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SEXUAL SEGREGATION AND FEMALE GRIZZLY BEAR AVOIDANCE OF MALES

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Abstract: We examined seasonal use of habitat for 14 male and 5 female grizzly bears (*Ursus arctos*) in southwestern Alberta, 1981–84, to test 2 competing hypotheses regarding segregation of the sexes. The male avoidance hypothesis predicts increasing differences in use of habitat with increasing male use of female-occupied areas because of female avoidance of males. The no avoidance hypothesis predicts decreasing differences in use of habitat with increasing male use of female-occupied areas because of increasing similarity of available habitat. Differences in use of habitat were greatest during late summer, when many males concentrated in the female-occupied area, and they were less during other seasons when few males were in the female-occupied area. Three of 4 habitat variables differed ($P \leq 0.10$) between the sexes during late summer, whereas 2, 1, and 2 variables differed during spring, early summer, and autumn, respectively. Grizzly bear females segregated from males and data support the hypothesis that females avoid males. If females avoid males and male-occupied habitats, reproduction could decline because of nutritional deprivation and survival could decline because of their increased use of human-occupied areas.

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Key words: Alberta, grizzly bear, habitat, sexual segregation, *Ursus arctos*.

Grizzly bears have disappeared from most of their historic range, largely by incremental population and habitat losses at the contracting edges of the species' range (Servheen 1990). In Al-

berta, there were an estimated 780 grizzly bears in 1990, and numbers were declining (Servheen 1990). Nagy and Gunson (1990) estimated 62 grizzly bears in southwestern Alberta, the edge of the species' range. In this study, we radio-monitored 19 of 38 bears in a declining population of Kananaskis Park and Bow Crow Forest, southwestern Alberta (Wielgus and Bunnell 1994). We must understand use of habitat and

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population dynamics in small peripheral populations to prevent further range contractions and eventual extinction of the grizzly bear. The sparse nature or small size of these populations, however, makes large samples impossible and impedes understanding of contracting populations.

Most studies of grizzly bear use of habitat have not examined seasonal differences between the sexes. The sexes often are not identified (Hamer and Herrero 1987a,b; Phillips 1987), are analyzed together (Blanchard 1983, Zager et al. 1983), or only one sex is studied (Hamilton and Bunnell 1987). Some researchers have examined family and single bear use of habitat (Atwell et al. 1980, Darling 1987) but did not discriminate between habitats used by females and those used by males. Only a few studies examined sex-specific seasonal use of habitat. Berns et al. (1980) found little difference between male and female use of habitat. Russell et al. (1979) found that females in Jasper National Park, Alberta, tended to use higher elevations more than did males, especially during spring. Nagy et al. (1983a) reported elevation differences in use of habitat between males and females in the Arctic Mountains but reported no sexual segregation in the Tuktoyaktuk Peninsula (Nagy et al. 1983b). Mattson et al. (1987) and MacLellan and Shackleton (1988) found that females used habitats nearer to roads more than did males. These findings indicate that sexual segregation may occur in some populations but not in others.

When sexual segregation has been observed in grizzly bears, it usually has been interpreted as female avoidance of aggressive or cannibalistic males (Russell et al. 1979, Nagy et al. 1983a, Mattson et al. 1987, McLellan and Shackleton 1988), but that inference has not been tested. This male-avoidance hypothesis predicts that sexual differences in use of habitat should increase with increasing male use of female-occupied areas; that is, females should shift their activity away from males when males move into their areas.

An alternative, no-avoidance hypothesis is that differences in use of habitat result from seasonal differences in habitat availability or diet. For example, males may have different habitats available to them because of their larger home ranges (LeFranc et al. 1987). In this case, differences in use of habitat should decrease with increasing male use of female-occupied areas because of increasing similarity of available

habitat. Differences in use of habitat also may result from females with offspring having reduced mobility and hence reduced access to various habitats. In this case, differences should be greatest early in the year when cubs are most sedentary. Finally, differences in use of habitat may result from sexual differences in dietary preference. In this case, differences should decrease as similarity in diet increases.

