HABITAT AND SPATIAL RELATIONSHIPS OF BLACK BEARS IN BOREAL MIXEDWOOD FOREST OF ALBERTA

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Abstract: Habitat and spatial relationships of 47 radio-collared black bears (*Ursus americanus*) were studied in 1975 and 1976 on 218 km^2 of boreal mixedwood forest in east-central Alberta. Mean sizes of areas occupied by bears were larger ($P < 0.05$) in 1976 when food was scarce than in 1975 when food was abundant; 102 km^2 and 39 km^2 in 1976 compared to 65 km^2 and 19 km^2 in 1975 for males and females, respectively. Bears engaged in 2 types of excursionary movements away from areas in which they were usually located. Short-range excursions occurred throughout the non-denning period, typically did not exceed 10 km in distance and 4 days in duration, and resulted in an expansion of areas occupied by bears when natural foods were scarce. Long-range excursions occurred during late summer and fall each year, averaged 23 km in distance and 47 days in duration, and were apparently a response to annual changes in the distribution of preferred foods. Home ranges of females, exclusive of short-range excursions, were generally stable in size and location each year regardless of food abundance. Scat analyses indicated the most important food-bearing plants were vetchling (*Lathyrus* sp.), wild sarsaparilla (*Aralia nudicaulis*), bearberry (*Arctostaphylos uva-ursi*), blueberry (*Vaccinium myrtilloides*) and hazelnut (*Corylus cornuta*). Aspen (*Populus tremuloides*) stands were the most abundant and important food-producing cover type because it contained foods eaten by bears during all seasons, whereas muskeg was the poorest food-producing cover type. Adult females selected aspen ($P < 0.05$) and avoided muskeg ($P < 0.05$) when natural foods were scarce; use of cover types reflected availability when natural foods were abundant. No differences were evident in the use of cover types by females with cubs and those without cubs. Adult males selected aspen ($P < 0.05$) and avoided muskeg ($P < 0.05$) each year regardless of food availability, and avoided jack pine (*Pinus banksiana*, $P < 0.05$) when blueberries were scarce there.

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The distribution and abundance of preferred foods are important factors in the daily lives of black bears. Bears adjust foraging strategies when natural foods are in short supply (Hatler 1967, Rogers 1976) and the sizes of bear home ranges, especially those of females, may reflect food availability (Amstrup and Beecham 1976, Garshelis and Pelton 1981). Moreover, Rogers (1976) intimated that bears are not always able to secure adequate food and that bears in poor physical condition are commonly observed during years when natural foods are scarce. Indeed, Hatler (1967) reported numerous emaciated bears in Alaska during a year when blueberries (*Vaccinium uliginosum*) were scarce.

Few studies, however, have described habitat availability and use among black bears and none has focused on the boreal mixedwood forest (Rowe 1959) of Canada. Furthermore, bear-habitat relationships usually have been determined indirectly through scat analysis (Tisch 1961, Hatler 1967, Beeman and Pelton 1980). This study directly examines the relationships between bears and their habitat in the boreal mixedwood forest and incorporates scat analysis and radiotelemetry. In this paper we describe the spatial relationships of bears in response to changes in food distribution and abundance, seasonal habitat use by different age and sex groups, and habitat use in relation to foods eaten by black bears.

This study is part of a long-term project initiated in 1968 by the Alberta Dep. of Energy and Nat. Resour. and continued from 1974 through spring 1978 under the auspices of the Dep. of Wildl. Ecology, Univ. of Wisconsin-Madison. We gratefully acknowledge the field assistance provided by B. Young, W. Tietje, T. Kemp, C. Ballweg, G. Kemp, J. Pelchat, and Fish and Wildlife Officers from the Alberta Dep. of Energy and Nat. Resour. Financial support was provided by the Alberta Dep. of Energy and Nat. Resour. (Fish and Wildl. Div.), the Natl. Sci. Found. (Grant BMSS75-09186), the Res. Comm. of the Grad. School, Univ. of Wisconsin-Madison, Gulf Canada Resources, Inc., and the Alberta Oil Sands Environ. Res. Prog.

STUDY AREA

Field studies were conducted on 218 km^2 of boreal mixedwood forest 240 km northeast of Edmonton, Alberta. The study area is on the north and west shores of Cold Lake and is bordered to the north by the Cold Lake Air Weapons Range and to the south by the Cold Lake Indian Reserve. The southern boundary also abuts agricultural land which is used primarily for beef cattle ranching and small-grain farming. The western boundary is the Medley River and the eastern boundary is the Martineau River and the Alberta-Saskatchewan border (Fig. 1). With the exception of river valleys and a 150 m hill on the northern boundary, terrain is flat with a mean elevation of 580 m. Mean temperature for July is 17 C

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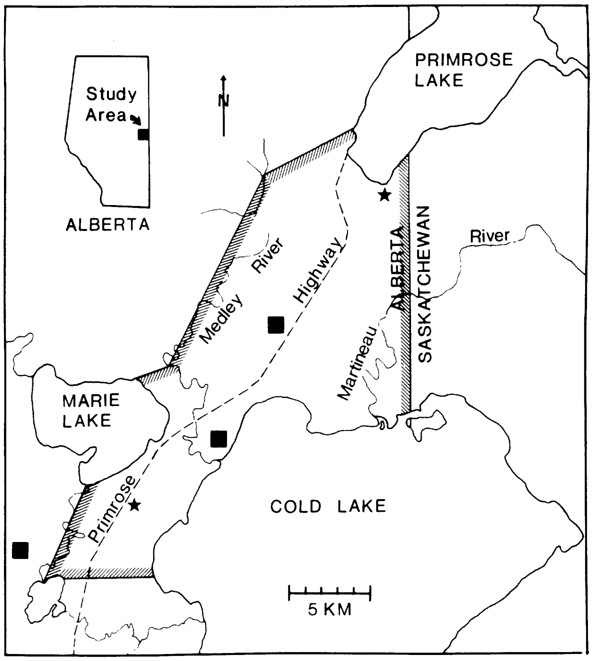

Fig. 1. Cold Lake study area (hatched line) showing major lakes and rivers, oil development sites (squares) and garbage dumps (stars).

and −19 C for January. Mean annual precipitation is 46 cm.

