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COMPARISONS OF SOME HOME RANGE AND POPULATION PARAMETERS AMONG FOUR GRIZZLY BEAR POPULATIONS IN CANADA

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Abstract: Kruskal-Wallis tests were used to compare annual and seasonal activity for adult males, adult females with cubs, and adult females without cubs among grizzly bears (*Ursus arctos*) of the northern Yukon Territory; Tuktoyaktuk Peninsula and Richards Island, Northwest Territories; west-central Alberta; and Jasper National Park, Alberta. Seasons were spring-early summer (15 May to 21 July) and mid-summer-early fall (22 July to 21 September). Multiple comparisons of mean class ranks from significant K-W tests ($P < 0.05$) were used to identify statistically distinct population subsets. These comparisons showed adult females without cubs in northern Yukon used annual and seasonal ranges that were significantly smaller than those for the same class of bears in the other study areas. Adult males in northern Yukon had the smallest annual home ranges. Bears in northern Yukon had lighter spring weights, were older, had the highest population density (26-30 bears/1,000 km²) and estimated standing biomass (243 kg/100 km²), and were unexploited. Differences in home range size estimates were primarily attributed to differences in population densities among study areas.

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Grizzly bear home ranges were reported to vary in size among regions in North America (Pearson 1975; Craighead 1976; Reynolds 1976; Nagy and Russell 1978; Russell et al. 1979; Reynolds and Hechtel 1980; Nagy et al. 1983a, b; IGBC 1987; Nagy et al. 1988); among sex, age, and reproductive classes within regions (Pearson 1975, Nagy et al. 1983b); among classes of bears within and among regions as changes occurred in habitat quality (Pearson 1977, Reynolds and Hechtel 1980, Knight et al. 1984), topographic structure (Pearson 1977, Hamer and Herrero 1983), and density caused by population growth or exploitation (Young and Ruff 1982). However, it is difficult to compare home range size estimates reported in the literature to determine if actual differences occur among populations and, if they occur, to identify the factors that may cause those differences. This is because the methods used to collect data (tracking, duration, location sample sizes, sampling intensity) and calculate areas vary among studies (IGBC 1987).

In this paper we compare home range sizes of grizzly bears in northern Yukon Territory (NY) (Nagy et al. 1983a); Tuktoyaktuk Peninsula and Richards Island, Northwest Territories (TP) (Nagy et al. 1983b); west-central Alberta (WCA) (Nagy et al. 1988, 1989); and Jasper National Park, Alberta (JNP) (Russell et al. 1979). Similar telemetry sampling techniques were used in all studies to obtain location data. We used a categorical approach (Slade and Swihart 1983) to derive indices of annual and seasonal range size from location data obtained for equivalent classes of adult grizzly bears. Classed indices of range size were compared to determine if differences occurred among populations. Age, weight, density, standing biomass, maximum growth rates, known

man-caused mortality, and reproductive data (Russell et al. 1979; Nagy et al. 1983a, b; Nagy et al. 1989; Kingsley et al. 1988; M. Kingsley pers. commun. 1989) were compared among populations to help interpret the results of home range comparisons. Standing biomass combines information on density estimates and body size of individuals in a population and thus provides more meaningful comparisons of relative habitat capacities (Miller and Ballard 1982). Maximum standing biomass of large mammals occurs near K (Fowler et al. 1980).

The 4 populations compared occupied interior type ecosystems where salmon were not available. Although we did not have quantitative data to compare habitat quality among the ecosystems, we felt that any differences would be small when considered on a continental scale. As a result our underlying assumption was that if differences occurred in range size among the populations, they were primarily caused by factors that influenced population sociality, structure, and/or density rather than by differences in habitat quality.