We use data collected during a study of grizzly bear use of habitat, movements, and food habits (Wielgus 1986) to determine if sexual segregation occurred and to evaluate consequences predicted by the male-avoidance and no-avoidance hypotheses of such segregation. The biological and behavioral reasons for female avoidance of males were addressed elsewhere (Wielgus 1993, Wielgus and Bunnell 1994).

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STUDY AREA

The study area covered 6,286 km² in Kananaskis Provincial Park and Bow Crow Forest, southwestern Alberta (50–51°N, 115–116°W). Elevation ranged from 1,300 to 2,700 m in mountainous terrain. Climate was continental with long, cold winters and short, cool summers. Vegetation was in the subalpine fir-Engelmann spruce (*Abies lasiocarpa*-*Picea engelmannii*) forest region (Rowe 1972). Forests comprised lodgepole pine (*Pinus contorta*), Engelmann spruce, and subalpine fir. Details of the study

area are given in Wielgus (1986) and Wielgus and Bunnell (1994).

Sport hunting of grizzly bears was closed in the study area from 1970 to 1981 but was reopened from 1982 to 1987. The study population showed high mortality of older adult males and a corresponding high immigration of younger males after 1981 (Wielgus and Bunnell 1994). The small population appeared to be declining from 1981 to 1984 (Wielgus and Bunnell 1994) and was designated as vulnerable by the Committee on the Status of Endangered Wildlife in Canada.

METHODS

Trapping

We trapped grizzly bears from 1980 to 1984 using Aldrich leg snares and immobilized them with ketamine HCl and xylazine HCl in a 1:1 ratio at a dosage of 6.5–10.0 mg/kg body mass. We weighed, eartagged, and aged bears by extracting a premolar (Stoneburg and Jonkel 1966). We then fitted them with activity-sensing radio collars. We trapped and radiocollared bears in the 254-km² Highwood trapping zone, which covered a 50-year-old burn in the mountains (1,800 m elevation) and was dominated by soapberry (*Shepherdia canadensis*) shrubfields. Surrounding areas were unburned and appeared to have comparatively little berry production (Wielgus 1986, 1993).

Seasonal Habitat Use

We monitored radioed bears (14 M, 5 F) from fixed-wing aircraft once every 1–2 weeks during the nonbreeding period (15 Apr–1 Dec), 1981–84. We estimated bear locations from the aircraft (Whitehouse and Steven 1977) and marked them on 1:50,000 topographic maps. We estimated radiolocation accuracy by noting signal strength when bears were sighted, then used signal strength for determining nonvisual locations. We visually confirmed 81 of 451 locations (18%). We only used locations judged to be accurate within 1 ha and within 1 habitat type (451 of 526 locations, 86%) in habitat analyses. The ratio of radiolocation error (1 ha) to mean forest stand size for a representative map-sheet (28.4 ha, SE = 7.8 ha, $n = 335$) was low, indicating little potential for error (White and Garrot 1986). Only 5% of forest stands had areas ≤ 1 ha. A self-developing photograph was taken and marked to indicate bear location within the

vegetational mosaic. We later transferred locations from topographic maps and photos to corresponding forest habitat maps.

Habitat variables for each location were forest type and age, elevation, aspect, and slope. We assumed those variables to be related to grizzly bear food and cover requirements (McCrory and Herrero 1981, 1983a,b; Zager et al. 1983; Holcroft and Herrero 1984), and they were already mapped and used for forest management. Habitat variables and criteria for designating them were determined in advance by the Alberta Forest Service. Prior to analysis, we reduced the number of forest types to facilitate statistical testing by combining similar classes into broader types on the basis of type and openness of vegetation. Our forest types were alpine (grassy meadows, alpine tundra, barren soil, rock), shrubfield (avalanche chutes, burns, clear-cuts, brushfields), pine-dominated forests (*Pinus* spp.), and spruce-dominated forests (*Picea* spp.). We recorded elevation, aspect, and slope from topographic maps.

