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

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Abstract: Spatial requirements of grizzly bears (*Ursus arctos horribilis*) in Montana are poorly understood, yet habitat management is based on attributes of female home ranges. We evaluated home range size, overlap, and spatial/temporal use of overlap zones (OZ) of grizzly bears inhabiting the Swan Mountains of Montana. Annual home ranges of adult males were larger ($\bar{x}$ = 768 km²), and adult female ranges smaller ($\bar{x}$ = 125 km²), than those of subadults. Overlap in annual home ranges of adjacent female grizzly bears averaged 24% (37 km²), varied from 0 to 94%, and was less when one or both females had young. Female home range overlap was greatest when one of both members of a pair were subadults. Male home range overlap with females averaged 19% for adult males and 30% for subadult males. Most simultaneous use of the OZ occurred during summer. We investigated both spatial and temporal interaction of grizzly bears having overlapping home ranges. Thirty-seven of 49 (76%) adjacent female pairs showed symmetrical and random spatial use of the OZ indicating lack of territoriality. In one of 49 (2%) cases, simultaneous use of the OZ exceeded solitary use. Temporal use of the OZ was random in 44 of 49 (90%) female interactions. Avoidance behavior within the OZ of home ranges was indicated for 1 of 2 pairs of sisters following dispersal from their mother. Most male/female pairs exhibited symmetrical and random use of the OZ. In 12 of 21 (57%) cases where the female home range was enclosed within a male range, the male exhibited spatial attraction to the female range. There was no evidence of spatial avoidance of the OZ for male pairs. Habitat availability in different portions of overlapping home ranges helped explain the observed patterns of spatial and temporal interaction among grizzly bears. The overlap zone of home ranges had higher proportional availability of avalanche chutes, rock/forb lands, and slabrock than home range areas outside the OZ. These home range and behavioral characteristics occurred at a female-dominated population density of 2–3 solitary grizzly bears/100 km².

J. WILDL. MANAGE. 61(1):39–52

Key words: barriers, behavior, grizzly bear, habitat, home range, overlap, Northern Continental Divide Ecosystem, Montana, spatial, temporal, territoriality, *Ursus arctos horribilis*.

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

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

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

We evaluated spatial characteristics of male and female grizzly bear annual home ranges, evaluated both spatial and temporal patterns of overlap at the home range scale of selection,

and characterized habitat attributes associated with those overlapping ranges.

We thank K. E. Aune, D. Hoerner, T. L. Manley, and field personnel who helped capture and radiotrack grizzly bears. We thank Flathead National Forest for hosting our studies. Research was funded by the U.S. Department of Agriculture Forest Service, the U.S. Department of Agriculture Intermountain Research Station, the National Fish and Wildlife Foundation, Montana Department of Fish, Wildlife and Parks, and the U.S. Department of Interior Fish and Wildlife Service.

STUDY AREA

The study area, located in the Swan Mountain Range of western Montana, extended from the northern terminus of the Swan Mountains on the north to the Bob Marshall Wilderness boundary on the south (Fig. 1). The 1,457 km² area was bounded on the east by Hungry Horse Reservoir and on the west by the edge of contiguous forest cover in the Flathead River and Swan River valleys. Grizzly bears are not tolerated by humans beyond much of this western boundary because of its agricultural and suburban nature. The area was administered by the U.S. Department of Agriculture Forest Service under a multiple-use management strategy, and had a history of hydroelectric development, roading, and timber harvest since the early 1950s.

The study area was characterized by heavily forested, rugged mountain topography; elevations varied from 914 to 2,736 m. More than 50% of the area was closed-canopy coniferous forest with the remainder broadly classified as rock lands, avalanche chutes, shrub lands, and timber harvest units. The area was under the influence of Pacific maritime weather patterns. Other characteristics of the study area and grizzly bear ecology were described by Manley et al. (1992), Mace et al. (1994), and Mace et al. (1997).

