ANNUAL AND SEASONAL MOVEMENT PATTERNS OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL NORTHWEST TERRITORIES

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Abstract: Between May 1995 and September 1997, we equipped 64 barren-ground grizzly bears (*Ursus arctos*) with satellite radiocollars within a study area of 200,000 km^2, centered 400 km northeast of Yellowknife, Northwest Territories. We estimated annual ranges of radiotracked animals ($\geq$38 locations/year) using the 95% fixed kernel technique with least squares cross-validating to determine bandwidths. The mean annual range for adult males was 6,685 km^2 (SE = 1,351, n = 19) and was larger ($P < 0.001$) than for females ($\bar{x}$ = 2,074 km^2, SE = 335, n = 35). There was no difference ($P = 0.42$) in the annual ranges among females of differing family status. Seasonal rates of movement, calculated from straight-line distances between successive locations, were higher for males than for females ($P < 0.001$). Both sexes decreased movement rates from their highest rates in spring (males) and summer (females) to lowest rates in autumn, which likely results from increased food availability as the year progresses. Annual ranges presented here are the largest ranges reported for grizzly bears in North America. Low primary productivity on the barrens may explain why the annual ranges of barren-ground grizzly bears are larger than the ranges of other grizzly bear populations.

Ursus 11:79–86

Key words: annual home range, fixed kernel, grizzly bear, minimum convex polygon, movement rates, Northwest Territories, *Ursus arctos*

The barren-ground grizzly bear population of the Slave Geological Province (SGP), Northwest Territories, is unique in that, for the most part, it has not been subjected to the exploitation and habitat changes that led to the extirpation of grizzly bears from much of North America. Recently, however, the discovery of diamond-bearing kimberlite pipes in the SGP has led to intense exploration activity and the development of the first of likely several diamond mines. In 1995, in response to concerns about the potential effects of human developments on barren-ground grizzly bears, the government of the Northwest Territories and the University of Saskatchewan initiated a multi-faceted research program on the ecology of grizzly bears inhabiting the SGP.

One of the objectives of the research program was to detail the spatial requirements of barren-ground grizzly bears in this region. Investigations into the relationships between human activity and grizzly bears (review in McLellan 1990) indicate that bears in the SGP may be at particular risk to impacts from human development. For instance, if bears in the SGP behave like bears from other barren-ground populations (see e.g., Reynolds 1980, Nagy et al. 1983*a*, Clarkson and Liepins 1989, Ballard et al. 1993), they may possess increased spatial requirements relative to more interior populations. Because large ranges may put individual bears in contact with humans even when developments are at considerable distance from the core of the home range, a better understanding of the spatial requirements of grizzly bears in the SGP, and in Arctic tundra environments in general, was considered necessary for effective management of this population.

Here we examine the annual ranges of grizzly bears in the SGP. Further, to understand seasonal fluctuations in movement patterns, we describe changes in the seasonal movement rates of grizzly bears in this region. We assess differences in range sizes and seasonal movement rates of grizzly bears of differing sex and breeding status. Then, we test a possible explanation for why home ranges of barren-ground grizzly bears are generally larger than interior and west-coastal populations of grizzly bears. We hypothesize that bears have responded to low primary productivity in Arctic tundra environments with large annual ranges to obtain requisite food resources.

STUDY AREA

The study area is located in the Slave Geological Province, central Northwest Territories (Fig. 1). The area encompasses approximately 200,000 km^2 of Low Arctic

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tundra, and is 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 temperatures 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 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 caribou >1 year of age in 1996 (Gunn et al. 1997). Muskoxen (*Ovibos moschatus*) occur sporadically in the northern half of the study area. 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. Major drainages in the study area include the Coppermine River, Burnside River, Hood River, and Back River systems.

METHODS

Animal Handling and Telemetry

Between May 1995 and September 1997, a Bell 206B or Hughes 500 helicopter was used to search for and capture bears. A 2-seat fixed-wing aircraft was sometimes used in addition to the helicopter for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 Jun) by following tracks in the snow. We immobilized each bear with an injection of titelamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Immobilized animals were marked with identifi-