Uplands comprise 76% of the area's land surface. Aspen dominates 53% of the uplands with an understory of aspen, willow (*Salix* sp.), and rose (*Rosa* sp.). Grass, blueberry, vetchling, sarsaparilla, and bearberry are common ground plants. Mixed forests of aspen, white spruce (*Picea glauca*) and jack pine cover 37% of the uplands. The understory is mostly birch (*Betula papyrifera*), cranberry (*Viburnum* sp.) and saskatoon (*Amelanchier alnifolia*) while common ground plants are bearberry, blueberry, and bog cranberry (*Vaccinium vitis-idaea*). The remaining uplands are covered by white spruce (6%) and pine (2%). Species common in the spruce understory are alder (*Alnus* sp.), white spruce, and rose, whereas birch, cranberry, and saskatoon are common in pine understories. Ground cover includes moss, dogwood (*Cornus canadensis*) and bog cranberry in spruce stands; bearberry, blueberry and bog cranberry are common in pine stands.

Muskeg lowlands comprise the remaining 24% of the area's land surface of which 90% is covered with a dense forest of scrubby black spruce. Swamp birch (*Betula pumila*), willow, and black spruce dominate the understory while sphagnum moss (*Sphagnum* sp.) and Labrador tea (*Ledum groenlandicum*) mat the ground. Open sphagnum bogs fringed by tamarack (*Larix laricina*) prevail in the wettest areas. Two small open-pit garbage dumps are located in the area. The northern dump is used year-round basis by military personnel, and the southern dump is used seasonally by campers and cottage owners. The study area is further described by Young and Ruff (1982), and Tietje and Ruff (1980, 1983).

METHODS

Bears were captured from May through September each year using Aldrich foot snares and culvert traps. After immobilization with phencyclidine hydrochloride (Sernalyn), bears were color-marked with numbered plastic ear tags and tattooed. A premolar was extracted and sectioned to determine the age of each bear (Stoneberg and Jonkel 1966).

Radiocollars were placed on 14 female bears in 1975 and on 17 male and 16 female bears in 1976. A mobile telemetry system consisting of dual yagi antennas and a peak/null switch was used in daily attempts to locate radio-collared bears. Each radiolocation was formed by the intercept of 2 or 3 compass bearings from known locations. Bears that moved beyond the 5 km range of the mobile telemetry system were located from fixed-wing aircraft.

A cover map (1:31,680) of the study area and surrounding terrain was prepared by the Alberta For. Serv. from 1974 aerial photos. All continuous blocks of cover in excess of 4 ha, and all streams, roads, trails, and buildings were mapped. The cover map represented overstory vegetation and classified potentially merchantable tree species. We used a point method to determine the ground cover within each overstory cover type. We sampled 47 sites: 8 in aspen, 4 in pine, 8 in spruce, 16 in mixed forest, 9 in muskeg and 2 in land previously cleared of timber. All were chosen randomly within areas representative of each cover type. At each site, 3 lines each of 30 paces in length, were marked at 0°, 120°, and 240° from true north. At each pace, the species of plant less than 1 m in height and whose base was closest to the toe of the boot was recorded.

The cover map was used to plot all radiolocations for home range determination and to measure cover available to and used by bears. Radiolocations were recorded to the nearest 100 m using the Universal Transverse Mercator (U.T.M.) Grid System. Plots of 3 compass bearings often produced error triangles of various sizes. The radiolocation was taken to be the mean of the coordinates of the vertices.

Areas occupied by bears were delineated by the minimum area method (Mohr 1947). In cases where bears occupied 2 separate ranges at different times of the year, the total area occupied was taken to be the combined area of both ranges. We also followed Burt's (1943:351) definition of home range as that area traversed by an animal in its normal activities of food gathering, mating, and caring for young. Occupied areas included all radiolocations of bears, whereas home ranges excluded up to 5% of the locations which were most distant from location clusters.

To delineate cover available to bears, the cover map was partitioned using a scaled grid of 200 m^2. This grid produced 4 ha cells that were coded with location and dominant cover type. Summation of the area and cover composition within these cells was considered as cover available within each bear's annual and seasonal home range. This recognizes that social, physical, and topographical factors play a role in the size and location of home ranges and, therefore, cover availability (Rogers 1977, Garshelis and Pelton 1981).

Only radiolocations for bears that were independent of each other were used to determine the cover type utilized by bears. To determine the time period required for independence, we plotted the distance against time between 2 consecutive locations for a number of bears. After a 24-hour time period, each bear was frequently moving distances greater than the radius of its home range. Consequently, after 24 hours we were unable to predict portions of the home range that the bear might traverse and hence, this time period was used as the minimum required for independence between locations.

