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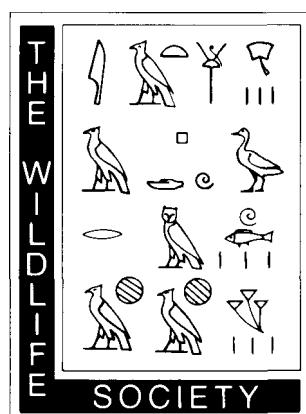
EFFECTS OF FOOD SUPPLY AND KINSHIP

ON SOCIAL BEHAVIOR, MOVEMENTS, AND

POPULATION GROWTH OF BLACK BEARS

IN NORTHEASTERN MINNESOTA

by

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FRONTICEPIECE. Above: Female F with 3 cubs in a shallow den on 19 March 1972. Female F was a member of 1 of 13 clans that had adjacent ranges and were studied through 2-4 generations each during 1969-84. Below: Looking southeast over aspen-birch-conifer habitat from near the center of the study area.

EFFECTS OF FOOD SUPPLY AND KINSHIP ON SOCIAL BEHAVIOR, MOVEMENTS, AND POPULATION GROWTH OF BLACK BEARS IN NORTHEASTERN MINNESOTA

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Abstract: Black bears *(Ursus americanus)* were studied in northeastern Minnesota from 1969 through 1985 to determine (1) the annual cycle of foraging and social behavior, (2) changes in mother-offspring relationships from birth through maturity, (3) the influence of food availability on social behavior, movements, and population growth, and (4) important habitat components. Studies were most intensive during 1971-76 when 28 males and 55 females were radio-tracked. The study area had relatively few fruit and mast species and a frost-free growing season of only 118 days. Crop failures were common and reduced the reproductive rate to less than half the biological potential. Females first reproduced at 4-8 years of age (average 6.3 years), depending upon food supply, and produced subsequent litters at 2-4-year intervals (average 2.28 years). Litters averaged 2.38 cubs. Cub survival was 59-88%, depending on food supply in the year of conception and the year of birth. Bears that supplemented their diets with garbage reproduced nearly twice as fast as the above. Density was 1 bear/4.1-6.3 km^2, including cubs.

The annual cycle of behavior was closely tied to the annual cycle of plant growth and fruiting. Bears emerged from dens in late March or April, depending in part on weather, but females and subadults remained lethargic until late April or early May when aspen *(Populus* spp.) catkins and young green vegetation became available. Mature females then re-established territories averaging 9.6 km^2, and mature males used overlapping mating ranges averaging 75 km^2. Mating began about 10 June and was essentially completed by 9 July when fruit began to ripen in abundance. Foraging then became the main activity until fruit and nuts disappeared in late summer. Sixty-seven percent of the males and 40% of the females foraged >7 km outside their territories or mating ranges in late summer or early fall, moving up to 200 km away before returning for denning. Adult males that remained in their mating ranges after the mating season spent a disproportionate amount of time in the buffer zones between female territories rather than inside them.

Despite generally solitary habits, bears behaved in accordance with kinship theory within a social order governed mainly by the distribution and abundance of food. Mothers recognized their independent offspring and tolerated them in their territories. Mothers avoided areas where their yearlings concentrated their activities, thereby allowing them to have nearly exclusive feeding areas. Young males voluntarily dispersed as subadults and settled 13-219 km away (average 61 km). Young females usually expanded their yearling ranges into adult territories. Mothers shifted away as their daughters expanded their ranges, thereby aiding daughters in obtaining territories. Adults of both sexes deterred immigration. The bears behaved as described above where food was dispersed, but formed hierarchies where food was clumped as at garbage dumps. There, female territories overlapped slightly, and males commonly tolerated individual distances of <2 m. Play was common among bears up to 4.7 years old around garbage dumps but was not seen elsewhere except among cubs. Adult females used garbage dumps in their territories but avoided other dumps where unfamiliar adult males congregated.

The denning period was 5-7 months. Very fat bears abandoned food and entered dens in late September. Less fat bears that found food continued to feed as late as early November. Bears in northeastern Minnesota achieved a deeper hibernation than has been reported from regions with shorter denning periods. Hibernating bears commonly did not awaken in midwinter until after several minutes of prodding. Overwinter mortality was <1% regardless of den type, but lightweight yearlings starved after emergence in spring. Starvation was the main cause of death among cubs and yearlings, and gunshot was the main cause of death among older bears. Bears commonly roamed farther in northeastern Minnesota than has been reported from other regions. A larger area of unbroken habitat may be needed to maintain this population than would be needed where food is more reliable and abundant. Habitat management practices beneficial to bears in northeastern Minnesota are identified.

CONTENTS

INTRODUCTION

The purpose of this study was to learn the social organization of black bears *(Ursus americanus)* in northeastern Minnesota and to identify factors that shape this organization and influence population growth. The study began in 1969. Social organization was a primary area of study through 1975 and was gradually reduced in emphasis as studies shifted to other aspects of bear biology during 1976-85. Study of social organization is a useful avenue toward understanding black bear movements, habitat use, population dynamics, and relations with

man. Information on social organization also is needed for development of social theory. Social relationships, and how they vary with kinship and food supply, have been studied much less in solitary mammals such as black bears than in the more gregarious species (Wilson 1975).

As has been found in other carnivores (Bekoff et al. 1984), black bear social organization is influenced by the distribution and abundance of food (Amstrup and Beecham 1976, Herrero 1978, Reynolds and Beecham 1980). Black bears may show territoriality (Jonkel and Cowan 1971),

home range overlap (Amstrup and Beecham 1976, Garshelis and Pelton 1981), or feeding aggregations (Herrero 1983). Jonkel and Cowan (1971) further found that mother-daughter relations were of long-term social importance, which suggests that black bears, although solitary, behave in accordance with kinship theory. The present study further investigated effects of food supply and kinship on behavior and social relationships.

Definitions of Terms.—In this report, cubs are bears <1 year old, yearlings are 1-year-olds, subadults are 2- and 3-year-olds, and adults are at least 4 years old. Residents are bears born in the study area and still living there or are immigrants that settled there. A territory is an area defended at least against members of the same sex and occupied more or less exclusively by an individual or a mother and her young. Family breakup is the more or less permanent separation of a mother from the close company of her offspring. Dispersal is movement from the mother's territory to a nonadjacent breeding area. Winter, spring, summer, and fall are used in the astronomical sense with equinoxes or solstices as the beginning and ending dates. Months are divided into thirds, with the 10-day portions referred to as early, mid-, or late.

DESCRIPTION OF THE STUDY AREA AND REGION

Studies were conducted mainly in the Superior National Forest in northeastern Minnesota. Studies were concentrated in a 300-km² area, termed the study area, where bears were captured and marked and where the majority of study individuals spent most of their time. However, bears were radio-tracked up to 200 km outside that area, and eartag returns were obtained from various parts of Minnesota, Ontario, and Wisconsin (Fig. 1). Bear habitat in the region was essentially continuous, with few physiographic barriers other than Lake Superior to restrict bear travel.

Vegetation in the study area and its close vicinity was 76% upland and 24% lowland with 59% being upland mixed coniferous-deciduous communities (Peek et al. 1976). Vegetation was typical of the northern Great Lakes region in that it contained components of both the boreal forest and the temperate deciduous forest (Maycock and Curtis 1960).
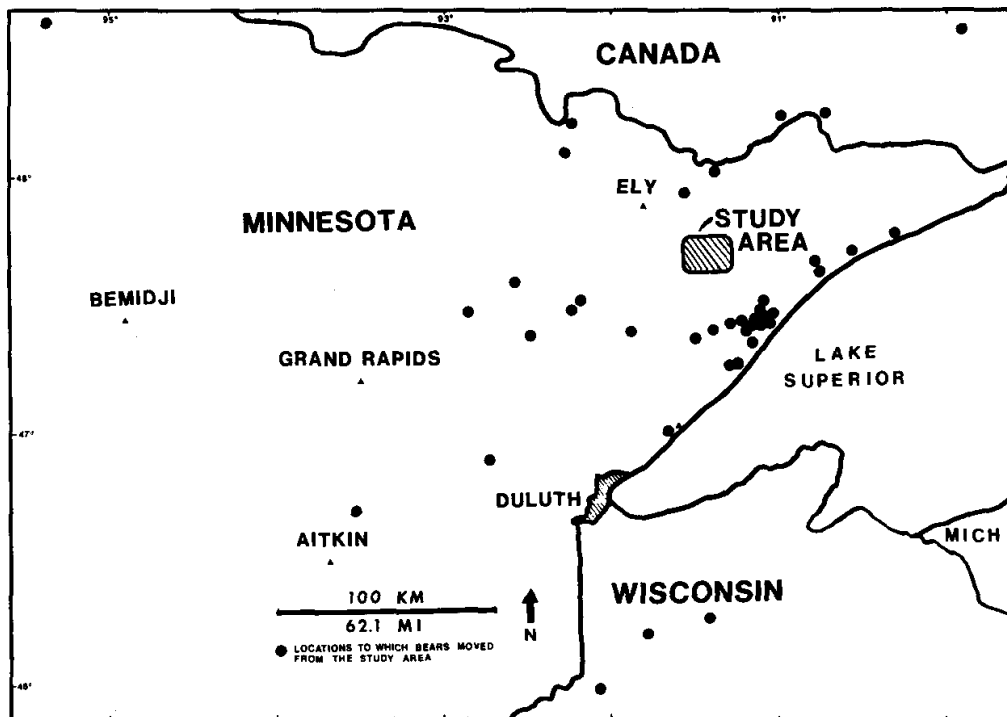
Fig. 1. The study area and the 40 longest movements outside it.

Common trees on uplands were quaking aspen *(Populus tremuloides)*, bigtooth aspen (P. *grandidentata)*, paper birch *(Betula papyrifera)*, red pine *(Pinus resinosa)*, white pine (P. *strobus)*, jack pine (P. *banksiana)*, white spruce *(Picea glauca)*, and balsam fir *(Abies balsamea)*. Common trees on lowlands were black spruce *(Picea mariana)*, balsam fir, white-cedar *(Thuja occidentalis)*, black ash *(Fraxinus nigra)*, and paper birch.

Climate of the region is cool-temperate. Temperatures at the Isabella Ranger Station in the study area ranged from —41 C to 33 C during 1969-75 and remained above freezing for an average of 118 consecutive days between mid-May and mid-September. Annual precipitation averaged 77 cm, including the water equivalent from 157 cm of snow. The ground typically was snow-covered from mid-November through at least mid-April except in 1973 when snow melted in late March and early April.

The study area was in an area of sandy and gravelly noncalcareous moraines formed by the southern edge of the Rainy lobe during the Wisconsin glaciation (Wright and Watts 1969, Ojakangas and Matsch 1982). Immediately to the north of the study area

was the vast Laurentian Shield characterized by abundant rock outcrops overlain by thin patches of glacial drift (Minn. Soil Atlas 1981). Fertility in both these areas was low due primarily to low moisture availability in the rooting zones (Minn. Cropland Resour. 1979, Minn. Soil Atlas 1981). In the study area, the low moisture was due mainly to the low moisture-holding capacity of the sandy soil on the moraines. On the Laurentian Shield, moisture availability was even lower because the soil was very shallow although somewhat loamier (Minn. Soil Atlas 1981). South and east of the study area and extending nearly to Lake Superior was an area of higher fertility (Minn. Cropland Resour. 1979) where soils were deposited by the Superior lobe of the Wisconsin glaciation (Wright and Watts 1969, Ojakangas and Matsch 1982). Soils there were deeper, loamier, and better able to hold water than those in the study area or farther north (Minn. Soil Atlas 1981).

An ecological inventory by soil scientists of the Superior National Forest revealed a general gradient of increasing vegetative productivity from north to south through the study area to Lake Superior.

Table 1. Ripening of major foods eaten by black bears in northeastern Minnesota.

Species	First ripe[a]	Peak availability[b]
Wild strawberries (*Fragaria* spp.)	Late Jun	Jul
Dwarf red raspberry (*Kubus pubescens*)	Early Jul	Jul
Serviceberry (*Amelanchier* spp.)	Early Jul	Mid-Jul-mid-Aug
Pin cherry (*Prunus pensylvanica*)	Early Jul	Mid-Jul-late Aug
Lowbush blueberry (*Vaccinium angustifolium*)	Mid-Jul	Mid-Jul-mid-Aug
Sourtop bilberry (*Vaccinium myrtilloides*)	Mid-Jul	Late Jul-late Aug
Wild sarsaparilla (*Aralia nudicaulis*)	Mid-Jul	Mid-Jul-mid-Aug
Red raspberry[c] (*Kubus strigosus*)	Mid-Jul	Mid-Jul-late Aug
Common chokecherry (*Prunus virginiana*)	Mid-Jul	Mid-Jul-late Aug
Red-osier dogwood[c] (*Cornus stolonifera*)	Mid-Jul	Late Jul-early Sep
Western thimbleberry[c] (*Kubus parviflorus*)	Late Jul	Aug
Rafinesque viburnum (*Viburnum rafinesquianum*)	Early Aug	Mid-Aug-mid-Sep
Roundleaf dogwood[c] (*Cornus rugosa*)	Early Aug	Late Aug-mid-Sep
Wild plum (*Prunus americana, P. nigra*)	Early Aug	Late Aug-mid-Sep
Beaked filbert (beaked hazelnut) (*Corylus cornuta*)	Early Aug	Late Aug-mid-Sep
Highbush-cranberrybush[c] (*Viburnum trilobum*)	Early Aug	Late Aug-late Sep
Hawthorn[c] (*Crataegus* spp.)	Late Aug	Early Sep-mid-Oct
Mountain-ash[c] (*Sorbus americana, S. decora*)	Late Aug	Early Sep-late Oct
Northern red oak[c] (*Quercus rubra*)	Early Sep	Mid-Sep-late Oct

[a] Months are divided into thirds: early, mid-, and late.
[b] Peak may persist longer in years of unusual abundance.
[c] More abundant on the loamier soil south and east of the study area than in the study area.

This gradient was due to differences in the soils of the 3 areas described above and to climate effects from Lake Superior (D. Prettyman, pers. commun.). Fruit and nut production also followed this gradient except in the cases of species adapted to dry or nutrient-poor soil. For example, although blueberries *(Vaccinium angustifolium* and V. *myrtilloides)* were initially very productive on the loamy soils following fire or other disturbance (Arimond 1979), they eventually tended to lose out to competing species (D. Prettyman, pers. commun.). Blueberries *(Vaccinium* spp.), wild sarsaparilla berries *(Aralia nudicaulis),* and pin cherries *(Prunus pensylvanica),* 3 of the more important foods of early summer, were more abundant in the study area than on the loamy soils to the south (D. Prettyman, pers. commun.) or on the shallow soils to the north (Arimond 1979). The species that were most abundant on the loamy soils to the south and east tended to be foods of late summer (Table 1). These included northern red oak acorns *(Quercus rubra),* mountain-ash berries *(Sorbus americana, S. decora),* dogwood berries

(Cornus rugosa, C. stolonifera), highbush-cranberries *(Viburnum trilobum),* red raspberries *(Rubus idaeus),* and thim-bleberries (R. *parviflorus)* (D. Pretty man, pers. commn.).

Human presence was concentrated along the southern edge of the study area where there were a paved road (Minn. Highway 1), 3 resorts, 2 campgrounds, and a logging community of approximately 35 homes. Loggers cut <1% of the study area per year. Summer use was mainly by fishermen and blueberry pickers. The study area was accessible by unimproved roads but had low human use except during fall grouse and deer hunting seasons. Bears were killed as nuisances or incidental to deer hunting prior to 1971 when a mid-September to late October bear season began. Hunter numbers were low the first few years of this season, but in 1974 the season began opening in early September. License sales began to increase rapidly, and the statewide kill began rising from 352 in 1973 to 701 in 1977 and 1,359 in 1981 (D. Schultz 1985, Minnesota black bear harvest 1984, unpubl. paper, Minn. Dep. Nat. Resour., St. Paul, Minn.).