We defined seasons by changes in plant phenology and corresponding shift in food habits as determined by scat analyses (Wielgus 1986). We identified 4 seasons: spring (15 Apr–11 Jul, pre-berry season), early summer (12 Jul–15 Aug, onset of berry season), late summer (16 Aug–17 Sep, peak of berry season), and autumn (18 Sep–1 Dec, end of berry season).

Data Analysis

We tested for sexual differences in seasonal use of habitat by comparing seasonal counts of male and female locations using the Chi-square test of homogeneity (Daniel 1978, Wilkinson et al. 1992). We pooled radiolocations of bears into male and female sex classes and across years (1981–84) into seasons, in a modified type-2 design (Thomas and Taylor 1990). Pooling of data allowed adequate sample sizes for tests of seasonal habitat segregation (Roscoe and Byars 1971), assuming no effect of years.

We ensured that our pooled sex-seasonal datasets were not biased toward individual bears or reproductive classes by balancing our radiotelemetry effort across individuals and classes. Data were not biased toward particular individuals because each bear contributed an approximately equal number of locations (Wielgus 1986). Pooled data were representative of individual bears and years because annual use of habitat did not vary among individual bears or

Table 1. Percent use and Chi-square tests (5 df) for homogeneity of forest age types used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84.

Forest type (age in yr)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
Alpine	17	29	15	12	16	21	10	25
Shrubfield	5	14	10	19	10	23	3	14
Pine (5–50)	22	27	36	42	51	41	18	39
Pine (>50)	31	14	21	15	12	7	33	4
Spruce (5–50)	5	2	4	6	0	4	4	0
Spruce (>50)	20	14	14	6	11	4	32	18
<i>n</i> locations	64	63	51	53	61	43	67	49
<i>n</i> bears	11	5	14	5	14	5	12	5
χ^2	10.87		4.37		8.65		28.81	
<i>P</i>	0.05		0.49		0.12		<0.01	

years, except between subadult and adult females (Wielgus 1993). We assumed data to be independent because all bears traveled alone and radiolocations were obtained at weekly or biweekly intervals (Swihart and Slade 1985). Analyses of annual, not seasonal, use of habitat by individual bears by year were treated elsewhere (Wielgus 1993).

We used log-linear models (Feinberg 1980, Wilkinson et al. 1992) to test if male locations for a given season were obtained during some years and female locations for the same season were obtained during other years. Any such findings would constitute a sex by season by year interaction and would invalidate our test of female seasonal avoidance of males. This analysis comprised 2 sexes, 4 years, and 4 seasons, for a total of 32 cells. Sample sizes and expected values were adequate (<20% of cells with expected values <5) for testing (Wilkinson et al. 1992).

We tested hypotheses of sexual segregation by determining seasonal numbers of individual male bears and percentage of male locations within the female 97.5% multi-annual, composite range of 868 km² (Ackerman et al. 1990). The female composite range was centered on the Highwood trapping zone. Most bears using that zone were believed to be captured and collared (Wielgus and Bunnell 1994). If differences ($P \leq 0.10$) between the sexes occurred for use of habitat variables during late summer, when many males concentrated in the female-occupied area, we interpreted that as support for the male-avoidance hypothesis. If differences were not significant ($P > 0.10$), or if differences were less during the late summer, we interpreted that as support for the no-avoidance hypothesis.