Not all radiolocations were sufficiently accurate to fix individual bears in a single cover type. Instead, the error triangle within which the bear was presumably located sometimes encompassed more than 1 cover type. In 1975, 27% of all radiolocations fell in this category, as did 14% in 1976. Exclusion of these locations from our analysis would have greatly reduced sample sizes. Therefore, we devised a method based upon probabilities to allow use of virtually all radiolocations. For example, if the cover within an error triangle was 60% aspen and 40% pine, the probability that the bear was in aspen or pine was 0.6 or 0.4, respectively. Error triangles composed of a single cover type, as was usually the case, had a probability of 1.0 assigned to that cover type. For an individual bear, the sum of the probabilities was equal to the number of radiolocations, and the sum of the probabilities for a cover type provided a relative index of time spent in that cover type. This method increased the proportion of usable locations to 98%. To evaluate preference or avoidance of a given cover type we employed the Bonferroni z statistic in conjunction with chi-square analysis (Neu et al. 1974).

Fresh bear scats were collected along roadsides, seismic lines and trails, and incidental to trapping and radio-locating bears. Scats were washed in graduated mesh screens (sizes 4, 7, and 10) to remove small unidentifiable food items. The remaining items were identified, dried, and weighed to the nearest decigram. Scats that could not be analyzed immediately after collection were preserved in a 10% formalin solution.

Thirty-seven permanent 1-m^2 plots were established to measure blueberry biomass each year. Eighteen plots were enclosed in wire cages with a 2.5 cm mesh. These were designed to measure blueberry production because they excluded birds and small mammals. The remaining 19 plots were enclosed by 15-cm-mesh cages that allowed passage of birds and small mammals and hence measured the availability of blueberries to bears.

RESULTS

Spatial relationships among bears were determined from telemetric observations of 12 females in 1975 and 14 females and 14 males in 1976 (Table 1). Radiolocations indicated that bears made excursions away from areas in which they were usually located. Short-range excursions typically did not exceed 10 km in length or 4 days in duration, whereas long-range excursions averaged 47 (range 28–62) days and 23 (range 14–35) km. Most bears engaged in short-range excursions whereas only a few individuals engaged in long-range excursions. Both types of excursions were much more common in 1976 than in 1975.

Bears engaged in short-range excursions throughout the entire non-denning period. The mean date for short excursions was 1 July (range 7 May–3 Sep, $N = 10$ bears) for females in 1975 and 8 July (range 13 Apr–30 Oct, $N = 13$ bears) and 24 July (range 23 Apr–26 Oct, $N = 8$ bears) for females and males, respectively, in 1976.

Short-range excursions were used to differentiate between home ranges and areas occupied by bears in a manner similar to that used by Alt et al. (1980) and Rogers (1977). Although the minimum area

Table 1. Black bear ranges in the Cold Lake study area in 1975 and 1976. Data are from bears > 1 year of age, tracked > 1 month and > 15 radiolocations.

	Females				Males			
	1975		1976		1975[a]		1976	
	Total	Mean	Total	Mean	Total	Mean	Total	Mean
Number of bears radio-tracked	12		14		14		14	
Age (years)		6.4		8.6		3.8		4.9
Days tracked	1,377	115	2,061	147	1,569	112	1,491	107
Number of locations	542	45	1,349	96	577	41	762	54
(A) area occupied (km^2)	225	19	548	39	916	65	1,431	102
(B) home range (km^2)	181	15	322	23	na	na	669	48
(A − B)	44	4	226	16	na	na	762	54

[a] From Young (1976).

method (Mohr 1947) was used to delineate both home ranges and areas occupied, home ranges typically excluded those locations associated with short-range excursions. Of the total locations obtained for any 1 bear, no more than 5% were excluded (Fig. 2). This method delineates an area of bear activity in close keeping with Burt's (1943:351) definition of home range.

Only bears > 1 year old and radio-tracked > 1 month with > 15 radiolocations were used for comparative purposes. The mean sizes of areas occupied by male and female bears that met these criteria were 65 km^2 (Young 1976) and 19 km^2 in 1975, whereas in 1976, these were 102 km^2 and 39 km^2, respectively (Table 1). These yearly differences were significant ($P < 0.05$) and because there was little difference in the number of days bears were tracked each year, it appeared that areas occupied by bears in 1976 were indeed larger than those in 1975. Home range sizes of female bears, however, were not significantly different (15 km^2 in 1975 vs. 23 km^2 in 1976; Table 1). Therefore the larger sizes of areas occupied by female bears in 1976 were due mostly to an increase in short-range excursions that year.

Long-range excursions generally occurred from August through September and were always directed south into agricultural or resort areas. In 1975, only 1 such excursion was observed, that of an adult female (No. 269) between 7 August and 26 September. In

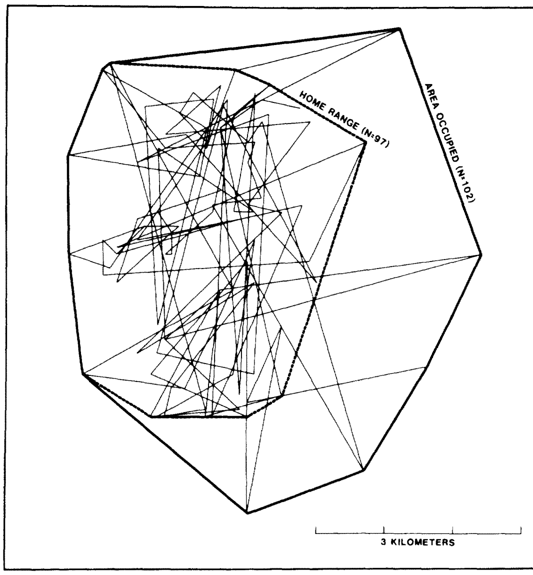

Fig. 2. Computer plot of radiolocations for a female black bear showing method of delineating occupied area and home range.

