

Possible negative effects of adult male mortality on female grizzly bear reproduction

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Abstract

We studied 2 grizzly bear (*Ursus arctos*) populations to test 3 hypotheses on the effects of adult male mortality on female reproduction. The “no effect” hypothesis predicts that reproduction should be higher in the population with superior overall diet quality, regardless of mortality of adult males. The “increased reproduction” hypothesis predicts that reproduction should be higher in the hunted population because of lowered numbers of competitive or cannibalistic adult males. The “decreased reproduction” hypothesis predicts that reproduction should be lower in the hunted population because of increased immigration by potentially infanticidal, nonsire males with subsequent reduced survival of cubs, and/or increased sexual segregation resulting in reduced production of cubs. Reproduction rates were 0.46 in a hunted population in Kananaskis, Alberta and 0.74 in non-hunted populations in the Selkirk Mountains of Idaho and British Columbia. Mean litter size was smaller in Kananaskis than in the Selkirks (1.40 vs 2.22) but age at first parturition was earlier in Kananaskis (5.50 vs 7.30 years). Mean birth intervals were not different between populations. Age of mothers, overall diet quality, and total population density were not associated with differences in litter size and age at first reproduction, but adult female avoidance (sexual segregation) of nonsire immigrant males and associated food-rich habitats were. Our results are inconsistent with the “no effect” and “increased reproduction” hypotheses but consistent with the “decreased reproduction” hypothesis. Higher hunting mortality of older males coincided with higher numbers of potentially infanticidal, immigrant males in Kananaskis. Adult females avoided those males and their food-rich habitats in Kananaskis and female reproduction appeared to suffer as a result. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Grizzly bears have disappeared from most of their historic range in North America and are classified as threatened in the lower US and vulnerable in Canada (Servheen, 1990). Despite these losses, adult males are hunted in many jurisdictions, even in very small peripheral populations at the edge of the species' range (Wielgus and Bunnell, 1994a; Wielgus et al., 1994; Swenson et al., 1997) because trophy hunting is believed to be beneficial or benign for population growth (Dood et al., 1986; Nagy and Gunson, 1990; Smith, 1990; British Columbia Ministry of Environment, 1995a,b). Although few, if any, rigorous tests of this hypothesis

have been conducted, many wildlife managers assume mortality of adult males reduces density of males and increases cub production by females, cub survival, and population growth through compensatory density dependent effects (see review by Miller, 1990).

Taylor (1994) reviewed the literature for density dependent effects on black bears (*Ursus americanus*), brown bears, and polar bears (*Ursus maritimus*). His review was inconclusive relative to the theories that hunting is either beneficial or detrimental for cub production and survival. This review and the work by McLellan (1989) and Hovey and McLellan (1996) has been interpreted as support for the beneficial or benign effects of hunting (British Columbia Ministry of Environment, 1995a,b). However, the studies reviewed in Taylor (1994) and conducted by McLellan (1989) and Hovey and McLellan (1996) were generally inconclusive

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because they were not designed to test effects of hunting, and any putative effects of hunting within and among populations were potentially confounded with several other factors (e.g. diet quality, population density, age of mothers, etc.).

More recently, Wielgus (1993) and Wielgus and Bunnell (1994a,b, 1995) studied a hunted and non-hunted population and controlled for some confounding factors using indices for diet quality and density. They suggested that removal of older adult males may have resulted in increased immigration of potentially infanticidal immigrant males. They reported that females avoided those immigrant males and the food-rich habitats they inhabited, and suggested that this resulted in small litter sizes and an estimated population decline. Swenson et al. (1997, in press) compared populations with high and low adult male mortality and controlled for some confounding factors using indices for diet quality and population density. They also suggested that hunting of adult males resulted in increased immigration of new males, reduced survival of cubs through sexually selected infanticide, and reduced population growth. The hypotheses and findings proposed by Wielgus and Bunnell (1994a,b, 1995) and Swenson et al. (1997) are considered highly controversial by some agencies (British Columbia Ministry of Environment, 1995a,b) and some researchers (B. McLellan and S. Miller, pers. comm.).

In this paper we use retrospective data and control for confounding factors including age of mothers, survival of females, population density, and indices of diet quality to conduct a mensurative experiment (Eberhardt and Thomas, 1991) to test competing hypotheses. We compare a hunted population in Kananaskis, Alberta to a non-hunted population in the Selkirk Mountains of Idaho and British Columbia (B.C.). Both populations were small (approximately 40 bears each; US Fish and Wildlife Service, 1990; Wielgus and Bunnell, 1994a), at the edge of the species' range, and appeared to be declining during the time of study (Wielgus and Bunnell, 1994a; Wielgus et al., 1994). Sample sizes were necessarily small in both of these threatened populations. Despite the problems associated with small samples, we suggest that small, declining, peripheral populations must be studied and reported on to understand the dynamics of such populations.