METHODS

Capture and Telemetry

We captured grizzly bears in leg-hold snares between 1987 and 1992 with a 3.2-km² capture grid, and fitted them with radiocollars (Mace et al. 1994). Bears were classified as belonging to one of 5 groups: adult (ad) male and solitary adult female (≥5 yr old), subadult (subad) male or female (<5 yr old), and adult females with attendant young (family). We located each bear once per week in 1988 and 1989 and twice each week from 1990 through 1992 from fixed-wing aircraft, weather permitting. Most flights occurred from 0600 to 1030 Mountain Standard Time. We photographed the location with a Polaroid camera and identified the location of each bear on the photograph before resuming the flight. We assigned Universal Transverse Mercator coordinates to each location from 1:24,000 orthophoto quadrangles. We evaluated telemetric error by placing radiocollars in the field and locating them from fixed-wing aircraft. The average error of 150 m was not large enough to significantly affect home range estimators.

Annual Home Range Size

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

Spatial and Temporal Interaction

We evaluated spatial and temporal patterns of home range interaction from 1990 to 1992

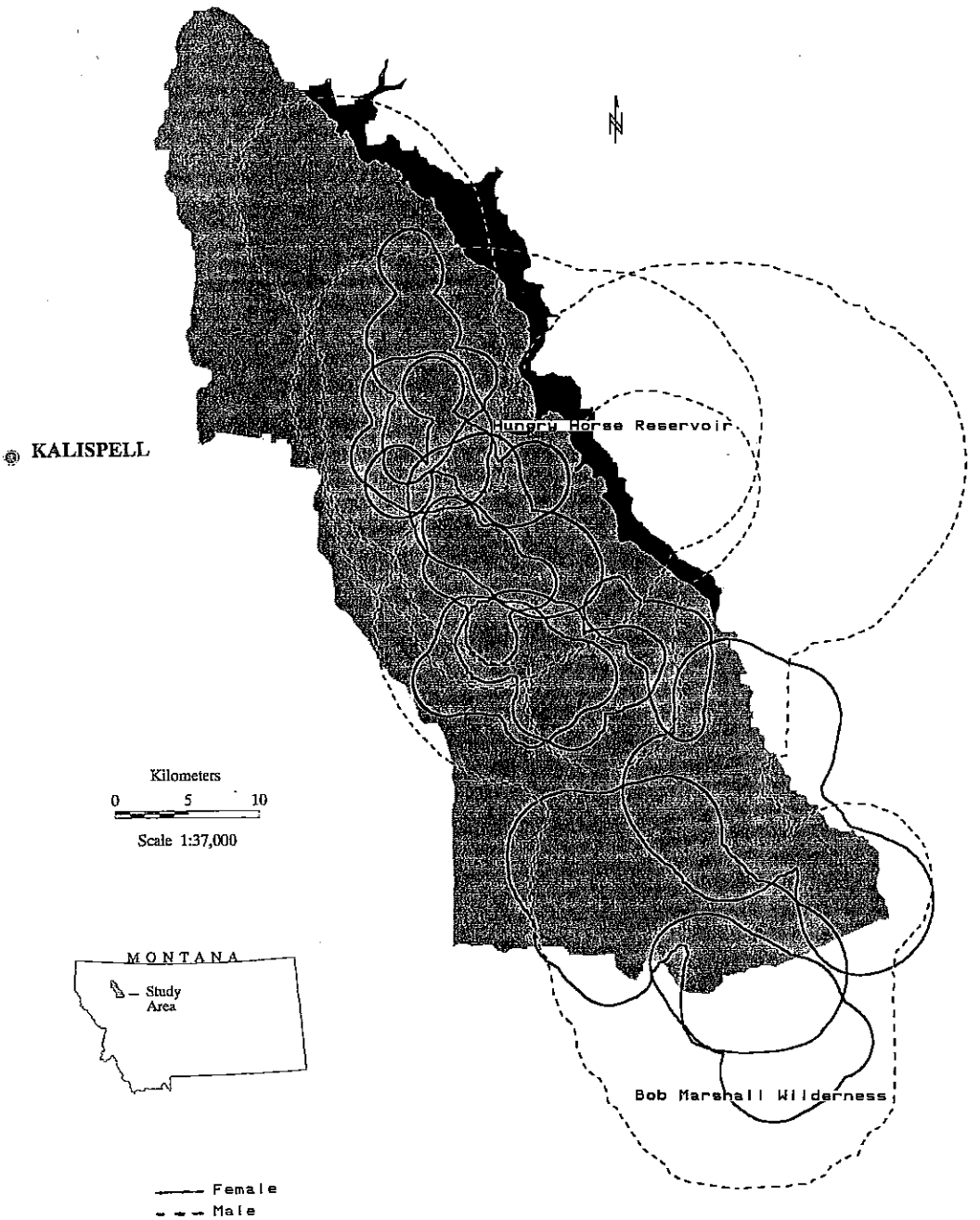

Fig. 1. The Swan Mountain study area in Montana showing 11 female and 3 male grizzly bear 95% annual home ranges during 1990. The shaded area is the primary study area where all bears were captured.

for each pair (α,β) of overlapping grizzly bears using 2 locations/week/bear. We included spatially adjacent yet nonoverlapping ($\leq$3 km) pairs in estimates of home range overlap. We used the 95% adaptive kernel isopleth to estimate annual home ranges and assessed the spatial and temporal interactions (Minta 1992) and simultaneous locations for each member of a pair. Minta's method reduces observations (telemetry locations) over space and time to a binomial distribution incorporating used and expected frequencies in different areas of a home range.

The technique replaces zero cells with pseudo-Bayes estimates that improves the stability of small-sample χ^2 inference from probability values. We defined simultaneous locations as those obtained within one hour of each other from fixed-wing aircraft. Locations were classified as occurring in one of 3 seasons: spring (den emergence–15 Jul), summer (16 Jul–15 Sep), or autumn (16 Sep-den entry).