METHODS

Barrel trapping was the main method of capturing bears in summer. These non-injurious traps made from 55-gallon drums allowed release of unnecessarily captured bears simply by lifting the sliding door. Capture success averaged a bear/34.8 trap-nights, excluding captures of 2 trap-prone bears (Female P and Male 569). Males over approximately 150 kg often tipped the traps over instead of entering them. These bears were foot-snared, as were the majority of bears the first year of study. A few bears were fortuitously treed and then drugged and lowered to the ground with ropes.

Four combinations of immobilizing drugs were used. Succinylcholine chloride and sodium pentobarbital were used the first month of study but proved unacceptable (Rogers et al. 1976o). After that, phencyclidine and promazine (Seal et al. 1970) were used until phencyclidine became unavailable in 1978. Then either ketamine and xylazine or preferably ketamine and promazine were used. Cubs weighing <5 kg were not tranquilized.

Captured bears were eartagged, weighed, measured, and examined for parasites (Rogers 1975a,fo). Natural markings were recorded (Rogers 1980). A first upper premolar was extracted for age determination (Willey 1974). Blood samples (up to 2 cc/kg lean weight) were taken from bears older than 1 year to determine hormone levels (McMillin et al. 1976), health, nutritional status, and seasonal changes in physiology. Blood samples were analyzed by Dr. U. S. Seal and others at the Veterans Administration Hospital in St. Paul, Minnesota.

Color-coded radio collars with individual frequencies and weighing 0.2-0.8 kg were fitted to bears older than 1 year. However, after 1972, no subadult males were given radio collars until they completed dispersal. Battery life was 1-2 years. Signal range to an airplane was typically only 1-7 km early in the study but improved to 5-20 km with equipment used later. Radio collars were fitted to the largest part of the bears' heads and hung loosely on the necks of all but the heaviest males. The collars were usually accepted and seemingly ignored within a few days. A lactating female (209) who lost 38% of her weight continued to wear her radio collar even though it was so loose it was removed with 1 finger when she was re-captured. Conversely, a few bears removed their collars or had them slip off, especially during the denning period. Males with necks at least as large as their heads lost 3 radio collars, with at least 2 of these being lost during fights.

Although some radio tracking was done each year during 1969-85, effort was most intensive during 1971-76. Effort those years was directed toward learning movements, social relationships, and population structure. Later studies were mainly to learn birth and survival rates in relation to habitat, approximate locations of adult ranges in relation to birthplaces, and

physiological changes between summer and winter. These studies required less radio tracking. During 1971-76, 28 males and 55 females aged 0.6-21.2 years provided meaningful telemetry data (Table 2; Appendixes 1, 2). Males were located in 1,526 (94%) of 1,625 attempts, and females were located in 5,478 (98.5%) of 5,562 attempts, excluding casual attempts from the ground and attempts to locate bears whose radio collars were later found to be nonfunctional (Table 2). Seventy-two of the 99 unsuccessful attempts to locate males were due to 4 males moving temporarily out of signal range in 1971 or 1972 (Appendix 1). Unsuccessful attempts to locate bears of either sex were mainly early in the study when signal range was short (Table 2). Bears typically were located 4-21 times/month except in 1973 when radio tracking was less frequent. Radio tracking was most frequent at times of year when behavioral changes were anticipated such as around the times of family breakup, mating, and entrance into or emergence from dens. Radio tracking by airplane allowed observation of the usually undisturbed bears in approximately 10-50% of the locations, depending on leaf growth, and provided most of the observations reported here. Supplemental radio tracking was done from the ground to determine activity patterns and to locate dens. Determining activity patterns involved several people working in shifts to radio track a bear (and sometimes its neighbors) for approximately 24 hours at a time. In this way, 12 bears were radio-tracked a total of 3,161 hours during 1972-76.

Each winter, old radio collars were replaced with new ones. This was done mainly in late March and early April during a 3-week period immediately before bears emerged from dens. The bears all used ground dens and were still sleeping soundly enough at that time of year to be approached and drugged. Newborn cubs were 2 months old by then and large enough to be weighed and eartagged. Cubs remained with their mothers past 1 year of age, so in some dens there were 14-month-old yearlings instead of cubs or no offspring.

Table 2. Number of telemetry locations of black bears in northeastern Minnesota during 1971-76.

Sex and year	No. of locations	No. attempts unsuccessful	No. adults radio-tracked	No. non-adults radio-tracked	No. bears
Males					
1971	315	67	6	3	9
1972	554	18	3	6	9
1973	37	2	1	2	3
1974	247	2	4	5	9
1975	222	4	3	6	9
1976	151	6	3	6	9
Total[a]	1,526	99 (6.5%)	11	18	28
Females					
1971	1,198	27	16	6	22
1972	1,579	41	16	11	27
1973	491	14	14	9	23
1974	1,013	2	22	9	31
1975	594	0	23	5	28
1976	603	0	21	6	27
Total	5,478	84 (1.5%)	37	27	55
Both sexes[a]	7,004	183 (2.6%)	48	45	83

[a] Totals for numbers of bears do not equal the sums of the individual years because some bears were radio-tracked > 1 year.

Data from den visits were used to determine growth rates, reproductive success, overwinter survival, and cub survival from 2 to 14 months of age. The 14-month-old yearlings were given their first radio collars. After emergence, the yearlings were radio tracked through family breakup and to their dens the next winter. Radio collars were then removed from males in anticipation of dispersal, but young females were given new radio collars each year as they grew to maturity and eventually raised cubs of their own. This cycle was repeated for up to 4 generations in 17 clans during 1969-84.

Radio collars apparently had little effect on social relations, behavior, or growth. Newly radio-collared yearlings were accepted by their mothers, and a newly radio-collared male (445) copulated with a radio-collared female (C) just 15 hours after he was initially drugged and fitted (page 30). Weights of 4 radio-collared vs. 4 nonradio-collared litter-mates (3 litters) showed no differences. In the only such comparison covering more

Table 3. Sex and age of resident black bears in the Minnesota study area each June during 1971-75.

Age (years)	1971 M:F	1972 M:F	1973 M:F	1974 M:F	1975 M:F	All years M:F	All years Total
Cub	8:6	9:5	7:7	6:9	9:6	39:33	72
1	3:6	6:6	8:4	5:4	4:6	26:26	52
2	3:3	5:6	6:6	8:4	3:4	25:23	48
3	0:2	3:3	4:5	3:5	2:2	12:17	29
4	2:4	0:2	2:2	3:4	1:4	8:16	24
5	2:0	3:4	0:1	3:1	4:3	12:9	21
6	1:3	1:0	3:4	0:1	1:0	6:8	14
7	0:0	1:2	0:0	2:4	0:1	3:7	10
8	0:0	0:0	1:2	0:0	2:4	3:6	9
9	0:2	0:0	0:0	1:1	0:0	1:3	4
10	1:3	0:2	0:0	0:0	1:1	2:6	8
11	0:0	1:3	0:2	0:0	0:0	1:5	6
12	0:0	0:0	1:3	0:2	0:0	1:5	6
13	0:0	0:0	0:0	1:3	0:2	1:5	6
14	0:1	0:0	0:0	0:0	1:3	1:4	5
15	0:0	0:1	0:0	0:0	0:0	0:1	1
20	0:1	0:0	0:0	0:0	0:0	0:1	1
All	20:31	29:34	32:36	32:38	28:36		

than a year, 2 littermates (Females q and r) that had each worn radio collars for 2.5 years weighed 42 and 55 kg as 3-year-olds in May; a third littermate (Female y) that had never worn a radio collar weighed 45 kg on 2 July of the same year.

Important plant foods were determined from examinations of scats and stomach contents and from observations of foraging bears. Relative abundance of those foods from year to year was estimated by counting berries and nuts at 30 permanent transects each year during 1974-77 (Arimond 1979) and by visual estimates during field operations during those and the remaining years. Food supplies were initially classified as scarce, moderately abundant, or exceptionally abundant (Rogers 1976), but the latter 2 categories were lumped into a single "abundant" category for this paper.

AGE STRUCTURE, SEX RATIO, AND DENSITY OF THE RESIDENT POPULATION

During 1969-75, efforts were made to capture most of the residents of the study area. Bears were intensively livetrapped through this period (and to a lesser extent thereafter), and radio-collared bears were followed to dens where accompanying cubs were eartagged and yearlings were given radio collars. Capture curves, sightings of marked vs. unmarked bears, and areas used by radio-collared females (page 13) indicated that nearly all residents were marked by 1971. At one time or another during 1971-75, 125 bears were found to be residents. Information on approximate date of recruitment or loss was complete for 103 of them. For the remaining 22, the following assumptions were made in order to estimate the age structure, sex ratio, and density of the resident population for each of the 5 years (Table 3):

1. Twelve males whose birth dates were known and whose weights as yearlings were normal are assumed to have dispersed from the study area as 2-year-olds, the age at which male dispersal commonly occurred.
2. Four underweight littermates (1 male, 3 females) that were not recaptured were assumed to have died. Their weights of 1.1-1.4 kg at 2 months of age were only half the average weight (2.26 kg) of cubs known to survive.
3. Three cubs of normal weight that were not recaptured and 3 eartagged yearling females that were not recaptured were assigned average mortality rates for purposes of population assessment.

June was chosen as the month for population inventory. Some of the first-year mortality among lightweight cubs had occurred by that month and most adults were not yet foraging outside their usual ranges (page 31). Subadult males that had been born in the study area and that were present in dens in March were included as residents in June even though a few may have dispersed, but no incoming transient males were included; these 2 influences are assumed to have been equal and thus not to have resulted in a meaningful change in density. There was no indication of a significant floating population of adults of either sex. Only 1 adult female (P, page 43) was found to be without a territory.

The population increased between June 1971 and June 1972 but then remained between 63 and 70 bears during 1972 and 1975 with an average density of 1 bear/ 4.5 km^2 (1.7 mi^2) (Table 3). Recruitment approximately balanced mortality and dispersal those 4 years. Increases in the June population were slight even though 65 cubs were born in the study area and several dozen transients (including 44 captured) passed through it. During that period, 16 females and 10 males became resident adults (at least 4 years old). Thirteen of the females but only 1 of the males were born in the study area.

Sex ratio declined with age (Table 3). Sex ratio remained approximately even through 2.5 years of age, but only a third of the adults were males, and only about half those males used the study area at a time; therefore, the true sex ratio among adults was probably closer to 1 male: 3-4 females. On the average during the 5 years, 28% of the males and 43% of the females were adults, with 0.43 female cubs/adult female (Table 3).

LAND TENURE SYSTEM OF ADULTS
Characteristics and Defense of Female Territories

Female black bears were found to be territorial in the mountains of Montana (Jonkel and Cowan 1971) and in the gently rolling forests of Alberta (Young and Ruff 1982). Poelker and Hartwell (1973) also found little overlap among 3 radio-collared adult females in western Washington, but Lindzey and Meslow (1977*a,b*) found considerable overlap in a very dense population (>1 bear/km^2) on an island in the same state. In Idaho, Amstrup and Beecham (1976) and Reynolds and Beecham (1980) also found considerable overlap among females.

In Minnesota, territoriality was apparent among females (but not among males) from telemetry data (below) and from observations of aggressive interactions (page 14). Telemetry data showed that home ranges of adult or near-adult females consisted of 2 parts—a territory that was used year after year, and areas of extensive movement that usually differed from year to year and that extended up to 92 km outside the territories. Excluding movements to places more than 7 km away from territories (approx. 2 territory diameters), more than 90% of the telemetry locations for 31 females after 10 June (beginning of mating season) were in the territories (Figs. 2, 3, 5, 6). Data in Figure 4 were too sparse to estimate territorial boundaries. Boundaries were drawn subjectively for the following 3 reasons: (1) to take into account behavioral data recorded with the location data, (2) to avoid inclusion of areas of extensive movement, and (3) to avoid exaggeration of territorial overlap. Individual locations are presented to permit other interpretations of boundary locations. Included in Figures 2-6 are locations for all resident females 3 years old or older, locations for 3 2-year-olds that took over portions of their dead mothers' territories (Female a. Fig. 3; Female t. Fig. 5; Female w. Fig. 6), and locations for 3 other 2-year-olds that were otherwise precocious in establishing exclusive territories (Females n, q, and r in Fig. 4). Blank spaces represent more or less vacant areas (such as around the Knotted Pine Community where several females had been shot), ranges of subadult offspring that were seldom visited by radio-collared mothers, and ranges of nonradio-collared
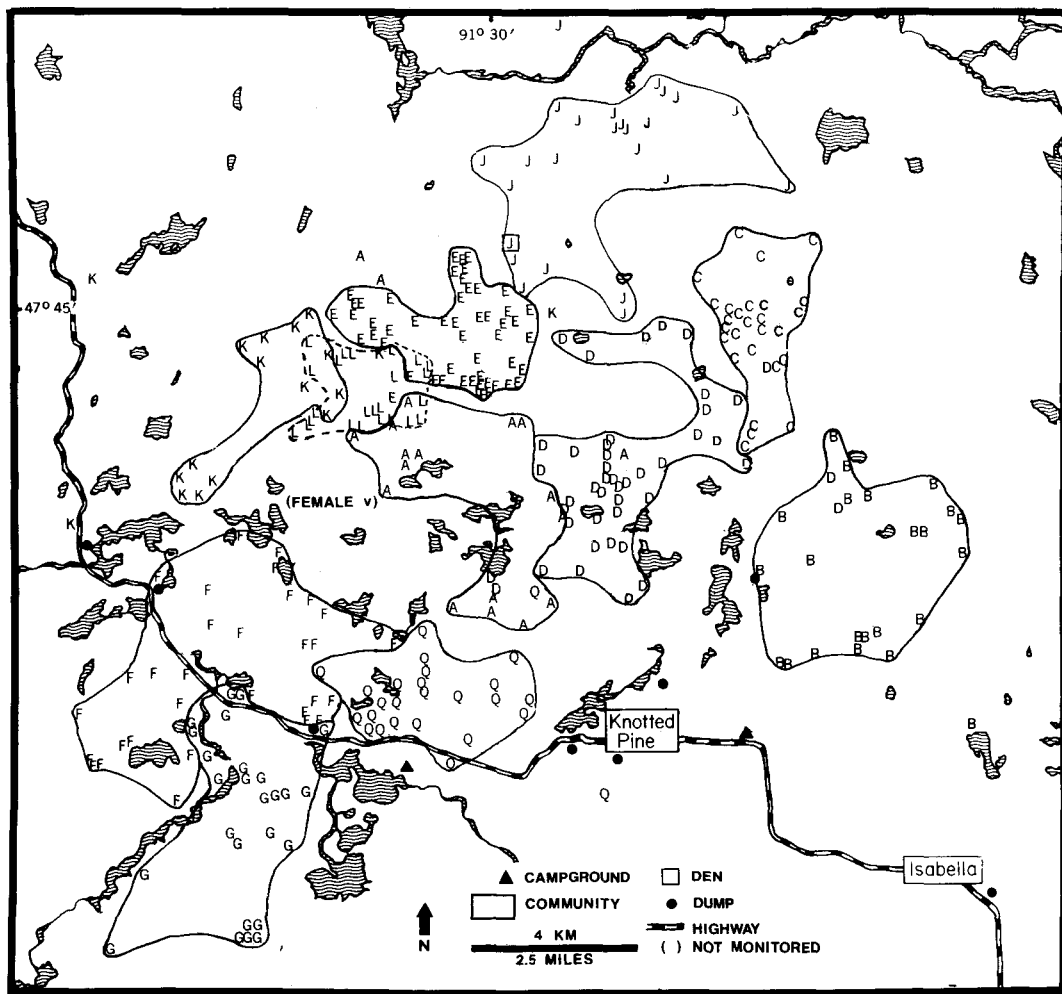
Fig. 2. Locations and territorial boundaries of resident females at least 3 years old in 1971.

adults. Areas near the edges of the figures were outside the trapping area.