The no effect hypothesis predicts higher cub production in the population with superior overall diet quality, regardless of mortality of adult males (Bunnell and Tait, 1981; Knight and Eberhardt, 1985; Rogers, 1987). The increased reproduction hypothesis predicts higher cub production in the hunted population because of lowered numbers or density of competitive and/or cannibalistic adult males (McCullough, 1981, 1986; Stringham, 1983; McLellan, 1989). The decreased reproduction hypothesis predicts lower cub production

in the hunted population because removal of adult males allows an increase in numbers and density of potentially infanticidal immigrant males (Stringham, 1980; Hrdy and Hausfater, 1984; LeCount, 1987; Wielgus and Bunnell, 1994a, 1995; Swenson et al., 1997, in press).

2. Study area

The Kananaskis study area covers 6300 km² in the Kananaskis Provincial Park (3400 km²) and Bow-Crow Forest (2900 km²) of southwestern Alberta (50–51° lat., 115–116° long.). Elevation ranges from 1300 to 2700 m in mountainous terrain. Climate is continental. Vegetation is in the subalpine fir/Engelmann spruce (*Abies lasiocarpa*–*Picea engelmanni*) forest region (Rowe, 1972). Hunting of grizzly bears was closed from 1970 to 1981, but was reopened in the Bow Crow forest from 1982 to 1988 because the population was believed increasing (Carr, 1989; Nagy and Gunson, 1990). Grizzly hunting seasons took place from 1 April–15 June. Wielgus and Bunnell (1994a) suggested the population was decreasing from 1981 to 1984. This population was classified as vulnerable (Banci, 1991).

The Selkirk Mountains Grizzly Bear Ecosystem (SMGBE) covers 5700 km² in northern Idaho, north-eastern Washington (3000 km²), and southern B.C. (2700 km²) (48–49° lat., 116–117° long.). Physiography is mountainous with elevations from 550 to 2500 m. Climate is Pacific maritime/Continental. Vegetation is in the Engelmann spruce/subalpine fir and cedar/western hemlock (*Thuja plicata*/*Tsuga heterophylla*) bigeoclimatic zones (Pojar et al., 1987). Hunting of grizzly bears was not allowed in the US SMGBE under the Endangered Species Act and hunting in the B.C. SMGBE did not occur during research (1985–1990). Wielgus et al. (1994) suggested the population was stable from 1985 to 1990 but that it would likely decline after hunting was reinstituted in B.C. in 1992. Hunting was again prohibited after 1995 (British Columbia Ministry of Environment, 1995a,b) because of public concern. This population was classified as threatened in the US (Servheen 1990) and vulnerable in Canada (Banci, 1991), and is now classified as threatened in both countries.

3. Methods

3.1. Trapping and monitoring

We trapped bears in 2 areas of Kananaskis (Highwood and Sheep trapping zones) and 2 areas of the SMGBE (Idaho and B.C. trapping zones) (Wielgus, 1993). We used Aldrich leg snares to trap bears and immobilized them with ketamine hydrochloride and

xylazine hydrochloride in both study areas. All bears were immobilized, weighed, ear-tagged, had a premolar tooth extracted for aging (Stoneburg and Jonkel, 1966) and were fitted with mortality-sensing radio-collars. We handled bears according to protocol of the Canadian Council on Animal Care, University of British Columbia Animal Care Certificate 890105. We monitored bears using fixed-wing radiotelemetry (Whitehouse and Steven, 1977) once every week or two during the non-denning period (early April–early November) from 1981 to 1984 in Kananaskis and from 1985 to 1990 in the SMGBE. There were no unusual weather occurrences such as droughts or excessive rainfalls resulting in food shortage during monitoring for either study area. Details on trapping, monitoring of bears, and habitat use are given in Wielgus (1993), Wielgus and Bunnell (1994a,b, 1995) and Wielgus et al. (1994).

3.2. Survival rates and ages of killed males

We estimated annual mortality rates for radiocollared males and adult females using the Micromort Program (Heisey and Fuller, 1985), which calculates the number of deaths recorded during the number of radio-days monitored. Details on mortality estimates are given in Wielgus and Bunnell (1994a) and Wielgus et al. (1994). We tested for differences in male mortality rates using the binomial z -test (Sokal and Rohlf, 1981). We tested for differences in age of killed males using the U -test. We also tested for differences in survival of adult females because lower survival of adult females may correspond with lower cub production (Miller pers comm.). P -values of <0.10 are considered statistically significant throughout.