We thank the Canadian Wildlife Service, Edmonton, Alberta for permission to use the data on the northern Yukon, Tuktoyaktuk Peninsula, and Jasper National Park and the Wildlife Biology Group, Alberta Environmental Centre, Vegreville, Alberta for the data on west-central Alberta. Studies in northern Yukon and Tuktoyaktuk Peninsula were supported by the Canadian Wildlife Service, and the Polar Continental Shelf Project contributed logistic and helicopter support on Tuktoyaktuk Peninsula. The west-central Alberta study was supported by the Alberta Government while that in Jasper National Park by Parks Canada and the Canadian Wildlife Service. We thank D.J. Mattson, M.C. Kingsley, and A.W.L. Hawley for their assistance and comments on interpretation of the data and 3 anonymous reviewers for their contributions to the manuscript.

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STUDY AREAS

Northern Yukon Territory

The NY study area encompassed the Arctic Coastal Plain, Arctic Plateau, Richardson Mountain, and British Mountain physiographic units (Bostock 1948, Oswald and Senyk 1977, Nagy et al. 1983a) (Fig. 1). The area features rugged mountains over 1,500 m above sea level, soils with continuous permafrost, and is north of tree line. The arctic climate is moderated by coastal influences (Oswald and Senyk 1977, Pearson and Nagy 1976, Nagy et al. 1983a). With the exception of fishing, hunting, and whaling camps along the coast, the area was unpopulated.

Indigenous fauna included grizzly bears, caribou (*Rangifer tarandus*), moose (*Alces alces*), wolves (*Canis lupus*), and ptarmigan (*Lagopus* spp.). The Porcupine caribou herd numbering approximately 172,000 animals migrated seasonally through the area (Urquhart 1983). Numerous migratory waterfowl and passerine species were seasonal residents. Primary foods consumed by bears included grasses and sedges, crowberries (*Empetrum nigrum*), soapberry (*Shepherdia canadensis*), roots of hedsarum (*Hedysarum alpinum*), and Arctic ground squirrels (*Spermophilus parryii*). Caribou remains were found infrequently in grizzly bear scats, but the importance of that food item may have been underestimated (Nagy et al. 1983a).

Tuktoyaktuk Peninsula and Richards Island, Northwest Territories

The TP study area encompassed part of the Pleistocene Coastlands of the Mackenzie Delta (Nagy et al. 1983b) (Fig. 1). The area is comprised of Pleistocene fluvial and deltaic deposits. Although some low hills occur on Richards Island and the south end of the Tuktoyaktuk Peninsula, most of the area is below an elevation of 60 m. Lakes cover about half of the total surface area. Vegetation includes boreal forest, forest-tundra transition, and tundra (Lambert 1973). Soils with continuous permafrost predominate. The climate is arctic and moderated by coastal influences. Oil and gas exploration activities occurred on- and off-shore on Richards Island. Fishing, hunting, and whaling camps were numerous in coastal areas. Human populations were centered around Tuktoyaktuk (pop. 500) and Inuvik (pop. 1,500).

Indigenous mammals included brown lemmings (*Lemmus sibiricus*), collared lemmings (*Dicrostonyx hudsonius*), Arctic ground squirrels, muskrats (*Ondatra zibethicus*), wolves, grizzly bears, and reindeer (*Rangifer tarandus tarandus*). The area encompassed the Reindeer

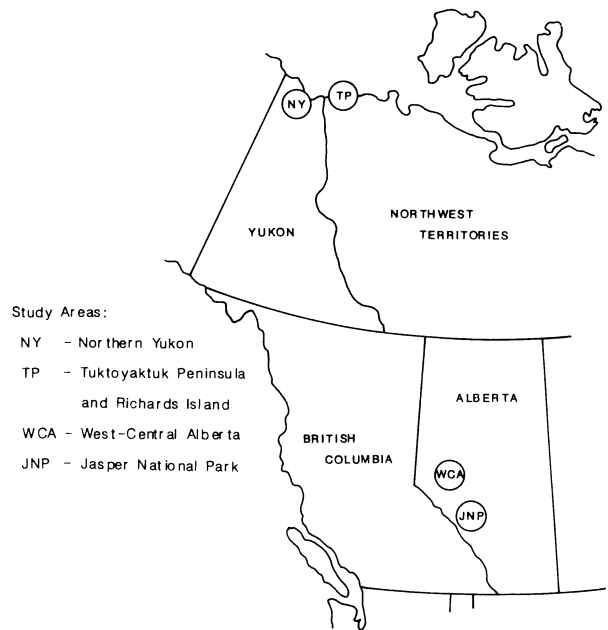


Fig. 1. Location of northern Yukon Territory; Tuktoyaktuk Peninsula and Richards Island, Northwest Territories; west-central Alberta; and Jasper National Park, Alberta grizzly bear study areas in Canada.

