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Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic

Abstract Using resource selection functions, we examined habitat selection patterns of barren-ground grizzly bears (*Ursus arctos*) in the central Canadian Arctic among and within home ranges. There was no difference between the sexes with regard to habitat selection patterns at the home range level (Wilks' λ, approx. $F_{11,11}=1.27$, $P=0.37$). Bear home ranges contain more esker habitat, tussock/hummock successional tundra, lichen veneer, birch seep, and tall shrub riparian areas relative to the proportional availability of habitats in the study area. We observed differences in habitat selection within home ranges among levels of sex/reproductive status (Wilks' λ, approx. $F_{20,412}=3.32$, $P<0.001$) and by season (Wilks' λ, approx. $F_{30,605}=2.71$, $P<0.001$). Eskers and tall shrub riparian zones were the habitats most preferred by bears throughout the year. Tussock/hummock successional tundra was also favored by males at varying times during the year and lichen veneers were favored in spring and autumn by most bears. Females with cubs tended to avoid the highest ranked habitat for males throughout the year. This pattern of habitat selection was not observed for females without accompanying young. Results of this study underline the importance of scale dependence in habitat selection. Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of habitat selection patterns.

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Introduction

The selection of habitats by animals can be viewed as a multi-level, hierarchical process (Johnson 1980; Senft et al. 1987). An organism first selects a home range in which to live and then makes subsequent decisions about the use of different habitats in which to forage and foods to eat (Johnson 1980). Patterns of habitat selection may be scale-dependent if the value of habitats to animals in terms of promoting long-term reproductive fitness differs from one level of habitat selection to the next (e.g., Orians and Wittenberger 1991; Schaefer and Messier 1995; Rettie and Messier 2000).

Rettie and Messier (2000) suggested that selection patterns of animals that permit them to avoid effects of those factors most able to limit individual fitness should be strongest at the largest scales (e.g., population range, home range). Less important limiting factors may influence habitat selection patterns only at smaller scales of selection (e.g., within the home range). Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of the value of habitats to animals.

Here we ask whether grizzly bears (*Ursus arctos*) differ in resource selection at different spatial scales. We examine the habitat selection patterns of barren-ground grizzly bears inhabiting Canada's central Arctic at two spatial scales. First, we compare the availability of habitat types in the home ranges of study animals with the availability of habitat types in the study area (Roy and Dorrance 1985; Thomas and Taylor 1990). Then, we compare the proportional use of habitat types within an animal's home range with the proportional availability of habitat types within the home range. Buffers around individual telemetry locations are used to determine the proportional use of habitats (Rettie and McLoughlin 1999; Rettie and Messier 2000). The area available for

habitat use varies from one location to the next and depends upon the amount of elapsed time between successive telemetry locations (Arthur et al. 1996). We use resource selection functions to determine the relative selection of habitats by grizzly bears (Manly et al. 1993; Boyce and McDonald 1999).

Materials and methods

Study area

The study area encompassed 75,000 km^2 of Low Arctic tundra in Canada's central Arctic (Fig. 1). The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10 °C and winter temperatures are commonly below –30 °C. Annual precipitation is around 300 mm, about half of which falls as snow (BHP Diamonds 1995). Drainages support willow (*Salix* spp) and dwarf birch (*Betula glandulosa*) as tall as 3 m; and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs, such as blueberry (*Vaccinium uliginosum*), cranberry (*V. vitis-idaea*), and crowberry (*Empetrum nigrum*), are common and their berries are important foods to grizzly bears (Gau 1998; Gau et al. 2002). Much of the study area is part of a well drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

Animal capture and telemetry

Satellite radio-telemetry (Service Argos, Landover, Md.) was used to obtain habitat-use data on barren-ground grizzly bears. Satellite telemetry provides locational information (approximately ±0.5 km, SD) on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars (Telonics, Mesa, Ariz.) were equipped with a VHF beacon to permit location of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five latitude–longitude locations during an 8-h duty cycle every 2 days from 1 May to 1 November. During other months, collars were programmed to transmit locations every 8 days to minimize output of battery power.

Between May 1995 and June 1999, a Bell 206B or Hughes 500 helicopter was used to search for and capture a random sample of bears in the study area. A Piper Supercub, Scout, or Aviat Husky aircraft equipped with skis or floats was sometimes used for searching the study area. Most bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow. We immobilized bears with Telazol (Ayerst Laboratories, Montreal, Quebec) in a projected dart. Immobilized animals were marked with identification numbers, applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac Systems International, Saskatoon, Saskatchewan), while suspended in a cargo net from a helicopter. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers; we extracted a vestigial premolar tooth for age determination (Craighead et al. 1970). Bears weighing >110 kg (males) and >90 kg (females) were fitted with satellite radio-collars prior to release.

