

INTERACTIONS OF SYMPATRIC BLACK AND GRIZZLY BEARS IN NORTHWEST WYOMING

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Abstract: As the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem (GYE) moves toward recovery, it will expand into more areas occupied by black bears (*U. americanus*). Interactions between the species may affect resident black bear populations and also influence the ease with which grizzly bears recolonize. We monitored movement and activity patterns of 17 radiocollared grizzly bears and 13 radiocollared black bears on a 450 km² area in northwest Wyoming during June–October in 1995 and 1996 and tested hypotheses predicting similarity in dispersion, activity, and habitat use patterns of sympatric black and grizzly bears. The larger home ranges of grizzly bears overlapped a number of black bear home ranges, yet core use areas were less likely to overlap. Adult male grizzly bears used open habitats more than expected ($P \leq 0.05$), whereas black bears selected against them and used forested habitats more than expected ($P \leq 0.05$). Patterns of black bear habitat use were more similar to those of adult female and sub-adult grizzly bears than adult male grizzly bears. Male grizzly bears were nocturnal, female grizzly bears were generally crepuscular, and black bears were diurnal. Differences in distribution, habitat use, and activity patterns suggested sufficient separation to reduce interactions between black bears and adult male grizzly bears. However, similarities between black bear and female and sub-adult grizzly bear patterns suggest that interactions between the species will become more common as adult female grizzly bears become established.

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Key words: activity, black bear, distribution, grizzly bear, habitat, interaction, *Ursus americanus*, *Ursus arctos*, Wyoming

Historically, substantial overlap occurred in geographic ranges of black and grizzly bears in western North America (Herrero 1972). Behavioral and physiological differences apparently allowed grizzly bears to exploit more open habitats, while black bears were restricted primarily to forests in areas of sympatry (Herrero 1978).

The grizzly bear was listed as threatened in the lower 48 states in 1975 due to decreasing numbers. Grizzly bear recovery efforts emphasized growth and expansion of the species with little consideration of how expanding grizzly bear populations might affect resident black bear populations or what effect black bears might have on grizzly bear recovery.

Many black bear studies have been conducted in areas devoid of grizzly bears (Lindzey and Meslow 1977, Quigley 1982, Young and Beecham 1986, Powell 1987, Braden 1991, Grogan 1997). Although grizzly bear research often has been conducted in areas where black bears were present, studies generally focused on the grizzly bear (Servheen 1983, Blanchard and Knight 1991, Craighead et al. 1995, Mace and Waller 1997). Comparisons of black and grizzly bear ecology, based on results of single-species studies, were limited to identifying areas of potential niche overlap between species. The studies that concurrently examined ecological characteristics of black and grizzly bears documented areas of niche overlap and identified behaviors that could result in ecological separation and promote coexistence (Shaffer 1971,

Lloyd and Fleck 1977, Kasworm and Manley 1988, Aune 1994).

Jonkel (1984) noted that coexistence of black and grizzly bears suggested niche separation between the species. Coexistence between similar species can be facilitated by spatial separation within an area of geographic sympatry, utilization of different habitats, temporal dissimilarities, and use of different food resources. We tested hypotheses predicting similarity in dispersion, activity patterns, and habitat use patterns of sympatric black and grizzly bears to identify behaviors that could facilitate coexistence.

STUDY AREA

The Blackrock study area in northwestern Wyoming (Fig. 1) encompassed about 450 km² of mountainous topography with elevations ranging from 2,070–3,360 m. Lower elevations were dominated by lodgepole pine (*Pinus contorta*) stands intermixed with stands of Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*). Sub-alpine fir (*Abies lasiocarpa*) and Engelman spruce (*Picea engelmannii*) stands were infrequent at lower elevations. Higher elevations were dominated by stands of sub-alpine fir, Engelman spruce, and lodgepole pine, intermixed with smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), and aspen. Both low- and high-elevation timber stands

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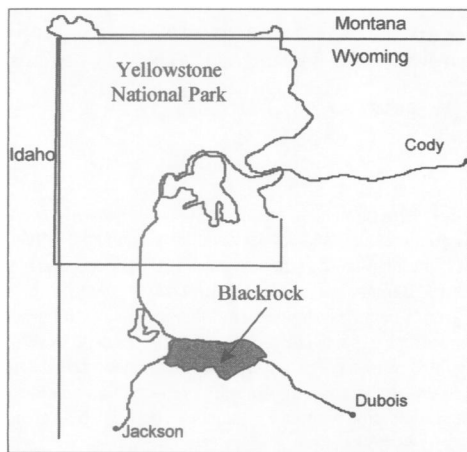


Fig. 1. Location of Blackrock study area in northwest Wyoming.

were typically interspersed with big sagebrush (*Artemisia tridentata*) and open grass-forb meadows. Riparian zones throughout the area were dominated by willow (*Salix* spp.). Precipitation averaged 14 cm from June–September, 1995–96, and mean annual temperature was 2°C, with a range of -12°C to 16°C (Cooper 1975, Anderson et al. 1997).