Extensive overlap, other than between mothers and young daughters, was seen only in the unusual situation when Female A died (page 43) and her former territory was invaded by Female D, forcing A's 2 offspring (Females a and b) to share an area temporarily in 1972 (Fig. 3). A second area that appears as extensive overlap (Fig. 5) actually represents shifting boundaries where Female d usurped part of Female C's territory in 1974. Slight overlap among territories occurred at each of the 5 garbage dumps, all of which were

at edges of territories. Delineated territories averaged 9.6 ± 0.5 km^2 (SE) (N = 49) for females that had produced cubs or that were in their first successful pregnancy. Territories averaged 6.7 ± 0.6 km^2 $(N = 13)$ for nonbreeding females (difference significant, $P < 0.01$).

Aggressive interactions included vigorous chases of intruders by mature territorial females. On 14 July 1971, Female A was observed from an airplane as she chased Female L 2.4 km over a twisting route to their mutual boundary (Fig. 2) where A turned back and L continued into her own territory. In a second observed
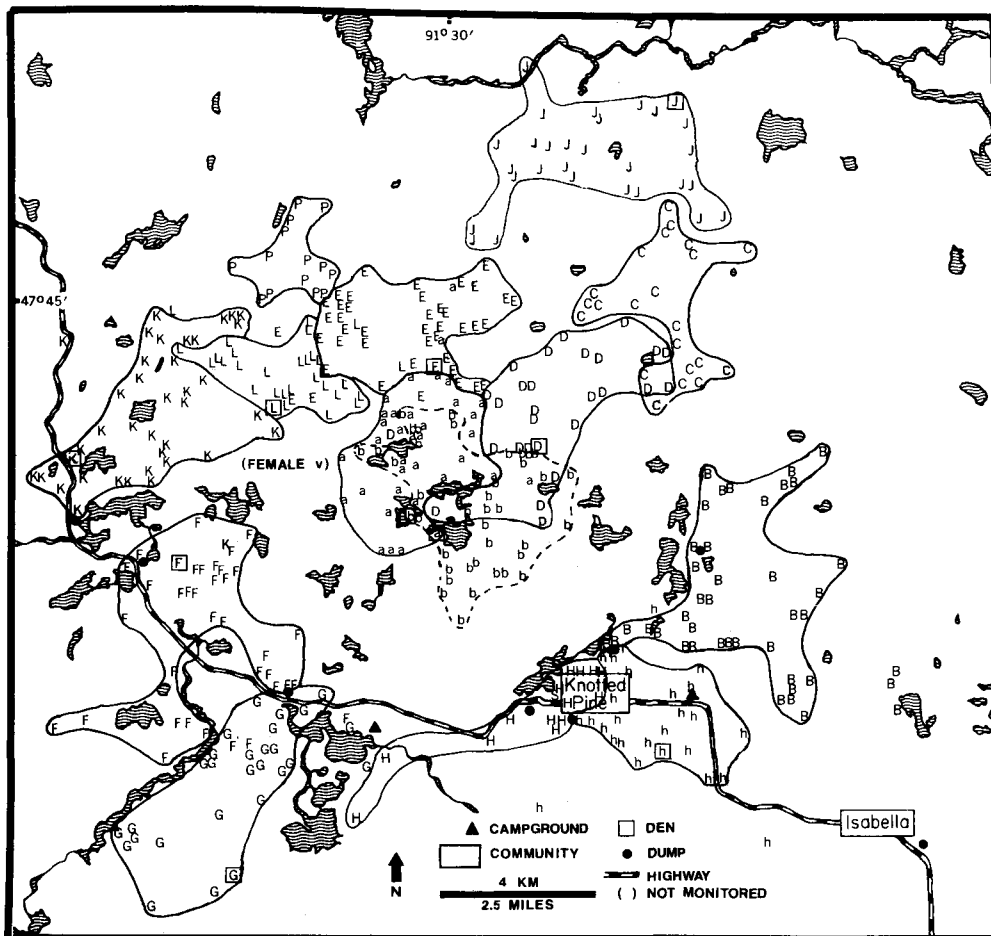
Fig. 3. Locations and territorial boundaries of resident females at least 3 years old in 1972.

chase, Female n, with cubs, vigorously chased a larger bear of unknown sex on 27 June 1976. Fights between adult females were not seen, but fresh wounds on 3 of them indicated that fights occurred. Two females with fresh punctures and lacerations on their heads and necks were captured on 23 and 25 June 1975. They held adjacent territories, and 1 of them, 11-year-old Female T, had been encroaching on the territory of the other, a 14-year-old (E) with cubs. Although the wounds on the 11-year-old appeared more extensive, it was the mother with cubs that was not subsequently found in the area of overlap. In a second instance of probable fighting, a 3-year-old female (S) had fresh lacerations on her head

and neck when captured on 6 June 1973. She was newly arrived in the study area and was in the process of establishing a territory where a territorial female (H) had been shot the previous August (Figs. 3, 4).

Boundary encounters probably did not usually involve physical contact because no other females had fresh wounds on their heads, necks, or forequarters. For example, no violence ensued when 2 territorial females (1 with cubs) encountered each other on 16 July 1976 in an open cutover area at or near their mutual boundary. Both fed on raspberries until the lone female (v) approached to 100 m. Then the mother (L) stood erect, her cubs bounded to her,
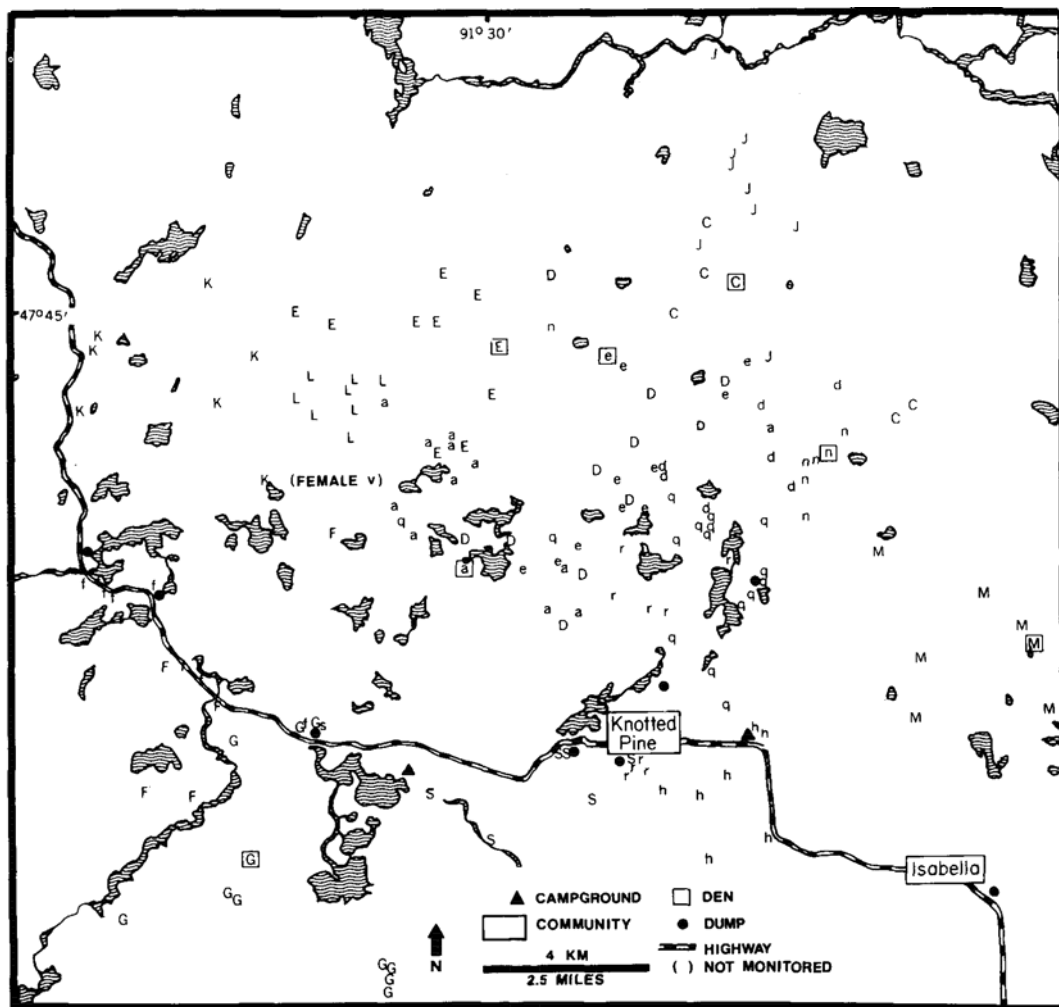
Fig. 4.   Locations of resident females at least 3 years old in 1973. Data were too sparse to estimate territorial boundaries.

and the family moved 30 m to forest cover. There they resumed feeding, and the lone female, who was downwind from the family, continued foraging as she moved away.

The importance of chemical communication in territorial defense by females is unclear. Black bears have greatly reduced anal scent glands and no specialized cutaneous scent glands (Pocock 1921). Only 3 of 553 observations of adult females were of possible scent marking (rubbing on trees). However, urine from either sex has a fairly strong odor, and females regularly

traversed their territories (page 19). Whatever the source, the scents females distributed as they traveled were sufficient to advertise their presence as evidenced by males scent trailing estrous females (page 29). However, responses of other females to the scent are unknown.

In late summer and fall, territorial defense may be less vigorous and less necessary than in spring and early summer. No female lost her territory in late summer or fall during absences as long as 69 days (page 33). Resident females did not pursue trespassers
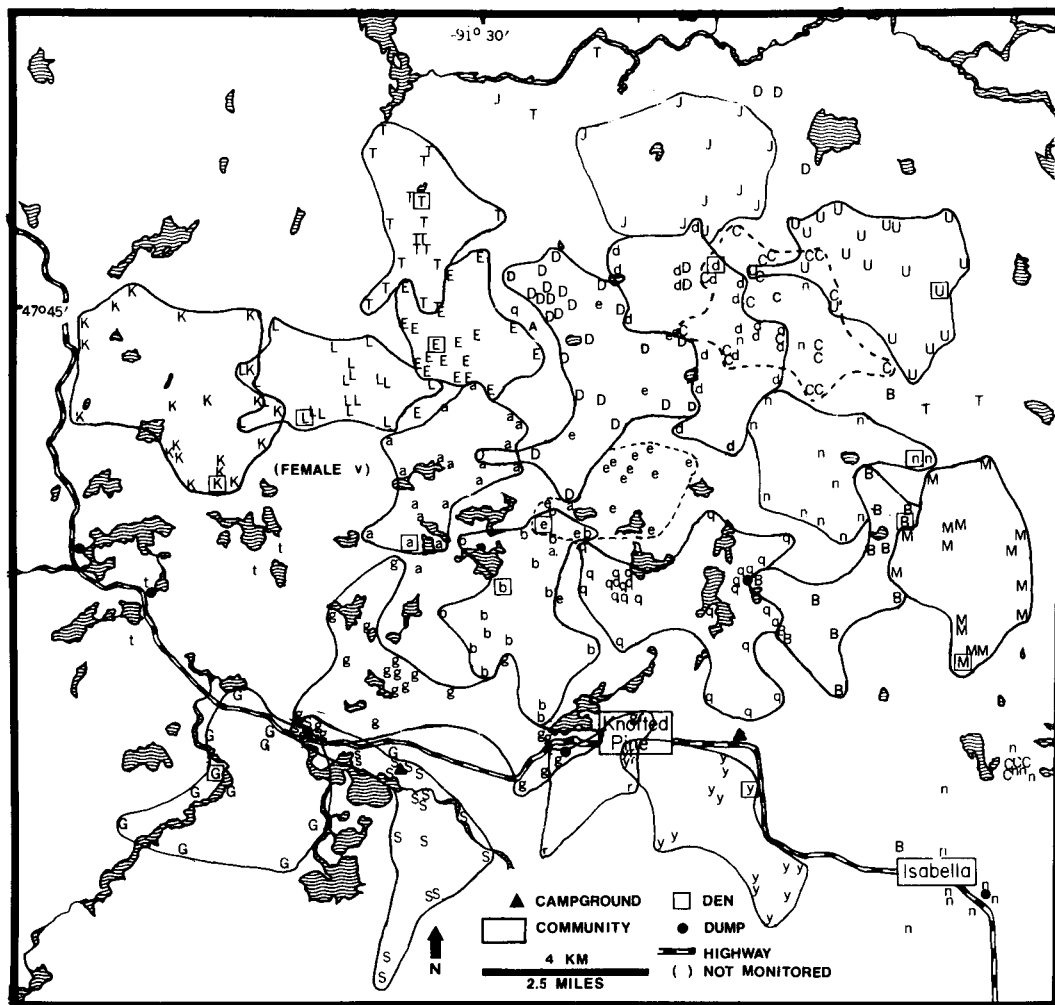
Fig. 5. Locations and territorial boundaries of resident females at least 3 years old in 1974.

in 10 encounters observed after 14 July, but in 9 of those encounters the trespassers avoided or fled from the residents. In the 1 instance in which the trespasser did not retreat, a female (841) and 3 cubs were at the edge of Female C's territory, 31 km outside their own territory on 19 August 1974. They fed to within 100 m of Female C and remained there during 40 minutes of observation. Female C had earlier seemed poorly able to maintain her territory and had lost half of it to a 3-year-old (Female d. Figs. 4-6). Her weight the past April had been her lightest in 9 years of study — 45 kg

compared with her peak of 110 kg. The possibility cannot be excluded that Females C and 841 were littermates because each was 13 years old. A more typical encounter in that it involved avoidance was observed in detail from an airplane on 25 August 1971. In that instance, Female P, an immigrant without a territory (pages 13, 25, and 43) was loping crosswind toward a mother (E) and 2 cubs that were feeding in their territory. Upon topping a rise 35 m from them. Female P doubled sharply back 40 m to the closest tree, looked toward the family, which had resumed feeding after brief
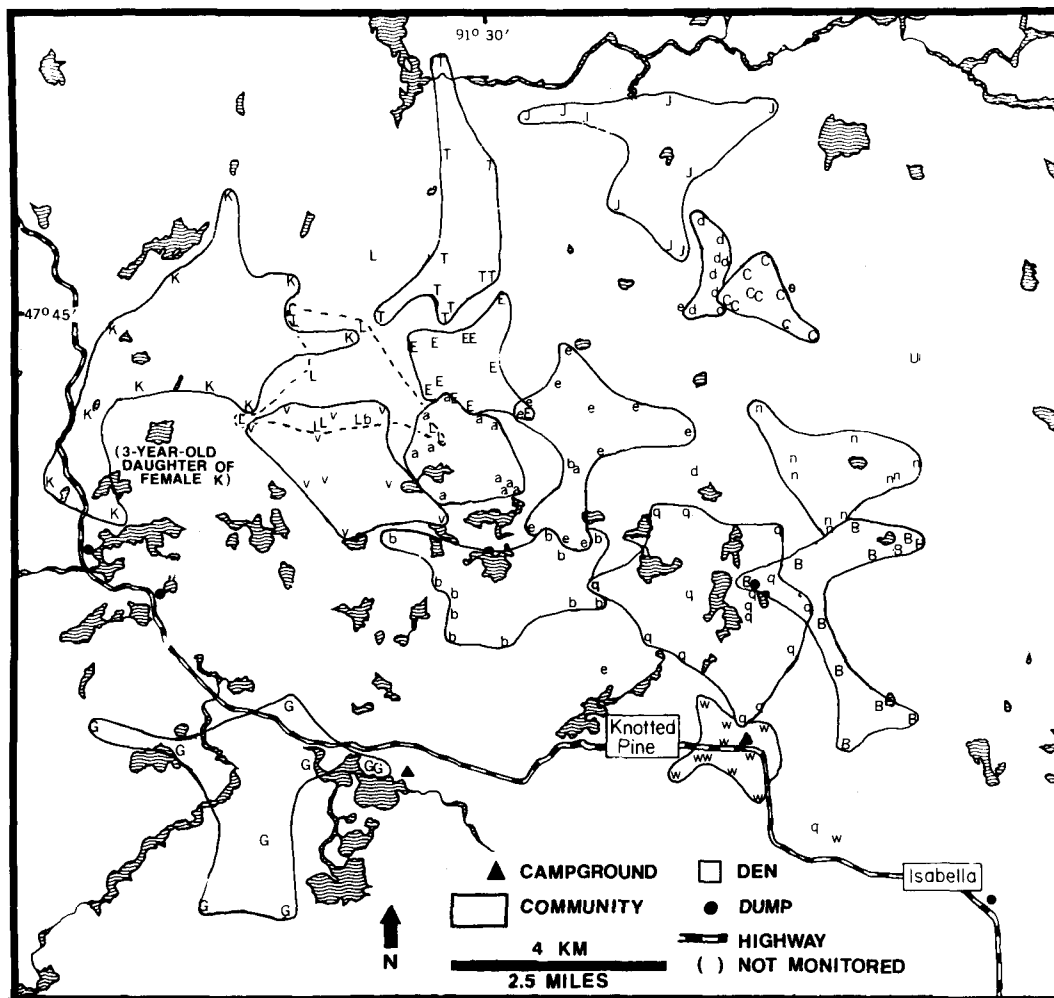
Fig. 6. Locations and territorial boundaries of resident females at least 3 years old in 1975.

alertness, and then circumvented them, passing approximately 100 m to the downwind side. She then continued in her original direction and was observed 1.5 hours later, 1.3 km away, feeding at the edge of the territory.