Habitat maps

Availability of habitats to grizzly bears in the study area was assessed from three Landsat thematic mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing (Epp et al. 2000). Twelve discrete habitat types, excluding water and ice, were represented in the classified Landsat TM scenes: esker
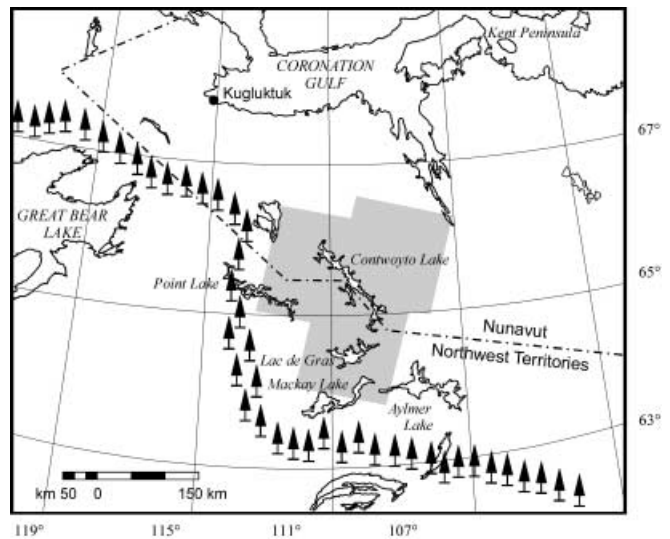

Fig. 1 Study area covered by classified Landsat thematic mapper images in the Canadian Arctic and available for the analysis of grizzly bear habitat selection patterns (*shaded region*). The *treeline* indicates the northernmost extent of coniferous forest in the study area

habitat, wetlands, tussock/hummock successional tundra, lichen veneers, spruce forest, boulder fields, exposed bedrock, riparian tall shrub habitat, birch seep, typical heath tundra, heath tundra with >30% boulder content, and heath tundra with >30% bedrock content. Epp et al. (2000) provide a detailed description of each habitat. Pixel size in the maps was 25×25 m. A smoothing algorithm was used to create minimum patch sizes of 3×3 pixels (5,625 m^2), excluding patches of linear habitat features (e.g., riparian zones, eskers). All spatial analyses described herein were conducted using SPANS Explorer 7.0 (Tydac Research, Nepean, Ontario).

Home range selection

The analysis of home range selection patterns (Johnson 1980) was based upon the methods of Manly et al. (1993). We considered proportions of habitats in the 75,000-km^2 study area as available to study animals; use of habitats by bears was determined from proportions of habitats occurring in each home range. We estimated home ranges (primarily annual ranges) for grizzly bears using the fixed kernel technique with least squares cross-validating to determine bandwidths (Silverman 1986; Worton 1989a, b, 1995), as this was the least biased method available (Seaman and Powell 1996; Seaman et al. 1999). We chose the 95% isopleth to measure home ranges, but exclude occasional movements outside the core range (<5% of locations). We calculated home ranges using the Home Ranger ver. 1.1 (F.W. Hovey, British Columbia Forest Service, Revelstoke, British Columbia). Radio locations used in calculating home ranges were a minimum of 48 h apart and included locations only of Service Argos classes 1, 2, and 3. (class 1: 68% of locations are accurate within 1,000 m, class 2: 68% of locations are accurate within 350 m, class 3: 68% of locations are accurate within 150 m). We included only those ranges that overlapped the mapped study area by a minimum of 60% for selection analysis at the level of the home range.

For both habitat availability and use, we divided the area of each of the 12 habitat types by the total study area or home range of an individual (excluding unclassified terrestrial areas, such as mine sites and areas of water), respectively. The resulting sets of used and available habitat ratios, which always totaled 1.0, were used to calculate a resource selection index (Manly et al. 1993)

for each of the H habitat types, for each bear in each home range. The selection ratios for each home range were first calculated as:

$$w_i = \frac{\text{proportion used}_i}{\text{proportion available}_i}$$

These were then standardized using the following equation:

$$bi = \frac{wi}{\sum\limits_{i=1}^{H} wi}$$

The resource selection function (the set of b_i values, where i ranges from 1 to H and H is the number of habitat types) for an individual bear was considered to be the basic datum for subsequent statistical analyses. A b_i value in such a resource selection function (sometimes referred to as a resource selection probability function; Manly et al. 1993) can be interpreted as the probability that, for any selection event, an animal would choose habitat i over all others, assuming all habitats are available to the animal in equal proportion.