The Blackrock study area was in the Buffalo–Spread Creek bear management unit of the Yellowstone Grizzly Bear Recovery Zone. Most land (85%) within the study area was administered by the U.S. Forest Service and managed for multiple uses including cattle grazing, timber harvesting, and outdoor recreational activities. Approximately 15% of the study area was administered by the National Park Service and was within Grand Teton National Park. Less than 1% of the study area was comprised of homesites on private land. Grizzly bear management designations were primarily management situation 1 (MS-1, 47%) and MS-2 (39%) (Anderson et al. 1997). Black bear hunting occurred on Blackrock during spring and fall.

METHODS

Bear Capture and Handling

We used Aldrich (Margo Supplies Limited, Calgary, Alberta, Canada) foot snares and culvert traps and began trapping at lower elevations in June 1995 and 1996 and progressed to higher elevations as snow melted. We immobilized captured bears with a combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Aveco Company Incorporated, Cherry Hill, New Jersey, USA) delivered via air pistol (Palmer Chemi-

cal and Equipment, Douglasville, Georgia, USA). We fitted immobilized bears >1 year old with a time delayed motion-sensitive radiotransmitter collar (Telonics Incorporated, Mesa, Arizona, USA) fastened with a cotton spacer. We uniquely marked all bears and extracted the first premolar for age determination by cementum annuli counts (Willey 1974). We assessed reproductive status of females and took morphometric measurements and blood samples from all bears. We classified black and grizzly bears as sub-adults until ≥ 4 and ≥ 5 years old, respectively.

We defined periods of high and low grizzly bear presence in Blackrock for habitat use, spatial distribution, and activity pattern analyses. The low grizzly bear period was June and July when a minimum of 2 marked grizzly bears were within the study area. The high grizzly bear period was August and September when a minimum of 8 marked grizzly bears were within the study area.

Telemetry Locations

We located bears from fixed-wing aircraft at 3–6 day intervals and from the ground at 12–48 hour intervals from time of capture or arrival on the study area (May–August) until mid-October. We assigned collared bears relocation schedules to assure that each was located throughout the diel period. We collected ground locations only within or immediately adjacent to Blackrock, but collected aerial locations further outside the boundaries of Blackrock. We collected ground locations with permanently fixed and mobile (truck mounted) null-peak antenna systems and hand-held “H” antennas from stations established along roads. We used portable computers loaded with the program Locate II v. 1.3 (Pacer, Truro, Nova Scotia, Canada) to translate bearings into UTM coordinates and provide error estimates. Bearings >1 hr apart were not used to determine locations. We tested aerial locations, null-peak antennas, and hand-held antennas for error following guidelines of White and Garrott (1990).

Spatial Distribution Analyses

We defined home ranges and core areas by 95% and 50% utilization distributions (UD), respectively, and generated them from combined aerial and ground locations with Ranges V (Natural Environment Research Council, Wareham, United Kingdom). We used the adaptive kernel method to determine ranges with contours modeled on the fix density, a smoothing parameter of 0.7, and a 40 x 40 (100m resolution) grid cell size (Worton 1989). We used only locations ≥ 48 hours apart to ensure independence (Swihart and Slade 1985) and attempted

to standardize the time between locations of individuals to further reduce potential biases (White and Garrott 1990). We compared range size with a 2-sample *t*-test at $\alpha = 0.05$.

We tested range center spacing with nearest-neighbor analysis (Ranges V; Clarke and Evans 1954). The ratio of the observed mean distance between range centers to the expected mean distance served as the measure of departure from randomness (*R*). Under conditions of maximum aggregation, $R = 0$; in a random distribution, $R = 1$; and under conditions of maximum spacing, $R = 2.15$. We used Student's *t* to test whether centers were more regularly spaced than a random distribution. We made both intra- and interspecific comparisons for both years.

We determined home ranges and core area overlap using values that indicated the percent of an individual bear's range covered by other bears ranges (Ranges V). Percent overlap was analyzed intra- and interspecifically and was limited to bears with $\geq 10\%$ overlap, which allowed us to disregard ranges with slight edge overlap while maintaining sample sizes and accounting for interspecific differences in the magnitude of range sizes.

Each grizzly bear had a unique period of occupation of Blackrock, which we subsequently compared to black bear ranges during the same period. We then compared the number of black bear ranges overlapped during joint occupation of Blackrock to the number of black and grizzly bear annual ranges with overlap to examine changes in black bear movement patterns due to grizzly bears. Home range and core area overlap was tested using a 2-sample *t*-test at $\alpha = 0.05$.