3.3. Number of bears

We documented the number of new bears captured/year to estimate potential immigration response to removal of adult males. We only included independent bears ≥ 2.5 years old because younger bears are typically offspring of resident females (Blanchard and Knight, 1991). Adult males were legally killed in Kananaskis starting in spring 1982 (hunting season was from 1 April to 15 June). We documented the number of new captures for 4 consecutive years in Kananaskis (pre-hunting 1980 and 1981, post-hunting 1982 and 1983) and 4 consecutive years in the Selkirks (1985–1987 and 1989 in US, 1988–1991 in Canada). A post-hunting (1982+) increase in capture of new males (especially 2.5–5.5 year-old males, Blanchard and Knight, 1991) in Kananaskis would suggest a male immigration response to removal of adult males. We controlled for potentially confounding temporal effects (e.g. higher trapping effectiveness in latter years) and geographic effects (higher trapping effectiveness in Kananaskis) by using

log-linear models (SYSTAT, 1997). We analyzed annual frequency of new captures for 4 years (years 1–4), for each sex (M, F), in each study area (K, S), in a 16 cell table (Table 1). We added a delta value of 1 to the one empty cell in the SMGBE data (SYSTAT, 1997). Mean expected values (3.18) were adequate for testing (>2 , Roscoe and Byers, 1971).

A simple model (e.g. main effects only: year, area, sex) would indicate temporal (more captures in latter years), geographic (more captures in Kananaskis), or sexual (more males than females in both areas) effects only with no male immigration response in Kananaskis. Significant 2-way interactions such as sex*area (more male than female captures in Kananaskis, more male captures in Kananaskis than in the SMGBE) and area*year (more captures in latter years in Kananaskis but not in the SMGBE) would suggest a male immigration response in Kananaskis.

3.4. Density of bears

We estimated mean annual density of bears by determining number of bears present annually in the female multi-annual composite ranges (Wielgus and Bunnell, 1994a; Wielgus et al., 1994). Mean densities were based on 5 years of data in the Kananaskis composite range, 6 years data in the US SMGBE composite range, and 3 years data in the B.C. SMGBE composite range. We averaged density data from both the US and B.C. SMGBE composite ranges to arrive at an average annual density for the Selkirks. That weighted the density estimate towards the US SMGBE (6 of 9 years), but cub litters (6 of 10) were also weighted towards the US. We tested for differences in mean annual density using the t -test.

3.5. Reproduction

We determined mean number of cubs per litter, birth interval, and age at first parturition from aerial and ground observations of females and their cubs. Reproductive rates and cub litter sizes include cubs <1

Table 1
Frequencies of new captures of male and female bears^a by year in Kananaskis, Alberta and the Selkirk Mountains Grizzly Bear Ecosystem of Idaho and British Columbia

Study area	Year 1	Year 2	Year 3	Year 4	Total
<i>Kananaskis</i>					
Males	4	3	2	8	17
Females	1	1	3	1	6
<i>Selkirk</i>					
Males	8	1	3	0	12
Females	7	2	4	2	15

^a Only includes independent bears ≥ 2.5 years-old.

year of age observed during June and July and do not incorporate any offspring that could have died in the den or shortly after leaving the den (e.g. February–May). We estimated reproductive rate for each population as average litter size of new cubs divided by average birth interval (Craighead et al., 1974). We tested for differences in mean litter size, birth interval, and age at first parturition using the Mann Whitney U test.

3.6. Age of mothers

We tested for differences in ages of mothers because such differences might affect cub litter size given that prime-age mothers (> age at first parturition) often produce larger litters (Caughley, 1977). We tested for differences using the *U*-test and controlled for the effects of age of mothers 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.

3.7. Indices of diet quality

We used 4 different measures to index diet quality. Following Garshelis (1994) and Swenson et al. (in press), we used body mass of subadult female, subadult male, and adult male bears as an index to diet quality. Bunnell and Tait (1981), Kingsley et al. (1983), Blanchard (1987), Rogers (1987), and Stringham (1990) all showed body mass of bears to be positively related to diet quality within and among areas. Rogers (1987) and Stringham (1990) further showed that litter size, birth interval, and age at first parturition were likewise related to diet quality within and among areas. More recently, Hildebrand et al. (in press) showed that body mass was highly correlated to diet quality, mean litter size was highly correlated to diet quality, and that mean litter size was highly correlated to body mass.

We used body mass of (1) subadult (pre-partum) females, (2) subadult males and (3) adult males as indices of overall diet quality because those age-sex classes used the best available habitats in both study areas (Wielgus and Bunnell, 1995). Adult females (including estrous adult females) avoided the best food areas in Kananaskis but not in the Selkirks so their body masses were not logical indicators of overall diet quality. We also did not use adult female body mass because this will fluctuate with current and past reproductive status (previous litter size and lactation, Kingsley et al., 1983) and we did not have enough data to control for these factors.

We also used (4) subadult female age at first parturition as a further index of diet quality because subadult females were not influenced by habitat segregation (Wielgus and Bunnell, 1995), lactation, or number of

accompanying cubs. We plotted body mass-at-age for both sexes in both study areas using non-linear PLOT (SYSTAT, 1997). We used all captures (e.g. 27 measurements from 18 males and 12 measurements from 6 females in Kananaskis; 21 measurements from 13 males and 20 measurements from 15 females in the SMGBE) to plot body mass at age and illustrate any differences in body mass between study areas.