Grazing Reserve (approximately 5,000 animals). Willow ptarmigan (*Lagopus lagopus*) were common while numerous migratory waterfowl, including snow geese (*Chen caerulescens*) and whistling swans (*Olor columbianus*), and passerine species were seasonal residents. Primary foods consumed by bears included: grasses, sedges, forbs, horsetails (*Equisetum* spp.), roots of hedsarum, crowberry, kinnikinnick (*Arctostaphylos uva-ursi*), blueberries (*Vaccinium* spp), Arctic ground squirrels, and reindeer.

West-central Alberta

The WCA study area encompasses portions of the Wapiti Plains, Western Alberta Plains, and Rocky Mountain Foothills physiographic regions of west-central Alberta (Rose 1981) (Fig. 1). Elevations ranged from 900 to 1,800 m (Nagy et al. 1989). Vegetation is characteristic of Boreal Upland ecoregions, with lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) the dominant overstory tree species throughout the region. Muskegs were common. Climate was continental. There were irregularly located roads resulting from petroleum extraction, but ground travel was generally limited to all-terrain vehicles or foot travel. Logging activities had commenced on a limited scale.

Although extensive seismic activity and limited development of oil and gas wells had occurred, the area was unpopulated.

Indigenous wildlife included grizzly bears, black bears (*Ursus americanus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), wapiti (*Cervus elaphus*), moose, and wolves. Primary foods consumed by grizzly bears included: blueberries, horsetails, roots of hedysarum, and foliar parts of legumes (*Trifolium* spp.) (Nagy et al. in press).

Jasper National Park, Alberta

The JNP study area encompassed part of the Rocky Mountains in Jasper National Park (Russell et al. 1979) (Fig. 1). Elevation ranged from 1,500 to 3,200 m. The area is characterized by alpine and subalpine vegetation. Subalpine areas were dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), whereas large meadows occurred along valley bottoms. The climate is continental. The study area receives extensive recreational use during the summer months.

Indigenous wildlife included grizzly bears, black bears, mule deer, white-tailed deer, wapiti, moose, mountain caribou, and wolves. Primary foods consumed by grizzly bears included: roots of hedysarum, grasses/sedges/rushes, horsetails, and berries (*Shepherdia* spp.). The use of wapiti was documented (Russell et al. 1979).

METHODS

Capture, instrumentation, and aerial telemetry tracking methods used to obtain population and movement data in each study were described by Russell et al. (1979), Nagy et al. (1983a, b) and Nagy et al. (1988, 1989). In NY and TP, helicopter-assisted capture techniques used in treeless habitats allowed for the capture of most resident bears. In JNP and WCA, bears were captured in Aldrich leg hold snares, placed in baited cubbies or on trails at bait stations (Pearson 1976, Nagy and Russell 1978). Bears in all studies were aged by counting cementum annuli of sectioned premolar teeth (Stirling et al. 1977). Weights were measured using dial-faced or digital scales (± 1 kg capacity). Weekly radio-tracking flights were conducted during each study, if weather permitted. Bear locations were described using Cartesian coordinates rounded to the nearest 100 m. Locations were assumed to be independent because each bear was located a maximum of once per week.