We compared intra- and interspecific distances between each same-time location and all possible distances between same-time locations of each black and grizzly bear with Jacob's index (Jacobs 1974) to detect attraction or avoidance. Jacob's index is centered at zero, thus a value rising toward 1 indicated attraction, while a value falling toward -1 indicated avoidance. We defined same-time locations as those occurring within a 2-hour window, and we analyzed only black bears that had ranges $\geq 10\%$ overlapped by grizzlies during each grizzly bear's period of occupation at Blackrock.

Activity Monitoring

We determined activity level (active, inactive) by monitoring signal and pulse rate characteristics of each bear's radiotransmitter collar (Lindzey and Meslow 1977, Garshelis and Pelton 1980) for one 3-minute period within each hour of the day. In 1995, we recorded activity once per hour during four 6-hour blocks (comprising the 24-hour period) within a 5-day period. In 1996 we recorded activity level once per hour during a continu-

ous 24-hour period once every 7–10 days. We scanned radiocollar frequencies from permanent towers in a random fashion within each 5 or 7–10 day period. We also determined the level of activity for each bear when it was located during ground-based telemetry. We compared activity patterns of black and grizzly bears for the entire field season and during the period of low and high grizzly bear presence. We included only bears with ≥ 50 activity bouts in analyses.

Habitat Analyses

Four U.S. Forest Service ARC-INFO vegetation coverages were combined to form a vegetation map for the study area. Because the ARC-INFO coverages had different classification schemes, and most bear home ranges overlapped more than 1, we combined habitat definitions from each coverage into 6 habitat types (non-forested, lodgepole, spruce–fir, aspen, Douglas-fir, cut) based on the classification scheme of the least well defined coverage. One coverage had been completely ground verified and 2 were partially ground verified. We estimated available habitat on the study area by calculating the mean proportion of the 6 habitat types included within 2 composite ranges (95% utilization distribution; UD) constructed using all bear locations from each year. We defined available habitat for each bear as the proportion of habitat types found within the boundaries of the annual home range or core area. We used ARC-INFO v. 6.0 (Environmental Systems Research Institute, Redlands, California) for habitat use analyses.

We identified habitat use patterns of individual bears and compared the 2 species at study area and home range scales by calculating selection ratios from use-availability data (Manley et al. 1993). We determined habitat use within the study area by comparing each bears' home range and core area habitat composition to available habitat on the study area. We examined use within home ranges by determining the percent of each habitat type included within a 400-m diameter circle (12 ha) centered over each location and comparing to home range habitat composition. A 12-ha circle was chosen to account for telemetry error and to address the observation that animals choose their location on the basis of more than immediate landscape features (White and Garrott 1990). Additionally, testing indicated that a 12-ha circle was an appropriate resolution to show habitat use patterns when they existed and did not simply reflect available habitat, thereby masking selection patterns. We did not use locations < 24 hours apart in analyses to address independence (Swihart and Slade 1985), and we included only data from bears with ≥ 25 locations to provide valid range estimates (Holm 1998).

We assigned selection ratios 90% confidence intervals derived from the mean of the ratios. If the confidence interval was >1, we assigned vegetation types a positive selection code (+, higher proportion selected than available). If the confidence interval was <1, we assigned vegetation types a negative selection code (-, lower proportion selected than available). However, if the confidence interval contained 1, we assigned vegetation types a neutral selection code (0 = selected in proportion to availability). We generated habitat selection ratios and mean proportions of each habitat type within home ranges and core areas for all bears and within age–sex classes. We tested habitat selection between the species, age–sex classes, and different times, with χ^2 contingency tables. Additionally, we tested mean proportions of each habitat type with a *t*-test at $\alpha = 0.01$ (Bonferroni correction).

RESULTS

Bear Capture and Telemetry Error

The Wyoming Game and Fish Department (WGFD) captured 8 grizzly bears and 14 black bears on Blackrock in 1994 (Anderson et al. 1997). Two black bears and 6 of the 8 grizzly bears received radiocollars in 1994, but only 2 grizzly bear collars and both black bear collars remained functional in 1995. We captured and radiocollared 8 additional grizzly bears and 13 black bears between 20 May and 8 September 1995, resulting in a minimum of 10 grizzly bears and 15 black bears present on the study area in 1995. Based on 1994 WGFD trapping (Anderson et al. 1997), 1995 black bear harvest, and observations of sign, we estimated that an additional 8–10 black bears and 4 grizzly bears were present periodically on the study area during 1995.

We captured 5 grizzly bears and 2 black bears between 4 June and 3 August 1996. Bears captured in 1996, along with bears retaining radiocollars from 1995, resulted in a minimum of 9 radiocollared grizzly bears and 9 radiocollared black bears present on the study area during 1996. Trapping data, 1996 harvest data, and sign

suggested an additional 10–12 black bears and 3 grizzly bears used the study area periodically during 1996. Three female and 2 male black bears were harvested during the study and there was one documented grizzly bear death (no. 209) at Blackrock during the study.