Activity Pattern and Movements of a Territorial Female

The activities of territorial Female E were studied during the summers of 1972-75 when she was 12-15 years old. She was radio-tracked an average of 23 hours/day on 64 days (total 1,480 hours), with 50 of those days being during June-July mating seasons. The 64 days included periods of 9, 11, and 16 consecutive days.

She showed a consistent activity pattern in which she became inactive 1.5-2 hours after sunset and remained inactive until 0.5-1 hour before sunrise, a period of about 6 hours. She commonly rested up to 2 hours during daylight hours for a total of 6-8 hours of rest/24 hours. She traveled 1.6-2.7 km/hour when moving crosscountry without foraging, but she usually foraged and meandered when active and therefore usually traveled more slowly. As a lactating mother in 1975, when nuts and berries were scarce, she spent

more than three-fourths of her active time foraging for ants. She smelled log after log, tearing some open. Her 3 cubs, when they were with her, crowded around logs she opened but were not observed tearing any open themselves.

Female E covered most of her territory every 1-4 days, with the interval depending at least in part upon her reproductive status. With cubs, she took 3-4 days (average 3.2 days) to complete each of 5 circuits of her territory, but when alone and nonestrous she took 2-3 days (average 2.7 days) to complete each of 6 circuits. During estrus, she traveled the periphery of her territory in <1 day with brief trespasses into an adjacent territory (page 29). Aside from the estrous movement around the periphery, she showed no tendency to make greater use of either the center or edges of her territory. Instead, she concentrated in 4 areas where tall shrubs predominated (page 40).

Female E spent <1% of her documented time in adjacent territories, probably trespassing less than most other females considering data presented in Figures 2-6. There were no documented encounters with 3 radio-collared females that held adjacent territories, but at least 3 transient subadults ran or rapidly walked away from her. The subadults probably were males because 24 of 27 unmarked subadults captured during those years were males.

Ranges of Males

Males were considered adults at 4 years of age because that was the youngest age that males (353, 442, and 569) were seen with females. Seven adult males were radio-tracked through 13 mating seasons (10 Jun-9 Jul), with mating ranges averaging 16.8 ± 0.7 km (SE) in length (range 10.1-20.6 km) by 7.7 ± 0.7 km in width (range 4.8-11.6 km). Each mating range included at least portions of 7-15 female territories, but mating ranges were probably indefensibly large and overlapped to the extent that no male had exclusive access to any female. Ranges of the 2 largest males (224 and 225) overlapped

only at a garbage dump, but each overlapped those of several smaller males. With 2 possible exceptions, all 28 male-female pairs seen in the study area included resident males with established mating ranges. Indeterminate roaming was not observed. There obviously is an upper limit to the number of potentially estrous females a male can efficiently monitor to determine receptiveness during the mating season, and this is probably reflected in the size of male mating ranges. Studies throughout the black bear range show adult male ranges to be disproportionately larger than adult female ranges considering differences in body size (Erickson et al. 1964, Jonkel and Cowan 1971, Poelker and Hartwell 1973, Amstrup and Beecham 1976, Lindzey and Meslow 1977&, Landers et al. 1979, Alt et al. 1980, Reynolds and Beecham 1980, Garshelis and Pelton 1981, Kohn 1982, Young and Ruff 1982). Female range size apparently is determined in part by habitat richness (Amstrup and Beecham 1976, Lindzey and Meslow *1977b,* Young and Ruff 1982), but male mating ranges may approximate a size that enables efficient monitoring of the maximum number of potentially estrous females.

After the mating season, some males foraged up to 200 km outside their mating ranges (page 31). Males that remained in their mating ranges avoided, or were excluded from, female territories. Telemetry locations for adult males more than 1.6 km from garbage dumps and in the area where most females wore radio collars showed that the males spent most of their time after the mating season between female territories or on the outer 0.4 km of them. The percentage of male locations more than 0.4 km inside female territories declined through the year as follows: mating season (10 Jun-9 Jul), 38 (84%) of 45 locations; transition period (10 Jul-3 Aug), 13 (45%) of 29 locations; foraging period (4 Aug to denning), 6 (19%) of 31 locations (differences significant, x^2 = 14.9, 2 df, P < 0.001). Whether males avoided or were excluded from the territories is unknown. Geist and Petocz (1977)

suggested that male bighorn sheep *(Ovis canadensis)* voluntarily vacated the home ranges of females in order to reduce feeding competition with pregnant mates and offspring. Evidence that black bear females might actively exclude males is that (1) Female n vigorously pursued a larger bear in her territory (page 15), (2) Male 224, whose annual weight range was 147-207 kg, walked away fast from a 65-kg female (E) in her territory on 11 June 1972, (3) 3 transient subadults moved rapidly away from a territorial female (E), and (4) a 74-kg 5-year-old male (338) that remained between the territories of 2 females from 17 to 23 July 1971 left that area when 1 of the females (F) moved through it. Whether due to avoidance or exclusion, the low use of female territories may explain further the disproportionately large areas used by adult males.

ANNUAL BEHAVIORAL EVENTS OF ADULTS
Overview

In northeastern Minnesota, as elsewhere, the annual cycle of behavioral and physiological events of black bears is tied to the annual cycle of plant growth and fruiting because much of the diet is plant material (Ewer 1973, Johnson and Pelton 1980). As will be detailed, adults emerged from dens in late March or April and typically remained lethargic until late April or early May when aspen catkins and green vegetation became available. Females then began roaming and re-establishing their territories. Later in spring or in early summer, mothers with yearlings separated from them, and females without cubs of the year mated. These events were completed by the time fruits began to ripen in abundance, about 10 July. During July, testosterone levels of males fell and males became less aggressive (McMillin et al. 1976). For both sexes, foraging became essentially the only activity until fruit and nuts disappeared. These disappeared from the main study area in September, but acorns, mountain-ash berries, and other

fruit and nuts often were available to the south and east through October, and some bears foraged far outside their usual ranges to obtain them. They returned to their usual ranges and prepared dens in late September, October, or early November. Pregnant females that had accumulated sufficient body stores gave birth during the denning period. Nonforaging activities took place mainly outside the period when fruit and nuts were available. This allowed maximum efficiency of feeding on the foods that were most critical to survival and reproduction and that were often in short supply in northeastern Minnesota (Rogers 1976,1983).

Hibernation

Cold seasons in northeastern Minnesota were long and harsh, and bears spent 5-7 months in dens each year. Snow typically covered the study area for at least 5 months, usually beginning in early to mid-November, and food was essentially absent for 7 months from October through April. In the shortest denning period, approximately 5 months, Male 353 constructed a den in early November 1970 and left it in early April 1971. In the longest denning period, 7 months, Female a entered a den between 26 and 29 September 1971 and emerged on 27 April 1972. A thread tied across the entrance of the female's den on 2 October 1971 was checked at approximately 4-day intervals through October and November. It was broken 4 times in October (on 2, 10, 14, and 29 Oct) when she emerged briefly to rake additional bedding, but it was unbroken 3 other times in October and on all checks in November. In the spring, snow still blocked the entrance when the den was checked on 26 April.

Hibernation enables survival through cold seasons of food scarcity (Watts et al. 1981). It is primarily an adaptation for prolonged survival without food or water. Hibernation and denning usually provided little protection against cold. Dens served as windbreaks and protection from

predators but usually did not accumulate significant heat. Most dens were shallow, had open entrances, and were only 1-2 C warmer than the ambient air, which was as cold as – 41 C and seldom above freezing. Dens with entrances closed by snow were approximately the temperature of the frozen soil, slightly below 0 C. Crusting of the inner surface of snow in closed dens caused oxygen levels to become reduced to as low as 15.9% (20.9% oxygen is normal) (Rogers, unpubl. data), but no mortality was found from that cause. Nearly all dens of either sex contained insulative nests of leaves, grass, clubmoss, cedar bark, conifer boughs, or other materials (Maxwell et al. 1972). Some bears hibernated in nests on the ground surface and produced surviving cubs. The fur of adults is sufficiently insulative on the back, shoulders, and neck that falling snow did not melt on an intensively studied individual at ambient temperatures ≤ - 8C (Moen and Rogers 1985). Bears protected their sparsely furred undersides, muzzles, extremities, and any newborn cubs by curling up.

Physiological readiness to hibernate apparently is controlled by a biological clock that varies regionally with norms of food availability (Johnson and Pelton 1980; Nelson et al. 1983*a,b*). In late summer or fall, black bears undergo neuroendocrine and metabolic changes that make hibernation possible (Nelson et al. 1975, 1983a, 1984; Nelson 1980). All study bears hibernated in winter, regardless of nutritional condition, as also has been reported in Montana (Jonkel and Cowan 1971). No bear died of starvation in a den, but some lightweight individuals starved after emerging in spring (page 52). By contrast, malnourished bears living in mild regions where food might be found in winter sometimes remain active (Carpenter 1973, Hamilton and Marchinton 1980). In Michigan, captive bears that were fed in winter remained active but lethargic (Erickson and Youatt 1961).

Bears in northeastern Minnesota achieved a deeper hibernation than has been found in mild regions. From late October to early April they seldom left their dens when closely approached, and during winter they commonly did not awaken until after several minutes of handling and prodding (Rogers 1981). Some that attempted to struggle or run when first awakened moved only slowly and stiffly at first. Blood supply to the limbs was markedly reduced during hibernation (Rogers and Durst 1987). By contrast, bears in Florida, Louisiana, North Carolina, and coastal Washington readily flee from their dens or beds (Baker 1956; Duffy 1971;Taylor 1971; Poelker and Hartwell 1973;Hamilton 1978; Hamilton and Marchinton 1980; J. Brady and D. Maehr, pers. commun.). Bears in Tennessee reportedly flee from open den sites but commonly move very slowly when first awake (Johnson and Pelton 1980). In Pennsylvania, a hibernating bear did not raise its head until after several minutes of prodding (G. C. Wakefield, pers. commun. to Folk et al. 1976).

Bears that enter hibernation usually do not emerge to forage during springlike periods in winter; bears in coastal Washington and Tennessee remained inactive through winter periods with temperatures higher than some in seasons of activity (Lindzey and Meslow 1976, Johnson and Pelton 1980). Interrupting hibernation to forage when food is not available would be maladaptive, and the physiological process of entering or leaving hibernation appears too slow for that kind of flexibility (Folk et al. 1976, Johnson and Pelton 1979, Nelson et al. 1984). However, bears may abandon or improve dens that become saturated with water (Hamilton and Marchinton 1980, Johnson and Pelton 1980). In Minnesota, the only healthy bear to emerge in winter was a female (C) that emerged briefly to gather additional bedding when meltwater accumulated in her den during a thaw between 12 and 15 March 1973 (maximum temperatures 3-5 C each day). She brought spruce boughs, shrubs, and pieces of birch bark into the den, elevating herself and her newborn cubs above the water. Eighteen other bears that were monitored through that thaw did not emerge. Two sick or wounded bears emerged

Table 4. Effects of spring thaws[a] on dates of emergence of female and subadult black bears from dens in northeastern Minnesota, 1971-75.

Year	Beginning of rapid thaw	Emerging before thaw began	Emerging <8 days after thaw began	Emerging <15 days after thaw began	Emerging later
1971	6 Apr	0/9[b]	4/7	9/9	0/9
1972	10 Apr	0/14	9/14	10/14	4/14
1973	24 Mar	0/19[c]	9/16	15/19	4/19
1974	9 Apr	1/18	10/13	17/18	0/18
1975	13 Apr	1/18	7/11	17/18	0/18
All years		2/78 (4%)	39/61 (64%)	68/78 (87%)	8/78 (10%)

[a] Daily maximum temperatures consistently exceeding 10 C with daily average temperatures exceeding 0 C.
[b] No. emerging/no, studied.
[c] Excluding Female C's brief emergence in mid-March to gather additional bedding (see text).

at other times. Femle A emerged briefly from her den a day or 2 before she died of natural causes at 21 years of age on 21 or 22 March 1972. A gutshot bear (Female 263) moved among several dens and beds until she died on 24 November 1970.

Emergence

Studies using telemetry showed that bears emerged from dens in late March or April in coastal Washington (Lindzey and Meslow 1976), Alberta (Tietje and Ruff 1980), coastal North Carolina (Hamilton and Marchinton 1980), and Tennessee (Johnson and Pelton 1980) despite considerable differences in climate. The probable reason for the common period of emergence in all these regions is widespread scarcity of winter food in most areas from Tennessee and North Carolina northward (Johnson and Pelton 1980). Weather conditions around the time of emergence in Washington (Lindzey and Meslow 1976) and Tennessee (Johnson and Pelton 1980) differed little from conditions found earlier in the hibernation periods except that a few bears in Tennessee left their dens when rainwater flooded them.

Bears in northeastern Minnesota also emerged during the late March and April period (see below). Snow still covered the ground, greenup had not begun, and ants were still below frostline. Food was essentially unavailable, and energy conservation rather than food gathering seemed to

dominate behavior (see below). Den temperatures at the time of emergence were near 0 C due to deeply frozen soil, but temperatures outside dens were typically above 0 C during the day. Meltwater dampened some dens. To determine possible effects of weather, particularly spring thaws, on the time of emergence, weather data and 78 dates of emergence were recorded for females and subadult males during 1971-75. No precise dates of emergence were obtained for adult males. Those bears were among the earliest to emerge (page 24).

In each of the 5 years, melting began to exceed snow accumulation between 6 March and 2 April. The melting became rapid each year between 24 March and 13 April when daily maximum temperatures began to exceed 10 C with daily average temperatures exceeding 0 C. Within a few days after these temperatures commenced, females and subadult males began to emerge; 39 (64%) of 61 emerged within 8 days, and 68 (87%) of 78 emerged within 15 days (Table 4). Two that emerged in the week before the 10 C temperatures emerged in 1974 or 1975 when warming was more gradual than in the other years. The weather influence was most apparent in 1973 when the warm weather and rapid melting began more than 2 weeks early, on 24 March, and 15 of 19 bears emerged earlier than any had emerged in the other 4 years (Table 4). The 15 emerged by 6 April, whereas all bears in other years (N = 59) emerged

between 7 and 30 April (Table 4) ($x^2 = 57.7$, 1 df, $P < 0.0001$). No earlier thaw reached 10 C, so whether the bears would have responded similarly before 24 March is unknown.

