

Effect of spatial differences in habitat on home ranges of grizzly bears¹

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Abstract: Between May 1995 and June 1999 we equipped 81 barren-ground grizzly bears (*Ursus arctos*) with satellite radio-collars within a study area of 235 000 km², centred 400 km northeast of Yellowknife, Northwest Territories. We estimated 71 annual ranges of radio-tracked animals (≥ 38 locations year⁻¹) using the 95% fixed kernel technique with least squares cross-validation. Annual ranges of males ($\bar{x} = 7\,245$ km², SE = 1,158, $n = 26$) were larger than ranges of females ($\bar{x} = 2\,100$ km², SE = 279, $n = 45$). Ranges increased in size as the proportional amount of exposed bedrock and other marginal habitats in the environment increased. Annual ranges are the largest reported for grizzly bears in North America.

Keywords: Arctic, fixed kernel, grizzly bear, habitat, home range, Northwest Territories, *Ursus arctos*.

Résumé : Entre mai 1995 et juin 1999, nous avons posé des colliers émetteurs dont les ondes peuvent être captées par satellite sur 81 ours grizzly de la toundra (*Ursus arctos*). L'aire d'étude couvrait 235 000 km² et son point central était situé à 400 km au nord-est de Yellowknife, dans les Territoires du Nord-Ouest. Nous avons estimé la superficie de 71 domaines vitaux annuels à partir des localisations télémétriques (≥ 38 localisations an⁻¹) en utilisant la technique du kernel fixé à 95 % avec validation croisée des moindres carrés. Les domaines vitaux annuels des mâles ($\bar{x} = 7\,245$ km², erreur type = 1158, $n = 26$) sont plus grands que ceux des femelles ($\bar{x} = 2\,100$ km², erreur type = 279, $n = 45$). La superficie des domaines augmente en fonction de la place occupée par le roc nu et par d'autres types d'habitats de moindre qualité. Les domaines vitaux annuels que nous avons observés sont les plus grands rapportés pour des ours grizzly en Amérique du Nord.

Mots-clés : Arctique, ours grizzly, habitat, domaine vital, Territoires du Nord-Ouest, *Ursus arctos*.

Nomenclature: Wilson & Reeder, 1993.

Introduction

The central problem of what determines home range size is the immensely integrative nature of the home range. McNab (1963) was first to demonstrate that home range size is positively associated with body size in mammals and suggested that home range size may be related to an animal's size-dependent metabolic rate. Other factors that may affect home range size include social organization (Darnuth, 1981), population density (Wolff, 1985; Desy, Batzli & Liu, 1990; Wolff, 1993; Wolff & Schaubert, 1996), and risk of predation (Desy, Batzli & Liu, 1990; Tufto, Andersen & Linnell, 1996). Further, because survival and reproduction are often food limited, habitat quality (abundance and predictability of food in time and space) is also an important factor influencing home range size (McLoughlin & Ferguson, 2000).

Here we describe the home ranges of grizzly bears in Canada's central Arctic (Figure 1). We assess the importance of habitat as a determinant of home range size by compar-

ing the size of home ranges across individuals within a single population (*i.e.*, the individual level; McLoughlin & Ferguson, 2000). We explore relationships between range size and proportional availabilities of habitat types within home ranges of grizzly bears. We hypothesize that if bears respond to availability of habitat, home range size should vary with the proportional availability of habitat types within the home range. For example, home ranges may increase as the proportion of habitats in the home range that provide marginal food value to bears increases or as high-quality habitats become more patchily distributed within a matrix of marginal habitats.