The standard deviation of 23 aerial locations of stationary test radiocollars was 99.5 meters, resulting in a 95% confidence ellipse around locations of 12 ha. Standard deviation of bearing errors ranged from 2.8°–5.3° for permanent towers ($n = 29$) and was 3.6° and 7.2° for mobile towers ($n = 25$) and hand-held antennas ($n = 33$), respectively.

Spatial Distribution

Home Range and Core Area Size.—Black bear home ranges and core areas averaged 234 km² and 67 km², respectively. Home ranges and core areas of adult male black bears were numerically larger than those of the other age–sex classes, but small sample sizes likely precluded detecting statistical differences. Grizzly bear home range and core area size averaged 508 km² and 104 km², respectively. Home ranges and core areas of all grizzly bear age–sex classes occupied areas comparable in size. Grizzly bear home ranges and core areas were larger than those of black bears only in 1996 ($T = 2.50$, $P = 0.02$; core areas: $T = 2.20$, $P = 0.04$). Black bears generally had numerically smaller home ranges and core areas than similar sex–age class grizzly bears, but differences were not significant (Holm 1998).

Range Distribution.—Black bear home range centers were spaced farther apart than expected only during 1996 ($r = 1.38$; $T = 2.33$; $P \leq 0.05$). Although grizzly bear home range centers tended to be aggregated during both years ($r = 0.82$, 0.68), spacing was not significant. When home ranges of the 2 species were combined, they were aggregated only during 1996 ($r = 0.46$; $T = -2.95$; $P \leq 0.05$).

Home Range and Core Area Overlap.—Home range and core area overlap among black bears did not differ between years ($T = 0.88$, $P = 0.38$; core areas: $T = 0.86$, $P = 0.40$ Table 1). Additionally, although grizzly bear home ranges overlapped significantly more in 1995 than

Table 1. Mean percent of overlap of marked black and grizzly bear home ranges and core areas (with $\geq 10\%$ overlap) on the Blackrock study area, northwest Wyoming, 1995–96.

| Type of overlap | Home range | | | Core area | | |
|---|------------|------|----------|-----------|------|----------|
| | 1995 | 1996 | <i>P</i> | 1995 | 1996 | <i>P</i> |
| Intraspecific, black bears | 29.4 | 25.2 | 0.38 | 28.2 | 21.8 | 0.40 |
| Intraspecific, grizzly bears | 35.8 | 25.0 | 0.01 | 46.4 | 34.3 | 0.18 |
| Grizzly bears overlapped by black bears | 25.4 | 20.3 | 0.19 | 28.5 | 28.0 | 0.94 |
| Black bears overlapped by grizzly bears | 37.2 | 33.1 | 0.37 | 29.1 | 27.7 | 0.84 |

