ranges (Compton et al. 1989) that encompassed road-closure areas and that may have increased their survival relative to subadult females.

#### *Population growth*

The estimated exponential rates of growth (0.00 to +0.02) appear considerably lower than that estimated (+0.08) for the Flathead Valley (McLellan 1989a). That difference is to be expected given the higher subadult female mortality and lower reproduction in the SMGBE. The rates appear higher than those estimated for Kananaskis (-0.01 to +0.01) but reproduction was lower there (Chapter 2). Knight and Eberhardt (1985) calculated a rate of  $r = -0.029$  for the Yellowstone population but their estimates of survival and reproduction were lower than those in the SMGBE.

Although I cannot say with certainty which, if any, of the two rates are correct, neither indicates a drastically declining or

increasing population. These data indicate that the population is stable or increasing slightly. Considering that my survival estimates for both adult and subadult females are maxima, the population is not likely to be increasing.

Populations can grow by increasing female survival or reproduction. Knight and Eberhardt (1985) and McLellan (1989a) indicated that female survival rates were the most important parameter for grizzly bear population growth, reproductive rates contributed comparatively little. Reproductive parameters are at or near the expected maximum in the SMGBE (LeFranc et al. 1987) so it is unlikely that reproduction can be increased sufficiently to spur population growth.

Because population recovery and growth is contingent upon survival of female bears, the prognosis for increased growth of the SMGBE population is not good. Any recolonization by subadult females is likely to occur outside their maternal ranges and those areas are now open to sport hunting in B.C. and are not subject to road closures. Unless those areas are protected from sport hunting and poaching, subadult female mortality will likely remain high and the population may have difficulty recovering. Reduced mortality can be accomplished by further road closures and/or increased education and vigilance of sport hunters. Increased law enforcement and higher penalties for illegal shootings would help. The grizzly bear hunting seasons in both the U.S. and B.C. SMGBE should remain closed since illegal killings alone appear to be limiting population growth.

**Chapter 4**  
**CAUSES OF SEXUAL HABITAT SEGREGATION**  
**IN GRIZZLY BEARS**

**INTRODUCTION**

Some researchers (Pearson 1975; Wielgus 1986; Mattson et al. 1987; McLellan and Shackleton 1988) reported that female grizzly bears, especially females with cubs, used habitats that were different from and less favourable than those used by males. They interpreted that as female avoidance of aggressive, cannibalistic males, but did not test this hypothesis. In this chapter, I test three competing models of sexual habitat segregation by examining and comparing habitat use of two different grizzly bear sample populations - one in Kananaskis, Alberta and the other in the Selkirk Mountains of Idaho.

The "no avoidance" model predicts that females do not avoid males and male-occupied habitats but simply have different habitats available to them within their range or choose to use different habitats. Habitat segregation should not occur in either study area if the same high quality habitat is equally accessible and available to all sex and reproductive classes of bears. If habitat segregation is observed, the degree of habitat segregation should be unrelated to the probability of females encountering males.

The "food competition" model predicts that female bears and other subdominants avoid adult males and their favoured habitats because those males compete with subdominants for food, and even cannibalize subdominants for food (Hornocker 1962; Egbert and Stokes 1976;

McCullough 1981; Stringham 1983). Subdominant reproductive classes should avoid adult males and male-occupied habitats in both study areas according to their size and vulnerability to predation or dominance and aggressiveness. The order of avoidance according to ascending size should be: females with cubs, females with yearlings, subadult females, subadult males, and lone adult females. The order of avoidance according to ascending dominance should be subadult females, subadult males, lone adult females, and adult females with offspring (Hornocker 1962; Egbert and Stokes 1976). Furthermore, habitat segregation should be more pronounced in the food-poor Selkirk study area and less pronounced in the food-rich Kananaskis study area (Chapter 5). Finally, habitat segregation should be most pronounced during seasons of food limitation, not seasons of food abundance.

The "sex competition" model predicts that females with cubs avoid adult males, especially immigrant adult males, because those males are unlikely to have sired cubs and will kill cubs to induce estrus to gain breeding opportunities (Stringham 1980, 1983; McCullough 1981; Hrdy and Hausfater 1984; LeCount 1987). Reproductive classes (e.g., adult females with offspring) that provide reproductive opportunities to non-sire males should avoid male-occupied habitats. Other reproductive classes (e.g., subadult females) should not avoid those habitats because they offer no reproductive opportunities to such males. Furthermore, habitat segregation should be more pronounced in the Kananaskis population where there are many potentially infanticidal, immigrant males (Chapter 2). Segregation should be less pronounced in the Selkirk population where there are fewer such males (Chapter 3). Finally, habitat segregation should be more pronounced in Kananaskis during the post-hunting period

when there were many immigrant males in the study area, and less so during the pre-hunting period when there were fewer such males (Chapter 2).

Wielgus and Bunnell (submitted) found that sexual habitat segregation in Kananaskis increased with increasing probabilities of females encountering males and that females moved out of previously occupied habitats when males moved in. Those observations do not support the "no avoidance" model. Wielgus and Bunnell (submitted) also found that sexual habitat segregation was greatest in Kananaskis during the fall berry season when food was super-abundant and that does not support the "food competition" model. In this chapter, I test for habitat segregation by sex and reproductive class in both study areas and test the remaining predictions of the three competing models.

## METHODS

### *Study area*

The Kananaskis study area is described in Chapter 2. Sport hunting of grizzly bears was closed in this area from 1970 to 1981, but was reopened from 1982 to 1987 because the population was believed to be increasing (Carr 1989, Nagy and Gunson 1990). I suggested that the population was decreasing from 1981 to 1984 because of low reproduction (Chapter 2).

The Selkirk study area is described in Chapter 3. Legal hunting of grizzly bears was not allowed in the U.S. Selkirk Mountains under the Endangered Species Act and legal hunting in the B.C. Selkirk Mountains

was prohibited during research (1985 to 1990). I suggested that the population was stable from 1985 to 1990 (Chapter 3).

#### *Trapping and habitat quality*

Trapping techniques are described in Chapters 2 and 3. Trapping and radio-collaring of bears in Kananaskis was done in 2 areas, the Highwood and Sheep trapping zones. The Highwood trapping zone (HTZ) encompassed 254 km<sup>2</sup> in the mountains (1800 m) and covered a 50 year-old burn dominated by soapberry shrubfields and forbfields. The HTZ was believed to be the best available grizzly habitat in the study area - bear foods and bear sign appeared more abundant there than in surrounding unburned areas and grizzly bears concentrated their activities in the HTZ (Wielgus 1986; Wielgus and Bunnell submitted). Hamer and Herrero (1987) found that burned-over habitats were more productive for bear foods than unburned habitats in a nearby area. Trapping in the HTZ took place from 1980 to 1984.

The Sheep trapping zone was a 225 km<sup>2</sup> area about 20 km to the east in the foothills (1400 m) and was chosen primarily for capture of black bears. It was not centered on a burned-over area and no grizzly bears were ever radio-located there (Wielgus 1986). Trapping in the Sheep zone took place from 1980 to 1983.

Trapping and radio-collaring of bears in the Selkirks was also done in 2 areas. The Idaho Trapping Zone (ITZ) encompassed 100 km<sup>2</sup> in northern Idaho and covered a 20 year-old burn dominated by Vaccinium globularum shrubfields and forbfields. The ITZ was believed to be the best available grizzly habitat in the study area - bear foods and bear

sign appeared more abundant there than in surrounding unburned areas and grizzly bears concentrated their activities in the ITZ (Knick 1988).