Selection within home ranges

For the analysis of selection patterns within home ranges (Johnson 1980), methods were adapted from those presented by Arthur et al. (1996), whereby areas available for habitat use by an animal from one location to the next (as determined from satellite telemetry) depended upon the amount of elapsed time between successive locations. Although most collars attempted to transmit locations hourly during 8-h duty cycles every 48h, some collars transmitted a cycle every 24 h, permitting successive location distance measurements after 24 h. We determined radii for measuring availability for each satellite location observation according to a function derived from the 95th percentile of distances moved over hourly periods by grizzly bears in this study (Fig. 2), bounded by the limits of the home range of each animal.

We defined use of habitats as the contents of a circle 2.0 km in radius, centered on a telemetry location (Rettie and McLoughlin 1999; Rettie and Messier 2000). Considering use as an area, rather than a point, has theoretical basis in reducing bias in habitat selection studies (Rettie and McLoughlin 1999). Specifying a radius of 2.0 km for each point of use ensured that the true habitat used by bears, regardless of telemetry error, was likely included for analysis. Although this method of measuring use can result in conservative estimates of selection because buffers will include both used and unused habitats, the procedure may be important for detecting use of habitat types by animals travelling along linear features (e.g., eskers, riparian habitats) or selection of habitat types which, on average, are of a smaller radius than telemetry error (Rettie and McLoughlin 1999).

For both use and availability, we divided the area of each habitat type within a buffer by the total area of that buffer. The resulting sets of used or available habitat ratios totaled 1.0 for each telemetry location. Data were processed with a program written in C^{++} to determine sets of standardized resource selection functions (i.e., the sets of H resource selection indices (b_i), where i ranges from 1 to H and H is the number of habitat types), according to formulae by Arthur et al. (1996).

Four seasons were defined for analysis of within-home range selection patterns by referring to temporal changes in the diet of barren-ground grizzly bears (obtained by analyzing the scats of study animals; Gau 1998). These include: spring (from den emergence to 20 June), summer (21 June–31 July), late summer (1 August–9 September), and autumn (from 10 September to denning).

The resource selection function for each animal season was considered the sampling unit for subsequent analyses within home ranges. For this level of analysis, the spruce forest habitat type was eliminated for both use and availability. Spruce forest was found only in the southern- and westernmost parts of the study ar-
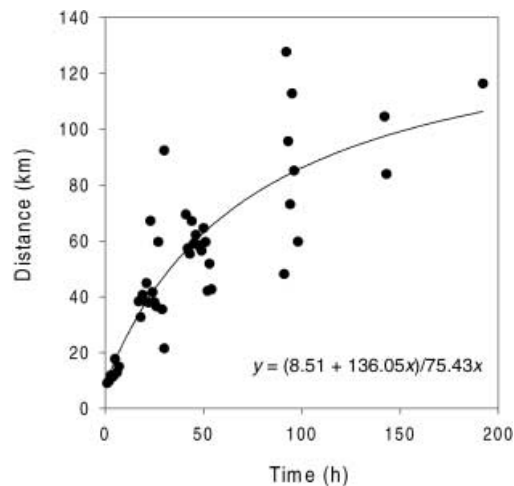

Fig. 2 Distance moved as a function of time for grizzly bears in the study area. Each data point represents the 95th percentile of distance moved for time intervals between successive satellite telemetry locations

ea and was outside the home ranges of several study animals. A habitat type must be greater than zero in availability for a resource selection index to be calculated.

Statistical analysis

For both home range and within-home range selection analyses, all b_i values were rank-transformed prior to statistical analysis to enable the use of parametric methods with non-normal data (Conover and Iman 1981). Following methods of Arthur et al. (1996), the selection indices for each bear or bear season were used to create $H-1$ synthetic variables based upon differences in adjacent pairs of ranked b_i values. We employed the synthetic variables to conduct multivariate analyses of variance (MANOVA) with the objective of examining the effects of sex and/or reproductive status in females and season (within-home range selection only) on habitat selection patterns (SPSS 1993). The MANOVA procedure employed is analogous to a multivariate repeated-measures ANOVA design (Johnson and Wichern 1982; SPSS 1993). For the MANOVA and subsequent post hoc analyses of selection within home ranges, we decided to weight each resource selection function (bear season) by the number of circular buffers used to determine the resource selection function with a weighted least-squares regression model (SPSS 1993). All post hoc multiple comparisons were conducted using the Welsch step-up procedure (Welsch 1977; Sokal and Rohlf 1995) on ranks of b_i values. An experimentwise α value of 0.1 was used for all tests of significance.