Indices of annual and seasonal home range size were derived for 3 classes of adult bears (age ≥ 5 years) includ-

ing: adult males, adult females with cubs (age of young < 1 year), and adult females without cubs (lone adult females and adult females with young ≥ 1 year). Seasons were defined as spring-early summer (season 1: 15 May to 21 July) and mid-summer-early fall (season 2: 22 July to 21 September). These seasons reflect broad shifts in activity, physiology, and use of seasonally available foods. Season 1 is characterized by mating activity (Russell et al. 1979; Nagy et al. 1983a, b) and normal physiology (e.g., normal urea/creatinine ratios and foraging activity); season 2 by hyperphagia and associated behaviors (Nelson et al. 1983, Nelson et al. 1984).

Average activity radii (AR) from arithmetic centers (Dice and Clark 1953) were calculated for seasonal and annual ranges. AR distance values were calculated using the FORTRAN program HRMIND (Matchett 1989). Raw distance values were pooled by bear class to produce classed estimates of seasonal and annual range size for each study area (Slade and Swihart 1983). This categorical approach increases the effective sample sizes for statistical tests when using small location sets, and/or few individuals (Slade and Swihart 1983). A minimum of 4 locations per seasonal, and 10 locations per annual range were required for inclusion in the analysis.

Nonparametric Kruskal-Wallis (K-W) tests (Nie et al. 1975, Gibbons 1985) were used to compare class AR distance values for seasonal and annual ranges, ages, and weights when sample sizes allowed comparisons among ≥ 3 populations. Multiple comparisons (Gibbons 1985) were conducted on mean class ranks when K-W tests indicated significant results ($P < 0.05$) to identify significantly different population subsets. We used overall significance levels of 0.15 and 0.20 during multiple comparisons of ≥ 3 populations (Gibbons 1985). Significance levels for multiple comparisons are usually larger than those ordinarily used in inferences involving single comparisons so that any possible single differences are more likely to be detected (Gibbons 1985). The level of significance used depends in part on the number of populations being compared simultaneously (Gibbons 1985). Mann-Whitney (M-W) tests were used for comparisons of values between 2 populations. Spearman rank correlation tests were used to determine if the sizes of annual and seasonal AR were associated with age and number of locations for individuals within each class of bears, within and among areas.

Minimum convex polygon (MCP) estimates of annual home range size (Mohr 1947) were obtained from the published reports. Mean home range size estimates, weighted by the number of locations, were calculated for bear classes in each population by: 1) multiplying the area

in each individual's MCP estimate by the number of locations used in the calculation of that polygon, 2) summing these values across individuals, 3) summing the number of locations used in the calculation of individual MCP's, and 4) dividing 2) by 3) (Matchett 1985).

An average age structure was calculated for males and females in each population and used to compare age distributions among populations and determine median ages. Because northern bears vary greatly in weight by age class and from spring to fall, we used data from physically mature bears (males ages ≥ 10 years; females ages ≥ 7 years) handled on or before 15 June (Kingsley et al. 1988) for comparisons of weights among populations.

Estimates of population density, rates of known man-caused mortality, median ages of first cub production, median litter sizes, and reproductive intervals used were those previously calculated or were derived from data presented for NY (Nagy et al. 1983a), TP (Nagy et al. 1983b), WCA (Nagy et al. 1989), and JNP (Russell et al. 1979).

Estimates of bear biomass were calculated for each population (Miller and Ballard 1982). Predicted weights were calculated by age class for NY, TP, and WCA using the growth curve equation $w(a) = W(1 - \exp(-k_w(a - A_w)))^3$. Coefficients for the growth curves equation were previously fitted to the age weight data by Kingsley et al. (1988) and Kingsley (pers. commun.). The resulting predicted weights were combined with the average age structures derived for comparisons of age distribution to estimate bear biomass. Data were insufficient to estimate standing biomass for JNP bears.

RESULTS

Comparison of Range Sizes

Median AR for annual ranges of adult males differed significantly among the populations (Table 1). Multiple comparisons of K-W mean ranks revealed 3 overlapping population subsets including: NY and TP males, TP and JNP males, and JNP and WCA males. Median AR for adult males in season 1 did not vary significantly among the populations (Table 1). For season 2 ranges, median AR for WCA males were significantly larger than those for TP males; those for males of TP, NY, and JNP and NY, JNP, and WCA were statistically similar. Median AR for male season 2 ranges were smaller than for season 1. Although the age distribution of radio-collared bears varied significantly for each sample period, AR values for males were not correlated with age or location sample size.