1976, 4 long-range excursions were observed, 3 by adult females (Nos. 301, 269, 236) and 1 by an adult male. The male occupied agricultural land 25 km south of his home range between 24 July and 23 August. Bear 301 left her home range on 5 August and was shot on 1 September at a small lakeside resort 35 km away. Bear 269 was 14 km south of her home range between 24 July and 31 August, and bear 236 was 16 km south of her home range between 4 August and 4 October. Bears 236 and 269 were most frequently observed at a dump during August; however, bear 236 extended her excursion south into agricultural land during September. We also suspected that bear 236 made a similar excursion in 1975 because she was not found on her home range between 29 July and 2 October of that year.

Telemetry data indicated that home ranges of adult females displayed little overlap (Fig. 3). Because the study area was trapped intensively, especially in 1976, the lack of overlap was not simply an artifact of a low proportion of radio-collared females. Where overlap between females occurred, bears usually utilized the shared area at different times.

We also strongly suspect that most females occupying shared areas were siblings or females and their offspring. This was supported in part by direct observations of known filial relationships determined from marked offspring. In other cases, the birthdates of suspected offspring coincided with years in which the parent female was known or suspected to have produced cubs. For example, bears 132 and 133, siblings born in 1971, were the offspring of bear 52, as possibly was bear 139 who was born in 1969, the previous cub-bearing year (Fig. 3). Bears 97 and 100 were born in 1968 and 1970, respectively, and were presumably the offspring of bear 49 who had cubs in 1970 and therefore could have produced cubs in 1968. Also, bear 100 was trapped only within the home range of bear 49 as a cub, yearling, and subadult, as was bear 97 as a subadult. And finally, bear 269, born in 1970, was likely the offspring of bear 236 because the latter bore cubs in even-numbered years and both bears made similar long-range excursions each year. In the latter regard, Rogers (1977) also noted similarities in movement patterns within families and suggested learning and genetic factors may be involved.

In contrast, home range overlap was the rule among adult males (Fig. 4) and shared areas were often used simultaneously. For example, in 1976, home ranges of 2 adult males overlapped extensively

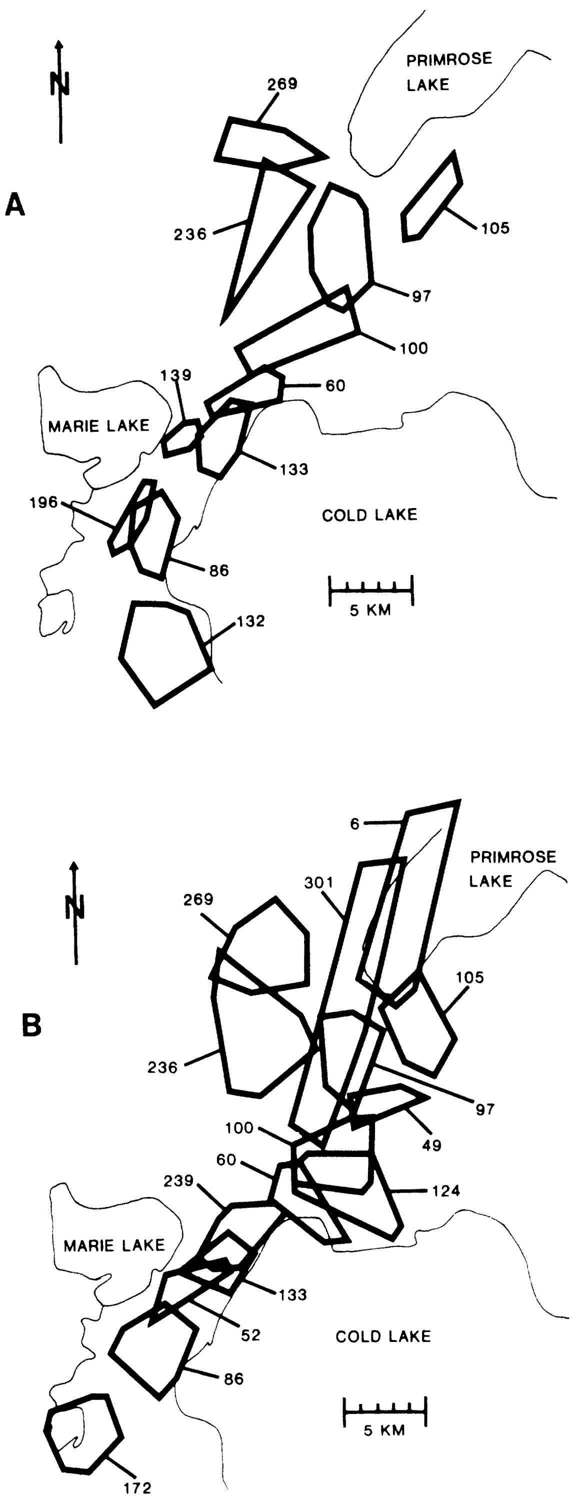

Fig. 3. Home ranges (exclusive of long-range excursions) of (A) 11 adult female bears in 1975 and (B) 15 adult female bears in 1976 at Cold Lake, Alberta.