Results

Home range selection

The 95% fixed kernel home ranges of males (mean = 7,245 km², SE=1,158, $n=26$) were larger than females without accompanying young (mean = 1,955 km², SE=349, $n=22$) and females with accompanying young (mean = 2,239 km², SE=437, $n=23$). These ranges represent the largest home ranges yet recorded for grizzly bears in North America (McLoughlin et al. 1999). Home ranges of nine male bears, six female bears without cubs, and

Table 1 Inclusion of habitat types into homogeneous subsets for which mean rankings of habitat selection indices (b_i) are not significantly different (experimentwise α=0.1, Welsch's multiple range test). Habitats included in the highest-ranked subset and not included in at least one lower-ranked subset are relatively preferred (+). Habitats included in the lowest-ranked subset and not included in at least one higher-ranked subset are relatively avoided (–). Habitats included in both the highest and lowest-ranked subsets are neither preferred nor avoided (·). *M* Males, F_0 females without accompanying young, F_y females with accompanying young

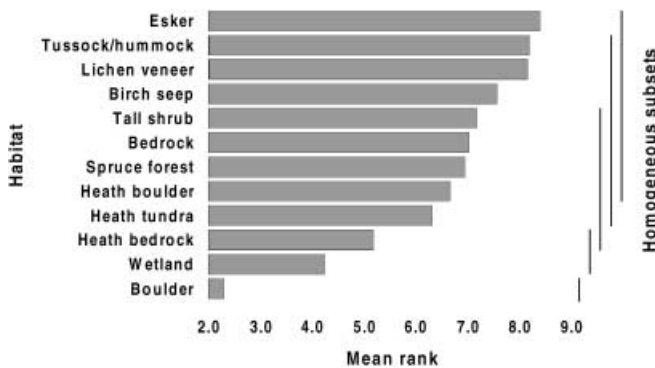| Habitat	Spring			Summer			Late summer			Autumn		
	M	F_0	F_y	M	F_0	F_y	M	F_0	F_y	M	F_0	F_y
Esker	+	+	+	·	+	+	+	+	–	–	+	·
Tall shrub	·	+	–	·	+	+	·	+	+	+	+	–
Tussock/hummock	+	·	–	+	·	·	+	–	+	–	·	·
Lichen	+	·	+	–	·	·	–	–	–	–	+	+
Heath tundra	·	·	·	·	·	+	·	–	–	+	·	+
Bedrock	+	+	·	·	·	·	·	–	–	–	–	+
Heath bedrock	–	–	–	·	–	·	–	–	+	–	–	·
Birch seep	–	–	·	·	·	·	·	·	·	–	–	·
Boulder	·	·	·	·	·	–	·	·	·	·	·	·
Heath boulder	–	–	·	·	·	·	·	–	·	–	–	·
Wetland	·	·	–	·	·	·	–	–	–	–	–	·

Fig. 3 Mean ranks of habitat selection indices (b_i) for grizzly bears (*n*=23) at the level of the home range. Homogeneous subsets of data are *indicated at the right* for mean ranks which are not significantly different (experimentwise α=0.1, Welsch's multiple range test)

eight female bears with cubs were available for analyzing home range selection patterns (i.e., possessed home ranges that overlapped the mapped study area by at least 60%). MANOVA indicated that there was no difference between sex or reproductive status with regard to habitat selection patterns at the level of the home range (Wilks' λ, approx. $F_{22,20}$=1.41, *P*=0.22). That is, males, females without cubs, and females with cubs were practicing the same selection patterns when establishing their home ranges in the study area. We also failed to detect a difference in habitat selection patterns between sexes after pooling the two female samples (Wilks' λ, approx. $F_{11,11}$=1.27, *P*=0.37).