Methods

STUDY AREA

The study area was located in Canada's central Arctic (Figure 1). The area encompassed approximately 235 000 km² of Low Arctic tundra and was delineated, clockwise, by Kugluktuk (formerly Coppermine), the Kent Peninsula, Aylmer Lake, MacKay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C, and winter tem-

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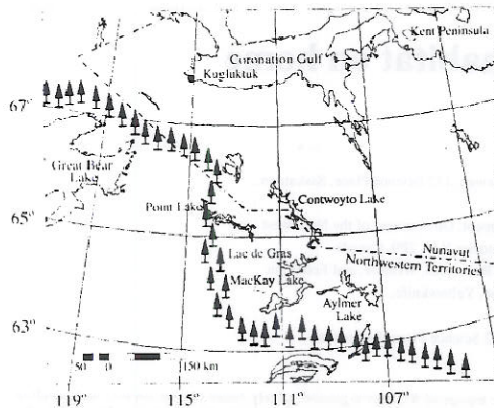


FIGURE 1. Study area in Canada's central Arctic. The shaded region indicates portions of the study area classified with Landsat TM images and used for estimating proportional habitat availability within home ranges. The treeline indicates the northernmost extent of coniferous forest in the study area.

peratures are commonly below -30°C . The area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995). Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (< 0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are also common, and their berries are important foods to grizzly bears (Gau *et al.*, 2002). Ungulate prey include caribou (*Rangifer tarandus*) of the Bathurst herd, which migrate annually through the study area. Muskox (*Ovibos moschatus*) occur sporadically in the northern half of the study area.

ANIMAL CAPTURE AND TELEMETRY

Between May 1995 and June 1999, we used a Bell 206B or Hughes 500 helicopter to search for and capture bears. A Piper SuperCub, Scout, or Aviat Husky aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured during the snow melt period (15 May–5 June) by following tracks in snow. Field crews immobilized bears with an injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol[®], Ayerst Laboratories Inc., Montréal, Québec, Canada) from 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 Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. Only those bears weighing >110 kg (males) and >90 kg (females) were fitted with radios prior to release.

Satellite radio-telemetry (Service Argos Inc., Landover, Maryland, U.S.A.) was used to obtain movement data on barren-ground grizzly bears (Fancy *et al.*, 1988; Harris *et al.*, 1990). Satellite collars (Telonics, Mesa, Arizona, U.S.A.) were equipped with a VHF beacon to permit loca-

tion of radio-marked animals from an aircraft and, eventually, enable the retrieval of collars. Most collars were designed to transmit approximately two to five latitude-longitude locations every two days (eight-hour duty cycle) from 1 May–1 November. During other months, collars were programmed to transmit locations every eight days to minimize use of battery power.

ANNUAL RANGES

From satellite telemetry locations we estimated annual ranges for grizzly bears using the fixed kernel technique with least squares cross-validating (LSCV) to determine bandwidths (Silverman, 1986; Worton, 1989a,b; 1995), as this was the least biased method available (Seaman & Powell, 1996; Seaman *et al.*, 1999). We chose the 95% isopleth to measure annual ranges, but excluded occasional sallies. We calculated annual ranges using "The Home Ranger", Version 1.1 (F. W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, P.O. Box 9158, R.P.O. No. 3, Revelstoke, British Columbia V0E 3K0, Canada). Radio locations used in all analyses were at least 48 hours apart. Most satellite collars in the study were designed to last for two years; hence, for some animals we obtained two annual range estimates. With these cases, to avoid sample pseudo-replication, we chose only a single annual range for inclusion in analyses (the estimate with the most locations), unless the animal underwent a change in family status between the two years (*i.e.*, cases where females gained or lost cubs or cubs aged). We included only those annual ranges composed of ≥ 38 locations for analysis, as kernel techniques tend to overestimate range size with smaller sample sizes (Seaman *et al.*, 1999). Also, ranges were not calculated for subadult males (2–5 years of age). Subadult male grizzly bears may wander extensively in search of a home region, and during this period they are not considered to possess a home range (Burt, 1943). McLoughlin *et al.* (1999) provide preliminary information on annual ranges for some bears sampled in this study.

We log₁₀-transformed ranges prior to statistical analyses to meet assumptions of normality and equal variance among groups of data (Sokal & Rohlf, 1995). Annual ranges of adult males and females of differing family status were compared using a one-way analysis of variance (ANOVA). Following significant ANOVAs, Tukey's HSD test (Zar, 1984) was used to compare individual means.