Eight (10%) of the 78 females and subadults remained in their dens for more than 15 days after rapid melting began. Emergence dates for these showed no obvious relation to weather. Four of the 8 were lactating females, but this proportion was not significantly larger ($x^2 = 0.93$, 1 df) than the proportion of lactating females among those that emerged earlier (23 of 70). However, it probably is significant that 2 of these were with the lightest cubs found; each cub weighed only 1.0-1.4 kg in late March. Both of those mothers (Female P in 1972 and Female B in 1973) emerged briefly the last week of April but then remained in or at their dens until the second or third week of May, which was as late as any bears remained. Female B did this in 1973 when most other bears emerged and left their dens unusually early. Sedentary behavior by these mothers might be expected because cubs weighing < 1.8 kg were poorly able to walk or climb and spent nearly all their time nursing, sleeping, or obtaining warmth under their mothers. Mothers with cubs too small to climb may be more secure from predators inside dens than outside them. Mothers with cubs were among the last to emerge in studies in Washington (Lindzey and Meslow 1976), Alberta (Tietje and Ruff 1980), Tennessee (Johnson and Pelton 1980), and New York (0'Pezio et al. 1983).

After their first, sometimes brief, emergence in spring, 56 (72%) of 78 females and subadults remained within 100 m of their dens for up to 18 days, and at least 24 of them continued to use their dens at least at night. Whether or not the 78 remained near their dens, they typically remained lethargic until at least late April. Radio-collared bears outside their dens were inactive in 52 (73%) of 71 aerial observations in April. A factor in this inactivity was speculated to be tender feet from newly shed foot pads (Rogers 1974),

but observations of males roaming in early April (page 24) indicate that tender feet may have little influence on movements. Studies using the ratio of serum urea to serum creatinine as a criterion of hibernation now show that at least some black bears remain in a semi-hibernation state for up to 3 weeks or more after emerging (Nelson et al. 1984; Mech, Seal, and Rogers, unpubl. data). During this period of lethargy, bears typically eat and drink very little (Hock 1958, Nelson et al. 1984). However, a lactating female that found a white-tailed deer *(Odocoileus virginianus)* carcass near her den, dragged it to the entrance and consumed most of it between 8 and 15 April 1974 before leaving the den. Lactating females would be expected to have higher protein requirements than other bears.

Three mothers with cubs (K in 1972 and 1974 and n in 1975) and 2 mothers with yearlings (K in 1973 and E in 1974) were observed intermittently from blinds as they emerged from dens, remained near the dens for 8-13 days, and left. One of the mothers (K in 1974) ate the deer carcass mentioned above. All 5 families continued to use their dens nearly throughout the period they remained near them, entering them at times during the day and for most or all of each night except the night before leaving the area. On that night, 2 of 3 families that were observed remained outside their dens. All 5 mothers were lethargic, spending the majority of their time resting in or near their dens. Each raked additional bedding into their dens or constructed beds outside them. One of the mothers with yearlings (K in 1973) nursed them several times although she had repeatedly rejected their attempts to suckle the previous October when the family was observed preparing the den. Nursing by the other mother with yearlings could have been missed due to poorer visibility and fewer observations at that den. All the mothers ate snow or drank meltwater. This was most frequent in the case of the mother that ate the deer. Protein from the deer probably increased her urea production and her requirement for liquid

Table 5. Snow depth and onset of roaming by radio-collared black bears in northeastern Minnesota in the springs of 1971-75.

	1971	1972	1973	1974	1975
Snow depth (cm)[a]					
16 Mar	124	86	51	70	102
24 Mar	91	74	36	58	66
1 Apr	97	79	tr	61	99
8 Apr	84	76	0	53	58
15 Apr	30	84	0	30	33
22 Apr	Patches[b]	74	0	Patches[b]	Patches[b]
29 Apr	tr	41	0	0	tr
6 May	0	0	0	0	0
Dates roaming began[c]					
Adult males					
N	3	2	1	1	3
Range	By 13 Apr	18 Apr-21Apr	By 7 Apr	By 16 Apr	12 Apr-29Apr
Males < 4 years old					
N		2	1	2	1
Range		26 Apr, 3 May	30 Apr	21 Apr, 16 May	27 Apr
Females without cubs					
x	27 Apr	3 May	23 Apr	27 Apr	29 Apr
N	5	8	12	7	16
Range	20 Apr-6 May	29 Apr-8 May	17 Apr-10 May	26 Apr-6 May	18 Apr-7 May
Females with cubs					
x	14 May	8 May	26 Apr	2 My	29 Apr
N	1	5	5	5	5
Range		1 May-21 May	18 Apr-10 May	25 Apr-11 May	28 Apr-29 Apr

[a] Snow depths were recorded at the Isabella Ranger Station.
[b] Snow cover was <50% in the open but was nearly continuous in the shade.
[c] Roaming is denned as bedding in a new location each night, usually bedding > 1 km from the previous night's bed.

for urination (Nelson et al. 1975). She was also the most active of the 4 mothers. The other mothers foraged occasionally but found little. Two of them ate aspen buds or catkins, which they obtained by climbing mature aspens near their dens, moving through snow up to belly deep to reach the trees. One ate a few willow buds, and another tore open a log near the den.

The yearlings, like the adults, were lethargic. They rested, raked, and the members of at least 1 family nursed, but they did not climb, wrestle, or otherwise play, and they were not observed to drink melt-water or eat snow. They sank more than belly deep in the snow and were not observed to forage. The cubs of the year rested, nursed, climbed, wrestled playfully, and leaped and lunged when trying to move through deep, soft snow. They did not rake. Unlike the yearlings and adults, they were active and vigorous upon emerging. This activity and their rapid growth indicate that newborn cubs do not hibernate.

Onset of Roaming

Bears were considered to have ended lethargy and begun roaming when they began bedding in new areas each night. Mature males emerged with near maximum levels of serum testosterone (McMillin et al. 1976) and usually began roaming earlier than other bears according to data from 1 to 3 males monitored each spring during 1971-75 (Table 5). The first indication of this early roaming was in 1971 when radio signals of all 3 mature males, but not of 9 other bears, were temporarily lost in mid- to late April. The next year, each of 2 mature males began roaming by 21 April while snow depths were more than 0.4 m and while 13 of 15 other

bears were still in or at their dens. The only females (B and J) that had left their dens by then were bedded at snow-free bases of trees where they remained for another 7-16 days, but the 2 males each were seen walking through chest-deep snow. In 1973 and 1974,1 adult male (295) was monitored in April; he began roaming by 7 April in 1973 and by 16 April in 1974. None of 37 other bears had begun roaming by those dates, and only 6 had emerged. In 1975, 2 of 3 adult males began roaming by 16 April, which was before any of 18 other bears began roaming and before 11 of them had emerged. By 3 May 1975, the 3 adult males (295, 442, and 445) were an average of 8.7 km (5.6-10.9 km) from their dens while an immature male and 19 females were an average of only 0.8 km (0-3.7 km) from their dens.

The decline in lethargy and the onset of roaming for females and subadult males typically coincided with the first availability of spring foods in late April or early May. During those 2-3 weeks, the last snow disappeared, ice melted from the lakes, and the ground began to thaw. Aspen and willow catkins, young green terrestrial and aquatic vegetation, and ants became available. Greenup continued through early June, with quaking aspen and birch trees leafing out in early May, most shrubs leafing out in mid-May, and bigtooth aspen and ash *(Fraxinus* spp.) trees leafing out in late May or early June. Bears began roaming only slightly earlier than usual in 1973 when they emerged unusually early and there was little or no snow to hamper movements (Table 5). Phenology of food plants (and perhaps bear physiology) is controlled in part by photoperiod (Ahlgren 1957, Sweeney 1963), and the early melt in 1973 did not cause an equal advance in phenology.

For the adult males, food apparently was not the major factor influencing the onset of roaming. Roaming began before greenup, and only 1 of 7 males visited dumps within their ranges by the end of April despite considerable roaming that month. Dump use by both males and females typically

began the first week of May.

Adults showed little tolerance for members of the same sex as the mating season approached in spring. Chases usually occurred when more than 1 male attempted to use 1 of the small garbage dumps in the study area. Only 1 territorial female used these dumps at a time. By contrast, at larger garbage dumps outside the study area, food was more abundant, bear densities were higher, and bears of either sex showed greater tolerance, as also was reported by Herrero (1983) for a large dump in Jasper National Park, Alberta.

The territorial pattern was blurred in spring when females made prolonged trespasses into adjacent territories as if investigating opportunities for territorial expansions. Some territories were vacant in spring due to fall and winter deaths (Rogers 1983). Others were occupied, but occupancy may have been difficult to detect because scent probably dissipates overwinter and new coverage probably was not complete yet. Mothers with newborn cubs probably distributed the least scent because they were the most sedentary. Intruders left upon encountering mature residents. For example, a 12-year-old mother (D) tended her litter in a small portion of her territory while an intruding 6-year-old female (a) occupied another part of it from 7 April until the 2 met on 4 May. The intruder then left the territory. In another observation, a nonterritorial 5-year-old female (P) denned and gave birth in the territory of another female (E, 11 years) and remained there until 24 May 1972 when she was seen moving away from the territorial bear toward a small adjacent area that she then used until midsummer (page 43). In a third observation, an 11-year-old female (E) extended her spring activities 2 km south into an area where the resident female (A) had died overwinter. The new area was soon taken over by a 5-year-old daughter (a) of the deceased bear, and the old female withdrew to her usual territory. Five additional encounters were noted at locations subsequently determined to be boundaries.

The territorial pattern was clear each year by the onset of the mating season (10 Jun). Most territories were reestablished in roughly the same locations each year (Figs. 2-6), which suggests overwinter memory of spatial relationships.

Marking Behavior

Before and during the mating season and to a lesser extent in other seasons, bears of several species rub, bite, and claw certain trees known as bear trees. This behavior has been reported for grizzly bears (Mills 1919), Old World brown bears (Meyer-Holzapfel 1957, Bromlei 1965, Tschanz et al. 1970), Himalayan black bears *(Ursus thibetanus)* (Bromlei 1965), and American black bears (Hamilton 1978, Burst 1979, Burst and Pelton 1983). Tschanz et al. (1970) reported that brown bears at the Municipal Bear Pit at Berne, Switzerland, marked mainly prior to and during the mating season. The small amount of marking by females, approximately 15% of the total annual marking, was mainly in late summer and fall.

Wild black bears in Minnesota showed the same pattern. Marking was seen in 16 (17%) of 92 observations of mature males but in only 3 (1%) of 553 observations of mature females and in none of 478 observations of subadult bears. Differences were significant between mature males and mature females ($x^2 = 72.5$, 1 df, $P < 0.001$) and between mature males and subadult bears ($x^2 = 79.2$, 1 df, $P < 0.001$) using chi-square with Yates' correction. Mature males were observed marking more frequently between 15 May and 17 July (in 14 [22%] of 65 observations) than during the remainder of the year (on 1 and 23 Aug, 2 [7%] of 27 observations), but the difference was not significant using chi-square and Yates' correction. Females were seen marking only on 15 August, 2 September, and 25 September, all within their territories. Fresh marks were found on at least some bear trees every month of the nondenning period. Burst and Pelton (1983) reported a similar distribution

in time for marking by black bears in Tennessee.

All marking was by resident rather than transient bears. The 2 largest males in the Minnesota study area (224 and 226) marked during 4 of 14 observations before or during the mating season, but during the same period the smallest male to be seen with a female (Male 338, 48 kg) did not mark during 8 observations (difference weakly significant, $x^2 = 2.79$, 1 df, $P < 0.1$). On 19 May 1972, the largest bear in the study area that year, 11-year-old Male 224, was seen marking trees as he walked approximately 1 km along a dirt road. At 3 locations he stood on his hind legs and rubbed his dorsal side, particularly his shoulders, neck, and head, on trunks of trees, frequently twisting his head around to bite the trunks. At 1 tree he also stood on all 4 feet and rubbed his hindquarters. At a fourth location, he rubbed on a fallen wooden signpost. He lay on it on his back and squirmed with all 4 feet in the air, twisting occasionally to bite it.

The same bear followed another forest road on 4 June 1972. Upon reaching an intersection, he turned and with no change in pace walked 20 m to a large balsam fir tree that bore signs of previous use. He stood erect, marked it, then retraced his steps to the intersection, and resumed his original direction. The tree was downwind from the intersection, making it unlikely that he noticed it by smell. His unhesitating, routine-like manner suggested that he was familiar with the tree's location within his range.

Another method of marking was shown by 5-year-old Male 295 on 29 May 1972 as he walked along a fire lane. He walked over 4 aspens 2-3 m in height. His chest and shoulder bent them to the ground and they rubbed along his underside until they sprang upright behind him. He returned and marked 2 of them repeatedly in this way and stood erect and embraced the foliage of another. These young, fast-growing saplings probably were not used in previous years.

Twenty-nine objects that showed signs

of previous use include a mature white pine, 2 jack pines, 2 red pines, a spruce, a balsam fir, 2 aspens, a paper birch, 18 telephone poles, and the fallen signpost. These bear trees (including the telephone poles and the signpost) showed numerous gouges from teeth and claws and had tufts of hair, some of them bleached, caught in crevices. Some of the trees had copious sap, whitened with age, covering their damaged sides. A large mature white pine that was used for each of 9 years showed no sign of recent use during the next 3 years but was used again in subsequent years. A drooping branch of a jack pine received frequent use in 1971 but died and showed no sign of recent use when it was rechecked 3 years later.

All except 1 of the 29 bear trees were in openings or at edges of openings, including roadsides. Those at edges were marked only on the side facing the opening. The majority of bear trees found were telephone poles along right-of-ways kept open by herbicide. The tendency for grizzly or black bears to mark trees or signposts along roadways or other travel lanes has been noted in previous studies (Meyer-Holzapfel 1957, Jonkel and Cowan 1971, Burst and Pelton 1983). Use of elevated objects in open areas probably maximizes dispersal of scent by wind. Vigorous rubbing of these objects probably ensures adequate deposition of odor (either body odor or urine odor [Meyer-Holzapfel 1957]), which may last longer in sap from bites or clawings than it might on dry ground where bear scent sometimes becomes undetectable to trained hounds within hours under hot, dry conditions. Freshly marked trees had sufficient odor for human detection, and a dog showed intense interest in a bear tree more than a month after all radio-collared bears in the area had denned.

Tschanz et al. (1970) concluded that rubbing places function in social communication among brown bears because the bears showed interest in each other's marks and because 7 of 9 strange young bears "shrank" from the marks of resident bears. Other functions that have been proposed

for tree marking in bears include sharpening of claws, testing of claw strength, reducing ectoparasite numbers, scratching insect bites, removal of fur during molt, causing sap to run for later feeding, play, and marking of boundaries. Although rubbing may be used in body care at times, all but the last of these proposed functions fail to account for the sex- and age-related differences observed by Tschanz et al. (1970) and in this study. Marking also did not appear to be a boundary-marking activity because it was rarely done by territorial females and it was not concentrated near edges of male ranges. In other mammals, scent communicates individual identity, sex, reproductive state, and mood (Eisenberg and Kleiman 1972, Schultz and Tapp 1973, Muller-Schwarze 1974). In carnivores, scent marking also may aid in the avoidance of encounters that could be mutually damaging (Leyhausen and Wolff 1959, Hornocker 1969, Eaton 1970, Eisenberg and Kleiman 1972, Ewer 1973, Mykytowycz 1974, Peters and Mech 1975). If a function of marking in black bears is to reduce conflict, dominant bears might be expected to mark most at times and places of likely conflict. Fourteen of the 16 observations of marking by males were between late May and early July when serum testosterone was highest and the most damaging fights occurred (McMillin et al. 1976). Unusually long and vigorous rubbing by Male 225 was seen immediately after he displaced Male 224 from a dump.