Median AR for annual and seasonal ranges of females

Table 1. Values of annual and season 1 and 2 activity radii (AR) for adult male grizzly bears in northern Yukon (NY), Tuktoyaktuk Peninsula (TP), west-central Alberta (WCA), and Jasper National Park (JNP).

Bear class	Area	Number of ranges	Number distance measures	Median distance (km)
Annual ranges				
	NY	4	54	10.0 ^a
	TP	7	99	13.3
	JNP	6	97	15.4
	WCA	17	427	17.6
K-W $P < 0.001$				
Season 1 ranges ^b				
	NY	9	52	12.8
	WCA	20	163	13.5
	JNP	8	63	14.6
	TP	7	35	18.4
K-W $P < 0.22$				
Season 2 ranges				
	TP	9	67	7.2
	NY	6	31	7.3
	JNP	3	22	7.6
	WCA	16	126	11.6
K-W $P < 0.02$				

^a Bars indicate statistically distinct populations at a combined alpha of 0.20.

^b Season 1: 15 May to 21 July; season 2: 22 July to 21 September.

without cubs differed significantly among populations (Table 2). Median AR for annual and season 1 ranges for NY females without cubs were significantly smaller than those for WCA, JNP, and TP; those for WCA and JNP and JNP and TP were statistically similar. Median AR for NY females without cubs were also significantly smaller than those obtained for the other 3 populations during season 2; those for WCA, JNP, and TP were statistically similar.

Location data for females with cubs were only available from WCA and TP. Median AR for annual and season 2 ranges did not differ significantly between these 2 populations (Table 3). However, AR for WCA females with cubs were significantly smaller than those for TP during season 1.

The age distribution of radio-collared females differed significantly only for those included in the analyses of annual AR. Median AR were correlated with age during season 1 for females without cubs in NY ($P = 0.05$; $n = 7$; $r = 0.80$) and WCA ($P = 0.03$; $n = 22$; $r = -0.47$).

Table 2. Values for annual and season 1 and 2 activity radii (AR) for adult female grizzly bears without cubs in northern Yukon (NY), Tuktoyaktuk Peninsula (TP), west-central Alberta (WCA), and Jasper National Park (JNP).

Bear class	Area	Number of ranges	Number distance measures	Median distance (km)
Annual ranges				
	NY	8	122	5.1 ^a
	WCA	22	518	8.5
	JNP	5	66	9.3
	TP	20	341	10.1
				K-W $P < 0.001$
Season 1 ranges ^b				
	NY	7	44	4.7
	WCA	22	200	8.2
	JNP	5	38	10.2
	TP	19	131	14.8
				$P < 0.001$
Season 2 ranges				
	NY	11	72	4.1
	WCA	19	150	7.8
	TP	21	186	8.2
	JNP	1	7	11.9
				M-W $P < 0.001$

^a Bars indicate statistically distinct populations at a combined alpha of 0.20.

^b Season 1: 15 May to 21 July; season 2: 22 July to 21 September.

Table 3. Values for annual and season 1 and 2 activity radii (AR) for female grizzly bears with cubs in northern Yukon (NY), Tuktoyaktuk Peninsula (TP), west-central Alberta (WCA), and Jasper National Park (JNP).

Bear class	Area	Number of ranges	Number distance measures	Median distance (km)
Annual ranges				
	WCA	4	100	7.3 ^a
	TP	3	55	7.5
				K-W $P < 0.16$
Season 1 ranges ^b				
	WCA	4	41	4.9
	TP	3	25	10.2
				K-W $P < 0.001$
Season 2 ranges				
	TP	5	32	6.1
	WCA	4	41	6.5
				M-W $P < 0.62$

^a Bars indicate statistically distinct populations at a combined alpha of 0.20.