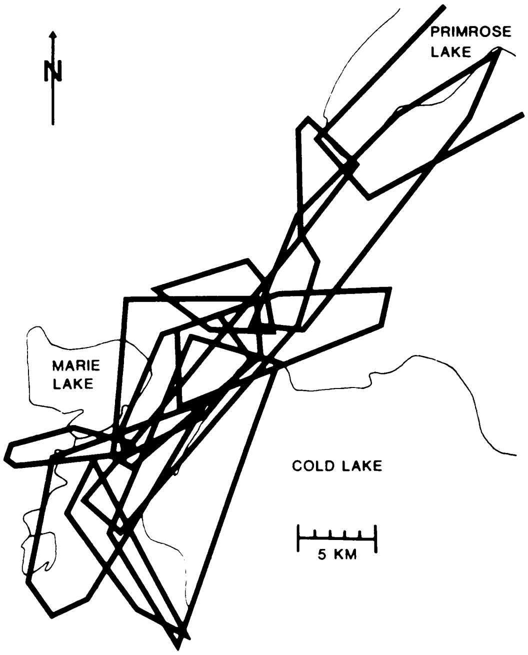

Fig. 4. Home ranges (exclusive of long-range excursions) of 12 adult male black bears at Cold Lake in 1976.

with those of 6 other adult males. Moreover, in 1976, less than 30% of the adult males on the study area were radio-collared, indicating that home range overlap was considerably more extensive than depicted.

Food Habits and Weights of Bears

Bear scats were collected on the Cold Lake study area and analyzed for contents each year from 1968 to 1976. However, the 1974 and 1975 data were lost and, therefore, the 1975 food habits reported here are based upon ocular estimates of scat contents made at the time of collection.

In 1975, most bear scats collected during spring and early summer contained green vegetation, probably vetchling because it was the primary food consumed by bears on our study area each year since 1968 (Alberta Fish and Wildl. Div., unpubl. proj. rep., 1973). From mid-July through mid-August, wild sarsaparilla and other early-ripening berries were the most abundant foods in bear scats. By mid-August blueberries had begun to ripen and correspondingly, a sudden and seemingly complete shift in bear diet was observed. Most scats collected from September to onset of hibernation consisted entirely of blueberries. This was similar to 1970 and 1973 when blueberries were abundant on the study area, and a composite of those years is presented here for comparison (Fig. 5).

Bear diets during the spring and early summer of 1976 were similar to those of 1975 in that bears ate mostly green vegetation. The percent dry weight of green vegetation in spring and summer bear scats was 73% and 62%, respectively, most of which was vetchling (Fig. 5). In addition, bears in spring fed on the buds and catkins of aspen trees and the berries of wild sarsaparilla during the late summer. The animal matter in scats was mostly bait, reflecting scat collection near bait sites incidental to trapping.

Bear diets during fall, 1976 varied dramatically from those of the previous year. Bears maintained a heavy reliance upon vetchling but use of blueberries was almost nonexistent (Fig. 5). Other fall foods important to bears in 1976 were bearberry and hazelnuts. Horsetail (*Equisetum* sp.), currants, and gooseberries (*Ribes* sp.), raspberries (*Rubus* sp.) and saskatoons were not commonly eaten by bears and probably reflected their scarcity on the study area. Cranberries, however, were plentiful during the fall of 1976, but few were eaten by bears.

Based on the assumption that food abundance should be reflected in well-nourished bears, we examined the seasonal weights and rates of weight change of individual bears with multiple captures during 1975 and 1976. Generally, the mean seasonal weights of bears > 1 year old were less in 1976 than in 1975 (Table 2). However, weights in spring of 1976 were still comparable to those in spring of 1975, and may have reflected the abundance of blueberries the preceding year which enabled bears to enter and emerge from their winter dens in good physical condition. The only cohort for which multiple captures

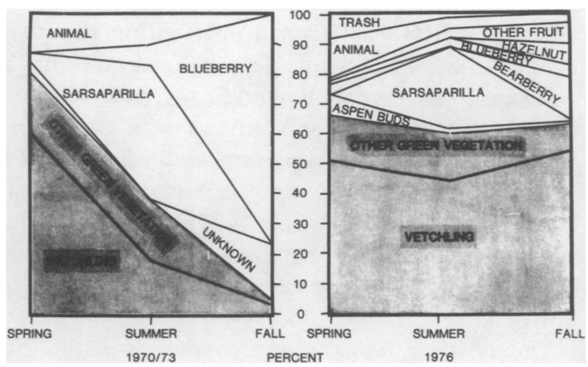

Fig. 5. Contents of bear scats collected at Cold Lake during years when blueberries were abundant (1970–73) and a year when blueberries were scarce (1976). Shaded areas indicate green plant matter.

Table 2. Seasonal weights (kg) of black bears in the Cold Lake study area, 1975 and 1976.

	Weight (kg)					
	Spring		Summer		Fall	
	1975	1976	1975	1976	1975	1976
Adults (≥4 years)						
Males						
N	7	19	3	53	2	6
Means	103	99	122	97	118	112
Females						
N	5	8	7	35	1	10
Means	56	69	82	77	121	89
Subadults (2–3 years)						
Males						
N	18	9	11	16	1	10
Means	59	56	67	57	89	68
Females						
N		3	1	5		2
Means		35	34	43		50

were obtained each year was that of subadult males. In 1975, most subadult males (7 of 10) gained weight throughout the trapping period, whereas in 1976, many (10 of 19) lost weight, especially during the spring (3 of 3) and fall (4 of 5) months. Weight loss by subadult bears indicated nutritional stress because these bears were still growing and should have gained weight.

Food Distribution and Abundance

Based on scat analysis, the more important food-bearing plant species on the study area were vetchling, wild sarsaparilla, bearberry, blueberry, and aspen buds and catkins. Vetchling was widely distributed in virtually every cover type except pine and muskeg, but was especially common along roadsides, streams and forest edges. Furthermore, it was abundant both years. Wild sarsaparilla occurred in moist aspen, mixed forest, and spruce sites. It appeared singly or in small patches, was not notably abundant either year, and was largely unavailable to bears after mid-August. Blueberry and bearberry were found in most cover types but were notably abundant only in pine and aspen types. Together, blueberry and bearberry comprised nearly two-thirds of the ground cover in open pine stands (Table 3).