Zager et al. (1983) found that burned-over habitats were more productive for bear foods than unburned habitats in a nearby area. Trapping in the ITZ took place during 1985, 1986, 1987, and 1989.

The B.C. trapping zone covered 235 km<sup>2</sup> about 20 km to the north in B.C. and was chosen to extend the study into Canada. It was not centered on a burned-over area and density was approximately one half that of the ITZ (Wielgus unpubl. data). Trapping in B.C. took place from 1988 to 1989.

For purposes of this study, both the HTZ and ITZ are defined as superior-quality habitats; surrounding unburned areas are defined as poorer-quality habitats.

#### *Habitat segregation*

Bears were monitored using fixed-wing radio-telemetry (Whitehouse and Steven 1977), conducted weekly during the non-denning period (early April to early November) from 1981 to 1984 in Kananaskis and from 1985 to 1990 in the Selkirks.

I analyzed habitat use by 6 reproductive classes: estrus adult females, adult females with cubs, adult females with yearlings, independent subadult females, adult males ( $\geq 6.5$  years), and independent subadult males (2.5 to 5.5 years). Only bears of known reproductive status were included in analyses. Sex of animal was determined during capture and age was determined from known birth date or estimated by counting cementum annuli (Stoneburg and Jonkel 1966).

I documented relative use of the HTZ and ITZ to determine which, if any, reproductive classes used the better quality habitats disproportionately. Only bears trapped and monitored in the HTZ and ITZ were analyzed. I used two methods to examine habitat segregation in the two study areas.

Method 1 compared the observed number of locations against the expected number of locations in the HTZ and ITZ for each reproductive class. The expected number was calculated from the percentage of total locations attributable to that class. For example, if adult females with cubs yielded a total of 100 out of 500 locations (20%), and they did not use the zones disproportionately, we would expect 20% of the locations in the zones to be from adult females with cubs. Method 1 satisfies the assumption of the no avoidance model in that all bears had equal access to the zones because all bears were trapped in and had home ranges overlapping the zones.

The chi-square goodness of fit (Daniel 1978) was used to test for apparent habitat selection. Locations of individual bears were pooled into their respective reproductive classes to ensure adequate sample sizes (Roscoe and Byers 1971; Alldredge and Ratti 1986). Bonferroni confidence intervals (Neu et al. 1974) were used to determine which reproductive classes used zones disproportionately.

Method 2 compared the observed number of locations in the zones for each individual bear against the expected number of locations for that bear. Data were analyzed separately for different reproductive phases of each bear. The expected number was calculated from the percentage of a bear's composite home range that covered the trapping zone multiplied by the number of locations for each reproductive phase

of that bear. For example, if 20% of a bear's home range were in the zone we would expect 20% of that bear's locations in the zone if that bear did not use the zone disproportionately. I used the chi-square goodness of fit (Daniel 1978) to test for second order selection within the home range (Johnson 1980). First order habitat selection was estimated as the relative percentage of a bear's home range in the zones (Johnson 1980). Method 2 satisfies the equal availability assumption of the no avoidance model because the use of a zone by each animal is compared to the availability of that zone to that animal.

## RESULTS

### *Trapping and monitoring*

Five females and 13 males were trapped and radio-monitored from 1981 to 1984 in the HTZ of Kananaskis. Seven females and 6 males were trapped and radio-monitored from 1985 to 1990 in the ITZ of the Selkirks. I did not analyze habitat use of B.C. bears because the B.C. trapping zone was not burned-over and did not represent superior quality habitat. Number of bears, number of bear-years, and number of radiolocations for each sex and reproductive class are given in Tables 7 and 8. Number of locations for different reproductive phases of each bear are given in Tables 9 to 12. Habitat use of one female reproductive phase (H9 with yearlings, Table 9) took place prior to the opening of the grizzly bear hunting season in Kananaskis (Chapter 2) - all other female habitat use was post-hunting in Kananaskis.

Table 7. Observed and expected number of locations in the Highwood trapping zone (HTZ) of Kananaskis, Alberta for different sex and reproductive classes of grizzly bears.

Repro <sup>1</sup> Class	No.	No.	Total No.	Observed No. Locations (%)	Expected No. <sup>2</sup> Locations (%)
	Bears	Bear-yrs	Locations (%)	in HTZ	in HTZ
AFe	5	5	84 (16)	33 (14)	38.0 (16)
AFc	4	4	62 (12)	8 (3) -	28.4 (12)
AFy	2	3	33 (6)	5 (2) -	14.2 (6)
SAF	2	3	57 (11)	49 (21) +	26.1 (11)
AM	7	13	139 (26)	58 (25)	61.6 (26)
SAM	8	11	151 (29)	84 (35)	68.7 (29)
Total			526 (100)	237 (100)	237.0 (100)

$$\chi^2 = 45.08, 5 \text{ df}, P < 0.001$$

<sup>1</sup> AFe = adult female estrus, AFc = adult female with cubs, AFy = adult females with yearlings, SAF = subadult female, AM = adult male, SAM = subadult male.

<sup>2</sup> Expected no. of locations in the HTZ for each reproductive class based on percentage of total locations for each reproductive class.

+ Observed percentage is statistically less than or greater than expected percentage ( $P < 0.05$ ) using Bonferroni confidence intervals (Neu et al. 1974).

Table 8. Observed and expected number of locations in the Idaho trapping zone (ITZ) of the Selkirk Mountains of Idaho for different reproductive classes of grizzly bears.

Repro <sup>1</sup> Class	No.	No.	Total No.	Observed No.	Expected No. <sup>2</sup>
	Bears	Bear-yrs	Locations (%)	Locations (%) in ITZ	Locations (%) in ITZ
AFe	4	6	122 (27)	46 (29)	42.4 (27)
AFc	3	3	71 (15)	28 (18)	23.6 (15)
AFy	1	1	10 (2)	6 (4)	3.1 (2)
SAF	3	4	33 (7)	8 (5)	11.0 (7)
AM	3	4	86 (19)	28 (18)	29.8 (19)
SAM	5	9	138 (30)	41 (26)	47.1 (30)
Total			460 (100)	157 (100)	157.0 (100)

$$\chi^2 = 5.45, 5 \text{ df}, P > 0.10$$

<sup>1</sup> AFe = adult female estrus, AFc = adult female with cubs, AFy = adult females with yearlings, SAF = subadult female, AM = adult male, SAM = subadult male.

<sup>2</sup> Expected no. of locations in the ITZ for each reproductive class based on percentage of total locations for each reproductive class.

Table 9. Observed and expected number of locations in the Highwood trapping zone (HTZ) of Kananaskis, Alberta for different reproductive phases of individual female grizzly bears.

Bear No.	Repro <sup>1</sup> Phase	Total No. Locations	Observed No.	Expected No. <sup>2</sup>
			Locations (%) in HTZ	Locations (%) in HTZ
H9	AFy <sup>3</sup>	9	4 (44)	4.3 (48)
	AFe	25	3 (12) -	12.0 (48)
	AFc	19	1 (5) -	9.1 (48)
	AFy	12	1 (8) -	5.8 (48)
H11	SAF	41	34 (83) +	25.8 (63)
	AFe	12	8 (67)	7.5 (63)
H12	SAF	16	15 (94) +	8.9 (57)
	AFe	22	19 (86) +	12.3 (57)
	AFc	12	7 (58)	6.7 (57)
H13	AFe	12	2 (17)	1.2 (10)
	AFc	19	0 (0)	1.9 (10)
	AFy	12	0 (0)	1.2 (10)
H20	AFe	13	1 (8)	1.4 (11)
	AFc	12	0 (0)	1.3 (11)

<sup>1</sup> AFe = adult female estrus, AFc = adult female with cubs, AFy = adult females with yearlings, SAF = subadult female.