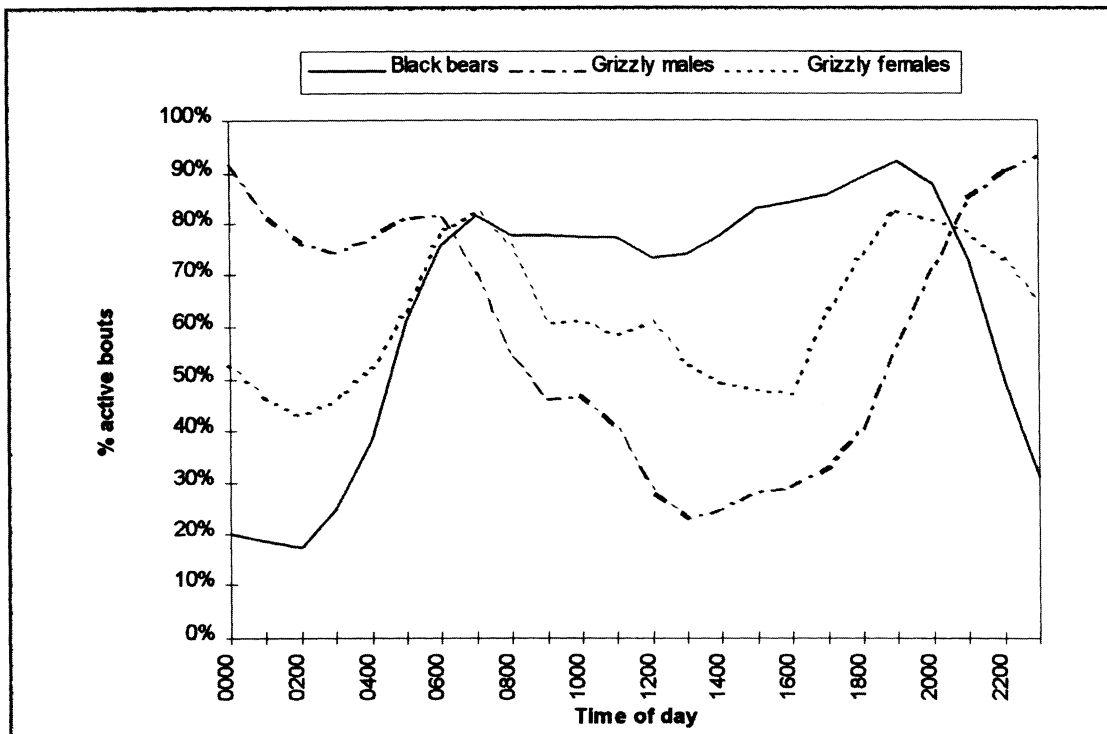


Fig. 2. Diel activity patterns of black and grizzly bears in northwest Wyoming, June–September, 1995–96.

1996 ($T = 2.52$, $P = 0.01$), core area overlap did not differ between years ($T = 1.34$, $P = 0.18$). Degree of overlap of grizzly and black bear home ranges and core areas was not different between years ($P > 0.05$). When years were combined, 33% fewer black bear home ranges were $\geq 10\%$ overlapped by grizzly bears during each grizzly bear's unique period of occupation of Blackrock. Core area overlap decreased by 35%, and the number of black bear core areas $\geq 10\%$ overlapped by grizzly bears was always lower than the number of home ranges overlapped ($P \leq 0.05$).

Same Time Locations.—Although positive index values, indicating attraction, were observed between species during both years, most values were quite low ($\bar{x} = 0.04$). The highest and lowest values were recorded for sub-adult female grizzly bears ($n = 2$, $\bar{x} = 0.11$) and sub-adult male black bears ($n = 5$, $\bar{x} = -0.02$), respectively. Although not significantly different from interspecific values, higher index values were reported among black bears ($\bar{x} = 0.11$) and among grizzly bears ($\bar{x} = 0.15$), suggesting stronger attraction within each species than between the species.

Diel Activity Patterns

We determined activity level during 3,399 ($n = 13$ bears) and 1,855 ($n = 14$ bears) activity bouts for black and grizzly bears, respectively. Activity patterns deter-

mined from permanent towers and ground locations during both years did not differ ($P > 0.05$) and were combined for analyses. Activity patterns within black bear age–sex classes did not differ ($P > 0.05$). However, male and female grizzly bears differed in activity patterns and were analyzed separately ($P \leq 0.05$).

Black bears ($n = 13$) were diurnal with activity peaks at 0700 and 1900 (Fig. 2). This pattern was not altered by the presence of grizzly bears. Male grizzly bears ($n = 10$) were nocturnal with activity peaks at midnight and 0600 and activity levels below 50% from 0800–1900. Female grizzly bears ($n = 4$) were crepuscular with activity peaks at 0700 and 1900. Females grizzlies were least active, and less active than males, from 0100–0300 ($P \leq 0.05$). Activity levels for both species were most similar during early morning (0600–0700).

Habitat Composition of Home Ranges and Core Areas

Comparison to Available Habitat.—Both species preferentially selected habitats ($P \leq 0.05$). Black bear home ranges and core areas contained less ($P \leq 0.10$) non-forested habitats and more ($P \leq 0.10$) lodgepole pine and spruce–fir than were available (Table 2). Grizzly bear home ranges contained more ($P \leq 0.10$) spruce–fir and less ($P \leq 0.10$) cut habitat than were available. Core

Table 2. Habitat selection patterns (mean proportion of habitat) of home ranges and core areas of black ($n = 13$) and grizzly bears ($n = 17$) compared to available habitat on the Blackrock study area, northwest Wyoming, 1995–96. Habitat was selected in either lower (-), equal (0), or higher (+) proportion than available ($P \leq 0.10$).

| Habitat | Black bear | | Grizzly bear | |
|--------------|------------|-----------|--------------|-----------|
| | Home range | Core area | Home range | Core area |
| Non-forested | - (0.31) | - (0.28) | 0 (0.36) | 0 (0.38) |
| Lodgepole | + (0.32) | + (0.34) | 0 (0.28) | 0 (0.27) |
| Spruce–fir | + (0.24) | + (0.25) | + (0.25) | + (0.27) |
| Douglas–fir | 0 (0.03) | 0 (0.04) | 0 (0.02) | - (0.01) |
| Aspen | 0 (0.03) | 0 (0.02) | 0 (0.02) | 0 (0.02) |
| Cut | 0 (0.06) | 0 (0.07) | - (0.05) | - (0.03) |