Whether or not the scent marks of male black bears are significant to females is unknown. In some mammals, the scent of mature males promotes estrus (Eisenberg and Kleiman 1972, Bronson 1974) and thus tends to synchronize estrus with the presence of a male. Natural selection for this trait might be expected in a solitary animal. In this study and that of Burst and Pelton (1983), marking was prevalent in the vicinities of estrous or near-estrous females, but this could simply reflect where mature males spend their time during seasons of frequent marking.

Bears' behavior at bear trees did not

support the popular notion that bears communicate their size by leaving claw marks as high as they can reach. The fallen signpost, even when it had been standing, was shorter than a standing bear. Rife (1972) reported that on open tundra where trees are absent, grizzly bears rub on rocks and gravel bars and sometimes lie on their backs among shrubs to rub. Available data are sufficient to refute some of the hypotheses regarding rubbing but are insufficient to conclusively identify its function (s) in bear biology.

Mating Season

Estrus.—The mating season is considered here to extend from 10 June through 9 July because it was during this period that 35 of 36 male-female pairs were seen. The remaining pair was seen on 3 August. Additionally, on 2 August, a male at a garbage dump approached a female, gave the licking signal sometimes seen in sexual encounters, and attacked a nearby male. Swollen vulvas were found for approximately a week before and for 2 weeks after the period of observed pairing; 49 of 51 swollen vulvas were observed between 4 June and 24 July. The remaining 2 were observed on 5 August and 30 March. The latter case, in a den, was probably abnormal. The June and early July peak for pairing and vulval swelling agrees with reports from other areas throughout the black bear range (Knudsen 1961, Rausch 1961, Stickley 1961, Wimsatt 1963, Erickson et al. 1964, Jonkel and Cowan 1971, Poelker and Hartwell 1973, Beeman 1975). However, mating activity terminated more abruptly after this peak in Minnesota than in milder regions where the growing season is longer, fall foods are more abundant, and there is a stronger tendency toward fall fattening (Stickley 1961, Beeman 1975, Graber 1981). For example, in Tennessee, where bears fatten significantly on acorns in fall (Garshelis and Pelton 1981), the mating season apparently stretches later into summer; 8 (24%) of 33 swollen vulvas were observed in August (M. Pelton, pers. commun.).

However, in northeastern Minnesota, bears fatten primarily on fruit in July and August. This may result in stronger natural selection to complete mating before fruit ripens in order to avoid interference with efficient feeding during the summer. In black bears, the time for mating may be influenced more by norms of food availability than by optimizing the time of parturition in view of the fact that they can delay implantation for up to approximately 6 months (Wimsatt 1963, Daniel 1974).

Although the mating season for the population was about a month, the estrous period for individual females was only a few days. The longest that any of 20 females was found to be receptive was 3 days (Female C in 1972, see below). Each of the 20 was observed to be alone or unreceptive 1-3 days before and after she was seen with a male. A wild-born, captive female was receptive for approximately 2 weeks during her first estrus as a 2-year-old and for 4 days or less as a 3-, 4-, and 5-year-old (0. Eggleston, pers. commun.). Females became attractive to males before they became receptive. This extended period of attractiveness may extend the period of male-male competition and increase the chances of a female being inseminated by a superior male. The longest that any of the 20 wild females was known to be attractive (including receptive) was 5 days. Three females (E, g, and K) were with males (224, 295, and 215) at the beginning and end of 5-day periods, but during those periods the males moved as far as 11 km away, and the 3 females, which appeared unreceptive during the initial observations, each were observed alone. The short estrous periods observed in Minnesota support a conclusion by Rausch (1961), in Alaska, that estrus is shorter in black bears than in other North American bears. Grizzly bears, for example, which usually live at lower densities than black bears (Nowak and Paradiso 1983), showed estrus for 1-4 weeks (N = 8) in Yellowstone National Park (Craighead et al. 1969). However, captive black bears in North Carolina showed estrus for

6-16 days with an average of 9.75 days (N = 8) (Ammons 1974).

Movements by Estrous Females and Their Offspring.—At the onset of estrus or shortly before it, mothers separated from their yearlings, a process termed family breakup (page 38). This took place between 1 June and 3 July in 26 of 28 families and during the last week of May in the remaining 2 families. Three mothers that were monitored closely through family breakup (E in 1972, E in 1974, and F in 1971) were joined by males 1-4 days later. Two other mothers (B and C in 1972) were observed alone 1 and 2 days after family breakup. No yearling was found near a male-female pair although an observation of this was reported for grizzly bears (Herrero and Hamer 1977).

Activities of a mother in the days following family breakup were best documented for Female E and her yearling (Male 628), which were monitored intermittently day and night from 3 to 12 June 1974. Mother and son remained together through at least 1500 hours on 8 June, but when next monitored on 9 June at 2252 hours, they were 300 m apart with the mother moving away from the yearling. They spent the night 1 km apart. The next day the mother walked most of the periphery of her territory and moved briefly outside it. She traveled at least 16 km that day, 3 times farther than she had on any day of similar monitoring earlier in the month. By the time she was halfway around her territory, she was joined by a 13-year-old, radio-collared male (224). (The same male had visited her 2 years earlier on 11 June 1972, approximately 4 days after family breakup that year.) The male left during the night, and the mother traveled alone for 1-1.5 days until the same male rejoined her. The pair remained together for at least 6 hours on 12 June until a second male (at 1830 hours) chased the first a minimum straightline distance of 1.5 km and fought with him. The new male rejoined the female (at 1854 hours) and remained with her until monitoring ended at 2105 hours. This observation and an observation of Female K (page 30) suggest that female

black bears become more active during estrus as has been reported for other solitary species such as red squirrels *(Tamiasciurus hudsonicus)* (Smith 1968) and white-tailed deer (Ozoga and Verme 1975). A female black bear that creates a large area of scent trails may increase the likelihood of several males competing for her and of her mating with a superior male.

Male Movements, Competition, and Scent Trailing.—In species in which males do not associate with their offspring, male reproductive strategy should be to maximize the number of offspring by inseminating as many females as possible. One factor in that strategy is judicious expenditure of time searching for and remaining with each female, especially when estrous periods are short as in black bears. Reproductive success of male black bears depends upon the ability to find and inseminate receptive females before other males do and upon the ability to defeat other males that find the same females. Mating privileges of males appeared to be won by contests between males rather than through selection by females. Encounters between mismatched males were settled by the larger ones simply chasing away the smaller, but when contestants were fairly even in size, clawing, biting battles with continuous contact up to 4 minutes were seen in some instances. Two fighting areas were examined, and both were characterized by clumps of fur and trampled, broken, or bent vegetation up to 8 cm in diameter. Because of fighting, old males had numerous scars on their heads, necks, and shoulders as has been reported for male black bears in Idaho (Beecham 1980) and Arizona (LeCount 1982).

Males found females by following scent trails. A male that temporarily lost a trail on a dry gravel road appeared frantic as he ran back and forth with nose to the ground until he found where the trail left the road. Most other males appeared less hurried as they followed scent trails, but they did not stop to forage. A typical example was observed from an airplane on 27 June 1971 as Male 215 tracked radio collared Female K

for 5.1 km. When first observed, the male was passing a point on Female K's trail that she had passed an hour and 45 minutes earlier. She was 2.8 km ahead of him and circling back to her territory after having moved 3 km outside it. She did not stop to forage while trespassing but did stop soon after entering her own territory where the male caught up to her. She probably was not receptive yet because 6 hours later (at 1845 hours) the male was resting 100–200 m downwind from her, and he eventually left. He returned and mounted her 4 days later on 1 July. In 2 other instances, males (215 on 12 Jun 1971 and 338 on 6 Jul 1971) were found 100–500 m downwind from near-estrous females (Q and L), and in at least 1 of those instances the male (338) and female (L) were together the next day.

While adult males were roaming their mating ranges they showed reduced use of garbage dumps. This was also noted at a dump in Alberta (Herrero 1983). Nine adult males, 4–13 years old (average 6.8 years), were within 2 km of garbage dumps in only 19 (24%) of 80 locations during the mating season as compared with 113 (42%) of 268 locations during the remainder of the period from 1 May to 30 September ($x^2 = 8.87$, 1 df, $P < 0.01$).

The 9 males also showed reduced use of territories of lactating females and increased use of territories of potentially estrous females. Prior to the mating season, they were found in territories of lactating females nearly as often (5 of 12 locations) as they were in territories of potentially estrous females (7 of 12 locations), but during the mating season, 36 (80%) of 45 locations were in territories of estrous or near-estrous females. Only 2 (4%) of the 45 locations were in territories of lactating females (excluding locations <2 km from garbage dumps) (difference significant, $X' = 52.7$, 1 df, $P < 0.001$).

Number of Mates.—The number of mates was not well documented for either sex. Both sexes were promiscuous, but males probably averaged more partners simply because receptive females outnumbered mature males (page 13). An indication of the minimum number of females or female territories that males visited was obtained in 1971 when 2 males (338 and 215) held mating ranges where most females were wearing radio collars. Male 338, a 5-year-old, was located on 8 of the last 17 days of the 30-day mating season (12 locations) and was found near 4 estrous females (F, G, L, and a), in the territory of a fifth (Q), and at the edge of the territory of a sixth (A). Male 215, a 6-year-old, was located on 9 of the 30 days of the mating season (14 locations) and was found in territories of 6 estrous females (D, K, L, M, Q, and T) but was seen mounting only 1 of them (K). In addition, Male 295, a 7-year-old with a mating range largely outside the area of radio-collared females, was observed 6 times during the mating season of 1974. He was alone twice (10 and 28 Jun) and was closely following females on 18 June (untagged female), 22 June (Female b), 26 June (Female g), and 30 June (Female g). None of these males was found in the territory of a lactating female.

The highest number of observed mates for a female was for Female C. In 1972, she mated with at least 1 male on 16 June, with at least 2 males on 18 June (see below), and possibly with a male (224) that lost his radio collar in a fight in her territory between 16 and 19 June. The male of 16 June could have been 1 of those copulating with her on 18 June. Thus, she had 2–4 or more mates that year. At least 16% of the estrous females were found with more than 1 male.

Copulation.—Events leading to copulation were seen from an airplane on 18 June 1972. At 1007 hours, radio-collared Male 445, a 5-year-old, was moving along the exact route a feeding radio-collared female (C) had taken 59 minutes earlier. She was by then feeding in brushy semi-open upland approximately 300 m downwind from him. He moved rapidly, turning his head quickly from side to side, thrusting his nose briefly toward logs, ground, and vegetation she had investigated. He closed to 25 m from her in about 5 minutes, whereupon she suddenly lifted

her head, ran about 50 m, stopped, and then ran a short distance farther as he continued to approach. She slowed to a walk, and, within a minute (at 1014 hours), the male mounted her and began thrusting. The female stood still at times but frequently walked forward while the male clasped her with his forelegs. He attempted to thrust as he walked on widely spread hind legs. The copulating bears moved out of sight after 13 minutes. Then a larger male (probably 7-year-old Male 450) appeared, slowly but steadily walking the route the female and first male had taken. Lack of fuel precluded further observations from the air, but additional data were obtained from the ground an hour later. By that time, the female had moved 200 m into a dense stand of alders *(Alnus rugosa)* where a muddy trail of large rear paw prints straddled a set of smaller front and rear tracks and led through the alders to where she was copulating with the second male. Upon seeing the observer, the copulating bears broke and ran. The first male was at least 100 m from the pair according to radio signals.

Foraging Period

Transition Period.—The end of the mating season corresponded with the first major ripening of fruit (Table 1), and foraging became the dominant waking activity for both sexes. The first 25 days of the foraging period was considered a transition period when a few males continued activities typical of the mating season. During this period (10 Jul-3 Aug), marking behavior of males declined (page 26) and testosterone levels decreased to late summer and fall levels. Serum testosterone levels were 153 ± 14 ng% (x ± SE, N = 16) before the transition period and 46 ± 7 ng% (N = 16) after it (P < 0.001) (McMillin et al. 1976). Three of 6 adult males reduced their roaming and increased their use of garbage in this period as compared with the mating season. Two of the 3 (215 and 225 in 1971) were found within 2 km of sources of garbage in 7 of 17 radiolocations during this period as

compared with only once in 19 radiolocations during the mating season (x^2 = 6.7, 1 df, P < 0.01). For the third male (295 in 1971-75), 23 (77%) of 30 radiolocations were near sources of garbage during the transition period as compared with only 12 (43%) of 28 during the mating season (x^2 = 6.9, 1 df, P < 0.01). The 3 males that did not increase their use of garbage dumps (338 in 1971 and 442 and 445 in 1974-75) continued to roam their mating ranges as they had during the mating season, and 1 of them (338) was seen following and attempting to mount a bear on 3 August. Vulval swelling also regressed during the transition period; only 1 of 51 swollen vulvas was found after 24 July (on 5 Aug).

Only a few bears from the study area began foraging outside their usual ranges during the transition period. Seven (24%) of 29 males (5 of 16 adults) and 5 (5%) of 111 females (3 of 81 adults) traveled more than 7 km outside their usual ranges for more than a week at a time (male-female difference significant, x^2 = 11.3, 1 df, P < 0.001) (Table 6). However, at least 4 females (222, 419, 502, and 706) from other areas entered the study area during the transition period, which suggests that conditions elsewhere might have been more conducive to travel this early in the summer. The latter 4 were found to have territories 18-26 km away in the loamy area where sarsaparilla berries and blueberries probably were less abundant than in the study area (page 9).

Late Summer and Fall Travels.— Wide-ranging travel became common among both sexes late in summer and remained more common among males. Between 10 July and the denning period, 22 (69%) of 32 males and 42 (40%) of 105 females foraged >7 km outside their usual ranges for more than a week (male-female difference significant, x^2 = 8.14, 1 df, P < 0.005). After midsummer, fruit and nuts tended to become relatively more abundant in the loamy area than in the study area, and 13 (72%) of 18 trips by males and 33 (69%) of 48 trips by females were to that area. The 46 trips there averaged

Table 6. Proportions of radio-collared black bears that traveled >7 km outside their usual ranges[a] for more than a week at different times of the year in northeastern Minnesota during 1971-76.

Time of year	Males				Females			
	Yearling	Subadult	Adult	Total	Yearling	Subadult	Adult	Total
Emergence								
Apr	[b]	1/5[c]	2/11	3/30		0/17	0/69	0/98
Greenup								
1 May-9 Jun	[b]	1/5	1/11	2/28		3/17	2/71	5/100
Mating								
10 Jun-9 Jul	0/10[c]	0/3	3/16	3/29	0/11	1/19	0/69	1/99
Foraging								
10 Jul-3 Aug	2/9	0/4	5/16	7/29	1/11	1/19	3/81	5/111
4 Aug-31 Aug	2/10	4/4	12/15	18/29	3/10	3/20	25/76	31/106
Sep	1/11	4/4	12/14	17/29	2/10	4/18	30/76	36/104
Oct	0/11	2/5	8/13	10/29	1/9	3/18	13/75	17/102
Nov	0/11	1/5	1/11	2/27	0/9	2/18	2/74	4/101
Total foraging								
period[d]	2/11	4/4	14/15	20/30	3/9	4/18	35/78	42/105
Denning	0/11	2/5	1/11	3/27	0/9	0/18	0/74	0/101

[a] Usual range is considered to be the mating range for adult males, the territory for adult females, the maternal territory for yearlings and predispersal subadults, and the area of concentrated activity for newly settled immigrant subadults.
[b] Yearlings remained with their mothers for most or all of this period.
[c] No, traveling/no, radio-tracked during the period. Summarized from Appendixes 1 and 2.
[d] Not a total of the months in the foraging period because most bears were radio-tracked for >1 month. See Appendixes 1 and 2 for specific dates of radio tracking.