RESULTS

Structure of Pooled Data

Mean number of locations/bear/season was 10.4 (SE = 0.8, $n = 20$) for females and 4.7 (SE = 0.4, $n = 51$) for males (Table 1). Male bears had fewer locations than did females because they suffered higher mortality (Wielgus and Bunnell 1994). Data were not biased toward particular age classes. Single adults (>5.5 yr, $n = 4$) contributed 35%, adults with offspring ($n = 4$) 42%, and subadults (2.5–5.5 yr, $n = 2$) 23% to the female radiolocation data. Adults (>5.5 yr, $n = 7$) contributed 46% and subadults (2.5–5.5 yr, $n = 9$) 54% to male location data.

Sample size or number of locations per cell in the log-linear model varied with sex, year, season, and 2 of their interactions. The most parsimonious log-linear model that fit our data was sex + season + year + sex by year + season by year ($\chi^2 = 13.23$, 12 df, $P = 0.35$). The sex main effect reflected differences between the sexes (M had 54% of locations, F had 46%). The year main effect reflected differences among years. Most data were obtained from 1982 to 1984 (6% of locations were in 1981, 29% in 1982, 48% in 1983, and 17% in 1984). One female was monitored in 1981, 4 in 1982, 5 in 1983, and 5 in 1984. There were 3 males in 1981, 6 in 1982, 10 in 1983, and 5 in 1984. The season main effect was included to account for the seasonal term of a significant year by season interaction. Percents of locations among seasons were similar (28% in spring, 23% in early summer, 23% in late summer, and 26% in autumn). The sex by year interaction reflected occurrence of proportionately more male locations in 1981 and more female locations in 1984. Percents of total