We evaluated spatial and temporal interaction between pairs of grizzly bears using raster-based Geographical Information System computer program EPPL7 (Minn. Land Manage. Inf. Cent. 1991). Overlap of 2 home ranges could take 2 forms. The entire home range of β could be enclosed within the range of α (termed an enclosed pair), or the OZ could be only a portion of each bear's range (termed an overlapping pair). For each pair, 3 areas of the combined ranges were mapped: the home range area unique to α ($area_A$), that unique to β ($area_B$), and the OZ of α and β ($area_{AB}$). For pairs with an enclosed range, $area_{AB} = area_B$. Simultaneous locations were overlaid on the combined home range map to determine where the simultaneous locations occurred relative to the 3 areas. For overlapping ranges, 4 possibilities existed for each pair of simultaneous locations: both bears were in the OZ, α alone was in the OZ, β alone was in the OZ, or neither bear was in the OZ. For enclosed ranges we needed to determine only the number of times α occurred in $area_B$. Percent overlap in home ranges was calculated as $[(area_{AB}/home\ range_A) * (area_{AB}/home\ range_B)]^{0.5}$.

Each pair was classified as belonging to a group depending on the gender, age, and reproductive status of both α and β. When both individuals were female, 6 groups were delineated; pairs consisting of 2 solitary adults, solitary adult-subadult, solitary adult-family, subadult-family, 2 subadults, and 2 families. Six groups were delineated when pairs consisted of a male and a female: adult male-solitary adult female, subadult male-solitary adult female, adult male-subadult female, 2 subadults, adult male-family, and subadult male-family. The basic sampling unit for all analyses were these groups. Because of mortality and loss of functional radiocollars, it was not possible to ascertain changes in spatial and temporal interactions of each unique pair over the course of the study. Our first hypothesis concerned only the spatial interaction between α and β. For overlapping ranges, we tested whether α and β influenced each other's spatial use of the OZ. That is, from location data, did α and β use their respective areas as expected in relation to the size of the OZ? Spatial relation to the OZ by each individual was categorized as either random, attraction, or avoidance with Minta's (1992) coefficients of interaction ($L_{A:A}$ for α and $L_{B:B}$ for β). As coefficients approached zero, use of the OZ became random. Coefficients >0 suggested attraction, and coefficients <0 suggested spatial avoidance. Probabilities of these coefficients ($P_{A:A}$ and $P_{B:B}$) were also calculated with α set at 0.05. Spatial response by each pair was further classified as symmetrical (same response by the pair), asymmetrical (opposite response), or singular (only 1 individual showing a significant departure from random use). In cases where β's range was enclosed within α's range, we tested the hypothesis that α used the OZ in a nonrandom fashion. Minta (1992) considered symmetrical avoidance of α and β evidence of territoriality, or defense of an area.