29.5 km (14-83 km) whereas all except 1 of the 20 trips to other areas were <19 km. The exception was a movement of 201 km lasting about 13 weeks (late Jul-24 Oct 1976) during a year of drought and food scarcity (Fig. 7). That movement by Male 450 was the longest recorded for a nondispersing bear. Other bears suspected of moving long distances in this study were beyond signal range for up to only 8 weeks; 7 of 8 bears that were beyond signal range for more than 2 weeks were radio-tracked in 1971 and 1972 when signal range was short (page 11). Although Male 450 found abundant acorns to the southwest, he did not travel the same direction the next year, moving instead 40 km east-southeast to a part of the loamy area that contained abundant mountain-ash berries, choke-cherries, hazelnuts, and highbush-cranberries (Fig. 7).

Bears from the Laurentian Shield, farther north, also moved to the loamy area during late summer, moving up to 92 km (mean = 46 km, range 24-92 km) in the 6 trips documented. The 4 territorial females (page 31) that moved from the loamy area to the study area in July returned to their territories in late July or August, and 1 of them (419 in 1974) then moved farther south to other parts of the loamy area. She repeated this pattern in 1976. This bear was earlier erroneously reported to be a resident of the study area (Rogers 1977:130).

Mothers with cubs of the year foraged >7 km outside their territories at least as frequently (12 [48%] of 25 left) as adult females without cubs (23 [43%] of 53 left). They also traveled at least as far, moving an average of 28.5 km (range 13-45 km, N = 11), compared with 22 km (range 8-38 km, N = 21) for lone adult females (difference weakly significant, t = 1.8, P < 0.1). The longest movements by females were 92 and 107 km, both by mothers with cubs (not included in the above comparisons of study area females). However, mothers probably traveled only about half as fast as lone females. Female C required 3.1 days for a 32-km trip with cubs in 1971 but made the same trip in less than a day when alone in 1972. The 3 fastest movements by mothers with cubs averaged only 12.1 km/day
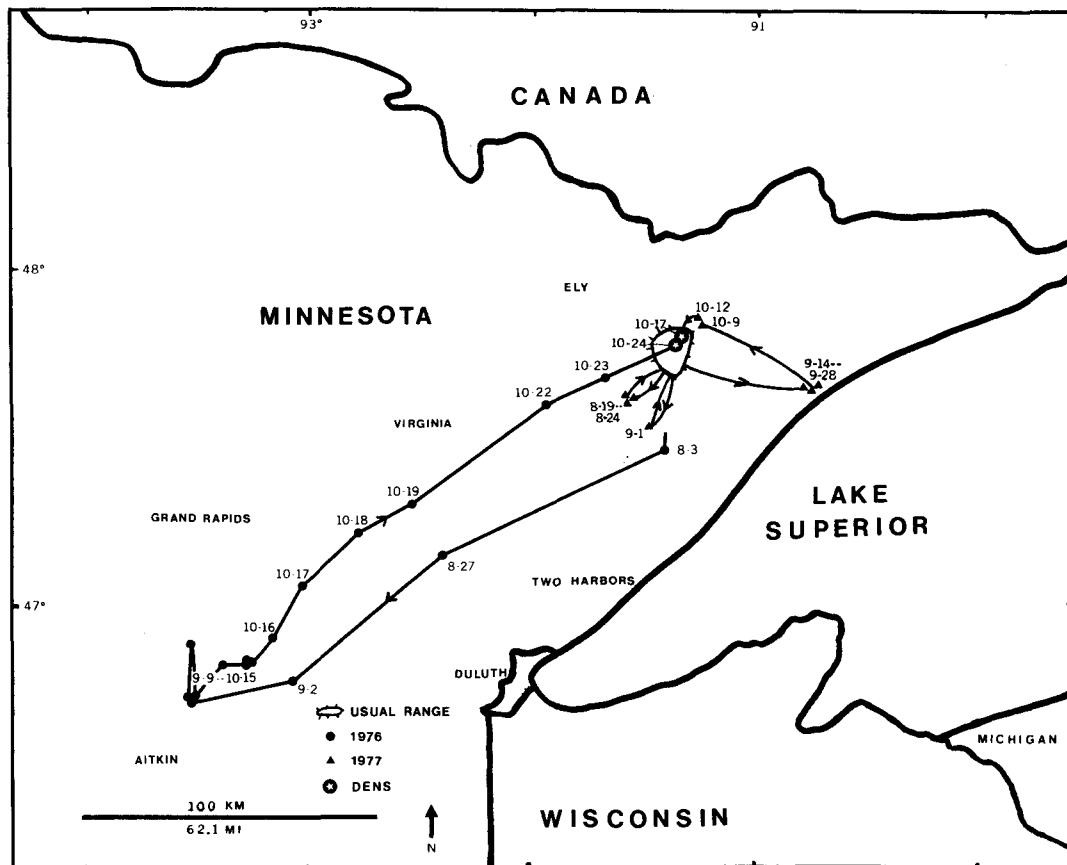
Fig. 7. Movements of Male 450 outside his usual range as an 11- and 12-year-old.

over distances of 23, 29, and 32 km, whereas lone females averaged 23.2 km/day over distances of 32 and 46 km. In shorter movements, a mother with cubs (E) moved 14.9 km in 25.25 hours on 7-8 September 1971, and a lone female (C in 1972) moved 16.7 km in <8.7 hours. A 4-year-old male (405), traveling a familiar path to a feeding area, moved 0.96 km in 8.2 minutes (7.0 km/ hour).

Cubs may remember as adults the food-rich areas they visited with their mothers. For example, in September 1976, Female n traveled 35 km to a 5-ha oak stand that she had been led to originally as a cub with her mother (C) 5 years earlier. Mother and daughter had foraged there from 30 August until 1 November in 1971. The mother had visited that stand, 30 km out side her

territory, in at least 3 of the 6 years she was monitored. The only other bear known to visit that stand from the study area was another of Female C's daughters, 3-year-old Female 324 in September 1972. Whether or not that daughter had been led to the stand as a cub in 1969 was not documented, but Female C is known to have led her cubs out of her territory in the direction of that stand in late August of that year.

Female C encountered her grown daughters at feeding sites up to 35 km outside her territory. Encounters with a 3-year-old daughter (n) in a hazelnut patch 11 and 7 km outside the mother's and daughter's respective territories were monitored in late August 1974. During 2 days of near-continuous radio tracking, the 2 seldom fed closer than 50 m except for a 3.4-hour

period when they fed in an area approximately 100 m in diameter. Then the mother moved away. When she returned 5 hours later, the daughter immediately left. No aggression or close interaction was detected.

Female C traveled more frequently than the other females studied, and she appeared to find the best food sources. Her knowledge of the oak stand and other distant food sources apparently minimized problems of local food shortage for herself and her offspring. She gained weight well in years of local food shortage, and her reproductive success was above average in both birth rate and cub survival (averages given on page 51). She produced 12 cubs (4 litters) in 7 years (age 8-14 years). Of 9 cubs that were studied closely, 8 survived to at least 1 year of age, and none died while accompanying Female C outside her territory. By fall, the 8 surviving cubs were significantly ($P < 0.001$) heavier, on the average (24.3 kg), than 57 other cubs born in the study area during the same period (17.3 kg). One of them (Female n) became the only female born in the study area to produce cubs at 4 years of age and raise them to independence without having access to garbage.

The percentage of bears traveling outside their usual ranges did not change significantly with changes in local food supply, which contrasts with an earlier finding (Rogers 1977). In years with abundant fruit and nuts in the study area (1971, 1973, 1977), 14 (38%) of 37 bears foraged >7 km away for more than a week, and in years of scarce food (1972, 1974-76), 50 of 100 left (difference not significant, $X^2 = 1.6$, 1 df, $P > 0.1$). Percentages also did not differ between females with access to garbage and those without (7 of 23 vs. 35 of 114 left, respectively). However, bears that forage widely in years of widespread food scarcity may move unusually far. Four of the 5 longest movements by adults (90, 107, 107, and 201 km) occurred in such years, with 3 of those movements occurring in 1985, a year when severe, widespread food scarcity led to a record number of nuisance bear com-

plaints in northeastern Minnesota (Garshelis 1986, Minnesota nuisance bear surveys—1981-85, office memorandum, Minn. Dep. Nat. Resour.). Those 3 movements (107, 107, and 90 km by bears 7, 15, and 24 years old, respectively) were to the outskirts of Duluth where 90 bears were reported killed as nuisances in 1985. The concentration at Duluth was due in part to wide-ranging bears being tunneled there by the shore of Lake Superior. Similarly 70 bears were killed as nuisances that year at Thunder Bay, Ontario, which is also on the shore of Lake Superior (B. Wall, Ontario Ministry Nat. Resour., pers. commun.). Similar concentrations have occurred in past years of food scarcity at Duluth (Schorger 1946), Thunder Bay (B. Wall, pers. commun.), and other places located mainly where waterways and population centers combined to act as barriers (Schorger 1949). Such locations were at population centers along the Mississippi, the Atlantic seashore, and the shores of each of the Great Lakes (Schorger 1949). Although bears have now been extirpated from most of those areas (Maehr 1984), they continue to be tunneled to Duluth and Thunder Bay in years of unusual food shortage.

Use of Garbage Dumps.—Although females left their territories to engage in what probably was scramble competition in the relatively food-rich loamy area in late summer, they avoided competing with adult males at garbage dumps there where food was even more abundant and concentrated. None of 33 females that traveled to the loamy area concentrated her activities near dumps, and only 2 females (n and r) were found even briefly near dumps. By contrast, adult males that traveled outside their usual ranges concentrated their activities around dumps in 5 of 10 cases. Seventeen of 22 bears foot-snared at dumps were males, with 14 of the males being ≥3 years old.

The avoidance of dumps by females outside their territories contrasts with their frequent use of dumps inside them. Inside their territories, mothers with cubs or yearlings avoided some individuals but

warned away other males larger than themselves. However, their avoidance of dumps outside their territories was consistent with their apparent fear of strange adult males. Some large bears are more likely than others to inflict injury, as has been noted for grizzly bears at dumps (Hornocker 1962), and small bears (including females) probably learn to recognize and avoid those individuals. Moreover, males at dumps far outside their mating ranges and the ranges of their kin (see below) may be more prone than usual to aggressive feeding and possibly cannibalism. Bears not yet familiar with individuals in a new area may at first be cautious of all large bears. For example, Female C, outside her territory and beyond the ranges of familiar males, turned and ran 0.4 km to forest cover upon encountering a feeding male that appeared unaware of her approach in a bog.

An attack by a large adult male on a subadult or young adult female was observed at a dump. The female continued to feed as the male entered the dump, and 2 other males fled. When the male moved toward food that people were throwing to him, the female followed. He whirled, leaped 3-4 m, caught her with his forepaws, and bit her behind the shoulders. She thrashed free and narrowly outdistanced him to cover 60 m away. This was the most aggressive and persistent attack witnessed outside the mating season. It contrasted with the situation commonly observed at garbage dumps in which 5-9 bears obtained feeding positions 0.5-2 body lengths apart and fed peaceably for more than an hour at a time with no apparent aggression other than occasional vocalizations. Infrequent clashes usually involved single bites or chases of <10 m, either of which caused nearby bears to scatter. However, when natural food was very scarce in 1985, fights at dumps were more frequent and severe. Injuries included a broken leg, a 12-cm laceration, and a nose pad being bitten off.

The avoidance by females of concentrations of strange adult males at dumps parallels observations in other studies of females avoiding concentrations of strange males in natural feeding areas. Jonkel and Cowan (1971) noted that in Montana, a female and cub remained near the edge of a large huckleberry area rather than moving into the center where berries were more plentiful but where 9 adult males had gathered. In Tennessee, Garshelis and Pelton (1981) reported that females avoided a mountainside where several males were feeding on acorns. The only female known to use that area remained there for a shorter time than any other bear studied.

Bears that fed at dumps in northeastern Minnesota continued to eat mainly the surrounding wild foods until those disappeared in late August. Ninety-nine (75%) of 132 fecal droppings at dumps contained mainly natural foods during 1-23 August 1982. However, as fruit abundance declined, the proportion of droppings containing mainly wild foods declined to 26 (35%) of 74 droppings during 24-31 August, to 7 (8%) of 89 droppings during 1-10 September, and to none of 10 droppings after that. Garbage supplements enabled bears to extend their growing and fattening period, leading to more rapid growth, earlier maturity, and higher reproductive success (Rogers 1976, Rogers et al. *197 6b)*. The largest bears captured during the study, including a 278-kg male (377), a 135-kg female (H), and all the dominant males of the study area, used dumps.

Male 295 used garbage dumps more than the other bears studied (page 31) and his travels to distant dumps were the best documented (Fig. 8). On 10 August 1971, as a 4-year-old, he left his mating range and moved from dump to dump until he arrived at the Finland town dump, 29 km away, on 20 August. From then until 9 October, he was found within 3.7 km of the dump on 19 of 27 monitoring attempts but left the dump for up to a week at a time, traveling 23 km to the Isabella dump and to points unknown. Natural food was abundant. In subsequent years he made additional trips to the Finland dump in August, and, with natural
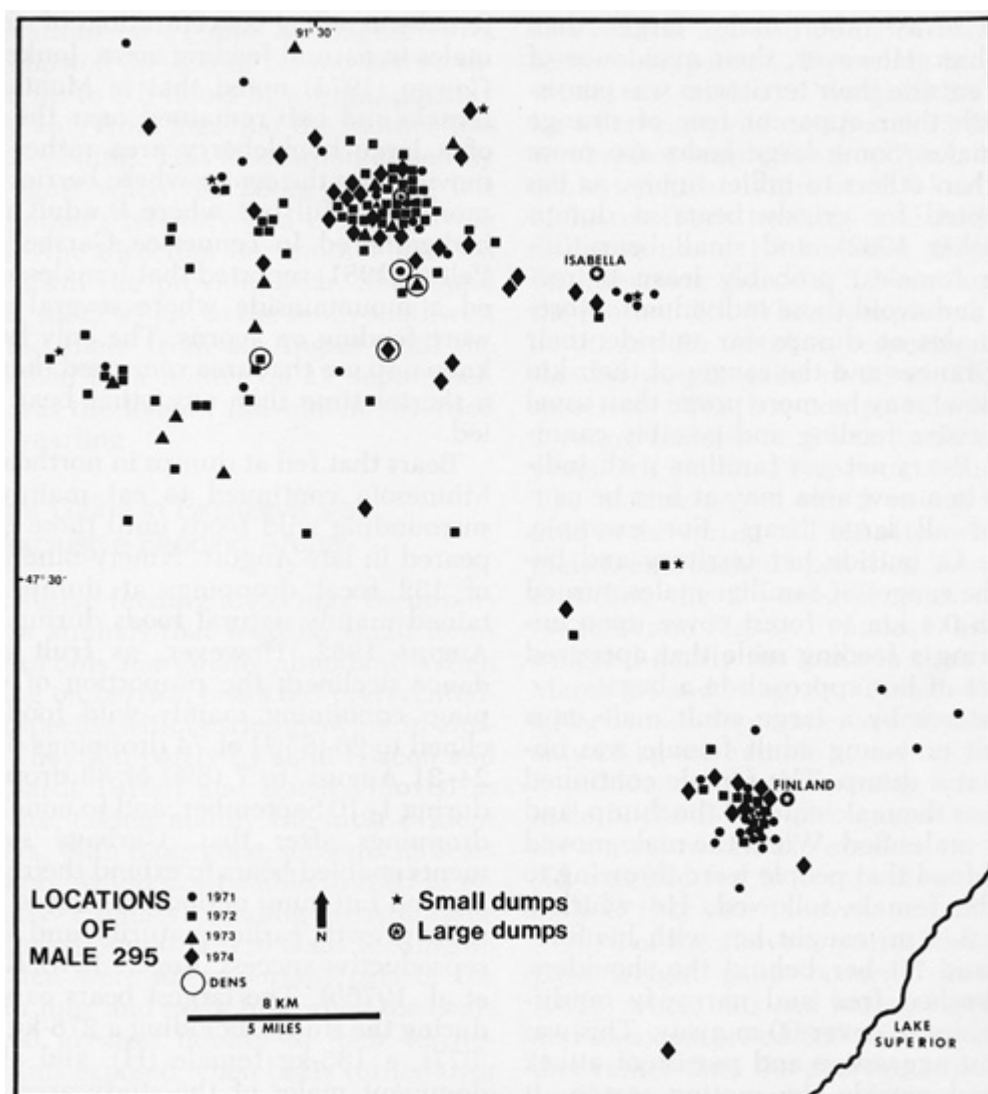
Fig. 8. Locations of Male 295 as a 4- to 7-year-old in northeastern Minnesota during 1971-74.

food scarce in each of those years, he concentrated his activities there more strongly. In 1972, he was found within 2 km of the dump on 11 of 12 monitoring attempts between 25 August and 25 September and was 9 km away once. His radio failed the next summer, but in 1974 he was within 2.7 km of the dump on 4 of 5 monitoring attempts between 15 August and 17 September and 11 km away once. Dumps were closed in 1975, a year when wild fruit and nuts were again scarce. That year he arrived at the Finland dump as usual in mid-August, found

it closed, and returned the 29 km to his mating range where he was killed at 0300 hours on 20 August while attempting to get garbage from a porch 0.2 km from a closed dump that he had frequented there.