We used the *t*-test to test for differences in mean body mass of males and females. Because body mass is influenced by age of bear and date of capture, as well as by food supply, we tested for differences in mean age and date of capture using *t*-tests. We controlled for the effects of age and date by analysis of covariance (ANCOVA; Tabachnick and Fidell, 1983). Sex specific ANCOVA models were: $\log(\text{body mass}) = \text{constant} + \text{area} + \log(\text{age}) + \text{date of capture}$. Area (Kananaskis vs SMGBE) was the main effect being tested, age and date were covariates. Both body mass and age were log transformed to linearize their relationship to meet the assumptions of the ANCOVA tests. We only used and report age at first capture (18 measurements for 18 males etc.) for the above tests (no recaptures) to ensure statistical independence among measurements.

4. RESULTS

4.1. Trapping and monitoring

Twenty-three grizzly bears (6 females, 17 males) were captured from 1980 to 1983 in the Kananaskis study area. Five females and 15 males were collared and radio-monitored from 1981 to 1984 (Wielgus, 1993). Seven of 17 males (4.5, 4.5, 5.5, 9.5, 12.5, 14.5, 15.5 years old) were captured during the first 2 years of trapping (1980–1981) (Table 1). The remaining 10 males (3.5, 3.5, 3.5, 3.5, 3.5, 5.5, 5.5, 6.5, 7.5, 15.5 years old) were captured during 1982–1983 after at least 2 collared resident males were shot (5.5 year-old in September 1981, 16.5 year-old in June 1982) and another collared resident male (15.5 year-old in July 1983) was suspected shot. This last bear stopped transmitting and disappeared only 2 months after capture. The 3 killed males spent an average of 95% (SE = 5%) of their time in the female composite home range.

Mean age of captured males was 9.5 years for 1980–1981 (SE = 1.8, $n = 7$) and 5.8 years for 1982–1983 (SE = 1.1, $n = 10$). Mean ages were statistically different at $P = 0.09$ ($t = 1.80$, 15 df). These observations indicate that 10 younger males were captured in the study area following removal of 3 resident older males. All new male captures were ≥ 3.5 years old when captured and none were previously observed as offspring of resident females, suggesting they were recent immigrants (Blanchard and Knight, 1991). Trapping effort or trap loca-

tions did not change (1806, 2074, 2124, 1868 trap-nights/year, Wielgus and Bunnell, 1994a) so that would not likely explain the increased number of males trapped after 1981. Most (5 of 6) females were captured when in estrus or as subadults because adult females with offspring avoided the male-occupied trapping area in Kananaskis after 1981 (Wielgus and Bunnell, 1995).

Twenty-eight grizzly bears (15 females, 13 males) were captured, collared, and radio-monitored from 1985 to 1990 in the Idaho and B.C. trapping zones of the SMGBE (Wielgus, 1993). Nine of 13 males were captured during the first year of trapping (one 1.5 year-old died shortly after capture) and 3 others were captured later as 2.5 year-old offspring of resident females. Only 1 older (13.5 years) male was captured during the second year of trapping, suggesting that all or most males were residents, not recent immigrants. Nine of 15 females were captured during the first 2 years of trapping or as offspring of resident females.

4.2. Mortality of adult males and females

Only 1 uncollared male bear was reported shot from 1980 to 1981 (5.5 year-old in September 1981) in Kananaskis. Four radioed males and 1 uncollared male (16.5 year-old in June 1982, 6.5 year-old in April 1984, 13.5 year-old in April 1984, and 10.5 year-old in June 1984) were reported shot and another radioed male (15.5 year-old in July 1983) was likely shot in the Kananaskis study area from 1982 to 1984. That yielded a total of 5 radiocollared deaths during 5508 radiodays in Kananaskis. A total of 3 males were killed during 7486 radiodays in the Selkirks. Mortality rate of males was higher in Kananaskis than in the SMGBE (0.30 vs 0.14, $z=1.33$, $P=0.09$). Killed males were also older in Kananaskis than in the Selkirks ($P<0.10$, $U=14.5$). Mean age of killed males was 11.3 years ($n=6$, $SE=1.8$) in Kananaskis and 6.1 years ($n=3$, $SE=1.4$) in the SMGBE. Survival rate of adult females was not different between populations (0.93 in Kananaskis and 0.96 in the SMGBE, Wielgus and Bunnell, 1994a; Wielgus et al., 1994).

4.3. Numbers of bears

Log-linear models of capture frequency (Table 1) suggested a significant post-hunting immigration response in Kananaskis. The main effects model did not fit the data (log likelihood $\chi^2=17.02$, 10 df, $P=0.07$) so temporal (higher trapping effectiveness over time), geographic (higher trapping effectiveness in Kananaskis), or sexual (more males in both areas) effects did not account for the increased numbers of males in post-hunting Kananaskis. The sex*area + year*area model showed the best fit to the data (log likelihood $\chi^2=4.63$,

6 df, $P=0.59$). Improvement χ^2 s were 8.4 (3 df, $P=0.03$) for the area*year effect (more captures in year 4 in Kananaskis) and 4.0 (1 df, $P=0.04$) for the area*sex effect (more males than females captured in Kananaskis, more males captured in Kananaskis than in the SMGBE). The sex*year interaction (more males in latter years for both areas) was not significant ($P=0.50$). In summary, there were increased captures of younger male bears in Kananaskis during latter post-hunting years, and this increase was not associated with increased trapping effort, increased trapping effectiveness overall, more males in Kananaskis to begin with, or easier catchability of males over time.