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

We evaluated the habitat composition of $area_A$, $area_B$, and the OZ for each pair of grizzly bears. Proportional availability of 6 cover types within the 3 home range areas were determined with GIS and a classified LANDSAT Thematic Mapper image (Mace et al. 1997). Habitats were classified as: rock/forb land, shrub land, closed forest (>40% conifer overstory), avalanche chute, slabrock, or timber harvest units (cutting units). Proportional availability of cover types was normalized with the arcsine transformation (Sokal and Rohlf 1969), and ANOVA was used to investigate the effects of group, home range area, and the proportional availability of cover

Table 1. Annual home range size (km²) for grizzly bears in the Swan Mountains, Montana, 1988–92.

Age/gender class	No. individuals	No. ranges	$\bar{x}$	SE	Range
Ad F	10	29	125	12	46–272
Family	8	18	127	17	59–272
Solitary ad F	9	11	121	19	46–229
Ad M	8	15	768	73	420–1,114
Subad F	9	16	228	40	35–456
Subad M	4	7	379	118	47–799

types. Separate analyses were conducted for each cover type as not all cover types were available to all groups. We used Tukey's statistic for post hoc analyses when significant ANOVAs were obtained ($P < 0.05$).

RESULTS

Annual Home Range Size

We estimated 67 annual home ranges of 24 individual grizzly bears (Table 1), varying in size from 35 km² for a subadult female to 1,114 km² for an adult male. On average, adult males had the largest ranges ($\bar{x}$ = 768 km², n = 15) and solitary adult females the smallest ranges ($\bar{x}$ = 121 km², n = 11). No females were known to cross the 1–3 km wide Hungry Horse Reservoir to suitable habitat on the other side although males did (Fig. 1).

Our sample of subadult males included 2 annual ranges from one individual who was orphaned as a yearling. This individual's ranges were smaller ($\bar{x}$ = 47 km²) than other members of the cohort ($\bar{x}$ = 512 km², SE = 118, n = 5), and were excluded from further analyses.

The 4 groups were significantly different in home range size (H = 37.0, 5 df, $P < 0.01$). Solitary adult females differed from adult males ($z = -4.3$, $P = 0.00$), adult males differed from families ($z = -0.5$, $P < 0.01$), subadult females differed from subadult males ($z = -2.06$, $P = 0.03$) and families ($z = -2.07$, $P = 0.03$), and subadult males differed from families ($z = -2.30$, $P = 0.02$).

Spatial and Temporal Interaction Between Females

Extent of Home Range Overlap.—Annual home range overlap of 49 overlapping and 4 adjacent pairs of female grizzly bears were evaluated. Females were well distributed throughout the study area (Fig. 1). Percent overlap varied from 0 to 94% and averaged 24% (Table 2). The size of the OZ for all overlapping female pairs averaged 37 km² (n = 49, SE = 6.2, 95% CI = 25–50 km²).

Percent overlap was greatest ($\bar{x}$ = 30%, n = 11) for the solitary adult-subadult group, and the least ($\bar{x}$ = 10%, n = 10) for the family-solitary adult group (Table 2). Percent overlap varied by the 6 groups (H = 11.3, 5 df, P = 0.04). Percent overlap varied significantly between the solitary adult-subadult group and the family-solitary adult group ($z = -2.5$, $P = 0.01$), and between the family-subadult group ($z = -2.6$, $P = 0.00$).