<sup>2</sup> Expected number based on % of home range in HTZ.

<sup>3</sup> Data are pre-hunting, all other data are post-hunting.

± Observed number of locations in HTZ is statistically less or greater than the expected number at  $P < 0.05$  using chi-square goodness of fit.

Table 10. Observed and expected number of locations in the Highwood trapping zone (HTZ) of Kananaskis, Alberta for individual adult male (AM) and sub-adult male (SAM) grizzly bears.

Bear No.	Repro Phase	Total No. Locations	Observed No.	Expected No. <sup>1</sup>
			Locations (%) in HTZ	Locations (%) in HTZ
H1	AM	36	9 (25) +	1.4 (4)
H7	AM	30	18 (60) +	8.7 (29)
H14	AM	19	10 (53) +	3.8 (20)
H15	AM	6	3 (50)	2.4 (40)
H17	AM	9	1 (11)	0.5 (6)
H19	AM	14	10 (71) +	3.5 (25)
S1	AM	25	7 (28) +	1.7 (7)
H6	SAM	11	8 (73)	7.3 (67)
H10	SAM	21	10 (48) +	5.4 (26)
H14	SAM	15	11 (73) +	3.0 (20)
H16	SAM	21	15 (71) +	4.3 (23)
H18	SAM	20	12 (60) +	3.2 (16)
H21	SAM	16	9 (56) +	2.4 (15)
S1	SAM	26	11 (42) +	1.8 (7)
S2	SAM	21	8 (38)	4.8 (23)

<sup>1</sup> Expected number based on % of home range in HTZ.

+ Observed number of locations in the HTZ is statistically less than or greater than the expected number at  $P < 0.05$  using chi-square goodness of fit.

Table 11. Observed and expected number of locations in the Idaho trapping zone (ITZ) of the Selkirk Mountains of Idaho for different reproductive phases of individual female grizzly bears.

Bear No.	Repro <sup>1</sup> Phase	Total No. Locations	Observed No.	Expected No. <sup>2</sup>
			Locations (%) in ITZ	Locations (%) in ITZ
867	AFe	50	26 (52) +	7.0 (14)
	AFc	37	18 (49) +	5.1 (14)
	AFy	10	6 (60) +	1.4 (14)
1015	AFe	34	9 (26)	6.4 (19)
	AFc	13	2 (15)	2.4 (19)
1087	AFe	15	5 (33)	2.8 (19)
	AFc	21	8 (38) +	3.9 (19)
1084	AFe	23	6 (26) +	2.7 (12)
1042	SAF	17	2 (12) -	7.6 (45)
1085	SAF	6	1 (17)	1.9 (33)
1089	SAF	10	5 (50) +	1.2 (12)

<sup>1</sup> AFe = adult female estrus, AFc = adult female with cubs, AFy = adult females with yearlings, SAF = sub-adult female.

<sup>2</sup> Expected number based on % of home range in ITZ.

± Observed number of locations in the ITZ is statistically less than or greater than the expected number at  $P < 0.05$  using chi-square goodness of fit.

Table 12. Observed and expected number of locations in the Idaho trapping zone (ITZ) of the Selkirk Mountains of Idaho for individual adult male (AM) and subadult male (SAM) grizzly bears.

Bear No.	Repro Phase	Total No. Locations	Observed No.	Expected No. <sup>1</sup>
			Locations (%) in ITZ	Locations (%) in ITZ
1005	AM	38	7 (18) ±	2.2 (6)
962	AM	19	9 (47)	9.3 (49)
1004	AM	29	12 (41) ±	2.3 (8)
962	SAM	22	13 (59)	10.7 (49)
1004	SAM	43	11 (26) ±	3.4 (8)
1077	SAM	18	5 (28)	3.6 (20)
1090	SAM	27	6 (22)	5.9 (22)
1091	SAM	28	6 (21) ±	1.9 (7)

<sup>1</sup> Expected number based on % of home range in HTZ.

± Observed number of locations in the ITZ is statistically less than or greater than the expected number at  $P < 0.05$  using chi-square goodness of fit.

*Habitat segregation*

Method 1 showed sex and reproductive class habitat segregation in Kananaskis (Table 7,  $\chi^2 = 45.08$ ,  $P < 0.001$ ). Adult females with cubs and adult females with yearlings were under-represented but subadult females were over-represented in the HTZ. Estrus adult females, adult males, and subadult males were neither over nor under-represented. No such habitat segregation was observed in the Selkirks (Table 8,  $\chi^2 = 5.45$ ,  $P > 0.10$ ) where all reproductive classes used the ITZ as expected.

Method 2 showed similar results to method 1. In Kananaskis, both subadult females (H11 and H12) used the HTZ more than expected (Table 9). One subadult female (H12) went on to use the HTZ more than expected during her first estrus. One adult female (H9) used the HTZ less than expected during all adult reproductive phases, except prior to the opening of the grizzly bear hunting season. The remaining 2 adult females (H13 and H20) used the HTZ as expected, but they had relatively small portions (10 and 11%) of their home ranges in the zone, indicating first order selection against the zone. They used the HTZ when in estrus and did not use the HTZ when accompanied by offspring.

By contrast, 5 of 7 adult males and 6 of 8 subadult males used the HTZ more than expected (Table 10). The remaining 2 adult males and 2 subadult males used the HTZ as expected, but 3 of those 4 bears had relatively large percentages (38 to 73%) of their home ranges in the zone, indicating first order selection for the zone.

Results were considerably different in the Selkirks. One adult female (867) selected for the ITZ during all adult reproductive phases (Table 11). Another adult female (1087) selected for the ITZ while

accompanied by cubs and another adult female selected for the ITZ when in estrus. One subadult female (1089) selected for and another (1042) against the ITZ. The remaining females did not select for or against the zone but, compared to similar non-selective females in Kananaskis, they had relatively larger portions of their home ranges (19 to 33% vs 10 to 11%) in the relatively smaller ITZ (ITZ = 100 km<sup>2</sup> vs HTZ = 254 km<sup>2</sup>), indicating first order selection for the ITZ.

Male bears behaved similarly to females in the ITZ. Two of 3 adult males and 2 of 5 subadult males selected for the ITZ (Table 12). The remaining males did not select for or against the zone, but they had large portions of their home ranges (20 to 49%) in the ITZ.

Overall, subadult females, subadult males, and adult males either selected for the HTZ or had large portions of their home ranges in the HTZ. Adult females with cubs and adult females with yearlings selected against or had small percentages of their ranges in the HTZ. Older estrus adult females (former mothers) were neutral or selected against the HTZ and younger estrus adult females (first-time breeders) were neutral or selected for the HTZ. By contrast, all sex and reproductive classes selected for or had large portions of their home ranges in the ITZ.

## DISCUSSION

### *Tests of habitat segregation*

Both methods 1 and 2 indicated sex and reproductive class habitat segregation in Kananaskis but not in the Selkirks. Although my sample sizes for locations were small, I am confident in my test results

because small  $n$  will result in increased type 2, not type 1 errors (Roscoe and Byers 1971; Alldredge and Ratti 1986). The small sample of bears and lack of experimental replication precludes extrapolation to other bears and other populations, so I do not extrapolate.