4.4. Density of bears

In Kananaskis, density of males was 0.57 bears/100 km² ($n=3$, $SE=0.06$) during pre-hunting 1980–1982 and 1.26 bears/100 km² ($n=2$, $SE=0.23$) during post-hunting 1983–1984. Density of females was 0.46 bears/100 km² during 1980–1982 ($n=3$, $SE=0.06$) and 0.57 bears/100 km² during 1983–1984 ($n=2$, $SE=0.01$) (Wielgus and Bunnell, 1994a). Densities did not appear to vary temporally for males or females in the SMGBE (Wielgus et al., 1994).

Total population densities (males, females, cubs) were similar between study areas; 1.61 bears/100 km² ($n=5$, $SE=0.26$) in Kananaskis and 1.68 bears/100 km² ($n=9$, $SE=0.15$) in the SMGBE. Density of adult females was 0.34 bears/100 km² ($n=5$, $SE=0.08$) in Kananaskis and 0.56 bears/100 km² ($n=9$, $SE=0.19$) in the SMGBE. Density of adult females was higher in the SMGBE ($P=0.03$, $t=2.36$, 12 df). Density of females (adults and subadults) was 0.50 bears/100 km² ($n=5$, $SE=0.04$) in Kananaskis and 0.72 bears/100 km² ($n=5$, $SE=0.064$) in the SMGBE. Density of weaned females was higher in the SMGBE ($P=0.04$, $t=2.27$, 12 df). Density of males was 0.85 bears/100 km² ($n=5$, $SE=0.17$) in Kananaskis and 0.48 bears/100 km² ($n=9$, $SE=0.06$) in the SMGBE. Density of males was higher in Kananaskis ($P=0.04$, $t=2.28$, 12 df).

4.5. Reproduction

Estimated reproductive rates were 0.46 for Kananaskis and 0.74 for the SMGBE. The apparent difference in reproductive rate was due to litter size (1.4 vs 2.2) or number of cubs produced (Table 2). Litter size was smaller ($P<0.05$, $U=42$) in Kananaskis than in the SMGBE. Mean birth interval was 3.0 years ($n=3$, $SE=0.0$) in Kananaskis and 3.0 years ($n=6$, $SE=0.25$) in the SMGBE. Mean age at first parturition was earlier ($P<0.05$, $U=14.5$) in Kananaskis (5.5 years, $n=3$, $SE=0.57$) than in the SMGBE (7.3 years, $n=5$, $SE=0.19$).

Table 2

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		Selkirk	
Litter size	Age	Litter size	Age
1	4.5 ^a	2 ^b	7.5 ^a
1	7.5	2	7.5 ^a
2	11.5	3 ^b	7.5 ^a
2 ^b	13.5 ^c	2	9.5
1	16.5	2	9.5
		2	10.5
		3	10.5
		2	11.5
		2 ^b	16.5
		2	20.5
Mean 1.4	10.7	2.2	11.1
SE 0.24	2.1	0.13	1.3

^a First-time mother.

^b This litter first observed when cubs were > 1 year old.

^c This litter produced prior to hunting season, all others post-hunting.

4.6. Age of mothers

Mean age of mothers (Table 2) was not different ($P > 0.10$, $U = 24.5$) between Kananaskis and the SMGBE. One of 5 litters in Kananaskis was produced by a young first-time mother, all other litters were produced by prime-age mothers. Three of 10 litters were produced by young first-time mothers in the SMGBE; the remaining 7 litters were produced by prime-age mothers. Differences in sample size between age at first reproduction (NK=3, NS=5) and litter size for first-time mothers (NK=1, NS=3) were because of unknown litter sizes for some known (lactating, cub tracks, cub sightings) first-time mothers in both study areas.

ANCOVA for cub litter size (Table 3) showed that the area effect (Kananaskis vs SMGBE) was significant ($P = 0.01$) but that age of mother had no effect on litter size ($P = 0.939$).