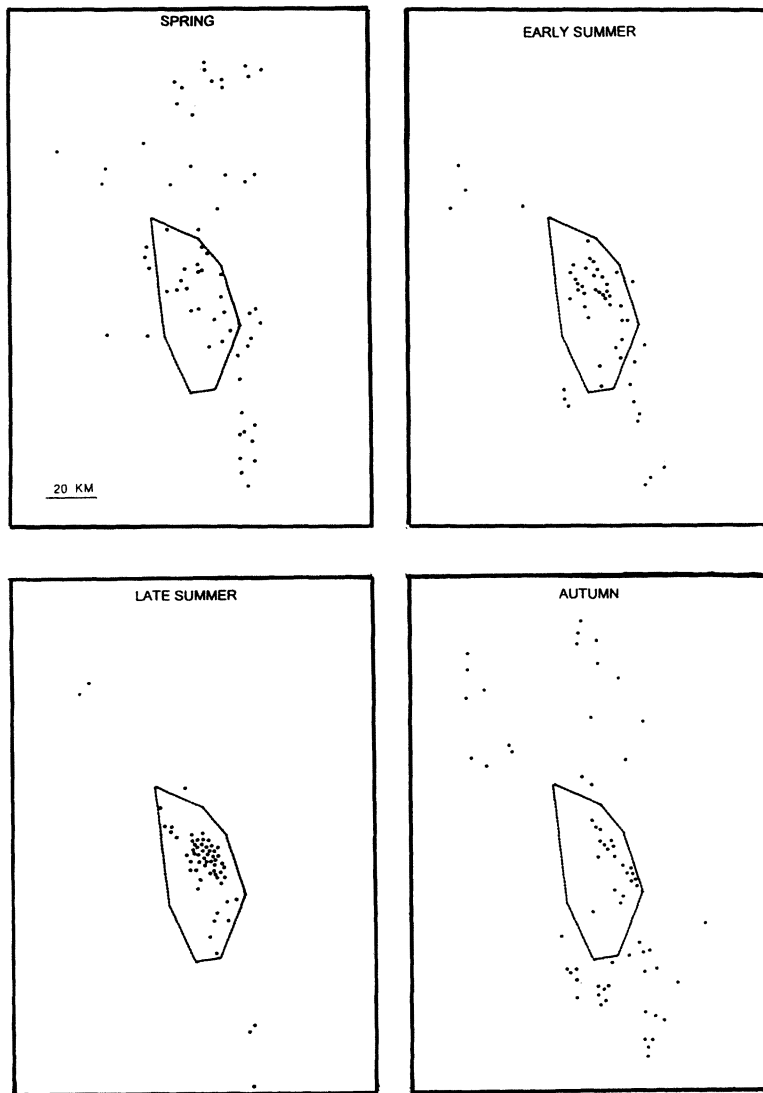


Fig. 1. Seasonal (spring = 15 Apr–11 Jul, early summer = 12 Jul–15 Aug, late summer = 16 Aug–17 Sep, autumn = 18 Sep–1 Dec) distribution of male grizzly bear radiolocations (dots) in relation to 97.5% multi-annual composite home range of female grizzly bears (polygon) in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84.

female locations distributed across years were 3, 27, 43, and 27% for 1981–84, respectively. Percents of total male locations distributed across years were 9, 30, 53, and 8% for 1981–84, respectively. The year by season interaction reflected scarcity of locations in spring and early summer 1981 and autumn 1984, because monitoring began in 1981 and ended in 1984.

Adding more interactions (e.g., sex by season or sex by season by year) to the model did not improve fit of the data ($\chi^2 = 1.1$, 3 df, $P > 0.10$). Therefore, seasonal data were not biased by the

uneven distribution of the sexes' locations among years.

Seasonal Segregation

Data on use of habitat (Tables 1–4) were presented as percentages rather than counts to facilitate comparisons (Hellgren et al. 1991, Wilkinson et al. 1992). During spring, overlap between males and females was low (Fig. 1). We observed 8 male bears and 20 of 64 male locations (31%) in the female composite range.

Table 2. Percent use and Chi-square tests (4 df) for homogeneity of elevation zones used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Elevation (m)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
<1,680	22	5	13	10	7	0	28	2
1,680–1,830	25	22	22	25	36	16	18	22
1,831–1,980	22	33	41	36	32	45	32	27
1,981–2,130	22	21	17	14	20	25	15	25
>2,130	9	19	7	15	5	14	7	24
χ^2	10.68		2.89		10.01		18.85	
P	0.03		0.57		0.04		<0.01	

Use of habitat differed between the sexes for forest age (Table 1) and elevation (Table 2).

In early summer, males began to converge on the female range (Fig. 1). We observed 9 males and 34 of 51 male locations (67%) in the female composite range. Use of aspect differed (Table 3) between the sexes.

During the late summer berry season, geographical overlap between sexes was most pronounced (Fig. 1), when we observed 11 male bears and 55 of 61 male locations (90%) in the female range. Sexual differences for use of habitat variables were greatest during late summer despite concentration of males and females in the same area. Three of 4 habitat variables differed: elevation, aspect, and slope. Location of females shifted to higher elevations (Table 2), different aspects (Table 3), and steeper slopes (Table 4) when males moved into the female area.

During autumn, overlap between the sexes declined as males moved out of the female range (Fig. 1). We observed 8 males and 20 of 67 male

locations (30%) in the female range. Use of 2 variables differed: forest age (Table 1) and elevation (Table 2).

DISCUSSION

Our results show differences between seasonal male and female use of habitat, so we reject the hypothesis that male and female bears used the same habitats. We are confident in our test results despite small sample size, because small sample sizes decrease statistical power, making rejection of null hypotheses more difficult (Allredge and Ratti 1986). Although large samples are desirable they cannot always be obtained, especially when studying small populations (Wielgus and Bunnell 1994).