There were 2 apparent inconsistencies in Kananaskis. Firstly, H9 did not select against the HTZ when accompanied by yearlings prior to the hunting season, but she selected against the HTZ during all reproductive phases post-hunting. Her avoidance of the HTZ corresponded with an influx of new immigrant males coincident with increased hunting mortality of older adult males (Chapter 2). Secondly, unlike other adult females, subadult female H12 selected for the HTZ during her first estrus and did not appear to avoid the HTZ after producing her first litter. That interpretation is incorrect because H12 and her new cub moved out of the HTZ during the onset of the fall berry season when large numbers of males arrived (Wielgus and Bunnell submitted). She established a new center of activity outside the HTZ during and after the berry season. Unfortunately, she could not be aerially monitored during that fall or the next year because aerial telemetry ended that fall. However, she was radio-located from the ground that fall and she was outside the HTZ. Furthermore, she was sighted outside the HTZ by rangers and hunters that fall and the following year and was not seen again in the HTZ. That suggests she avoided the HTZ when accompanied by offspring. Perhaps females with their first litters learned to avoid the HTZ only after encountering many males there during the fall berry season.

*Competing hypotheses of habitat segregation*

I reject the no avoidance model because habitat segregation occurred in Kananaskis despite the fact that the better quality habitat (HTZ) was equally accessible and available to all sex and reproductive classes. Unequal access or availability of habitat did not account for the habitat segregation observed there. Also, it seems unlikely that females with offspring would choose the lower quality unburned area because of diet preference.

Furthermore, Wielgus and Bunnell (submitted) showed that seasonal sexual habitat segregation in Kananaskis increased with increasing numbers of males and male use of the female composite range - females vacated previously occupied habitats when males moved in. These results suggest that females avoided males and male-favoured habitats in Kananaskis.

I reject the food competition model because sub-dominant reproductive classes did not avoid adult males and their favoured habitat (HTZ) according to their size or dominance. Smaller, low dominance, subadult females selected for the male-occupied HTZ while larger, high dominance adult females of all reproductive phases, including estrus adult females, selected against or were neutral for the HTZ. No sex or reproductive classes avoided the ITZ. The three other predictions of the food model were also rejected. Habitat segregation occurred in the food-rich Kananaskis study area but not in the food-poor Selkirks study area (Chapter 5) - the reverse should have occurred if competition for food were the causal factor. Habitat segregation was observed in Kananaskis but not in the Selkirks despite similar densities

in both study areas (Chapter 5) - density or competition for food did not account for habitat segregation. Habitat segregation was greatest in Kananaskis during the fall berry season when food was super-abundant (Wielgus and Bunnell submitted) - habitat segregation should have been more intense during other seasons of food limitation if competition for food or cannibalism for food were causative (Egbert and Stokes 1976).

My results support the sex competition model because only reproductive classes that offered breeding opportunities to potentially infanticidal immigrant males avoided the HTZ. Furthermore, habitat segregation was only observed in Kananaskis where there was an abundance of potentially infanticidal, immigrant males (Chapter 2), not in the Selkirks where such males were rare (Chapter 3). Finally, H9 did not avoid the HTZ prior to the hunting season when immigrant males were rare but she did avoid the HTZ during and after the hunting season when immigrant males were abundant.

Immigrant males are unlikely to have sired cubs and can be expected to attempt sexually selected infanticide to increase their breeding opportunities, and females with offspring should avoid such males (Hrdy and Hausfater 1984; LeCount 1987). Increased mortality of older adult males coincided with increased immigration by younger males in Kananaskis (Chapter 2). Older adult males are believed to limit immigration of subadult males (Bunnell and Tait 1981) so their removal can be expected to result in increased immigration. Kemp (1976) and Young and Ruff (1982) observed a 3-fold increase in immigrant subadult male black bears after removing 30% of adult males. By contrast, there was little mortality of older adult males in the Selkirks and few

immigrant males there (Chapter 3) and females with offspring are not expected to avoid resident sires (Hrdy and Hausfater 1984).

Reproductive data corroborated the sex competition model (Chapter 5). Cub litter size was lower in Kananaskis despite superior food there. However, age at first parturition for subadult females appeared earlier in Kananaskis. That corresponds with the observed patterns of habitat segregation. Sexually immature subadult females did not avoid the male-occupied, food-rich HTZ in Kananaskis so they reached sexual maturity and produced cubs earlier than in the Selkirks (Chapter 5). By contrast, sexually mature adult females avoided the food-rich, male-occupied HTZ in Kananaskis and produced smaller litters than females in the Selkirks.

It is unclear whether the "sex competition" model accounts for other instances of habitat segregation in grizzly bears, perhaps the "no avoidance" and "food competition" models are applicable elsewhere. What is clear is that the sex competition model does explain the observed segregation in Kananaskis and the lack of segregation in the Selkirks. This study should be replicated to determine if the "sex competition" model is applicable elsewhere.

**Chapter 5**  
**EFFECTS OF ADULT MALE MORTALITY ON**  
**FEMALE GRIZZLY BEAR REPRODUCTION**

**INTRODUCTION**

A controversy exists on the effects of hunting of adult male bears. It is not known if female reproduction is independent of density of males with male mortality having additive effects on reproduction; dependent on density of males with male mortality having compensatory effects; or dependent on density of males with male mortality having depensatory effects (Miller 1990). No rigorous tests of those hypotheses have been conducted, to date, yet many wildlife managers assume the compensatory model (Miller 1990). In this chapter, I test the three competing hypotheses by comparing a hunted population in Kananaskis, Alberta to a non-hunted population in the Selkirk Mountains of Idaho and B.C.

The density independent, additive model predicts that higher reproduction should occur in the population with superior food supply, regardless of mortality of males (Bunnell and Tait 1981; Knight and Eberhardt 1985; Rogers 1987).

The density dependent, compensatory model predicts that higher reproduction should occur in the population with high mortality of adult males because of lower density of competitive or cannibalistic adult males (McCullough 1981, 1986; Stringham 1983; McLellan 1989a).

The density dependent, depensatory model predicts that lower reproduction should occur in the population with high adult male

mortality because removal of adult males allows an increase in density of potentially infanticidal, immigrant males (Hrdy and Hausfater 1984; Chapter 2) with increased cub mortality (Stringham 1980; LeCount 1987) or reduced cub production because of sexual habitat segregation (Wielgus 1986; Wielgus and Bunnell submitted; Chapter 4).

The Kananaskis sample population had high mortality of old adult males, corresponding high immigration of subadult males, subsequent high densities of young adult immigrant males, and a reproductive rate of 0.46 (Chapter 2). The Selkirks sample population had low mortality of old adult males, few immigrant males, subsequent low density of adult males, and a reproductive rate of 0.74 (Chapter 3). In chapter 4 I showed that adult females avoided food-rich, male-occupied habitats in Kananaskis but not in the Selkirks, which could account for the lower reproduction in Kananaskis.

Those observations support the density dependent, depensatory model. However, differences in reproduction, mortality of males, ages of killed males, and density of males were not statistically tested and any differences in reproduction may have been due to variation in age of mothers, environmental productivity, or total population density. In this chapter, I test those alternative null hypotheses as well as the three competing models of adult male mortality.

## METHODS

### *Study area*

The Kananaskis study area is described in Chapter 2. Sport hunting of grizzly bears was closed there from 1970 to 1981, but was reopened

from 1982 to 1987 because the population was believed to be increasing (Carr 1989; Nagy and Gunson 1990). I suggested that the population was decreasing during 1980 to 1984 because of low reproduction (Chapter 2).