^b Season 1: 15 May to 21 July; season 2: 22 July to 21 September.

Median AR were correlated with location sample size for females without cubs in NY during season 1 ($P = 0.04$; $n = 7$; $r = 0.85$) and TP during season 2 ($P = 0.03$; $n = 21$; $r = -0.45$).

Average annual MCP's for adult males, weighted by sample size, were 645 km² in NY ($n = 6$), 948 km² in JNP ($n = 4$), 1154 km² in TP ($n = 7$), and 1,918 km² in WCA ($n = 17$). Weighted mean MCP values for females without cubs were 210 km² in NY ($n = 8$), 393 km² in JNP ($n = 3$), 476 km² in WCA ($n = 22$), and 644 km² in TP ($n = 18$). Weighted mean MCP values for females with cubs were 252 km² in WCA ($n = 4$) and 695 km² in TP ($n = 5$). These data support the results of our comparisons of annual AR values that adult males and females without cubs in NY used smaller annual ranges than those in WCA, TP, and JNP.

Comparisons of Population Parameters

Median ages of females did not differ among populations (K-W $P = 0.86$), however those for males did (K-W $P < 0.01$). Median ages of males in TP and WCA were similar; TP males were younger than JNP and NY males; and ages of males in WCA, JNP, and NY were similar (Table 4). Males were oldest in the NY and youngest in the TP populations.

Median spring weights of physically mature females differed significantly among the populations (Table 4). NY females were significantly lighter than those in TP and WCA. Median spring weights of TP and WCA females did not differ significantly. Jasper females were excluded from comparisons because only 1 spring weight was obtained. Median spring weights of males in NY and TP did not differ significantly (Table 4). NY males were significantly lighter than those in JNP and WCA. Median spring weights of males in TP, JNP, and WCA did not differ significantly.

Estimates of population densities for the NY were 2 to 6 times higher than those in the TP, WCA, and JNP (Table 4). Although helicopter-capture techniques used in the open habitats of NY and TP were undoubtedly more efficient than saturation snare capture techniques used in WCA and helicopter-assisted snare capture techniques used in JNP, differences in the methods did not account for the magnitude of differences in density estimates derived. These differences in population densities may be explained in part by the magnitude of estimated man-caused mortality rates reported for bears in the study areas (Table 4).

Median age of first cub production, litter sizes, and reproductive interval was similar among populations (Table 4). These reproductive parameters were not tested

Table 4. Some population parameters for grizzly bears in northern Yukon (NY), Tuktoyaktuk Peninsula (TP), west-central Alberta (WCA), and Jasper National Park (JNP).

	Study area			
	NY ^a	TP ^b	WCA ^c	JNP ^d
Median age (years):				
Males	10.5 (n = 51)	3.5 (n = 43)	6.5 (n = 21)	8.5 (n = 8)
Females	7.5 (n = 55)	6.5 (n = 43)	6.5 (n = 21)	8.5 (n = 8)
Median weight (kg):				
Males	172 (n = 22)	189 (n = 12)	243 (n = 9)	234 (n = 6)
Females	90 (n = 17)	105 (n = 21)	114 (n = 8)	91 (n = 1)
Density (bears/1,000 km ²)	26-30	4.2-4.7	4.4-4.7	9.8-11.7
Known man-caused mortality (%)	<1	12	9	15
Median age first cub production	7 (6-8 yrs) (n = 3)	7 (5-8 yrs) (n = 9)	6 (6) (n = 2)	7 (7) (n = 2)
Median cub litter size	2 (1-3) (n = 6)	2 (1-3) (n = 18)	2 (1-3) (n = 5)	2 (1-3) (n = 3)
Reproductive interval (yrs)	3-5	3-4	3-4	3-4

^a Nagy et al. (1983a)

^b Nagy et al. (1983b)

^c Nagy et al. (1989)

^d Russell et al. (1979)

statistically because of small sample sizes. Median age of first cub production was 6 years in WCA and 7 years NY, TP, and JNP (Table 4). Median litter size was 2 young per litter of cubs in all areas (Table 4). Reproductive (birth) interval was estimated at 3-4 years in TP, WCA, and JNP and 3-5 years in NY.