SPATIAL EFFECTS OF HABITAT ON HOME RANGES

We assessed effects of spatial differences in habitat on range size by first determining the proportion of different habitat types contained within home ranges of grizzly bears. We then tested for linear relationships between home range size and proportional habitat availability within home ranges. Here, home ranges were primarily annual ranges. To avoid pseudo-replication of data, however, a composite range based upon data from more than one year was used when more than one annual range could be calculated for a bear. Annual ranges of bears in this study did not differ significantly from multi-year composite ranges for both females (paired *t*-test, $t_{34} = 1.79$, $P = 0.08$) and males (paired *t*-test, $t_{25} = 1.70$, $P = 0.10$).

Availability of habitats to bears in the study area was assessed from three Landsat Thematic Mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing (Epp, Matthews & Smith, 2000). Twelve discrete habitat types excluding water and ice were represented in the classified Landsat TM scenes: esker 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, Matthews, and Smith (2000) provide details of habitat types. Pixel size in the maps was 25 m × 25 m. A smoothing algorithm was used to create minimum patch sizes of 3 × 3 pixels (5,625 m²), excepting patches of linear habitat features (e.g., riparian zones and eskers). All spatial analyses described herein were conducted using SPANS[®] Explorer[™] 7.0 (Tydac Research Inc., Nepean, Ontario, Canada).

We included only those ranges that overlapped the mapped portion of the study area by at least 60.0% for habitat analysis. To determine proportional habitat availability within each range, we projected the perimeter vectors of each home range (or portions thereof) upon the habitat map and calculated the area of each habitat type contained within home range vectors. We then divided the area of each of the 12 habitat types by the total terrestrial area of the range contained within the habitat map. Because habitat selection analysis indicated no differences in the proportional availability of habitat types within the home ranges of males and females of differing family status (McLoughlin *et al.*, 2002), we pooled observations across sex and reproductive status for this analysis. Stepwise multiple regression (SPSS Inc., 1993; Sokal & Rohlf, 1995: 610–664) was used to identify relationships between range size and proportional habitat availabilities within home ranges.

Results

ANNUAL RANGES

We calculated 71 annual ranges from radio-collared bears, including 26 adult males, 22 lone females, and 23 females with cubs. Annual range size differed significantly across sex and family status ($F_{2,68} = 14.2$, $P < 0.001$). The annual ranges of males ($\bar{x} = 7,245$ km², SE = 1,158) were significantly larger than those of lone females (Tukey's HSD, $p = 3$, $q = 6.75$, $P < 0.001$) and females with cubs (Tukey's HSD, $p = 3$, $q = 6.08$, $P < 0.001$); however, the annual ranges of lone females ($\bar{x} = 1,955$ km², SE = 349) and females with accompanying young ($\bar{x} = 2,239$ km², SE = 437) did not differ (Tukey's HSD, $p = 3$, $q = 0.72$, $P = 0.87$). We pooled females across family status and tested again for a sex effect. The mean annual range of males was larger ($F_{1,69} = 28.4$, $P < 0.001$) than the mean annual range of females pooled across family status ($\bar{x} = 2,100$ km², SE = 279).

SPATIAL EFFECT OF HABITAT ON HOME RANGES

Stepwise multiple regression of home range size on proportional habitat availability produced a significant regression model including the predictor variables (habitats): bedrock, heath boulder, wetlands, heath bedrock, tall shrub riparian, lichen veneer, and spruce forest (Figure 2, $F_{7,15} = 2.25$, $r = 0.72$, $P < 0.10$). Partial regression coefficient

icients (b) and their standard errors (SE of b), standardized partial regression coefficients (β), t -scores, P -values, and partial correlation coefficients (r_{YX}) for each predictor variable can be found in Table 1.