The Selkirk Mountains Grizzly Bear Ecosystem (SMGBE) is described in Chapter 3. Legal hunting of grizzly bears was not allowed in the U.S. SMGBE under the Endangered Species Act and legal hunting in the B.C. SMGBE was prohibited during research (1985 to 1990). The population appeared to be stable from 1985 to 1990 (Chapter 3).

#### *Trapping and monitoring*

Bears in Kananaskis and the SMGBE were trapped using Aldrich leg snares and immobilized with Ketamine hydrochloride and Xylazine hydrochloride. Immobilized bears were weighed, ear-tagged, had a premolar tooth extracted for ageing (Stoneburg and Jonkel 1966) and were fitted with activity and/or mortality sensing radio-collars. Details on trapping are given in Chapters 2 to 4.

Fixed-wing radiotelemetry (Whitehouse and Steven 1977) was conducted weekly during the non-denning period (early April to early November) from 1981 to 1984 in Kananaskis and from 1985 to 1990 in the SMGBE.

#### *Reproductive rates*

Number of cubs per litter, birth interval, and age at first parturition were determined from aerial and ground visual observations of females and their cubs. Reproductive rates reported here do not

incorporate new-born cubs that died in the den or shortly after leaving the den.

I estimated reproductive rate for each sample population as the average litter size of new cubs divided by the average birth or breeding interval (Craighead et al. 1974). Details are given in Chapters 2 and 3. I tested for differences in mean cub litter size, mean birth interval, and mean age at first parturition using the Student's t-test (Sokal and Rohlf 1981).

#### *Age of mothers*

I examined age of mothers because that might effect cub litter size, with prime-age mothers producing larger litters (Caughley 1977). Age of mothers was determined by counting cementum annuli (Stoneburg and Jonkel 1966). I tested for differences in mean age using the t-test and controlled for the effects of age of mother on litter size by analysis of covariance (ANCOVA; Tabachnick and Fidell 1983). ANCOVA models were: litter size = constant + area + age of mother. Area (Kananaskis vs SMGBE) was the main effect being tested; age of mother was the covariate.

#### *Environmental productivity*

Weights of captured male and female bears were used as indices for environmental productivity or food supply. Bunnell and Tait (1981), Kingsley et al. (1983), Blanchard (1987), Rogers (1987), and Stringham (1990) all showed that weight of bears was positively related to food

supply. They also showed that litter size, birth interval, and age at first parturition were similarly related to weight and food supply.

I used weights of male bears as an unbiased index of food supply because males used the best available habitats in both study areas; I did not use adult female weight because females avoided the better quality male-occupied habitats in Kananaskis (Chapter 4) and because adult female weight fluctuates with reproductive status or lactation (Kingsley et al. 1983). I used subadult female age at asymptotic weight and age at first parturition as indices of food supply because neither were influenced by habitat segregation (Chapter 4) or lactation. I expressed weight at age for both sexes in both study areas using non-linear least squares regression (Wilkinson 1990).

I tested for differences in mean weight of males and females using the t-test. Because weight is influenced by age of bear and date of capture, I tested for differences in mean age and date of capture using t-tests. I controlled for the effects of age and date by analysis of covariance (ANCOVA; Tabachnick and Fidell 1983). Sex specific ANCOVA models were:  $\log(\text{weight}) = \text{constant} + \text{area} + \log(\text{age}) + \text{date of capture}$ . Area (Kananaskis vs SMGBE) was the main effect being tested, age and date were covariates. Weights and ages were log transformed to linearize their relationship to meet the assumptions of the ANCOVA tests.

#### *Survival of adult males*

I estimated annual survival rates for adult males using the techniques of Heisey and Fuller (1985), which calculates the number of deaths recorded during the number of radio-days monitored. Details on

estimating survival rates are given in Chapters 2 and 3. I tested for differences in survival rates using the binomial z-test (Sokal and Rohlf 1981). I estimated ages of killed males by counting cementum annuli (Stoneburg and Jonkel (1966). I tested for differences in age of killed males using the t-test.

### *Density*

I estimated the mean annual density of all bears and adult (> 5.5 years) males by dividing the known number of bears present annually by the size of the area they occupied. Details on density estimation are given in Chapters 2 and 3. Mean densities were based on 5 years of data in Kananaskis, 6 years data in the U.S. SMGBE, and 3 years data in the B.C. SMGBE. I averaged density data from both the U.S. and B.C. SMGBE to arrive at an average annual density for the Selkirks. This weighted the density estimate towards the U.S. SMGBE (6 of 9 years), but cub litters (6 of 10 litters) were also weighted towards the U.S. I tested for differences in mean annual density using the t-test (Sokal and Rohlf 1981).

## **RESULTS**

### *Trapping and monitoring*

A total of 24 grizzly bears (6 females, 18 males) were captured from 1980 to 1984 in Kananaskis. Five females and 15 males were collared and radio-monitored. A total of 28 grizzly bears (15 females, 13 males)

were captured, collared, and radio-monitored from 1985 to 1990 in the SMGBE.

#### *Reproductive rates*

Estimated reproductive rates were 0.46 for Kananaskis (Chapter 2) and 0.74 for the SMGBE (Chapter 3). The apparent difference in reproductive rate was due to cub litter size. Mean litter size for cubs of the year was 1.40 ( $n = 5$ ,  $SD = 0.54$ ) in Kananaskis and 2.22 ( $n = 10$ ,  $SD = 0.42$ ) in the SMGBE (Table 13). Litter size was statistically different ( $P = 0.008$ ,  $t = 3.15$ ,  $df = 13$ ). Mean birth interval was 3.00 years ( $n = 3$ ,  $SD = 0.00$ ) in Kananaskis and 3.00 years ( $n = 6$ ,  $SD = 0.63$ ) in the SMGBE. Mean age at first parturition was 5.50 years in Kananaskis ( $n = 3$ ,  $SD = 1.00$ ) and 7.30 years ( $n = 5$ ,  $SD = 0.44$ ) in the SMGBE. Mean age of first parturition was statistically different ( $P = 0.011$ ,  $t = 3.00$ ,  $df = 6$ ).

#### *Age of mothers*

Mean age of mothers was 10.70 years ( $n = 5$ ,  $SD = 4.76$ ) in Kananaskis and 11.05 years ( $n = 10$ ,  $SD = 4.12$ ) in the SMGBE (Table 13). Mean age did not differ statistically ( $P = 0.88$ ,  $t = 0.14$ ,  $df = 13$ ). One of 5 litters in Kananaskis was produced by a young (4.5 years) first-time mother (Table 13). All other litters were produced by prime-age mothers. One 2-cub litter was produced prior to the opening of the hunting season in Kananaskis. The same female produced a 1-cub litter after the hunting season. All other litters were post-hunting. Three of

Table 13. Cub litter size and age of mother (years) for female grizzly bears in Kananaskis, Alberta and the Selkirk Mountains Grizzly Bear Ecosystem of Idaho and British Columbia.

Kananaskis		Selkirks	
Litter size	Age	Litter Size	Age
1	4.5 <sup>a</sup>	2	7.5 <sup>a</sup>
1	7.5	2	7.5 <sup>a</sup>
2	11.5	3	7.5 <sup>a</sup>
2 <sup>b</sup>	13.5	2	9.5
1	16.5	2	9.5
		2	10.5
		3	10.5
		2	11.5
		2	16.5
		2	20.5
Mean	1.40	2.22	11.05

a First-time mother.

b This litter produced prior to opening of hunting season, all other litters were post-hunting

10 litters were produced by young (7.5 years) first-time mothers in the SMGBE; the remaining 7 litters were produced by prime-age mothers.