Mean ranks of selection index values and significant differences among habitat types, as determined from multiple comparison tests on ranks of habitat selection indices (both sexes combined), are presented in Fig. 3. Esker habitat was preferred above all other habitats. Next, relative to other habitats, bears preferred tussock/hummock successional tundra, lichen veneers, and birch seep habitat. Selection for these three habitats was followed by selection for tall shrub riparian areas, exposed bedrock, spruce forests, heath/boulder habitat, and heath tundra. Wetlands were significantly less preferred when compared with these habitats. Boulder fields were significantly less preferred when compared with all other habitat types, including wetlands.

Selection within home ranges

Collars often failed to successfully uplink to satellites at scheduled intervals. We obtained 2,833 class 1, 2,435 class 2, and 1,121 class 3 locations from 26 male and 20 female grizzly bears for analyzing selection patterns within home ranges. A mean of 15.5 locations/season (SD=3.3) were obtained from study animals. MANOVA indicated differences in patterns of habitat selection among levels of sex/reproductive status (Wilks' λ, approx. $F_{20,412}$=3.32, *P*<0.001) and season (Wilks' λ, approx. $F_{30,605}$=2.71, *P*<0.001). We observed no interaction between sex/reproductive status and season (Wilks' λ, approx. $F_{60,1084}$=1.04, *P*=0.41). Post hoc analyses revealed that, for at least one synthetic variable in the MANOVA, the mean for males significantly differed from females without cubs and, for at least one synthetic variable the mean for males significantly differed from females with cubs. Further, for at least one synthetic variable, the mean for females without cubs differed significantly from females with cubs. Post hoc analyses also revealed significant differences among means of all possible pairs of seasons for at least one synthetic variable.

For all levels of sex/reproductive status in each season, we present significant differences among habitat types as determined from multiple comparison tests on ranks of habitat selection indices (Table 1). In spring, grizzly bears (*n*=32 males, *n*=14 females without cubs, *n*=19 females with cubs) demonstrated greatest preference for esker habitat, regardless of reproductive status. Exposed bedrock and lichen veneers were also favored by bears over other habitat types. In addition, males

showed high preference for tussock/hummock successional tundra. Females without accompanying young also showed preference for tall shrub habitat.

In summer, males ($n=28$) continued to demonstrate significant preference for tussock/hummock successional tundra. Females without cubs ($n=18$) and females with cubs ($n=16$) demonstrated highest preference for tall shrub riparian habitat and eskers. Heath tundra was also preferred by females with accompanying young.

In late summer, esker and tall shrub riparian habitat again emerged as preferred habitats. Although esker habitat was highly preferred by males ($n=24$) and females without accompanying young ($n=22$), it was significantly avoided by females with accompanying young ($n=11$). High ranks of tall shrub riparian habitat were observed for bears regardless of sex/reproductive status, although the habitat was significantly preferred by only females. Males continued to prefer tussock/hummock successional tundra and females with accompanying young also expressed some preference for this. Heath bedrock, which was significantly avoided by males and females without accompanying young, was actually preferred by females with cubs.

Males ($n=19$) and females without cubs ($n=15$) showed highest preference for tall shrub riparian zones in autumn. This selection pattern was not, however, shared by females with cubs ($n=9$): tall shrub habitat was significantly avoided by family groups. Eskers continued to be highly ranked by females without accompanying young. Lichen veneers were preferred or at least highly ranked by bears of all levels of sex/reproductive status.

Overall, esker and riparian tall shrub habitats were preferred by bears throughout the year. Tussock/hummock successional tundra was also favored by males at varying times during the year. In addition, lichen veneers were favored in spring and autumn by most bears. There was a general pattern that the highest-ranked habitats for males were avoided by females with cubs in spring (e.g., tussock/hummock tundra), late summer (e.g., esker), and autumn (e.g., tall shrub). This pattern of habitat use was not observed for females without accompanying young.

Discussion

Rettie and Messier (2000) suggested that habitat selection patterns should permit animals to avoid effects of those factors most able to limit individual fitness and selection patterns that allow for this should be strongest at the coarsest (largest) scales of selection. Less important limiting factors may influence selection patterns only at smaller scales. For example, woodland caribou (*Rangifer tarandus*) likely select habitats at higher orders of selection to minimize wolf (*Canis lupus*) predation, or exposure to the lethal meningeal worm (*Parelaphostrongylus tenuis*; Rettie and Messier 2000). Only at finer scales do foraging decisions of caribou determine habitat selection patterns (Rettie and Messier 2000).