Discussion

The home ranges of barren-ground grizzly bears in the central Canadian Arctic are the largest ranges yet reported for grizzly bears in North America. The relatively large spatial requirements of grizzly bears in the study area agree with results of other studies of barren-ground grizzly bears

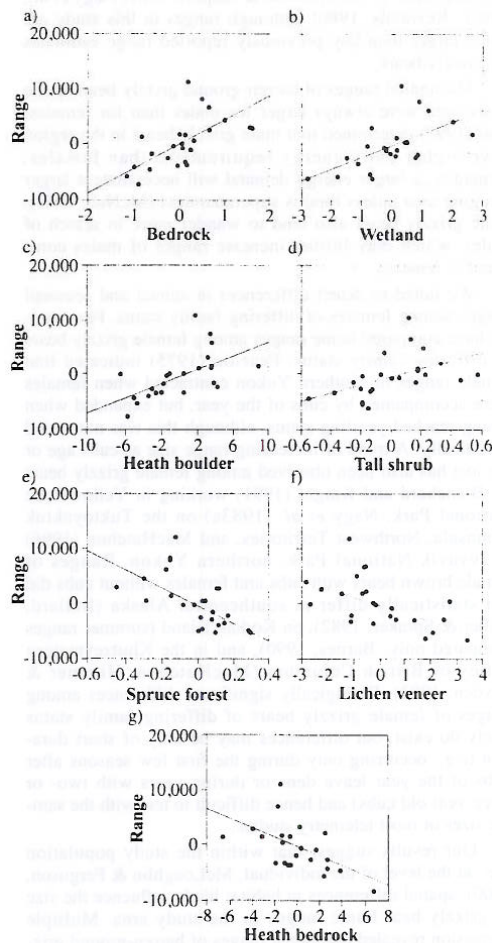


FIGURE 2. Standardized partial regression plots of home range size versus predictor habitat variables for grizzly bears in the central Canadian Arctic, 1995–1999. Graphs are home range size versus proportional amounts of habitat within the home range: a) Bedrock; b) Wetlands; c) Heath boulder; d) Tall shrub riparian; e) Spruce forest; f) Lichen veneer; g) Heath bedrock.

TABLE 1. Table of coefficients for significant predictor variables in a multiple regression of home range size versus proportional habitat availability within the home ranges of grizzly bears in the central Canadian Arctic, 1995–1999.

	b	SE	Coefficients			
			β	t	P	r
(Constant)	-17,579.3	7,714.3		-2.279	0.038	
Lichen veneer	-1,495.7	536.7	-0.986	-2.787	0.014	-0.58
Wetland	2,154.8	751.4	1.100	2.868	0.012	0.60
Spruce forest	-16,393.6	5,005.7	-2.163	-3.275	0.005	-0.65
Bedrock	4,368.3	1,381.5	1.220	3.162	0.006	0.63
Tall shrub	7,268.4	3,406.6	1.245	2.134	0.050	0.48
Heath boulder	650.8	237.7	0.779	2.738	0.015	0.58
Heath bedrock	-857.9	322.6	-1.009	-2.659	0.018	-0.57

(Ballard *et al.*, 1993; Clarkson & Liepins, 1989; Nagy *et al.*, 1983a; Reynolds, 1980), although ranges in this study are much larger than any previously reported range estimates for grizzly bears.

The annual ranges of barren-ground grizzly bears in the study area were always larger for males than for females. Gau (1998) determined that male grizzly bears in the region have higher daily energy requirements than females. Generally, a larger energy demand will necessitate a larger foraging area unless food is superabundant (McNab, 1963). Male grizzly bears also tend to wander more in search of mates, which may further increase ranges of males compared to females.

We failed to detect differences in annual and seasonal ranges among females of differing family status. Few studies have compared home ranges among female grizzly bears of differing family status. Pearson (1975) indicated that female ranges in southern Yukon contracted when females were accompanied by cubs of the year, but expanded when young reached yearling status, although this was not tested statistically. A trend of increasing range size as cubs age or are lost has also been observed among female grizzly bears by Blanchard and Knight (1991) working in Yellowstone National Park, Nagy *et al.* (1983a) on the Tuktoyaktuk Peninsula, Northwest Territories, and MacHutchon (1996) in Ivvavik National Park, northern Yukon. Ranges of female brown bears with cubs and females without cubs did not statistically differ in southcentral Alaska (Ballard, Miller & Spraker, 1982), on Kodiak Island (summer ranges compared only; Barnes, 1990), and in the Kluane National Park of British Columbia (MacHutchon, Himmer & Bryden, 1993). Biologically significant differences among ranges of female grizzly bears of differing family status likely do exist, but differences may be only of short duration (*e.g.*, occurring only during the first few seasons after cubs of the year leave dens or during years with two- or three-year old cubs) and hence difficult to test with the sample sizes of most telemetry studies.