ANCOVA for cub litter size showed that the area effect (Kananaskis vs SMGBE) was statistically significant ( $P = 0.01$ , Table 14). Age of mother had no effect on litter size ( $P = 0.939$ ). Mean litter size was larger in the SMGBE controlling for the effect of age of mother.

#### *Weight and environmental productivity*

Twenty-seven weight measurements were obtained from 18 males during 1980 to 1984 in Kananaskis and 21 weights from 13 males during 1985 to 1990 in the SMGBE. Mean weight at capture for male bears in Kananaskis was 149.89 kg ( $n = 27$ ,  $SD = 25.84$ ) and mean weight of males in the SMGBE was 109.23 kg ( $n = 21$ ,  $SD = 39.64$ ) for a difference of about 40 kg. Mean weights were statistically different ( $P < 0.001$ ,  $t = 4.29$ ,  $df = 46$ ).

Mean age at capture was 6.55 years ( $n = 27$ ,  $SD = 4.18$ ) in Kananaskis and 5.95 years ( $n = 21$ ,  $SD = 3.37$ ) in the SMGBE. Mean age was not statistically different between the 2 study areas ( $P = 0.600$ ,  $t = 0.528$ ,  $df = 46$ ).

Mean Julian date at capture was 192 days ( $n = 27$ ,  $SD = 27.95$ ) in Kananaskis and 175 days ( $n = 21$ ,  $SD = 27.86$ ) in the SMGBE for a difference of about 17 days. Mean date at capture was statistically different between the 2 study areas ( $P = 0.042$ ,  $t = 2.08$ ,  $df = 46$ ). ANCOVA for weight of males (Table 15) showed that the area effect was statistically significant ( $P < 0.001$ ). Male bears were heavier in

Table 14. Analysis of covariance (ANCOVA) for cub litter size in Kananaskis and the Selkirk Mountains Grizzly Bear Ecosystem.

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Source	SS	df	MS	<u>F</u>	<u>P</u>
Area	2.134	1	2.134	9.150	0.011
Age of Mother	0.001	1	0.006	0.006	0.939
Error	1.799	12	0.233		

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$\bar{n} = 15, r^2 = 0.43$

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ANCOVA model: cub litter size = constant + area + age of mother.

Table 15. Analysis of covariance (ANCOVA) for weight of male grizzly bears in Kananaskis and the Selkirk Mountains Grizzly Bear Ecosystem.

Source	SS	df	MS	<u>F</u>	<u>P</u>
Area	1.26	1	1.26	39.45	< 0.001
log(Age)	2.55	1	2.55	79.97	< 0.001
Date	0.04	1	0.04	1.34	0.25
Error	1.40	44	0.03		

$\underline{n} = 48, r^2 = 0.75$

ANCOVA model:  $\log(\text{weight}) = \text{constant} + \text{area} + \log(\text{age}) + \text{date of capture}.$

Kananaskis controlling for the effects of age and date. Since age at capture was not different between the 2 study areas, and since date of capture had no effect on weight, the difference of approximately 40 kg can be attributed primarily to the area effect or environmental productivity. Differences in weight at age were most pronounced for younger (< 10.5 years) males (Fig. 1.). Maximum weight was about 180 kg for both populations but that maximum was reached at about 7.5 years in Kananaskis and 15.5 years in the SMGBE.

Twelve weight measurements were obtained from 6 females from 1980 to 1984 in Kananaskis and 20 weights from 15 females during 1985 to 1990 in the SMGBE. Mean weight at capture for female bears was 100.83 kg ( $n = 12$ ,  $SD = 12.73$ ) in Kananaskis and 81.65 kg ( $n = 20$ ,  $SD = 26.04$ ) in the SMGBE for a difference of about 20 kg. Mean weights were statistically different ( $P = 0.024$ ,  $t = 2.37$ ,  $df = 30$ ).

Mean age at capture for females was 6.75 years ( $n = 12$ ,  $SD = 5.51$ ) in Kananaskis and 9.40 years ( $n = 20$ ,  $SD = 7.89$ ) in the SMGBE. Mean age was not statistically different ( $P = 0.316$ ,  $t = 1.02$ ,  $df = 30$ ).

Mean date at capture for females was 196.92 days ( $n = 12$ ,  $SD = 22.76$ ) in Kananaskis and 181.95 days ( $n = 20$ ,  $SD = 23.77$ ) in the SMGBE. Date at capture was not significantly different between the 2 study areas ( $P = 0.90$ ,  $t = 1.751$ ,  $df = 30$ ).

ANCOVA for weight of females (Table 16) showed that the area effect was statistically significant ( $P = 0.018$ ). Female bears in Kananaskis were heavier controlling for the effects of age and date. Both age at capture and date at capture also had significant effects on weight. The effect of reproductive status (e.g., lactation) was unknown,

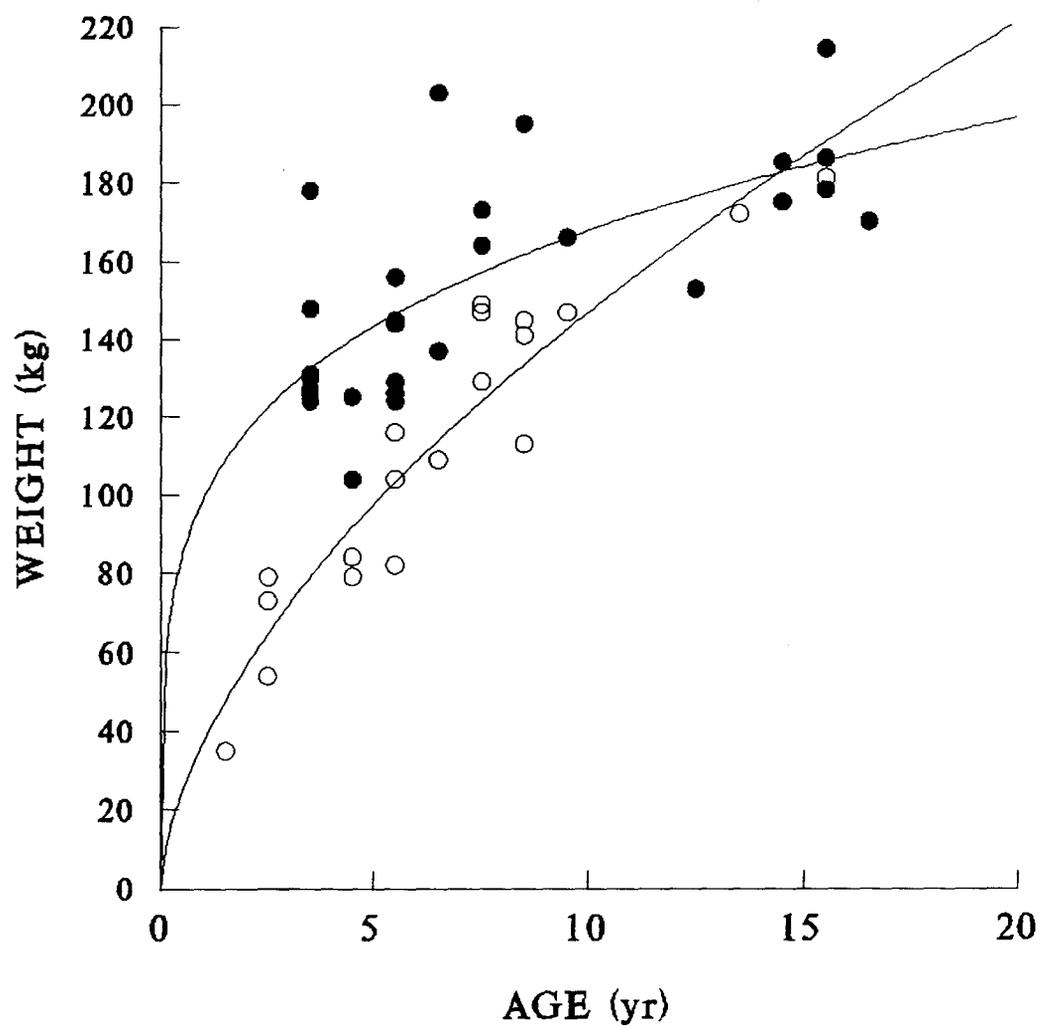


Fig. 1. Non-linear least squares regression for weight (kg) and age (years) of male grizzly bears in Kananaskis (●) and the SMGBE (○).