Table 2. Spatial interactions of adjacent and overlapping female grizzly bears. Swan Mountains, Montana, 1990–92. (No. in parentheses indicates column percentages.)

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

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

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

Spatial/Temporal Interaction of Females.—Forty-nine of 53 pairs of female grizzly bears exhibited some spatial overlap. There were no enclosed ranges for female pairs. When pooled, 76, 22, and 2% of the pairs, respectively, exhibited symmetrical, singular, and asymmetrical spatial responses to the OZ (Table 2). Thirty-five of 37 (95%) symmetrical responses were random. Eleven singular responses to the OZ were calculated (9 positive, 2 negative), and they exhibited greater percent overlap ($\bar{x}$ = 41, SE = 6, n = 11) than symmetrical groups ($\bar{x}$ = 22, SE = 4, n = 37) (H = 8.03,1 df, P = 0.00). Two of these singular and positive responses were adult female/daughter pairs. In all other singular and positive cases, the younger of the 2 individuals was positively attracted to the OZ.

Solitary female pairs were least symmetrical in their response to the OZ relative to other pair groups (Table 2). Rather, the spatial relation between solitary females was more singular (43%).

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

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

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

Spatial and Temporal Interaction Between Males

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

Spatial and Temporal Interaction Between Males and Females

Extent of Home Range Overlap.—The mean percent overlap in annual home range for all male/female pairs was 29% (n = 51, SE = 1.9). Subadult males exhibited significantly greater overlap with females than did adult males (H = 4.47, 2 df, P = 0.03; Table 3). For adult males, the amount of overlap did not vary by female group (H = 2.6, 2 df, P = 0.27). Similarly, no difference in percent overlap was observed for subadult male relative to female group (H = 4.2, 2 df, P = 0.12).

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

Patterns of spatial/temporal use of the OZ were evaluated for 24 adult male/female pairs: 13 were overlapping ranges and 11 were enclosed ranges. Ten of 13 adult male/female pairs exhibited symmetrical and random use (P > 0.05) of the OZ (Table 3). The remaining adult male/female pairs were singular, 2 were singular attraction by males to the OZ, and one was singular avoidance of the OZ by a family/adult male pair. Temporal use of the OZ was

Table 3. Spatial interactions of overlapping male and female grizzly bears. Swan Mountain, Montana, 1990–92. (No. in parentheses indicates column percentages).

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

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

random for 12 of 13 adult male/female pairs ($P_{\alpha n} > 0.05$), thus our second hypothesis concerning temporal interaction was not rejected.

The home ranges of 11 adult male/female pairs were enclosed. In 5 and 6 instances respectively, the adult male used the OZ (the entire female range) randomly, or was spatially attracted to the OZ (Table 4). No spatial avoidance of a female range was observed for adult males.

Ten of 17 subadult male/female pairs exhibited symmetrical and random spatial use of the OZ (Table 3). One subadult male (positive spatial interaction) and family (negative spatial interaction) pair were asymmetrical. The remain-

Table 4. Spatial interaction of male grizzly bears to enclosed home ranges of female grizzly bears. Swan Mountains, Montana, 1990–92.

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

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

Table 5. Simultaneous seasonal use of the OZ by pairs of male and female grizzly bears. Swan Mountains, Montana, 1990–92.

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

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

ing 6 pairs of subadult male/female were singular. Temporal use of the OZ was random for 16 of 17 subadult male/female pairs ($P_{txn} > 0.05$), thus our second hypothesis concerning temporal interaction was not rejected. Solitary temporal use was greater than simultaneous use in one instance ($P_{txn} < 0.05$).

The home range of 10 subadult male/female pairs was enclosed. In 4 and 6 instances respectively, the subadult male used the OZ (the entire female range) randomly, or was spatially attracted to the OZ (Table 4). No spatial avoidance of the female range was observed for subadult males.