Estimates of minimum grizzly bear biomass were 243 kg/100 km² for NY, 61 kg/100 km² in WCA, and 35 kg/100 km² in TP. WCA also had an estimated minimum black bear biomass of 23 kg/100 km².

DISCUSSION

Estimates of annual and seasonal ranges differed significantly among the 4 populations studied. Females without cubs in NY consistently used annual and seasonal ranges that were significantly smaller than those used by the same class of adult females in the other 3

study areas. The fact that season 1 ranges of males did not differ suggests that males in all areas used similar sized ranges during the breeding season. The decrease in range size from season 1 to season 2 that was evident for males and females without cubs likely reflects a cessation of breeding activity and increased foraging efforts during the late summer hyperphagic period.

The pattern of differences among annual home ranges for adult males could have been a result of regional differences in the length of the active season for grizzly bears. Bears in all 4 areas began emerging from dens in mid-April to early May. Grizzly bears in NY and TP began denning during October (Nagy et al. 1983a, b) whereas those in JNP and WCA began during November (Russell et al. 1979, Barrett et al. in prep). Adult males in WCA occasionally remained active until January, although food resources were largely unavailable by the end of October. The generally larger home ranges of WCA and JNP males may have been because they were active for at least 1 month longer than those in NY and TP. However, home ranges of adult males in JNP were not significantly larger than those for TP males despite a longer active season. Similarly, home ranges of adult females without cubs in TP were significantly larger than those of the same class of females in NY where emergence and denning times were the same.

The pattern of differences that we observed in home range size could have been a direct result of differences in location sample sizes, in ages of bears radio-collared, and in topographic relief among the study areas. Although ages of collared animals differed significantly among study areas, AR index values generally were not correlated with age. Additionally, AR values generally were not correlated with location sample sizes. The average local topographic relief was estimated at less than 60 m on TP, 300 to 600 m in WCA and NY, and 1,200 to 1,700 m in JNP. Therefore, the indices of home range size would have been underestimated most in JNP, to a lesser extent in WCA and NY, and the least in TP. However, the magnitude of differences between median AR values for males and females without cubs among the populations was large enough that the patterns of significance would likely remain the same had we compensated for differences in topographic relief.

Habitat quality and population density have been recognized as primary factors influencing home range size (Sanderson 1966, Simon 1975, Pearson 1975, Slade and Swihart 1983, Knight et al. 1984, Miller 1984). Territory range size in some species correlates inversely with availability of food (Ricklefs 1973). Rogers (1977) speculated that this may be the case with black bears on

a broad geographic scale. Young and Ruff (1982) speculated that home range size among female black bears in northeastern Alberta was inversely related to population density. Female black bears may have been more sensitive to crowding and responded by occupying smaller home ranges when the population doubled over a 3-year period (Young and Ruff 1982). Rogers (1977) reported that average territory size for black bears in northeastern Minnesota did not differ significantly during years of abundant or scarce food supply, but speculated that the lack of difference may have been due to high bear densities. However, females did extend their activities into adjacent ranges left vacant when neighboring females were killed (Rogers 1977). The observations of Rogers (1977) and Young and Ruff (1982) suggest that the size of bear home ranges can vary not only on a geographic scale as quality varies among habitat types, but also within single habitat types as population density varies.

Population density data were available for the 4 populations studied, but we did not have quantitative data with which to compare habitat quality. However, body weights have been used as "surrogate indices" of habitat quality for grizzly bear populations (IGBC 1987). Blanchard (1987) found that females in areas with reliable, high value foods (meats, berries) during summer and fall attained greater size, matured earlier, and had larger litters than females with relatively low value foods (roots).