4.7. Indices of diet quality

Twenty-seven body masses in total and 18 first-capture body masses were obtained from 18 males during 1980–1984 in Kananaskis. Twenty one masses in total and 13 first-capture masses were obtained from 13 males during 1985–1990 in the SMGBE. Mean body mass at first capture was greater ($P < 0.01$, $t = 4.12$, $df = 29$) in Kananaskis (153.7 kg, $n = 18$, $SD = 29.1$) than in the SMGBE (100.0 kg, $n = 13$, $SD = 43.5$). Mean age at first capture did not differ ($P = 0.37$, $t = 0.90$, $df = 29$) between Kananaskis (7.3 years, $n = 18$, $SD = 4.32$) and the SMGBE (5.9 years, $n = 13$, $SD = 4.40$). Mean Julian date at first capture was 190 days ($n = 18$, $SD = 30.7$) in

Table 3

Analysis of covariance (ANCOVA)^a for cub litter size in Kananaskis and the Selkirk Mountains Grizzly Bear Ecosystem

Source	SS	df	MS	F	P
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		

$n = 15$, $r^2 = 0.43$

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

Kananaskis and 180 days ($n = 13$, $SD = 28.5$) in the SMGBE. Mean date at first capture was not significantly different ($P = 0.37$, $t = 0.90$, $df = 29$).

ANCOVA for body mass of males showed that the area effect was significant ($P < 0.001$, Table 4). Male bears were heavier in Kananaskis controlling for the effects of age and date. Differences in body mass at age were most pronounced for younger males (<10.5 years). Maximum mass 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 (Fig. 1).

Mean body mass of 2 subadult females were significantly greater in Kananaskis than 5 subadults in the SMGBE (90.5 vs 66.6 kg, $t = 2.08$, 4.4 df, $P = 0.10$) despite younger ages of subadults in Kananaskis (Kananaskis = 2.5, 2.5 years; SMGBE = 2.5, 2.5, 2.5, 5.5, 5.5 years). Differences in mass at age were apparent for subadult (<6.5 years) females (Fig. 2). Body mass appeared to asymptote at about 100 kg for both populations but females reached that mass at about 3.5–5.5

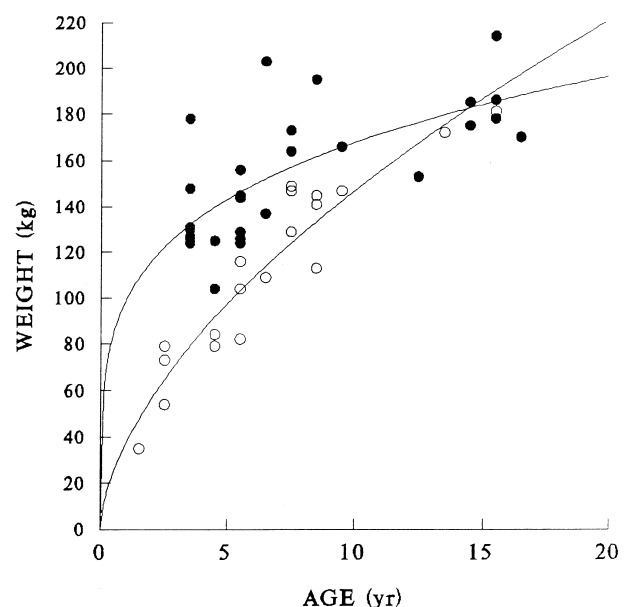


Fig. 1. Non-linear least squares regression for weight (kg) and age (years) of male grizzly bears in Kananaskis (●) and the SMGBE (○).

Table 4

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

Source	SS	df	MS	F	P
Area	1.07	1	1.07	30.16	<0.001
Log(age)	2.07	1	2.07	58.42	<0.001
Date	0.10	1	0.10	3.06	0.09
Error	0.96	27	0.03		

$n = 31$, $r^2 = 0.81$

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

years in Kananaskis and 5.5–7.5 years in the SMGBE. Those ages correspond to mean age at first breeding and parturition.

5. Discussion

5.1. Mortality and numbers of males

Our results indicate that mortality rate and age of killed males was higher in Kananaskis. Our results also indicate that numbers of new younger males increased after removal of adult males in Kananaskis. The increased numbers of younger males was not likely due to increased trapping effort or varying trap locations because number of trap-nights and trap locations remained the same throughout the study.

Nor were the increased captures of males likely due to increased trapping effectiveness over time (year effect), higher numbers of bears to begin with (area effect), or

higher catchability of males (sex effect), otherwise the main effects log-linear model should have fit the data, and it did not. The increased number of males was not likely due to higher catchability of males over time, otherwise the sex*year interaction would have been significant. The increased numbers of younger males also did not appear to be due to reproduction by resident females in previous years. That would not explain the area*year effect or why these males were captured in 1982–1983 but not in 1980–1981 when all males would have been independent (≥ 2.5 years old) from their mothers and presumably easy to catch.

Another reason why reproduction by resident females is unlikely to account for these males is that this would have required reproductive rates that are unheard of in grizzly bears. Three of the resident females were not old enough at the time to have produced any of these males. It seems most unlikely that the remaining 2 females could have produced five 3.5 year-old, two 5.5 year-old, one 6.5 year-old, and one 7.5 year-old male, in addition to 2 known 4.5 year-old female offspring consecutively from 1977 to 1981. That would require an annual reproductive rate of 2.2 cubs/year to account for these males. A reproductive rate of 2.2 cubs/year is 3–5 times higher than those observed in the Selkirks and Kananaskis and has never been documented for grizzly bears (IGBC, 1987).