Interspecific predation, human hunting, and disease are not likely to be important limiting factors for barren-ground grizzly bears (LeFranc et al. 1987; McLellan 1994). Therefore, we predicted that patterns of selection observed by grizzly bears at the coarser scale (home range) examined in this study would likely correspond to factors such as food abundance or availability (i.e., bears are likely food-limited). We also predicted that patterns of selection for barren-ground grizzly bears at the finer scale of study (within the home range) would focus on vegetation communities identified at the coarser scale, but selection for these habitats would vary throughout the year (i.e., selection patterns would reflect food availability in time and space).

Selection of habitats by grizzly bears corresponded well with the spatial and temporal availability of food on the landscape. For example, concentrations of fruit-bearing shrubs along esker slopes likely attract bears in both autumn and spring, when over-wintering berries are consumed by bears (Gau 1998). Arctic ground squirrels (*Spermophilus parryii*) are an important component of the diet of barren-ground grizzly bears (e.g., Tuktoyaktuk Peninsula, Northwest Territories, Nagy et al. 1983; Western Brooks Range, Alaska, Hechtel 1985; central Canadian Arctic, Gau 1998; Gau et al. 2002), ground squirrels preferentially burrow in eskers (Mueller 1995). Tall shrub riparian zones contain concentrations of several foods that are used by grizzly bears in summer and late summer, such as horsetail (*Equisetum* spp), sedges (*Carex* spp, *Eriophorum* spp), and willow buds (Gau 1998; Gau et al. 2002). Early successional stages of tussock tundra provide concentrations of sedges (*Carex* spp) and Arctic cotton grass (*E. vaginatum*), both of which were major constituents of summer scats of study animals (Gau 1998; Gau et al. 2002). Lichen veneers may attract caribou, which are specialist foragers of lichens, and offer hunting habitat for grizzly bears during spring and autumn when caribou migrate through most of the home ranges of bears in this study. Caribou are preyed upon extensively by grizzly bears at these times (Gau 1998; Gau et al. 2002).

In addition to food availability, McLellan (1994) suggested that intraspecific predation by males on females and their cubs may be an important limiting factor for grizzly bears. If true for the central Canadian Arctic, we would expect sexual segregation in habitat use to be apparent at one or both scales of habitat selection examined. Our results support this prediction. Within the home range, females with accompanying young did not exhibit the same patterns of habitat selection throughout the summer, late summer, and autumn as males and females without accompanying young. Intraspecific predation by males on females and their cubs in the Arctic has been documented (Reynolds 1980; Nagy et al. 1983; Case and Buckland 1998) and sexual segregation in habitat use may be a strategy by females with cubs to avoid predatory males (Ballard et al. 1993; Wielgus and Bunnell 1995a,b).

No differences in habitat selection patterns between males, females without accompanying young, and fe-

males with accompanying young were found to occur at the level of home range selection. That sexual segregation in habitat selection appears to be scale-dependent concurs both with the results of Bowyer and Kie (1996) and, for grizzly bears, with the results of Wielgus and Bunnell (1995a,b) and Mace and Waller (1997). As in this study, Mace and Waller (1997) concluded that, at the home range level of selection, female avoidance of males did not occur. Although Mace and Waller did not examine male/female interactions at finer levels of selection, the results of Wielgus and Bunnell (1995a,b) agree with our results by suggesting that differences in habitat selection between sexes does occur at smaller spatial scales. Whereas food availability may be the limiting factor affecting habitat selection patterns at the higher level of selection, intraspecific predation, in concert with food availability, may influence habitat selection at the finer level of selection.

Patterns of habitat selection at larger scales may differ from patterns of habitat selection at smaller scales (Johnson 1980; Senft et al. 1987; Wiens et al. 1987; Wiens 1989; Orians and Wittenberger 1991; Schaefer and Messier 1995). The results of this study suggest that, at higher scales, food availability is the most important limiting factor for grizzly bears; patterns of habitat selection at the level of the home range appeared to emphasize foraging habitats. This pattern was also generally demonstrated within home ranges, although, unlike at the level of the home range, sexual segregation in habitat use was also evident. This suggests that the potential for intraspecific predation influences habitat selection within home ranges. That intraspecific predation affects habitat selection patterns at the finer but not the coarser level of selection suggests that it may be less able to limit population size than those factors governing higher order selection patterns (Rettie and Messier 2000). Selection patterns for animals should permit them to avoid effects of those factors most able to limit individual fitness; selection patterns that allow for this should be strongest at the highest scales (Rettie and Messier 2000). The results of this study underline the importance of scale dependence in habitat selection. Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of the value of habitats to animals.

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