Comparisons of spring body weights showed that median spring weights of physically mature males and females were largest in WCA, followed by JNP, TP, and NY. In predicted asymptotic spring weights and lengths of both sexes, the WCA bears were largest at most ages, the TP bears second largest, and NY bears the smallest (Kingsley et al. 1988, M. Kingsley pers. commun.). In addition, maximum growth rates for male grizzly bears were 20 kg/year in NY, 24 kg/year in TP, and 30 kg/year in WCA (Kingsley et al. 1988, M. Kingsley pers. commun.). Similarly, those for females were 15 kg/year in NY, 19 kg/year in TP, and 25 kg/year in WCA. If spring body weights are used alone as indices of habitat quality, then it would appear that habitat quality was the poorest in NY and the best in WCA and JNP.

If grizzly bear home range sizes were inversely correlated with food supply among our study areas (i.e., large range size-poor habitat), and body weights are a good indices of habitat quality, then NY bears should have had the largest home ranges and those for WCA and JNP bears the smallest. However, if home range size for NY bears was small because of better habitat, why were the NY bears the lightest in weight and why did they have the

lowest maximum growth rates?

Rogers (1977) reported that young black bears with relatively exclusive feeding areas grew faster than those that fed in competition with older bears. Better nourished bears achieved larger body size and began reproducing sooner than did less well nourished ones (Rogers 1977). In Texas, white-tailed deer had greater body weights in high quality habitats with medium to low population density (Cook 1984). Weight and antler measurements of bucks declined as their populations increased in density and as competition for preferred forage intensified (Cook 1984).

Population densities in NY were 2 to 6 times greater than those reported for TP, WCA, and JNP. The NY population occupied a relatively stable undisturbed environment, was in a state of long term equilibrium (Nagy et al. 1983a), and was undoubtedly at carrying capacity. Populations in TP, WCA, and JNP had been subjected to substantial rates of man-caused mortality for at least a decade (Nagy et al. 1983a, b, 1989). The estimated minimum standing grizzly bear biomass in NY was approximately 7 times greater than in TP and 4 times greater than in WCA. In general, the NY study area supported more small body size, slow growing bears but had a higher standing biomass of bears than the other areas.

As a result, we suspect that the differences we observed in annual home range size among the study areas were largely due to differences in population density. The small home ranges, body weights, and lower maximum growth rates of NY bears were most likely a result of competition for available space and food resources within a population at or near carrying capacity. In TP, WCA, and JNP, where man-caused mortalities have reduced grizzly bear densities below carrying capacity, competition for space would have been reduced allowing bears to use resources over larger annual ranges. The energetic costs to individuals of movements within larger home ranges may have been offset by greater exclusive use of foods, resulting in larger body size and higher maximum growth rates. This conclusion appears to be substantiated by TP, WCA, and JNP having fewer but larger, faster growing bears with larger home ranges.

Habitat quality undoubtedly determines the minimum size of an annual home range that will support a bear within a given habitat type. However, it seems clear that population density plays an important role in determining the actual range size used. We suggest that accurate inferences about the relationship between home range size and habitat quality can only be derived by comparing populations that are at carrying capacity.

CONCLUSIONS

Based on our comparison of home range indices and population parameters we concluded that:

1. Grizzly bear home range size is a function of both habitat quality and population density.
2. Physical fitness as measured in body weights is a function of habitat quality and population density.
3. If body weights of grizzly bears increase as population density decreases, and reproductive success is related to body weight, then the overall physical fitness and reproductive success of a population may increase when numbers are maintained below maximum carrying capacity.
4. As density increases, population growth may be progressively limited by the proportion of females that can adequately meet nutritional requirements for successful reproduction. In a high density population, the home ranges of all breeding females may be adequate in size to allow them to produce cubs in years of abundant or average food production. However, only those breeding females that occupy home ranges in the best habitats may produce cubs during years of poor food production.
5. Body weights cannot be used as reliable indices of habitat quality in the absence of information on population density.
6. Studies are required that quantitatively assess habitat quality through estimates of per unit area biomass available to bears before comparisons of habitat quality can be made among areas occupied by grizzly bears.

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