The increased numbers of males was best explained by the combined area*year (more captures in latter years in Kananaskis) and area*sex (more captures of males in Kananaskis) effects model. The simplest and most logical explanation for these effects is increased immigration after 1982. Blanchard and Knight (1991) found that 2.5–5.5 year-old males are the most likely age-sex class to emigrate/immigrate. A number of other researchers also found that weaned males are highly unlikely to remain in the natal area and almost always emigrate (IGBC, 1987). Weaned females are much less likely to emigrate far from the natal range. The sex and age of the new captures is consistent with that group of animals that typically immigrate into new areas. The fact that males ≥ 3.5 years old were observed copulating (Wielgus, unpubl data) suggests that these males were sexually mature, hence even more likely to disperse out of their natal ranges and immigrate (Blanchard and Knight, 1991). The removal of resident adult males could have facilitated new males settling into this area (Kemp, 1976; Young and Ruff, 1982; LeCount, 1987; Swenson et al., 1997, in press).

5.2. Reproduction

Our results indicate that mean litter size was larger in the SMGBE than in Kananaskis (2.2 vs 1.4). We are confident in our test results despite the small sample sizes because small n will result in increased type 2 not

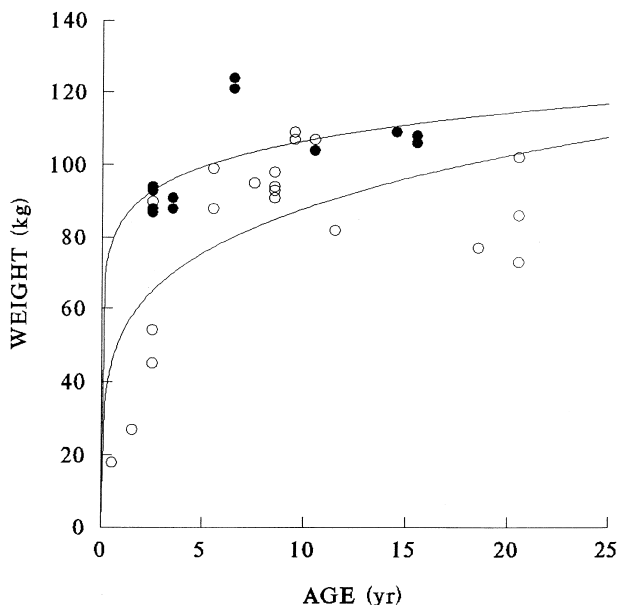


Fig. 2. Non-linear least squares regression for weight (kg) and age (years) of female grizzly bears in Kananaskis (●) and the SMGBE (○).

type 1 errors (Sokal and Rohlf, 1981). The small samples may also raise the question of whether or not the statistical difference in litter size was due to sampling bias. The lower power of small sample tests are because of higher potential bias so bias is accounted for (Taylor and Gerrodette, 1993). We also monitored reproduction for 4 of 8 estimated adult females in Kananaskis and the Bow Crow (Wielgus and Bunnell, 1994a) and 10 of 20 estimated females in the SMGBE (US Fish and Wildlife Service, 1990). Those samples comprise very large proportions of the populations (50%).

Our results are inconsistent with the hypothesis that age of mothers accounted for the difference in litter sizes. Age of mothers did not differ between the 2 populations and age of mother had no effect on litter size. There were no differences in adult female survival between populations so lower survival of females did not account for the smaller litters in Kananaskis.

The most parsimonious explanation for the higher body mass of males and subadult females is greater diet quality in Kananaskis (Hildebrand et al., in press). That is also consistent with the earlier age at first parturition for females in Kananaskis. Diet quality (as indexed by body mass and age at first reproduction) appeared superior in Kananaskis yet mean litter size was smaller there so we reject the hypothesis that overall diet quality accounts for the difference in litter size. Short term changes in food supply (e.g. berry crop failures) did not appear to account for differences in reproduction since no berry crop failures were evident in Kananaskis during the period of study. Furthermore, any such failures should probably have been reflected in weight of males, weight of subadult females, and age at maturity for subadult females.

5.3. *Competing hypotheses*

Results are inconsistent with the “no effect” hypothesis because litter sizes were smaller in Kananaskis despite apparently superior diet quality there and similar population densities. Results are also inconsistent with the “increased reproduction” hypothesis because higher mortality of older adult males in Kananaskis did not result in lower numbers of males and larger litter sizes for females. Our results are consistent with the “decreased reproduction” hypothesis because higher mortality of older adult males in Kananaskis coincided with increased numbers of younger, potentially infanticidal males and smaller litter sizes for females.