Aspen was the most important food-producing cover type on the study area because it was the most

Table 3. Percent relative frequency of ground cover (< 1 m tall) in each cover type in the Cold Lake study area, 1976.

Plant species	Aspen (*N* = 720)	Spruce (*N* = 720)	Pine (*N* = 360)	Mixed forest (*N* = 1,440)	Muskeg (*N* = 810)	Cleared land (*N* = 180)
Green vegetation	30	9	15	12	32	42
Fruit						
Bearberry	12	5	33	2	T	1
Blueberry	15	2	30	2	3	
Wild sarsaparilla	T	1	T	T		
Other (gooseberry, rose, raspberry)	4	12	1	14	3	1
Subtotal	31	20	64	18	6	2
Non-Food Items (rock, bare ground, and vegetation not eaten by bears)	40	71	21	69	63	57
Total	101	100	100	99	101	101

abundant (39% of land area) and it contained foods that were important to bears during all seasons. These included aspen buds and catkins, and vetchling in early spring; sarsaparilla berries and vetchling in summer; and blueberries, bearberries and vetchling in fall. In contrast, pine comprised only 2% of the study area and produced blueberries and bearberries that were available to bears only during the fall; moreover, in some years blueberries were scarce.

To measure blueberry production and availability to bears, 37 permanent plots were established each year in blueberry patches under stands of open pine and aspen. Of these plots, 12 were destroyed by vandals in 1975 and 15 were destroyed in 1976. The remaining plots provided estimates of blueberry biomass each year.

The estimated biomass of blueberries produced and available to bears in 1975 declined significantly ($P < 0.001$) in 1976 (Table 4). These declines of 83% in biomass production and 88% in biomass available from 1975 to 1976 were paralleled by nearly identical percentage declines in the number of blueberries produced (82%) and available (88%), and clearly illustrate the inherent risks to bears for heavy reliance upon a single food item or source. Moreover, the fact that so few blueberries were observed in bear scats in 1976 may indicate that a mean density of 44 berries per m2 was too low for bears to forage efficiently.

The biomass of blueberries apparently consumed by animals other than bears in 1975 was 2.9 gm dry weight/m^2, or 28% of the biomass produced. In 1976, it was 0.9 gm dry weight/m^2 or 50% of the biomass of blueberries produced (Table 4). Consequently, it appears that as blueberry abundance decreases the proportion taken by animals other than bears increases.

Habitat Utilization

The 6 major cover types on the study area were aspen, pine, mixed forest, spruce, muskeg, and cleared land. Aspen and pine were single species stands, whereas mixed forest contained various combinations of aspen, pine, and spruce. Muskeg encompassed open and treed bog, and wet scrubby areas. The remaining vegetation consisted mainly of mature stands of white spruce and small parcels of cleared land. Excluding those areas covered by water, the study area was comprised of 39% aspen, 27% mixed forest, 24% muskeg, 2% pine, and 7% other vegetation.

Aside from the hibernation period, the number of independent radiolocations that could be used to assess cover type use was 460 for 10 female bears in 1975, 1,033 for 14 females and 581 for 14 males in 1976, respectively. Use of cover types by adult females in 1976 differed from that in 1975 ($P < 0.01$) and the cover types contributing most of the variation were aspen and muskeg. Adult females spent more time in aspen in 1976 (45%) than in 1975 (39%), caused largely by a shift in home range boundaries that made aspen more available in 1976 (Table 5). These same bears also spent less time in muskeg in 1976 (18% vs. 24% in 1975), again the result of a shift in home range boundaries. Adult females avoided muskeg in 1976 (Table 5).

In 1976, 40% of the radio-collared adult females had cubs with them during the entire instrumentation period. We found no differences in the use of cover between adult females accompanied by cubs and those without cubs that year. Apparently all adult females, regardless of their reproductive status, utilized cover in a similar manner.

In 1976 the use of cover by adult male and female bears was significantly different ($P < 0.001$). Adult males showed a strong preference for aspen, whereas adult females did not (Table 5). Adult males and females avoided muskeg ($P < 0.05$) that year, males more so than females. Adult males avoided pine ($P < 0.05$). All other cover types were used in proportion to their availability.

The use of cover by subadult bears is less clear because few females were radio-collared and 3 of the 5 males were sibling yearlings whose home ranges

Table 4. Numbers and dry weights of blueberries per m^2 in 2.5-cm- and 15-cm-mesh exclosures in the Cold Lake study area, 1975 and 1976.

	Number of berries				Dry weight of berries (gm)			
	1975		1976		1975		1976	
Mesh size	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$
2.5 cm	14	468	12	85	14	10.4	12	1.8
15 cm	11	366	10	44	11	7.5	10	0.9
Mean	25	423	22	66	25	9.1	22	1.4

Table 5. Percent of cover types available to (Av) and used by (Ut) black bears in the Cold Lake study area, 1975 and 1976.