Sexual differences in grizzly bear use of habitat were greatest during the late summer berry season when the most spatial overlap between the sexes occurred. Sexual difference in diet was unlikely to account for habitat segregation in late summer because of hyperphagia (Nelson et al. 1983) by both sexes on soapberries (McCrory

Table 3. Percent use and Chi-square tests of homogeneity (8 df) for aspects used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Aspect	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
Flat	17	11	19	30	18	11	16	8
Northwest	14	10	2	6	1	16	6	12
North	9	3	15	9	10	5	10	10
Northeast	0	10	9	6	15	7	25	16
East	17	22	26	4	13	14	17	23
Southeast	9	6	4	9	7	9	7	4
South	9	12	9	9	5	9	5	2
Southwest	6	10	5	4	13	2	3	10
West	19	16	11	23	18	27	11	15
χ^2	10.79		16.34		14.95		8.21	
P	0.21		0.03		0.06		0.41	

Table 4. Percent use and Chi-square tests of homogeneity (3 df) for slope categories used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Slope (°)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
≤10	56	44	52	55	56	34	48	35
11–20	19	19	24	17	15	30	29	41
21–30	23	27	19	25	28	21	21	22
>30	2	10	5	3	1	15	2	2
χ ²	4.68		1.14		13.30		2.74	
P	0.19		0.76		<0.01		0.43	

and Herrero 1983*a,b*; Wielgus 1986; Hamer and Herrero 1987*a,b*). Low cub mobility was unlikely to account for habitat segregation in late summer because cubs are mobile relative to earlier seasons. These results lead us to reject the no-avoidance hypothesis and accept the male-avoidance hypothesis of habitat segregation.

Males converged on the female composite range in late summer and concentrated in burned-over, young (5–50 yr) pine forests at low to mid-elevations (1,680–2,130 m), on northeasterly aspects, and on shallow (≤10°) slopes. These sites contained the best soapberry patches in our study area (McCrary and Herrero 1981, 1983*a,b*; Hamer and Herrero 1987*a,b*). Females also concentrated in young pine forests and shrubfields during the early summer onset of berry season, but they shifted to higher, drier, steeper, and apparently poorer sites (McCrary and Herrero 1981, 1983*a,b*; Hamer and Herrero 1987*a,b*) when males arrived in late summer. We feel it is unlikely that females would select for poorer quality berry patches if males had not arrived.

Females also may have avoided old forests in spring and autumn because of the likelihood of encountering male bears there (Table 1). Wielgus (1986) suggested that males may have used those forests for predation and consumption of elk (*Cervus elaphus*) calves during the spring calving season and elk bulls during the autumn rut and hunting season.

Hornocker (1962), Egbert and Stokes (1976), McCullough (1981), and Stringham (1983) hypothesized that female bears and other subdominants avoid adult males because males compete with, behave aggressively toward, and even kill subdominants for food. Stringham (1980), Wielgus (1986), and LeCount (1987) hypothesized that adult females, especially females with offspring, avoid non-sire, immigrant males because

those males may kill cubs to induce estrus and gain a breeding opportunity (Hrdy and Hausfater 1984). The only tests of those hypotheses were conducted by Wielgus (1993), and results supported the latter hypothesis. Hunting of older adult males resulted in an influx of younger immigrant males (Wielgus and Bunnell 1994) and subsequent female avoidance of those males.

MANAGEMENT IMPLICATIONS

If female grizzly bears use food-poor habitats to avoid males, identification and protection of only food-rich habitats (Mace and Bissell 1986, McCrary et al. 1986) could leave essential habitats for females unidentified and unprotected. That could result in dangerous conflicts between humans and female bears if humans venture unaware into such unidentified female-occupied areas (Herrero 1985). Avoidance of food-rich, male-occupied habitats by females also could slow or stop population growth because of increased female mortality or reduced female reproduction. For example, Mattson et al. (1987) suggested that females avoided males by using habitats close to roads and this led to increased deaths of female grizzly bears by humans. In small populations, the loss of even a few females can cause population declines (Bunnell and Tait 1981, Eberhardt 1990). Wielgus (1993) found that females avoided food-rich habitats occupied by immigrant males and that female reproduction suffered, contributing to population decline. We recommend that other researchers replicate our tests and examine these phenomena to see if results are applicable elsewhere.

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