5.4. *Possible effects of trophy hunting*

The opening of the grizzly bear hunting season resulted in deaths of older resident males and apparent increased immigration by younger, but sexually mature males in Kananaskis (Wielgus and Bunnell, 1995). No

evidence of such immigration was observed in the SMGBE (Wielgus and Bunnell, 1995) where mortality was lower and restricted to younger animals. Older males may limit immigration of younger males (Bunnell and Tait, 1981; Rogers, 1987) so their removal may result in increased immigrants. Previous research on black and grizzly bears (Kemp, 1976; Young and Ruff, 1982; LeCount, 1987; Swenson et al., 1997, in press) has shown a probable increase following removal of adult males.

Sexually mature females avoided potentially infanticidal immigrant males and male-favored habitats in Kananaskis but subadult females did not (Wielgus and Bunnell, 1995). Those results also support and corroborate the findings presented here. The apparent contradiction of smaller litter size and earlier age at first parturition in Kananaskis can be reconciled by that habitat segregation. Subadult females, subadult males, and adult males all concentrated in food-rich habitats in Kananaskis. That may have allowed subadult females to gain weight rapidly and produce cubs at an early age. Sexually mature adult females rarely used those food-rich habitats. They restricted most of their activities to high elevation, food-poor habitats where immigrant males were rare and food supply was likely inferior, and that could account for their small litters. One of the 2-cub litters (Table 2) was produced by an adult female using the food-rich habitat (Wielgus and Bunnell, 1995), but she produced that litter prior to the opening of the hunting season and the corresponding influx of immigrant males — the same female produced a 1-cub litter after avoiding the food-rich habitat when immigrant males increased.

No such sex and age habitat segregation was observed in food-rich habitat in the SMGBE where there appeared to be no immigrant males (Wielgus and Bunnell, 1995). All sex and age classes, including adult females, selected for the food-rich habitats (Wielgus and Bunnell, 1995). That could account for the larger litters in the SMGBE.

McCullough (1981) and Stringham (1983) also documented an apparent inverse relationship between reproductive success and number of adult male bears. They suggested that adult males depress reproduction directly by infanticide or indirectly by denying females access to superior food sources; the second appears to be the case in Kananaskis. Our results suggest, however, that adult females avoid potentially infanticidal immigrants or nonsire males (e.g. Kananaskis), but not resident sires (e.g. Selkirks). Therefore, it may not be the number of males per se that determine female reproductive success, but rather the number of non-sire males.

Our results suggest that the female counter-strategy to infanticide (habitat segregation, Wielgus and Bunnell, 1995) may have a strong effect on litter size, reproductive rate, and population growth. The small litter sizes observed in Kananaskis were directly responsible for an

estimated population decline (Finite rate of growth = 0.99, Wielgus and Bunnell, 1994a). That suggests that trophy hunting of adult males may have contributed to, and perhaps even caused this population to decrease. Swenson et al. (1997, in press) found that brown bear cub survival decreased from 0.98 in a population with low adult male mortality to 0.72 in a population with high adult male mortality, consistent with sexually selected infanticide. Finite population growth rates appeared to be reduced by 0.034 because of adult male mortality in that study area (Swenson et al., 1997). LeCount (1987) found that 50% of black bear cub mortality was due to intraspecific killing. He also suggested that the high cub mortality in his study area was due to large numbers of immigrant males because of high mortality of resident adult males. We did not observe intraspecific killing or lower survival of cubs in Kananaskis but it may have occurred prior to our observations (e.g. in April–May). However, we did observe sexual habitat segregation consistent with a counter-strategy to infanticide, and that did appear to reduce litter size and reproductive success.

The most parsimonious explanation for the smaller litters yet earlier age at first reproduction in Kananaskis was the sexual segregation observed there. Adult females avoided immigrant males and their food rich habitats but subadults did not (Wielgus and Bunnell, 1994b, 1995). Confounding factors such as age of mothers, survival of adult females, indices of diet quality, and population density did not account for the smaller litter sizes. We have no basis for supposing that other potential confounding factors such as congenital defects, disease, parasites, or ingestion of unknown toxic substances accounted for simultaneous smaller litters and earlier age at first reproduction. However, because causation cannot be demonstrated here we urge other researchers to replicate studies of this type to increase experimental sample size (Hurlbert, 1984; Sinclair, 1991) and provide a stronger basis for judging the effects of hunting adult males.

Our acceptance of the decreased reproduction hypothesis is not unequivocal because of limited experimental replication (e.g. LeCount, 1987; Swenson et al., 1997, in press; this paper). Nonetheless, these studies do suggest that the commonly accepted hypothesis that increased reproduction derives from trophy hunting could contribute to further declines in some grizzly bear populations. We believe that wildlife managers should be cautious when dealing with small populations of vulnerable and threatened grizzly bears on the edge of the species' range. This research needs to be replicated to determine if our findings are also applicable to other species that show potential for sexually motivated infanticide (Packer and Pusey, 1984) such as African lions (*Panthera leo*), black bears, cougars (*Felis concolor*), and tigers (*P. tigris*).

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