Cover types	1975				1976								
	Female				Female				Male				
	Subadult		Adult		Subadult		Adult		Subadult[a]		Adult		Study area
	Av	Ut	Av	Ut	Av	Ut	Av	Ut	Av	Ut	Av	Ut	
Aspen	68	82[b]	37	39	56	35[b]	42	45	48	54	39	59[b]	39
Pine	0	0	1				1	0	0	0	3	1[b]	2
Mixed forest	10	6	28	30	20	42	25	28	23	28	28	24	27
Muskeg	12	5	28	24	23	20	24	18[b]	24	12[b]	21	10[b]	24
Other	9	7	6	5	0	2	8	10	5	7	8	6	7
Total	99	100	100	99	99	99	100	101	100	101	99	100	99
No. of bear locations	115		347		49		1,005		198		501		
No. of bears radio-collared	2		9		1		15		5		12		

[a] Includes 3 yearlings.
[b] Significantly different ($P < 0.05$) from cover available to bears as determined by Bonferonni z statistic (Neu et al. 1974).

were small and largely reflected cover used by the parent female. Nonetheless, subadult females preferred aspen in 1975, whereas they avoided aspen in 1976, and subadult males avoided muskeg in 1976 (Table 5).

DISCUSSION

Spatial relationships of bears differed between 1975 and 1976. Female bears engaged in more short-range excursions in 1976 and as a result, occupied larger areas that year. These differences cannot be explained by changes in bear densities or population age structure which varied little during this study. Food abundance, however, varied greatly and may provide the most plausible explanation for the observed changes in the spatial relationships of bears at Cold Lake.

Natural foods were abundant in 1975, especially during the fall when blueberries were so plentiful that most bear scats were comprised entirely of blueberries. As a result, bears were heavier and in better physical condition in 1975 compared to 1976. They were able to obtain adequate nutrition from foods close at hand and there was little need to engage in foraging excursions away from their home ranges.

In contrast, in 1976 some preferred foods were scarce. Many young bears and females with cubs were in poor physical condition, especially during late summer and fall. Green vegetation, consisting mostly of vetchling, made up approximately 60% of the food consumed by bears throughout the year. As noted by Jonkel and Cowan (1971) and Rogers (1976), when black bears are forced to feed on grasses and other green plants that are high in cellulose and relatively non-digestable, bears lose or only slowly gain weight. This apparently was the case in 1976. In apparent response to this shortage of preferred foods, bears engaged in foraging excursions away from their home ranges and occupied areas larger than those of bears in 1975.

Indeed, if areas occupied by bears fluctuate in response to food abundance, then the size of these areas, as determined by similar methods, should provide a relative index of food abundance between years and regions. Amstrup and Beecham (1976) suggested that regional variability in the sizes of areas occupied by black bears may reflect differences in the quantity, quality and distribution of preferred foods. Their estimates of the sizes of areas occupied by male (112 km^2) and female (49 km^2) bears in Idaho were only slightly larger than our estimates (102 km^2 for males, 39 km^2 for females) at Cold Lake in 1976. These figures are comparable because methodologies were similar and Idaho bears experienced a shortage of huckleberries (*Vaccinium globulare*) much like the shortage of blueberries at Cold Lake. Reynolds and Beecham (1980) reported home range sizes of 60 km^2 and 13 km^2 for adult males and females on this same Idaho study area in 1975. These data are remarkably similar to our estimates at Cold Lake in the same year. Combined with similar estimates of density and other population parameters, home range size may serve as a valuable index to annual and regional differences in habitat quality.

Short-range excursions occurred throughout the non-denning period each year. In 1976, a food-poor year, these excursions resulted in significant range expansion and suggested that bears were ranging widely in search of new food sources. Amstrup and Beecham (1976) noted that daily movements of bears in Idaho were significantly longer in a year when foods were scarce compared to a year when foods were abundant. Rogers (1977), however, found that short-range excursions of territorial females in Minnesota were more pronounced during the spring and early summer of each year and suggested that these females were investigating opportunities for territorial expansion. Hence, short-range excursions may serve a dual function, but the magnitude of change in home range during food-scarce years points to the former as being most important.

Long-range excursions are thought to be a response to changes in the distribution of preferred foods. All excursions of this type were during late summer and fall, and away from areas where natural foods were scarce and toward agricultural and berry-producing areas where foods were more abundant.

During the 2 years of this study, most long-range excursions (4 of 5) occurred during 1976 and most (4 of 5) were undertaken by female bears. These differences however, may simply reflect the larger number of bears radio-collared during the 2nd year as well as the larger number of radio-collared female bears compared to males. Furthermore, the size of male home ranges may mask the presence of long-range excursions as defined herein.

Bear 269 and probably bear 236, both adult females, engaged in long-range excursions in both 1975 and 1976. The area occupied by these bears during most of the year was dominated by treed muskeg and completely devoid of pine. As a result, they probably experienced food shortages during late summer and fall of each year, although natural fall foods were generally abundant elsewhere on the study area. These bears apparently undertook extensive foraging excursions each year to maintain their nutritional well-being.

According to Bray and Barnes (1967:8), similar types of excursionary movements have been reported in Colorado, Pennsylvania, Virginia, Wisconsin, and Yellowstone National Park. Piekielek and Burton (1975) and Kelleyhouse (1980) reported excursions of 14 km and 17 km by male black bears into food-rich areas in northern California. In Montana, Jonkel and Cowan (1971) described areas that did not support bears permanently but were used seasonally by bears from adjacent areas when food was abundant there.

Adjustments in the spatial relationships among bears in response to changes in the distribution of preferred foods have also been reported in Minnesota by Rogers (1977). Wide ranging foraging activities were observed for many male and female bears during late summer and early fall and, for some bears, these were annual occurrences. Thirty-seven female bears in Minnesota traveled an average of 27 km to food-rich areas, compared to 21 km for 4 females at Cold Lake. The longest distance recorded was 201 km by an 11-year old male in Minnesota.