Our results suggest that within the study population (*i.e.*, at the level of the individual; McLoughlin & Ferguson, 2000), spatial differences in habitat likely influence the size of grizzly bear home ranges in the study area. Multiple regression revealed that home ranges of barren-ground grizzly bears increased with increasing proportions of bedrock, wetland, and heath boulder habitats within home ranges.

Habitat selection analysis indicated that throughout most of the year these habitats are not highly ranked by bears (McLoughlin *et al.*, 2002). Food in these habitats may be limited or only accessed by bears during very short junctures in the year (*e.g.*, bedrock during the snow-melt period as it may be one of the first habitat types to become snow-free; McLoughlin *et al.*, 2002). Here, home ranges likely increase in size as the proportional amount of energetically "useless" space in the environment increases, in order to supply constant amounts of quality habitat, such as esker, tall shrub riparian habitat, and tussock/hummock successional tundra (McLoughlin *et al.*, 2002). Although tall shrub riparian areas, a highly ranked habitat by bears (McLoughlin *et al.*, 2002), also showed a positive relationship with home range size, the partial correlation with home range size was the weakest of all habitats included in the regression model ($r^2 = 0.23$). Further, the decision to include tall shrub riparian habitat in the regression was based on only a marginally significant ($P = 0.05$) improvement in the model.

The proportions of spruce forest and lichen veneer (two habitats that are closely associated with the treeline of the southwest portion of the study area) in home ranges showed strong negative relationships with home range size. This suggests that bears that are closer to treeline require smaller home ranges to meet food demands. Bears closer to treeline may access more abundant or different foods than those bears in areas of open tundra, such as the highly favoured roots of alpine *hedysarum* (*Hedysarum alpinum*) that are unavailable in the central study area (Porsild & Cody, 1980; Gau, 1998; P. McLoughlin, pers. observ.). The roots of alpine *hedysarum* are an important source of seasonally available protein for grizzly bears in most other northern environments (Nagy *et al.*, 1983a,b; Hechtel, 1985; Phillips, 1987; MacHutchon, 1996). Within populations, home range size generally shares an inverse relationship with food abundance (McLoughlin & Ferguson, 2000). This is true for several species, including voles, *Microtus townsendii* (Taitt, 1981); bandicoots, *Isodon obesulus* (Broughton & Dickman, 1991); roe deer, *Capreolus capreolus* (Tufto, Andersen & Linnell, 1996); black bears, *Ursus americanus* (Powell, Zimmerman & Seaman, 1997); lizards, *Sclerophorus jarrovi* (Simon, 1975); and birds (Hixon, 1980).

Apart from habitat-specific food availability, other factors governing home range size within populations may include conspecific density and risk of predation (McLoughlin & Ferguson, 2000). For example, low densities may reduce competition for space and allow animals to use resources over larger ranges than at higher densities. Rogers (1977) observed that female black bears extended their home ranges into areas left vacant when neighbouring females were killed. Conversely, increased intruder pressure by conspecifics may decrease home range size (Wolff & Schaubert, 1996). If the density of grizzly bears near treeline is higher than in open tundra, the observation of smaller ranges in treed habitats versus open habitats may proximately result from density, rather than food effects. Ultimately, however, observed differences in home range size may be determined by habitat quality as habitat quality influences density (at least in food-limited populations). It is

difficult to separate the effects of density from habitat quality on home range size as the two factors are correlated (McLoughlin & Ferguson, 2000).

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