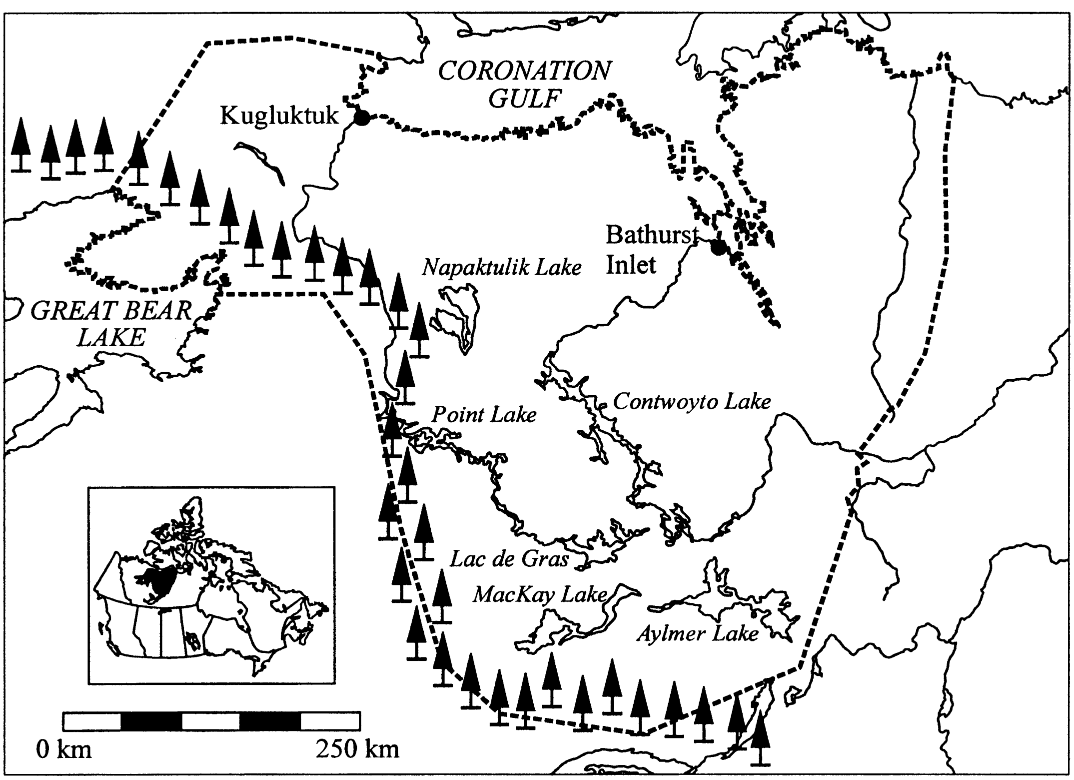

Fig. 1. Location of the study area in the Slave Geological Province, central Northwest Territories. The treeline indicates the approximate northern limit of coniferous forest in the region.

cation 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. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers, and extracted a premolar tooth for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical impedance analysis and blood sampling (Gau 1998). Captured bears weighing >110 kg (males) and >90 kg (females) were equipped with a radiocollar containing both a satellite telemetry transmitter (platform terminal transmitter; Service Argos Inc., Landover, Maryland, USA) and a VHF beacon in the 150–154 MHz range (Telonics, Mesa, Arizona, USA). Most satellite transmitters were designed to transmit locations every second day during the active season (1 May–31 Oct), and every eighth day when bears were in their dens (1 Nov–30 Apr). Bears were recaptured and collars replaced or removed near the end of radio battery life.

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 1989*a*,*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 annual ranges, but exclude occasional sallies. We calculated annual ranges using "The Home Ranger", Version 1.0 (F.W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, P.O. Box 9158, R.P.O. No. 3, Revelstoke, BC V0E 3K0, Canada). Radiolocations used in all of our analyses were a minimum of 48 hours apart. Most satellite collars in the study were designed to last for 2 years; hence, for some animals we obtained 2 annual range estimates. With these cases, to avoid sample pseudo-replication, we chose only a single annual range for inclusion in our analyses (the estimate with the most locations), unless the animal underwent a change in family status between the 2 years (i.e., cases where females gained or lost cubs, or cubs aged). We included only those annual ranges comprised of ≥38 locations for analysis, as kernel techniques tend to overestimate range size with smaller sample sizes (Seaman et al. 1999). Also, annual ranges were not calculated for subadult males. Subadult male grizzly bears may wander extensively in search for a home region, and during this period they are not considered to possess a home range (Burt 1943).