Table 3. Habitat selection patterns (mean proportion of habitat) within home ranges and core areas of black and grizzly bears by age–sex class in northwest Wyoming, 1995–96. Habitat was selected in lower (-), equal (0), or higher (+) proportion than available ($P \leq 0.10$).

| Habitat | Home range | | | Core area | | |
|---------------|------------|--------------|-----------|------------|--------------|-----------|
| | Adult male | Adult female | Sub-adult | Adult male | Adult female | Sub-adult |
| Black bears | $n = 6$ | $n = 2$ | $n = 5$ | $n = 6$ | $n = 2$ | $n = 5$ |
| Non-forested | - (0.29) | - (0.26) | 0 (0.38) | - (0.25) | 0 (0.25) | 0 (0.36) |
| Lodgepole | + (0.32) | + (0.38) | 0 (0.30) | + (0.36) | 0 (0.35) | 0 (0.30) |
| Spruce–fir | + (0.25) | 0 (0.22) | 0 (0.23) | 0 (0.25) | 0 (0.24) | 0 (0.25) |
| Douglas–fir | 0 (0.04) | 0 (0.03) | 0 (0.02) | 0 (0.04) | 0 (0.05) | 0 (0.01) |
| Aspen | 0 (0.03) | - (0.01) | 0 (0.03) | 0 (0.02) | - (0.01) | 0 (0.03) |
| Cut | 0 (0.06) | 0 (0.10) | 0 (0.04) | 0 (0.08) | 0 (0.10) | 0 (0.04) |
| Grizzly bears | $n = 6$ | $n = 3$ | $n = 7$ | $n = 6$ | $n = 3$ | $n = 7$ |
| Non-forested | 0 (0.38) | 0 (0.30) | 0 (0.36) | + (0.47) | 0 (0.29) | 0 (0.33) |
| Lodgepole | 0 (0.27) | 0 (0.29) | 0 (0.28) | 0 (0.25) | 0 (0.25) | 0 (0.30) |
| Spruce–fir | 0 (0.24) | 0 (0.27) | + (0.25) | 0 (0.21) | + (0.40) | + (0.29) |
| Douglas–fir | 0 (0.02) | 0 (0.04) | - (0.01) | 0 (0.02) | 0 (0.02) | - (0.01) |
| Aspen | 0 (0.02) | 0 (0.03) | 0 (0.02) | 0 (0.03) | - (0.01) | - (0.01) |
| Cut | - (0.05) | - (0.03) | 0 (0.07) | - (0.01) | - (0.01) | 0 (0.06) |

area habitat selection was similar to home range habitat selection patterns for both species.

Comparison between Species.—Both grizzly and black bears used habitats disproportionate to availability within their home ranges and core areas ($P < 0.001$). Black bears included less non-forested habitat ($P = 0.017$) and more lodgepole ($P = 0.008$) and cut habitat ($P = 0.013$) within core areas, and more lodgepole ($P = 0.013$) within home ranges than grizzly bears (Table 2). Spruce–fir, Douglas–fir, and aspen were used similarly ($P > 0.05$) between species.

Comparisons among Black Bear Age–Sex Classes.—Adult black bears had less ($P \leq 0.10$) non-forested habitat and more ($P \leq 0.10$) lodgepole within their home ranges than expected, but sub-adults used habitats in proportion to availability (Table 3). All age–sex classes used

non-forested, lodgepole, Douglas–fir, and cut habitat in similar proportions.

Comparisons among Grizzly Bear Age–Sex Classes.—Sub-adult grizzly bears included more ($P \leq 0.10$) spruce–fir and less ($P \leq 0.10$) Douglas–fir within home ranges, whereas adults selected against cut habitat ($P \leq 0.10$; Table 3). Habitat inclusion within core areas was generally similar to home range patterns, but adult males included more ($P \leq 0.10$) non-forested habitats in their core areas than expected.

Comparison between Species Age–Sex Classes.—Home ranges of adult male grizzly bears included more ($P = 0.016$) non-forested habitat than home ranges of adult male black bears. Adult black bears selected against non-forested habitat and for lodgepole habitat (Table 3).

Table 4. Habitat selection patterns (mean proportion of habitat) of black bears during low (June–July), and high (August–September) grizzly bear presence on the Blackrock study area, northwest Wyoming, 1995–96. Habitat was selected in lower (-), equal (0), or higher (+) proportion than available ($P \leq 0.10$).

| Habitat | Grizzly presence | |
|--------------|-----------------------|-----------------------|
| | Low | High |
| Non-forested | - (0.26) | - (0.22) |
| Lodgepole | 0 (0.30) | 0 (0.34) |
| Spruce fir | + (0.28) | + (0.31) |
| Douglas-fir | + (0.07) ^d | - (0.02) ^d |
| Aspen | 0 (0.04) | - (0.02) |
| Cut | 0 (0.06) ^d | 0 (0.09) ^d |

^a“d” denotes a significant difference between time periods within each habitat type.