Forty-two of 51 male/female pairs used the OZ simultaneously. Most overlap occurred during summer (Table 5). Simultaneous seasonal use of the OZ did not vary by male/female group ($P > 0.05$). When groups were pooled, the percent simultaneous use of the OZ differed by season ($H = 37.0$, 2 df, $P = 0.00$). Simultaneous use differed between spring and summer ($z = -4.91$, $P = 0.00$), and between summer and autumn ($z = -5.3$, $P = 0.00$).

Habitat Characteristics of Home Range Areas

Female Pairs.—The proportional availability of several cover types within combined home ranges varied by female groups. Significant differences were observed for shrub lands ($P = 0.04$) and avalanche chutes ($P = 0.00$; Table 6). Post hoc comparisons showed that the solitary adult-subadult group had more ($P = 0.01$) shrub lands ($\bar{x} = 14\%$) in their ranges than did the family-solitary adult group ($\bar{x} = 8\%$). The family-solitary adult group and 2-family group had significantly less ($P < 0.05$) proportional availability of avalanche chutes in their home ranges ($\bar{x} = 6$ and 7%, respectively) than did the solitary adult-subadult group ($\bar{x} = 13\%$). The family-solitary adult group had less proportional availability of avalanche chutes than did the 2-subadults group ($P = 0.02$). The unique portion of each pairs home range differed significantly for avalanche chutes ($P = 0.04$). There was a higher proportion of avalanche chutes within the OZ ($\bar{x} = 10\%$) relative to areas of the home ranges outside of the OZ ($\bar{x} = 8\%$).

We conducted ANOVA tests on the relations among the area of the home range, spatial pattern of interaction (symmetrical or singular), and proportional availability of each cover type. No significant interactions were observed ($P > 0.05$; Table 7).

Male/Female Pairs.—The shrub land, avalanche chute, and slabrock cover types differentiated male and female ranges. The propor-

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

We conducted ANOVA tests on the relations among the area of the home range, spatial pattern of interaction (symmetrical or singular), and proportional availability of each cover type. A significant interaction was observed for the shrub land type only ($P = 0.00$; Table 9). Pairs exhibiting a symmetrical interaction had more proportional shrub lands in the OZ than outside the OZ ($\bar{x}$ = 11 and 8%). Pairs exhibiting symmetrical interaction had more shrub land in the OZ than the unique portion of the home range for singular pairs ($\bar{x}$ = 7%).

DISCUSSION

Population size, demography, and habitat condition can influence home range size and extent of overlap (Sanderson 1966, Rogers 1977, Young and Ruff 1982). Home range size and overlap data for grizzly bears in the Swan Mountains were difficult to compare with those from other areas because of variable data collection methods and lack of a standard home range estimator (Interagency Grizzly Bear Comm. 1987). However, it is apparent from published literature that the size of grizzly bear home ranges varies in North America by region, age, gender, and reproductive status (Interagency Grizzly Bear Comm. 1987, Nagy and Haroldson 1989). Our results concur with other findings that the home ranges of males were larger than females, and that subadult ranges were larger than those of adult females (Interagency Grizzly Bear Comm. 1987). Even though we used a different home range estimator than did Blanchard and Knight (1991) for grizzly bears in the GYE, and Aune and Kasworm (unpubl. data) for the RMEF, the magnitude of differences suggests that they can be compared generally. Both male and female grizzly bears in the GYE occupied areas that were at least 5 times the

Table 6. Mean squares (MS), degrees of freedom (df), and probability levels (*P*) for cover type comparisons among overlapping female home ranges relative to group and area of overlapping range. Swan Mountains, Montana, 1990–92.

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

[a] Six female groups were evaluated: 2 ads, 2 subads, solitary ad-family, solitary ad-subad, 2 families, and subad-family.
[b] Two areas of the overlapping home range were considered: the unique portion of each individual's range, and the OZ.
[c] df error, MS error.