Table 16. Analysis of covariance (ANCOVA) for weight of female grizzly bears in Kananaskis and the Selkirk Mountains Grizzly Bear Ecosystem.

Source	SS	df	MS	F	P
Area	0.29	1	0.29	6.23	0.018
log(Age)	0.92	1	0.92	19.60	< 0.001
Date	0.24	1	0.24	5.17	0.031
Error	1.27	27	0.04		

$\underline{n} = 31, r^2 = 0.53$

ANCOVA model:  $\log(\text{weight}) = \text{constant} + \text{area} + \log(\text{age}) + \text{date of capture}.$

however, 1 of 6 adult female weights in Kananaskis and 5 of 13 adult female weights in the SMGBE were from lactating females.

Differences in weight at age were most pronounced for subadult (< 6.5 years) females (Fig. 2.). Weight appeared to asymptote at about 100 kg for both populations but females reached asymptotic weight at about 3.5 to 5.5 years in Kananaskis and 5.5 to 7.5 years in the SMGBE. Those ages correspond to mean age at first breeding and parturition.

#### *Survival of adult males*

Survival rates of adult males appeared lower in Kananaskis (0.70, Chapter 2) than in the SMGBE (0.81, Chapter 3) but the rates were not statistically different ( $P > 0.10$ ,  $z = 0.71$ ) because of large variances due to small sample sizes. Mean age of killed males was 11.12 years ( $n = 8$ ,  $SD = 4.98$ , range = 5.5, 6.5, 7.5, 9.5, 10.5, 13.5, 16.5, and 19.5 years) in Kananaskis and 6.16 years ( $n = 3$ ,  $SD = 2.51$ , range = 3.5, 6.5, and 8.5 years) in the SMGBE. Killed males were older in Kananaskis than in the Selkirks ( $P = 0.06$ ,  $t = 2.17$ ,  $df = 7.5$ ).

#### *Density*

Total population densities were similar between study areas; the Kananaskis sample population had a mean annual total density of 1.61 bears/100 km<sup>2</sup> ( $n = 5$ ,  $SD = 0.58$ ) and the SMGBE had a mean total of 1.68 bears/100 km<sup>2</sup> ( $n = 9$ ,  $SD = 0.45$ ). Density of adult males was 0.48 bears/100 km<sup>2</sup> ( $n = 5$ ,  $SD = 0.21$ ) in Kananaskis and 0.23 bears/100 km<sup>2</sup>

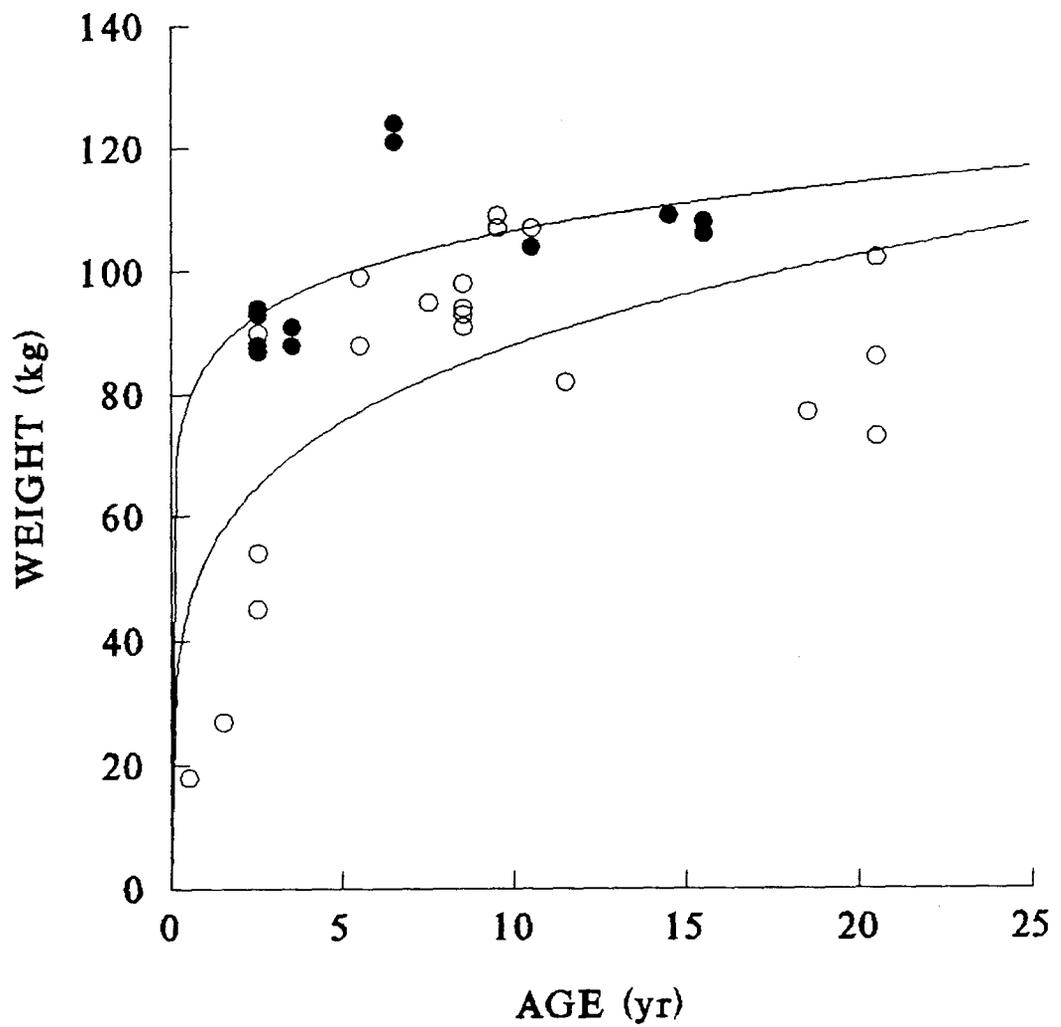


Fig. 2. Non-linear least squares regression for weight (kg) and age (years) of female grizzly bears in Kananaskis (●) and the SMGBE (○).

( $n = 9$ ,  $SD = 0.16$ ) in the SMGBE. Density of adult males was higher in Kananaskis ( $P = 0.03$ ,  $t = 2.41$ ,  $df = 12$ ).

## DISCUSSION

### *Reproduction*

My results reject the null hypothesis that reproductive rates were not different between the 2 sample populations; larger litters in the SMGBE accounted for the higher reproduction there. I am confident in my test results despite the small sample size because small  $n$  will result in increased type 2 not type 1 errors (Sokal and Rohlf 1981).