Table 5. Habitat selection by black and grizzly bears when active and inactive on the Blackrock study area, northwest Wyoming, 1995–96. Habitat was selected in lower (-), equal (0), or higher (+) proportion than available ($P \leq 0.10$).

| Habitat | Black bears | | Grizzly bears | |
|--------------|------------------------|-------------------------|------------------------|--------------------------|
| | Active ($n = 13$) | Inactive ($n = 8$) | Active ($n = 17$) | Inactive ($n = 17$) |
| Non-forested | - | 0 | + | - |
| Lodgepole | + | - | - | 0 |
| Spruce fir | + | + | 0 | + |
| Douglas fir | 0 | 0 | - | - |
| Aspen | 0 | 0 | 0 | 0 |
| Cut | 0 | 0 | 0 | - |

Adult black bears included more ($P = 0.02$) cut habitat within their ranges than adult grizzly bears.

Habitat Use Within Home Ranges

Habitat Use within Black Bear Home Ranges.—We recorded ≥ 25 locations for 2 black bears in 1995 (1 adult male, 1 adult female) and 8 (6 adult male, 1 adult female, 1 sub-adult male) in 1996. Eight of 10 black bears used non-forested habitats in their ranges less ($P \leq 0.10$) than expected; 1 adult male used it in proportion to its availability and another selected it. Five of the 8 bears used spruce–fir habitats more ($P \leq 0.10$) than expected, and the other 3 used it in proportion to its availability. Aspen was either used in proportion to availability (4 bears) or used less ($P \leq 0.10$) than expected (4 bears).

Habitat Use within Grizzly Bear Home Ranges.—We recorded ≥ 25 locations for 2 grizzly bears (1 adult male, 1 adult female) in 1995 and 5 (1 adult male, 1 adult female, 2 sub-adult males, 1 sub-adult female) in 1996. One adult male and 1 adult female used non-forested

habitat more ($P \leq 0.10$) than expected. Both sub-adult male grizzly bears used non-forested habitat less ($P \leq 0.10$) than expected. Only female grizzly bears used the spruce–fir habitats more ($P \leq 0.10$) than expected. Grizzly bears either selected against Douglas–fir habitat (3 bears) or used it as expected (4 bears).

Habitat Selection of Black Bears during Low and High Grizzly Periods

Black bears selected ($P \leq 0.10$) Douglas–fir when grizzly bears were absent, but avoided it when they were present (Table 4). Black bears also avoided ($P \leq 0.10$) aspen when grizzly bears were present. In the presence of grizzly bears, the amount of non-forested habitat included in the home ranges of black bears decreased and the amount of lodgepole, spruce–fir, and cut habitat increased.

Habitat Selection during Diel Active and Inactive Periods

Habitat used by active versus inactive bears differed within and between species (Table 5). Active black bears selected ($P \leq 0.10$) lodgepole, but avoided ($P \leq 0.10$) it when inactive; they used spruce–fir more ($P \leq 0.10$) than expected during both periods. Active black bears used non-forested habitat less ($P \leq 0.10$) than expected, while active grizzly bears used it more than expected. Inactive grizzly bears used spruce–fir more than expected ($P \leq 0.10$).

DISCUSSION

Black bear home ranges at Blackrock were 2–3 times larger than reported in other areas with similar habitat characteristics (Mack 1988, Carriles 1990, Beecham and Rohlman 1994), which may reflect increased movements necessary to avoid more aggressive grizzly bears (Herrero 1978, Mattson et al. 1992). Mean home range size of grizzly bears on Blackrock was similar to those reported in other areas of the Greater Yellowstone Ecosystem (Knight et al. 1984, Reagan et al. 1994).

Dispersion of black and grizzly bear home ranges on the Blackrock study area indicated substantial spatial overlap of the 2 species. Dispersion patterns when grizzly bears occupied the study area suggested that black bears may have adjusted their movements to reduce contact with grizzly bears. However, black bears commonly shift activities within their ranges in response to seasonal food distribution (Pelchatt and Ruff 1986). Reduction in the number of black bear home ranges and core areas overlapped by grizzly bears during the high

grizzly bear period may have reflected distribution of seasonal food rather than an attempt by black bears to minimize contacts with grizzly bears. Although black bear home ranges tended to be overlapped less by other black bears home ranges than by those of grizzly bears, this was most likely a reflection of the magnitude of difference in range size between the species rather than increased avoidance by black bears.

Neither the spacing of home range centers or distances between same-time locations indicated strong avoidance of one species by the other. Although the centers of black bear home ranges were spaced farther apart than expected during both years, this pattern was likely a reflection of having a smaller portion of black bears radiocollared compared to the grizzly bear sample. Jacob's index values also indicated a slightly stronger attraction within each species than between species, indicating that black bears may have avoided grizzly bears to a greater degree than they avoided other black bears.