Seasonal Rates of Movement

We defined seasons according to changes in the diet of barren-ground grizzly bears during the active period (adapted from Gau 1998), including: spring (den emergence–20 Jun), summer (21 Jun–31 Jul), late-summer (1 Aug–9 Sep), and autumn (10 Sep–den entrance). Den emergence generally occurs in the last week of April and den entrance in the last week of October (data on file). Because sample sizes for bears within seasons were generally <20 locations, we employed calculations of rates of movement to determine possible seasonal fluctuations in movement patterns. Where the number of fixes is low or data is collected within a restricted time period, indices of space use such as observed range length or rate of movement, which make no attempt to measure home range area, may be more appropriate than estimates of home range to document space-use patterns (Harris et al. 1990). We calculated rates of movement with program Tracker (Version 1.1, Camponotus AB, Solna, Sweden) by examining straight-line distances between successive locations. Only those animals that transmitted ≥8 locations/season in every season of the year were included for analysis.

Range and Movement Statistics

We $\log_{10}$-transformed range and movement rate estimates prior to analyses to meet assumptions of normality and equal variance among groups of data (Sokal and Rohlf 1995). The annual ranges of adult males and females were compared using a 1-way analysis of variance (ANOVA). We performed a preliminary 1-way ANOVA to determine whether family status among females (i.e., females without accompanying offspring, with cubs of the year, with yearlings, or with 2-year olds) influenced annual range size. Estimates of seasonal movement rates for each grizzly bear across a single year were related through time; hence, to compare seasonal rates of movement between males and females and among seasons, we performed a 2-way repeated-measures ANOVA (SigmaStat, Version 2.0, Jandel Corporation, San Rafael, California, USA). Following significant ANOVAs, Tukey's honestly significant difference (HSD) test was used to compare individual means.

Annual Ranges versus Primary Productivity

We used site-specific measures of habitat quality to help explain observed differences between the size of grizzly bear ranges in the SGP and the reported ranges of several other North American grizzly bear populations. Habitat quality was estimated as net annual above ground primary productivity, which can be predicted through calculating actual evapotranspiration (Rosenzweig 1968) and using the following equation from Leith (1976):

$$PP = 3000[1\text{-}e^{-0.00009695(E\text{-}20)}]$$

where *PP* is primary productivity (g/m^2), *E* is actual evapotranspiration (mm), and *e* is the base of natural logarithms. For each study area in our comparison, we computed *E* values using the Thornthwaite method (Thornthwaite and Mather 1957, Willmot et al. 1985). To determine whether the regression of mean annual ranges of grizzly bears against primary productivity was significant and to explore any differences between males and females, we used an analysis of covariance (ANCOVA). Because most studies of grizzly bears made reference to the minimum convex polygon (MCP) technique to calculate annual ranges, we provided mean 95% MCP annual ranges for bears in the SGP for comparison purposes. Primary productivity estimates and mean male and female ranges were $\log_{10}$-transformed prior to analysis to ensure normality of data.

RESULTS

Annual Ranges

We calculated 54 annual ranges from data on 64 collared bears, including: 19 adult males, 18 lone females, 4 females with cubs of the year, 6 females with yearlings, and 7 females with 2-year olds. The annual ranges of females of different family status did not differ ($F_{3,31}$ = 0.99, P = 0.42), thus we pooled annual ranges of females across family status for comparison with adult males. The mean annual range of males (6,685 km^2, SE = 1,351, n = 19) was larger ($F_{1,52}$ = 20.2, P < 0.001) than the mean annual range of females (2,074 km^2, SE = 335, n = 35).

Seasonal Rates of Movement

We calculated seasonal movement rates for 15 male and 19 female bear-years, and detected a sex effect ($F_{1,96}$ = 34.88, P < 0.001), season effect ($F_{3,96}$ = 3.38, P < 0.05), and sex by season interaction ($F_{3,96}$ = 4.73, P < 0.005; Fig. 2). The full model was reduced by sex, and both

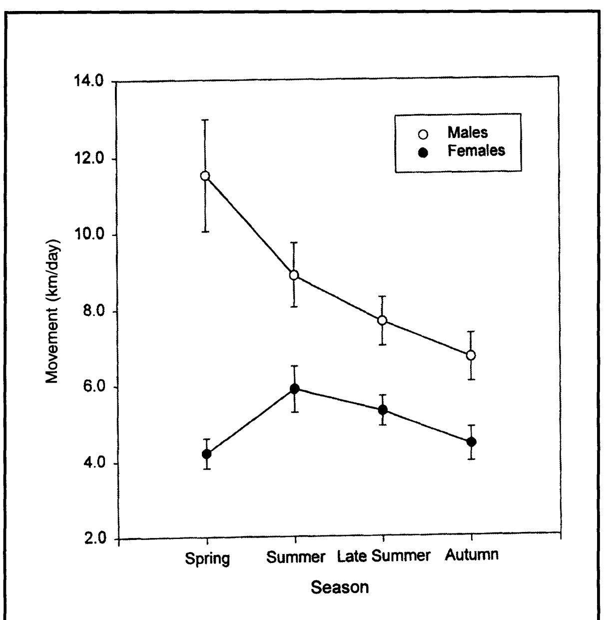

Fig. 2. Seasonal movement rates (km/day) of barren-ground grizzly bears in the Slave Geological Province, Northwest Territories, 1995–97. Error bars are ±1 SE.