The small sample also raises the question of whether the statistical difference was due to sampling bias - perhaps these litters were not representative of the Kananaskis and SMGBE populations. That has no bearing on my tests of hypotheses because I do not attempt to infer to some larger populations - I simply predicted and observed that the Kananaskis sample population had statistically smaller litters than the SMGBE sample population. Although large samples are always desirable they cannot always be obtained, especially from sparse populations; the total estimated number of adult females was only 8 animals in Kananaskis (Chapter 2) thereby making large samples very difficult to obtain.

### *Age of mothers*

My results reject the null hypothesis that age of mothers accounted for the difference in litter sizes. Age of mothers did not

differ between the two sample populations and age of mothers had no effect on litter size (Table 14).

#### *Environmental productivity*

My results reject the null hypothesis that environmental productivity or food supply accounts for the difference in litter size. Food supply (indexed by male weight) appeared superior in Kananaskis (Fig. 1) yet mean litter size was smaller there. Earlier age at asymptotic weight and earlier age at first parturition for females in Kananaskis further supports the notion of superior food there (Fig. 2).

#### *Competing hypotheses of reproduction*

The density independent, additive mortality model was rejected because reproduction was lower in Kananaskis than in the SMGBE despite superior environmental productivity or food supply in Kananaskis.

The density dependent, compensatory model was rejected because reproduction was lower in Kananaskis despite high mortality of adult males. Density of adult males was higher in Kananaskis despite that high mortality.

My results support the density dependent, compensatory model because reproduction was lower in Kananaskis coincident with high mortality and higher density of adult males there. Survival rates were not statistically different between the 2 populations (0.70 vs 0.81) because of small sample sizes in the sparse populations (Chapters 2 and 3). However, 8 of 18 male bears collared in Kananaskis were reported

shot by 1987 and 7 others simply disappeared by 1984 (Chapter 2). By contrast, only 3 of 13 males collared in the SMGBE were reported shot by 1990 and none disappeared (Chapter 3). That also suggests that adult male survival was lower in Kananaskis. Regardless of survival rates, those males that were killed were older in Kananaskis than in the SMGBE and removal of old males may be responsible for the higher densities of adult males in Kananaskis.

The opening of the grizzly bear hunting season coincided with increased immigration of subadult and young adult males in Kananaskis (Chapter 2). Few immigrant males were observed in the SMGBE where adult male mortality appeared to be lower and was restricted to younger age classes (Chapter 3). Older adult males are believed to limit immigration of subadult males (Rogers 1987; Bunnell and Tait 1981) so their removal can be expected to result in increased numbers of younger, immigrant males. Kemp (1976) and Young and Ruff (1982) experimentally induced a 3-fold increase in immigrant subadult male black bears by removing 30% of adult males. LeCount (1987) also observed an abundance of subadult males in a black bear population with high adult male mortality.

Sexually mature females avoided potentially infanticidal, immigrant males and male-favoured habitats in Kananaskis; subadult females did not (Chapter 4). The apparent contradiction of smaller litter size and earlier age at first parturition in Kananaskis can be reconciled by that sexual habitat segregation. Subadult females, subadult males, and adult males all concentrated in a burned-over, food-rich habitat in environmentally superior Kananaskis. That may have allowed subadult females to gain weight rapidly and produce cubs at an early age. Sexually mature adult females rarely used that burned-over,

food-rich area. They restricted most of their activities to unburned areas where immigrant males were rare and food supply was likely inferior, and that could account for the small litter sizes.

No such sex and reproductive class habitat segregation was observed in a burned-over, food-rich habitat in the environmentally inferior SMGBE where there appeared to be few or no immigrant males (Chapter 3). All sex and age classes, including adult females, selected for the burned area (Chapter 4), and that could account for the larger litters in the SMGBE.

McCullough (1981) and Stringham (1983) also documented an inverse relationship between reproductive rate and number of adult male bears. They suggested that adult male bears depress reproduction indirectly by denying females access to superior food sources and that appears to be the case in Kananaskis. I suggest, however, that adult females avoid sexually mature, immigrant or non-sire males, not resident sires.

My results suggest that habitat segregation may have an equal or greater negative impact on cub litter size than direct infanticide. LeCount (1987) found that 50% of black bear cub mortality was due to intraspecific killing. He suggested that the high cub mortality in his study area was due to large numbers of immigrant males because of high mortality of adult males. I did not observe intraspecific killing of cubs in my study areas but it may have occurred in early spring, prior to first observation of cubs.

*Possible effects of trophy hunting*

Increased hunting mortality of older adult males corresponded with increased immigration of younger males (Chapter 2) and that appeared to result in sexual habitat segregation (Chapter 4) and small litter sizes (this chapter). The small litter sizes were directly responsible for an estimated population decline in Kananaskis (Chapter 2). That dynamic suggests that trophy hunting of adult males may not be compensatory for reproduction and population growth as commonly believed, but that hunting of adult males can actually be depensatory, at least for some small, peripheral populations where the potential for male immigration is high. I concur with Miller (1990) that a compensatory model should not be assumed for bears. This research needs to be replicated to determine if my findings are applicable elsewhere.

## Chapter 6

### GENERAL CONCLUSIONS

This thesis suggests that hunting of adult males may have compensatory effects on female reproduction because of increased immigration by potentially infanticidal, non-sire males and resulting sexual habitat segregation. Although my results are consistent with my initial predictions, I had no prior knowledge of the habitat use patterns and population parameters of the Selkirk Mountains grizzly bears. Predictions that I made grew from discussions with coworkers at the University of British Columbia and review of my earlier work. Selection of the Selkirks population was opportunistic and data derived from it led to my conclusions. I am aware that my tests of hypotheses are not replicated; I cannot extrapolate and make generalizations to other populations, however, I hope that subsequent research will do so.

Despite my inability to replicate studies of populations, this thesis makes four contributions to conservation biology of grizzly bears. In Chapter 2 I estimated the population dynamics including density and numbers, sex and age composition, reproduction, survival, and population growth for a heavily hunted but sparse grizzly bear population at the edge of the species' range. That population was previously believed to be increasing because of numerous subadult males (Carr 1989). I showed that high mortality of older adult males corresponded with increased density of younger immigrant males, not increased production by resident females, and that the population was probably decreasing.

In Chapter 3 I estimated the population dynamics of a non-hunted, but threatened population at the edge of the species' range. That population was previously believed to be decreasing but I showed that the population was probably stable.

In Chapter 4 I tested three competing hypotheses of sex and reproductive class habitat segregation. My results rejected the "no avoidance" and "food competition" models but supported the "sex competition" model of habitat segregation. Sexually mature adult females avoided food-rich, male-occupied habitats in Kananaskis where there were many potentially infanticidal, immigrant males but did not in the Selkirks where there were few such males. Sexually immature, subadult females did not avoid those food-rich, male-occupied habitats in either study area.

In Chapter 5 I tested three competing hypotheses on the effects of adult male mortality on female reproduction. My results rejected the "additive" and "compensatory" models but supported the "depensatory" model of male mortality. High hunting mortality of older adult males in Kananaskis corresponded with increased density of younger, potentially infanticidal immigrant males. Adult females avoided food-rich habitats occupied by immigrant males in Kananaskis and their reproduction appeared to suffer as a result. My results suggest that hunting of older adult males is not beneficial for reproduction and population growth as commonly believed but that such hunting may be detrimental for reproduction and can contribute to population decline.

I have no doubt that my findings will be controversial but I also have no doubt that other grizzly bear researchers will test my conclusions to determine if my findings are applicable elsewhere.

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