Activity patterns of black and grizzly bears differed. Black bears were principally diurnal and grizzly bears nocturnal. These patterns have been documented in other studies (Schleyer 1983, Garris and Pelton 1984). However, variation among individuals and between seasons allowed individuals of both species to appear largely crepuscular. Schleyer (1983) noted differing activity schedules contribute to the ecological separation of the species.

Black and grizzly bears included similar habitats within their home ranges, but the proportion of each habitat type included and degree of use of these habitats within the home ranges differed between the species. Black bears included more forested habitats within their home ranges, whereas grizzly bears selected for more open habitats, although variation between age–sex classes was noted. Grogan (1997) found that black bears in southeastern Wyoming avoided open habitats without cover, and Aune (1994) noted that black bears were strictly confined to the forested mountains of his Montana study area. Sub-adult black bears selected habitats in proportion to their availability, perhaps suggesting exclusion from preferred habitats by adult black and grizzly bears. In Montana, Waller and Mace (1997) indicated forested areas were among the least selected cover types by grizzly bears during all seasons, and Servheen (1983) reported lower than expected use of timber and timber–shrubfield habitat by grizzly bears. However, in the GYE grizzly bears used timbered habitats more than expected (Blanchard 1983, Reagan et al. 1994). Differences in grizzly bear habitat selection patterns likely reflect regional variation in food availability, individual bear preferences, and data collection methods.

Choice of habitat by active versus inactive bears served to further differentiate habitat use patterns between the species. Differences in habitat use were most pronounced at night, when male grizzly bears were active in open habitats and black bears rested in closed, forest habitats. Diurnal activity patterns of black bears may have evolved to avoid grizzly bears when sympatric. However, black bears are diurnal even in areas without grizzly bears (Beecham and Rohlman 1994) suggesting they probably were not utilizing resources at night before grizzly bears began to reoccupy Blackrock. Researchers have suggested that black bear visual acuity limits effective foraging time to the daylight hours, especially when feeding on vegetation (Bacon and Burghardt 1976).

Spatial, activity, and habitat-use patterns of black and grizzly bears on the Blackrock study area indicated sufficient ecological separation for the species to coexist at current numbers and age–sex composition. However, our sample sizes were low for many comparisons, and data were dominated by patterns of adult and sub-adult male grizzly bears and adult male black bears. Although we felt that a majority of the grizzly bears that used the Blackrock area were radiocollared, we did not feel that a representative sample of adult and sub-adult female black bears in the Blackrock area were radiocollared. Hence, inferences about black bear patterns should be viewed with caution. Additionally, variation was noted in habitat use patterns among individuals of both species, which may have masked patterns when sample size was low.

We believe grizzly bears were in the early- to mid-stage of re-establishment on the Blackrock area during our study. The Blackrock grizzly bear population was dominated by adult and sub-adult males, and although females were present, it was not until 1994–96 that we captured females with young. Also, grizzly bears were only seasonal residents on the study area until 1 denned there in 1996. If grizzly bears continue to recolonize the Blackrock area, lone females and females with young will likely increase in the population and more grizzly bears likely will remain in the area year-round. Black bears will have to share the area with grizzly bears in spring and early summer, when they had been almost exclusive occupants. Additionally, black bears will encounter more female grizzly bears, with whom they have greatest similarities in activity and habitat use patterns.

Our results were dominated by patterns of male grizzly bears, those bears typically first to pioneer new areas. Female grizzly bears (Weilgus and Bunnell 1994), and presumably black bears, choose behaviors that minimize interactions with male grizzly bears, so it is not surprising that their habitat-use and activity patterns would tend

to converge. Activity and habitat-use patterns of black bears and female grizzly bears were more similar to one another than either were to male grizzly bears on the Blackrock area. Given the more aggressive nature of grizzly bears and generally greater size within sex–age groups, as more female grizzly bears colonize the area, they likely will restrict black bear distribution further through interference competition (McLellan 1993). Nonetheless, the increase in the number of female grizzly bears on the Blackrock area may be retarded by the presence of a larger black bear population utilizing similar resources.

While we expect black bear numbers to decrease in the Blackrock area with establishment of the grizzly bear, we do not expect them to be totally excluded. As Jonkel (1984) noted, forested habitats and the presence of humans tend to favor black bears. Although grizzly bears are currently protected under the Endangered Species Act (16 U.S.C. 1531–1544), human-caused deaths and management removals occur annually (Interagency Grizzly Bear Committee 1995), which likely will limit grizzly numbers, especially outside of and on the edge of the Yellowstone Grizzly Bear Recovery Zone.

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