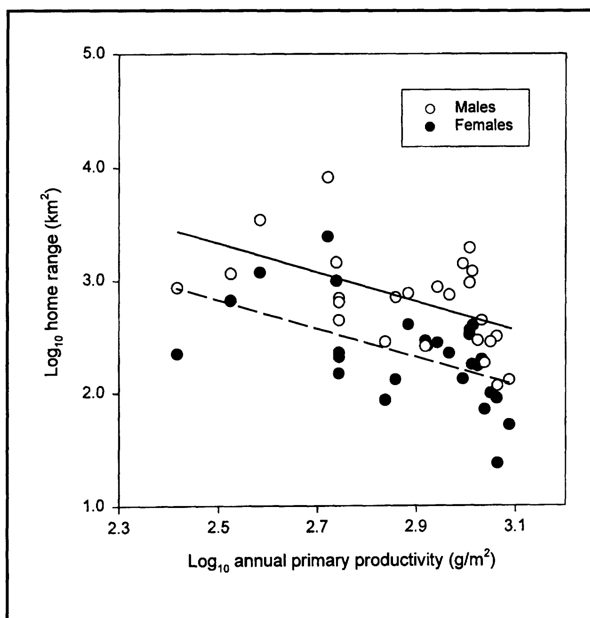

Fig. 3. Log_{10} mean home ranges (km^2) of grizzly bears for selected North American populations versus $\log_{10}$ mean annual primary productivity (g/m^2). The equation for the male regression line (solid line) is $y = 6.21 - 1.24x$. The equation for the female regression line (dashed line) is $y = 6.07 - 1.24x$. R^2 for the ANCOVA was 0.45.

Table 1. Estimated mean home ranges of grizzly bears in North America as reported in the literature. Ranges are primarily adult annual home ranges and were calculated using the minimum convex polygon (MCP) approach unless otherwise indicated. Weighted means were calculated if ranges were estimated with small or variable numbers of locations (if data permitted).

		Males		Females	
Study Area	Source	km²	*n*	km²	*n*
Admiralty Island (Hawk Inlet), Alaska	Schoen et al. (1986)	115	6	24	12
Akamina-Kishinena/Flathead, B.C.	McLellan (1981)	446	5	200	5
Alaska Peninsula	Glenn and Miller (1980)	262	4	293	30
Alaska Range	Reynolds and Hetchel (1983)	710	6	132	11
Anderson-Horton Rivers, N.W.T.	Clarkson and Liepins (1989)	3433	7	1182	14
Central Northwest Territories	This study	8171	19	2434	35
Copper River Delta, Alaska	Campbell (1985)[a]	295	2	174	4
East Front Montana	Schallenberger and Jonkel (1980)	747	5	226	3
Eastern Brooks Range, Alaska	Reynolds (1976)[b,c]	702	5	230	8
Ivvavik National Park, Yukon	MacHutchon (1996)[d]	447	8	149	15
Jasper National Park, Alberta	Russell et al. (1979)[d]	948	6	331	6
Kananaskis, Alberta	Wielgus (1986)	1198	4	179	5
Khutzeymateen River Valley, B.C.	MacHutchon et al. (1993)[d]	130	4	52	13
Kluane National Park, Yukon	Pearson (1975)	287	5	86	8
Kodiak Island, Alaska	Barnes (1990)	185	6	71	33
Mackenzie Mountains, N.W.T.	Miller et al. (1982)			265	6
Mission Mountains, Montana	Servheen and Lee (1979)	1398	3	133	2
Noatak River, Alaska	Ballard et al. (1993)	1437	15	993	33
Northern Yukon	Nagy et al. (1983*b*)[e]	645	6	210	8
Revelstoke, B.C.	Woods et al. (1997)[c]	318	23	89	14
Selkirk Mountains, Idaho	Almack (1985)			402	2
South Fork Flathead, Montana	Mace and Jonkel (1979,1980)	286	5	99	2
Tuktoyaktuk Peninsula, N.W.T.	Nagy et al. (1983*a*)[e]	1154	7	670	
Upper Susitna River Basin, Alaska	Ballard et al. (1982)[c]	769	10	408	13
West-Central Alberta	Nagy et al. (1988)[e]	1918	17	364	
Western Brooks Range, Alaska	Reynolds (1980)	872	14	225	35
Yellowstone National Park, Wyoming	Blanchard and Knight (1991)	874	28	281	48