By deleting short-range excursions from adult female home ranges at Cold Lake, areas were delineated comparable to those defined as territories by Rogers (1976) in Minnesota. Territorial overlap appeared greater in the Cold Lake study but this was probably due to a difference in methodologies. At Cold Lake, territories were delineated by the minimum area method (Mohr 1947), whereas in Minnesota they were outlined subjectively by drawing lines between areas used by neighboring territorial females. Regardless, the territories of adult females in these 2 studies show striking similarities. First, they are occupied by the same bear in the same area each year and, secondly, they are about the same size each year regardless of gross variations in the annual abundance of forage. Alt et al. (1980) also found geographic stability for bear home ranges in Pennsylvania.

Not all studies of bear spatial relationships report territorial behavior among adult females. In Washington, the home range distribution of 6 female bears age 3 years and older showed considerable overlap (Lindzey and Meslow 1977). However, this study did not examine filial relationships or excursionary movements. In addition, when the home ranges of only adult females were mapped, overlap was substantially reduced. Home range overlap among adult females in Idaho was also extensive, but when the smallest areas within which 75% of all locations were delineated for each female, overlap was minimal (Reynolds and Beecham 1980). The Idaho study also did not examine kinship relationships among female bears.

Adult females at Cold Lake were believed to be territorial even though our method of delineating individual home ranges showed overlap between some female bears (Fig. 4). Most overlap appeared to be between parent females and their progeny. Such range sharing has been reported in Montana (Jonkel and Cowan 1971) and Minnesota (Rogers 1977). Because adult females spend much time within their territories, these areas must produce sufficient forage to sustain them each year. However, territories probably did not evolve to protect foraging areas because adult females often forage on food-rich areas away from their territories. Moreover, the distribution of forage is often too unpredictable to be defended (Brown 1964).

Instead, territorial behavior by adult females may be a compromise between enhancing the survival of female offspring and obtaining an adequate diet from a dynamic and heterogeneous food resource. By establishing territories, by tolerating female offspring within these territories, and by subsequently allowing these offspring to establish territories adjacent to and overlapping that of the parent, adult females enhance the survival of their female offspring. This type of behavior ensures that the genotypes of the female parent will have a greater chance for perpetuation. On the other hand, because the distribution and abundance of food is at times highly variable, adult females must occasionally dispense with territorial behavior to obtain an adequate diet. Adult females will make excursions to more food-rich areas before denning, adequate nutrition being tantamount to survival and pregnancy success (Rogers 1976).

Home ranges of individual bears varied little in size and location from 1 year to the next and were areas within which bears spent at least 95% of their time. For this reason, cover types within home ranges were more representative of cover available to bears than was the composition of cover in the study area as a whole. This was especially true for individual adult females who spent most of their time in relatively small portions of the study area.

Bears use their habitat for such activities as resting, feeding, mating, playing and traveling. Because bears are often on negative energy budgets during much of their active year (Jonkel and Cowan 1971, Poelker and Hartwell 1973) and because fat deposition before denning is tantamount to survival and reproductive success (Rogers 1976), feeding must certainly be the most important of these activities. Consequently, use of cover by bears largely reflects their foraging activities, especially when natural foods are scarce. Foods were indeed scarce in 1976 and, because aspen was the principal food-producing cover in the study area, adult female bears spent more time in aspen that year than in 1975. Moreover, because muskeg provided little in the way of food for bears, it was avoided by adult females in 1976. At Fort McMurray, 300 km to the north of Cold Lake, Fuller and Keith (1980) reported that black bears also favored cover types that produced food and avoided those that did not in 1976.

The proportion of time bears spent feeding was probably much less in 1975 because nutritious food was more abundant that year. As a result, the use of cover by bears in 1975 was not nearly as selective as in 1976. This may be why, solely on the basis of food availability, we were unable to explain the observed use of cover by adult females in 1975. Moreover, it demonstrates that when natural foods are abundant, adult females are less selective in their use of available cover. When natural foods are scarce, adult females prefer covers that produce food and avoid those that do not.

Mixed forest and muskeg were not valuable food-producing covers on the study area. Most plant species in these areas were non-food items for bears and bears never selected these cover types. Muskeg occurred in the wet lowland areas, was difficult to traverse, and was a constant, and presumably aggravating, source of mosquitoes and blackflies. Mixed forest occurred in the drier upland areas, was comprised of stands of the largest trees in the study area, and was 1 of the easier areas to traverse. Bears probably used mixed forest for resting cover because it afforded more protection (Herrero 1972) and as travel corridors between feeding sites. Similarly, Kelleyhouse (1977) noted that black bears in northern California used mixed conifer forests for traveling, resting, and escape cover during all months of the year.

The use of pine by bears reflected the abundance of blueberries in that cover each year. Adult females used pine during the fall of 1975. Blueberries, however, were so abundant in 1975 that they were reasonably plentiful even after the bears had denned. As a result, blueberries were also a source of food for bears in 1976 and we observed blueberries in spring bear scats that year. In 1976, adult males avoided pine and adult females appear to have adjusted the boundaries of their home ranges such that pine was not available to them.

No age-related differences were evident in cover use by male bears. Previously at Cold Lake, Young and Ruff (1982) observed twice the percentage of subadult male (28% of 634) as adult male (14% of 346) radiolocations in the immediate vicinity of dumps. Exclusive of radiolocations in dumps, aspen use by adult males (55% of 297 radiolocations) was not significantly different than that of subadult males (50% of 455 radiolocations). These percentages are essentially identical to those of 1976, 59% and 54%, respectively. Hence, subadult males did not avoid habitat occupied by adult males and the 2 cohorts shared large portions of their ranges with each another. However, as evidenced by radiotelemetry, immediate spatial and temporal separation was achieved largely through subadult avoidance of adults.

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