Table 7. Mean squares (MS), degrees of freedom (df), and probability levels (*P*) for cover type comparisons among overlapping female home ranges relative to spatial interaction and area of overlapping range. Swan Mountains, Montana, 1990–92.

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

[a] Symmetrical or singular spatial interaction.
[b] Two areas of the overlapping home range were considered: the unique portion of each individual's range, and the OZ.
[c] df error, MS error.

Table 8. Mean squares (MS), degrees of freedom (df), and probability levels (*P*) for cover type comparisons among male and female home ranges relative to group, and area of overlapping range. Swan Mountains, Montana, 1990–92.

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

[a] Six male-female groups were evaluated: 2 ads, 2 subads, ad M-subad F, subad M-ad F, ad M-family, and subad M-family.
[b] Two areas of the overlapping home range were considered: the unique portion of each individual's range, and the OZ.
[c] df error, MS error.

Table 9. Mean squares (MS), degrees of freedom (df), and probability levels (*P*) for cover type comparisons among male and female home ranges relative to spatial interaction and area of overlapping range. Swan Mountains, Montana, 1990–92.

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

[a] Symmetrical or singular spatial interaction.
[b] Two areas of the overlapping home range were considered: the unique portion of each individual's range, and the OZ.
[c] df error, MS error.

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

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

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

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

Interactions by sex could feasibly vary with demographic differences among local populations. For example, in local populations skewed

towards females, the probability of a female encountering a male would be low relative to a population dominated by males. Two recent publications by Wielgus and Bunnell (1995*a*,*b*) highlight the importance of scale and demography in interaction studies.

Wielgus and Bunnell (1995*a*) studied the seasonal habitat use of grizzly bears in Alberta, Canada and tested hypotheses regarding gender segregation. The population under study had a female:male ratio of about 1:3, which was nearly the opposite of our Swan Mountain population (4:1 ratio). The authors proposed that female avoidance of males would be manifested by increasing differences in habitat selection between sexes as male use increased in areas occupied by females. Using telemetry data, the authors compared use of habitat between sexes among seasons and not within seasons. Based on differences in specific use of habitat between the sexes in different seasons, the authors concluded that females avoided males due to the presence of immigrant males (Weilgus and Bunnell 1995*b*).

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

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

The importance of cover type availability in different portions of overlapping home ranges helped explain the patterns of spatial and temporal interaction among individual grizzly bears (Brown and Orians 1970). The OZ of all pairs had higher proportional availability of avalanche chutes than home range areas outside the OZ. Avalanche chutes are forage-rich areas during all seasons and provide both thermal and security cover. Although all individuals had avalanche chutes outside of OZs, forage quality varied widely for this cover type (Mace and Bissell 1986). Areas where numerous bears overlapped were often distinguished by numerous and productive avalanche chutes. These findings lend further evidence that this cover type is a vital and shared component of grizzly bear habitat throughout the year in the Swan Mountains. Mace et al. (1997) found that the generally negative response of grizzly bears to roads was lessened for bears using avalanche chutes. For female pairs, the rock/forb land cover type was more prevalent in the OZ than in the individual portion of the home range. Rock/forb lands are also food-rich areas, and were used by females while foraging and for digging underground roots and bulbs.

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

Our study design to assess spatial and temporal interaction was conducted over 3 years. The design would have been improved if the same focal individuals were maintained longer. If this had been possible, we would have treated the individual bear as the basic analysis unit. Unfortunately mortality, loss of functional collars, and budgets required that we pool data within cohorts. Interpretation of our results was also hampered for other reasons. We did not know the lineage of all individual bears in the study area. For example, the relation between a 22-year-old adult female and 4 overlapping

younger females was unknown. Likewise, we could not confirm the birthplace or mother of any of the males. We recommend that future studies of this type incorporate genetic testing for lineage (Craighead et al. 1995).

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

MANAGEMENT IMPLICATIONS

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

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Received 11 September 1995.
Accepted 11 September 1996.
Associate Editor: Murphy.