[a]Cited in LeFranc et al. (1987:28–30).
[b]Ranges calculated using the modified exclusive boundary technique.
[c]Estimate contains same multiannual ranges. J.G. Woods, B.N. McLellan, D. Paetkau, M. Proctor, and C. Strobeck, 1997, West slopes bear research project: second progress report, Parks Canada, Revelstoke, British Columbia, Canada.
[d]Weighted means calculated from data presented.
[e]Weighted means cited in Nagy and Haroldson (1990). For females, data is presented as the midpoint between the mean for females with and without young except for the Northern Yukon, where the mean is only for females without young.

females ($F_{3,54} = 4.79$, $P = 0.005$) and males ($F_{3,42} = 3.35$, $P < 0.05$) continued to reveal season effects. Females increased movement rates from spring to summer (Tukey's HSD test, $P < 0.05$), and decreased rates from summer to autumn (Tukey's HSD test, $P < 0.05$). Males decreased movement rates between spring and autumn (Tukey's HSD test, $P < 0.05$). A general trend from a high rate of movement in spring (males) and summer (females) to lower rates in autumn was clear (Fig. 2).

Annual Ranges versus Primary Productivity

The mean 95% MCP annual range for adult males in this study was 8,171 km² (SE = 1,309, $n = 19$); for females it was 2,434 km² (SE = 647, $n = 35$). Both means were larger than the mean ranges calculated using the 95% fixed kernel technique with LSCV; however, results of a paired t-test indicated no difference ($t_{53} = 0.18$, $P = 0.86$) between the estimates produced by the 2 methods.

A survey of the published and unpublished literature revealed 27 study areas in North America for which estimates of grizzly bear home ranges have been reported (Table 1). We found a significant negative relationship between documented North American grizzly bear range sizes and primary productivity for respective study areas ($F_{1,49} = 19.0$, $P < 0.001$; Fig. 3). Male grizzly bears, in general, possessed larger ranges than female grizzly bears ($F_{1,49} = 20.5$, $P < 0.001$; Fig. 3). Slopes for male and female samples did not differ ($F_{1,48} = 0.04$, $P = 0.85$).

DISCUSSION

Annual ranges and seasonal movement rates for barren-ground grizzly bears in the SGP were always greater for males than for females. Gau (1998) determined that male grizzly bears in the SGP have higher daily energy requirements than females. Generally, a larger energy demand will necessitate a larger area for food gathering unless food is superabundant (McNab 1963). Male grizzly bears also tend to wander more in search of mates, which would further increase male ranges and movement rates.

We failed to detect differences among females of differing family status with regard to annual ranges. Few studies have compared ranges and movement rates 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 also has been observed among female grizzly bears by Blanchard and Knight (1991) in Yellowstone National Park, Nagy et al. (1983*a*) on the Tuktoyaktuk Peninsula, Northwest Territories, and MacHutchon (1996) in Ivvavik National Park, northern Yukon. Non-significant differences in ranges of females with cubs and females without cubs have been obtained from brown bears in southcentral Alaska (Ballard et al. 1982), on Kodiak Island (summer ranges compared only; Barnes 1990), and in the Khutzeymateen valley of British Columbia (MacHutchon et al. 1993). Real differences among ranges of female grizzly bears of differing family status likely do exist, but the differences may be only of short duration (e.g., occurring only during the first few seasons after cubs of the year leave dens) and hence difficult to test with the sample sizes of most telemetry studies.

Seasonal trends in movement rates for barren-ground grizzly bears in the SGP likely reflect seasonal changes in behavior. For example, male barren-ground grizzly bears travel at their highest rates during spring, when they are searching for mates. The increase in female seasonal movement rates from spring to summer and the high rates of movement exhibited by both sexes at that time probably results from low summer food availability, which may predispose bears to wander more in search of food. Fat stores reach annual lows in the summer, when female caribou aggregate on calving grounds beyond the ranges of most study animals and prior to the ripening of berries (Gau 1998). The subsequent decrease in movement rates by both sexes as the summer progresses likely reflects increased food availability. By late summer, caribou return to the central study area (where the majority of bears in this study were collared) and berries peak in abundance. Movements of bears likely lessen when food supply increases, and vice versa. For example, an inverse relationship between range size and annual hard mast (acorns [*Quercus* spp.], hickory nuts [*Carya* spp.], hazel nuts [*Corylus* spp.]) production was documented for female black bears in North Carolina (Powell et al. 1997). Following the closure of garbage dumps in Yellowstone National Park (1968–70), the mean annual ranges of male and female grizzly bears increased 5-fold before apparently levelling off in the mid-1980's (Craighead et al. 1995).

The annual ranges of barren-ground grizzly bears in the SGP are the largest ranges yet reported for grizzly bears in North America. This may be a result of several factors, including low density and habitat quality. Nagy and Haroldson (1990) concluded that differences in the size of annual ranges among 4 populations of grizzly bears were due largely to differences in population density. Low densities resulting from substantial human-caused mortality or other factors could feasibly reduce competition for space and allow bears to use resources over larger ranges than at higher densities. Results of our review show a significant inverse relationship between grizzly bear range size and primary productivity. This leads us to conclude that habitat quality is likely a primary determinant of grizzly bear home range size at the geographic scale, hence the large annual ranges of barren-ground grizzly bears relative to other populations. However, variation about our regression lines suggests that factors other than habitat quality (including density), acting on local or geographic scales, may also be of importance in determining range sizes in grizzly bears.

Although some variation in the data on range sizes no doubt resulted from differences in annual range estimation techniques and sample sizes among studies, there are several other possible contributors. For example, the use of ecocenters (Craighead et al. 1995) by some brown bear populations may contribute to smaller ranges than would be expected from primary productivity alone. Ranges may also be inflated beyond those predicted by primary productivity if bears travel with migrating food sources such as caribou. We suspect that several bears in this study tracked the spring migration of caribou, a behavior that has been documented in barren-ground grizzly bears of northern Alaska (Reynolds and Garner 1987). Topography (Pearson 1975) and availability of denning sites (Schallenberger and Jonkel 1980) may further affect range sizes, as might individual variation and human influences (Jonkel 1987); however, these factors are probably important only at local scales.

MANAGEMENT IMPLICATIONS

Grizzly bears in the SGP have large spatial requirements. This agrees with results of other studies of barren-ground grizzly bears (e.g., Reynolds 1980, Nagy et al. 1983*a*, Clarkson and Liepins 1989, Ballard et al. 1993), although ranges in this study are much larger than any previously reported range estimates for grizzly bears. Large ranges may put individual bears in contact with humans even when camps or mine sites are of considerable distance from the core of the home range of an animal. Furthermore, individual ranges could encompass several camps that are tens or even hundreds of kilometers apart. Barren-ground grizzly bears, especially those of the SGP, may therefore be highly susceptible to human activity. Management of bears in the SGP should focus on maintaining low levels of human-caused mortality, with the realization that communities, hunting camps, and mining-exploration camps may impact bears from more than just the general vicinity. Estimates of bear population status and trends should be monitored for the region to ensure that the cumulative effects of human activity on bears, including mortality, are within sustainable limits.

It is important to note that primary productivity accounts for considerable variation in the average size of grizzly bear ranges. This may help us interpret why the ranges of barren-ground grizzly bears are so large relative to interior and Pacific-coastal populations, but it may also be used to predict the spatial requirements for grizzly bear populations that have yet to be studied. For instance, we predict that grizzly bears to the east of our study area ranging to Hudson's Bay, where primary productivity is lower, will possess annual ranges that are larger than those obtained for the SGP.

ACKNOWLEDGMENTS

We gratefully acknowledge H.D. Cluff and R. Mulders for their dedicated assistance with fieldwork and planning. Numerous private sector and government sponsors contributed to the project, including: BHP Diamonds Inc., BHP Minerals, the West Kitikmeot/Slave Study Society, the Government of the Northwest Territories, the University of Saskatchewan, RESCAN Environmental Services Ltd., Axys Environmental Consulting Ltd., Diavik Diamond Mines Inc., the Federal Department of Indian Affairs and Northern Development, the Polar Continental Shelf Project, Nunavut Wildlife Management Board, Echo Bay Mines Ltd., the Northern Scientific Training Program, and the Natural Sciences and Engineering Research Council of Canada.

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