Another male (453), a 7-year-old, also demonstrated familiarity with dumps over a large area. During 6 days after a dump he had been using was covered with soil, he moved southeast and south during the next 6 days to the Murphy City, Finland, and Silver Bay dumps, 18, 29, and 41 km away. He visited the Silver Bay dump almost daily from 16 July until 19 September when

he began moving 25 km north to a den. He had gained more than a kilogram per day during the summer and had achieved an above average weight (approximately 245 kg) as is common for bears that supplement their diets with garbage (Rogers et al. 1976*b*).

Prehibernation Activities

Fruit and nuts became scarce in the study area by mid-September and were essentially absent in the region by late October (Table 1). Bears typically began denning between late September and early November, with at least half of them settling at den sites by 15 October each year. The fattest bears were the first to move to dens. These abandoned available food as was reported for very fat bears in good mast years in Pennsylvania (Matson 1946). The heaviest bear, weighing 278 kg on 13 September, moved 13 km from a dump to a den site between 18 and 24 September and dug his den by 4 October. The second heaviest bear, 245 kg (see above), began moving from a dump to a den on 19 September. A very fat, pregnant female (103 kg) raked bedding into a crevice den during 2-9 September, moved up to 1.6 km away in mid-September, returned by 18 September, and remained thereafter. Leaner bears also denned in late September or early October if food was scarce but were the last to den if they found late-lasting foods such as garbage, acorns, or mountain-ash berries. The latest den construction was in early November when adult Male 353 dug a den 4 km from the dump he had been using and Female C renovated an old rock den after returning 34 km from an oak stand. Black bears in Montana (Jonkel and Cowan 1971), Idaho (Reynolds 1977), Alberta (Tietje and Ruff 1980), and Tennessee (Johnson and Pelton 1980, Garshelis and Pelton 1981) also entered dens later when food remained available in late fall.

As the time of denning approached, wide-ranging females returned to their usual ranges in 42 of 43 instances, and males did so in 20 of 23 instances. The

female that did not return in fall (Female Q, 2 years old) denned 21 km away and returned in spring. The 3 instances of males not returning all involved Male 569 who denned in either of 2 dens 20 km north of his usual range as a 2-, 3-, and 4-year-old and who also returned to his usual range each spring. Although he was atypical in denning outside his usual range, he was typical of other males in returning each year to a particular small area for denning. He moved to that denning area each year from foraging areas 55-65 km away. His 2 dens (1 used twice) were 5.2 km apart. Similarly, Male 295 returned each of 4 years to an area 6x3 km after roaming an area larger than 49 x 24 km (Fig. 8). Male 445 returned each of 3 years to an area 2.2 x 0.5 km after roaming an area larger than 37 x 14 km. Male 224 used dens 2.6 km apart, and Male 450 used dens 2.0 km apart.

In the days before denning, movements and activities declined. Johnson and Pelton (1979) found that activity began to decline up to a month before hibernation in Tennessee where bears entered dens in late December or early January. The decline may have been more rapid in northeastern Minnesota where bears denned 2-3 months earlier. For example, Female F remained active through at least 29 September before becoming abruptly lethargic in October. On 3 October, she slowly left her bed of 3 days after allowing an approach to 2 m. Her movements appeared difficult for the first few seconds after arising, but she gradually moved more freely and, after moving 10-20 m, bounded away. Four to 6 days later she constructed a den and ceased roaming for the year. Bears that foraged outside their usual ranges began this lethargy before returning in some cases. Female C and her cubs largely rested for several days in November before moving 34 km to an old den in the mother's territory. Male 295 was found at a single location on 22 and 25 September before moving 27 km and constructing a den by 6 October. Male 450 remained at a single location for approximately 6 days (4 aerial locations   during   10-15   October)

immediately before moving 174 km to a den in his usual range.

Only 8 (<4%) of over 200 dens found during the study were reused. Similarly, only 22 (<7.3%) of over 300 dens were reused in Pennsylvania (Alt and Gruttadauria 1984), and only 2 (6%) of 34 dens were reused in Alberta (Tietje and Ruff 1980). The low incidence of reuse is not due to study-related disturbance at dens because bears not previously studied also constructed new dens in most cases, as was also noted by Tietje and Ruff (1980). The 8 reused dens included 4 rock crevices, a hollow tree, an aboveground nest, and a burrow. Five of these were used the next year by the same bear. All were reused by bears of the same sex and approximate size. The reused burrow was re-excavated after having collapsed in spring as was common for burrows. Hollow trees were probably the preferred den sites (Bromlei 1965, Johnson and Pelton 1981) but were rare in the study area. The only 2 large hollow trees found during the study were both used as dens, and 1 of them was reused 2 years later by the same bear. Some of the rock dens were probably used for centuries. One was used 3 times during this study—in 1971-72 by adult Female E, in 1977-78 by adult Female L, and in 1984-85 by adult Female T, none of which were close relatives. Another rock den was used by a large adult male (224, 205 kg) in 1971-72 and by a male (450) of similar size in 1976-77.

EVENTS ASSOCIATED WITH GROWING TO MATURITY
Overview

Young bears remained with their mother for 16-17 months. Family members separated about the time the mother began estrus. Yearlings then began living alone in small ranges within the maternal territory. Males dispersed 1 or 2 years later, but females usually remained and expanded their yearling ranges into territories as they grew to maturity. Mothers avoided the ranges of their yearlings and shifted away from their daughters as the latter expanded their ranges. This behavior aided yearlings in obtaining exclusive feeding areas and aided daughters in obtaining territories. Adults of both sexes deterred immigration. Exclusive feeding areas appeared to increase feeding efficiency and may be particularly important in northern regions where relative shortages of food (as defined by Andrewartha and Birch 1954) are common. When fruit and nut crops failed, cubs and yearlings starved and adult females failed to reproduce.

Relationships Between Mothers and Yearlings

Family Breakup.—When yearlings reached 16-17 months of age, mothers and littermates all separated. This occurred between 1 June and 3 July for 26 families and during the last week of May for 2 families. Breakups probably were prompted by the mothers because all yearlings within a family left at about the same time in each of 5 families (families of Females B, C, and E in 1972; E in 1974; and F in 1971).

Events around the time of family breakup were most closely monitored for the family of Female B in 1972. The yearlings of Female B had grouped closely around her and fed without strife at a garbage dump 4.5 days before a man reported a bear blowing near his cabin. Three hours after the blowing, telemetry signals showed that the 3 radio-collared yearlings were within 0.4 km of the cabin but no longer together. In another 2 hours, the 3 were more than a kilometer away in different directions. The yearlings did not regroup despite repeated encounters with each other at the garbage dump. The blowing sounds reported were those used primarily in agonistic encounters, which further suggests that yearlings are forced on their own by threats as has been reported for grizzly bears (Murie 1961) and other solitary animals (Altmann 1958, Hafez 1970, Trivers 1974).

Only 1 of 51 families reunited after family breakup. Reuniting also was reported as uncommon by Schorger (1949), Jonkel and Cowan (1971), and S. M. Herrero (pers. commun.). The mother (D) in this family separated from her yearlings (Females d and e) as usual in June (1971) but reunited with them after the mating season; 1 rejoined her in late July and the other later in summer. She was recaptured during the mating season and showed the unusual condition of lactating (lightly) while having a swollen vulva. She probably was unreceptive to males as she was alone in each of 7 observations during the mating season, and radio-collared males that overlapped her territory were found in it only briefly (Male 215) or not at all (Male 224). She produced no cubs the following winter. She separated from the 2-year-olds the following June (1972), conceived, and subsequently produced a litter from which she separated at the usual time.

Establishment of Yearling Ranges.— Excluding the 2 that reunited with their mother (above), 24 yearlings (10 males, 14 females) were radio-tracked after family breakup. Littermates separated from their mothers and from each other and moved to portions of their mothers' territories where they concentrated their activities for at least the next year. All were in those areas by the time they were first located after family breakup, with 11 of them being located within 4 days. Yearling Male 628 was monitored at about the time of family breakup. He and his mother (Female E) had been together at 1500 hours on 8 June 1974, but when monitoring resumed on 9 June at 2252 hours, the 2 were 300 m apart and the mother was moving farther away (page 29). For the next 3 days, he remained in an area of only 1 km^2 while his mother traveled more widely than usual and attracted a male (page 29). The square kilometer remained part of his core area until at least the next June when his radio collar was removed.

Twenty-two of the 24 yearlings concentrated their activities in areas of 1-7 km^2. These areas included up to a fourth of each mother's territory and, in some cases, adjacent areas. The other 2 yearlings (Male 433 and Female 890) used the majority of their mothers' territories rather than a small portion. Overlap between yearlings or between yearlings and older siblings varied from practically none with clear mutual boundaries *(N* = 3), through separate core areas with shared low-use areas (N = 8), to concentrated use of a shared dump with largely separate areas away from it (2 families). Five of the 24 yearlings (3 males, 2 females) moved more than 7 km outside their usual ranges for 1-6 weeks in late summer and fall.

Movements by Mothers in Relation to Yearling Ranges.—Mothers seldom used the ranges of 22 of the 24 radio-collared yearlings, giving them nearly exclusive use of those areas as has been reported for various primates (Aldrich-Blake and Chivers 1973, Tenaza 1975, Chivers and Raemakers 1980, Tilson 1981, Waser and Jones 1983). The 2 remaining ranges were shared by mother and yearling in early summer, but each of those yearlings (Male 433 and Female 890) traveled extensively outside their mothers' territories in late summer. The avoidance by mothers of yearling ranges was examined closely for adult Female E during 429 hours of radio tracking between 21 June and 23 September 1972. Although the range of her yearling (Male 431) occupied 8-15% of her territory, she spent only 2.4% of her time in it (Fig. 9). The yearling range apparently was not deficient habitat because the year after the yearling dispersed the mother concentrated her activities in a portion of it that she had previously avoided (Fig. 10). Avoidance undoubtedly also was not due to threats from yearlings because mothers were still at least 3 times heavier than yearlings in early summer and yearlings were clearly subordinate members of the social order as Hornocker (1962) reported for grizzly bear yearlings. By allowing her yearlings in her territory and avoiding their core areas, each mother provided her yearlings with territorial protection from nonkin, a spatial nucleus
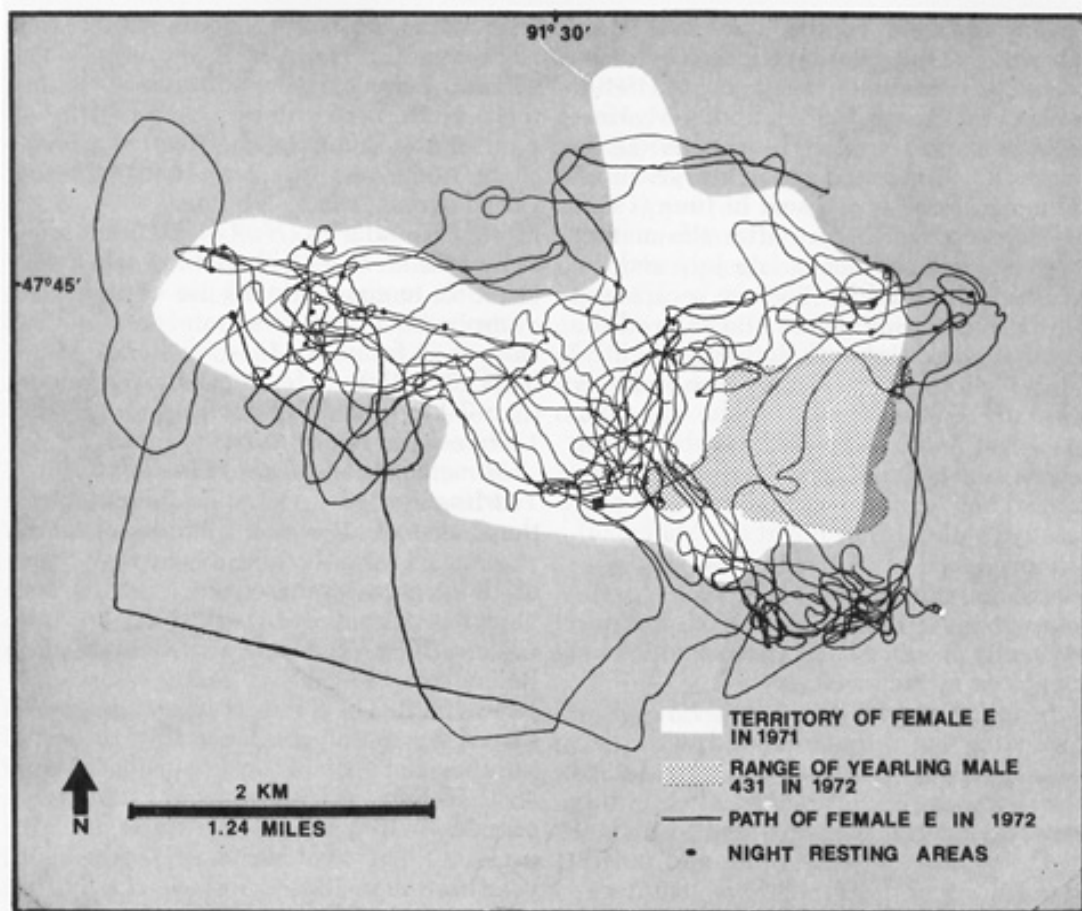
Fig. 8. Movements of 11-year-old Female E in 1972, showing avoidance of her yearling's home range in her territory. Female E was radio-tracked 439 hours from June until she denned on 23 September. The yearling (Male 431) was radio tracked 206 hours during this same period. Both bears were absent from the territory and not located in late July and early August.

from which young females could establish territories (page 42), and decreased competition for food. Exceptions were at sites with unusually abundant, clumped food supplies such as garbage dumps. Those were shared rather than avoided by mothers.

Alt and Beecham (1984) demonstrated that mothers recognize their offspring primarily by smell. This type of recognition seemed to underlie an interaction between a mother (812) and her independent male yearling when the 2 met at the edge of their territory near an artificial feeding station on 27 July 1984. The 2 approached a clearing from opposite directions with a strong crosswind preventing scent recognition.

When the yearling appeared, the mother immediately ran full speed toward him while he climbed quickly to the top of a mature red pine. She leaped up the trunk and climbed fast after him. Suddenly she slowed. The 2 extended noses to within 0.5 m, and she calmly climbed down and left. From her vigor, demeanor, and persistence, she had seemed inclined to attack the yearling, but she desisted when she apparently identified him as her own. The next year the same mother, with cubs, chased an unrelated young male up a tree at the same location. That time she showed no restraint, biting the male, throwing him out of the tree, and chasing him further. The
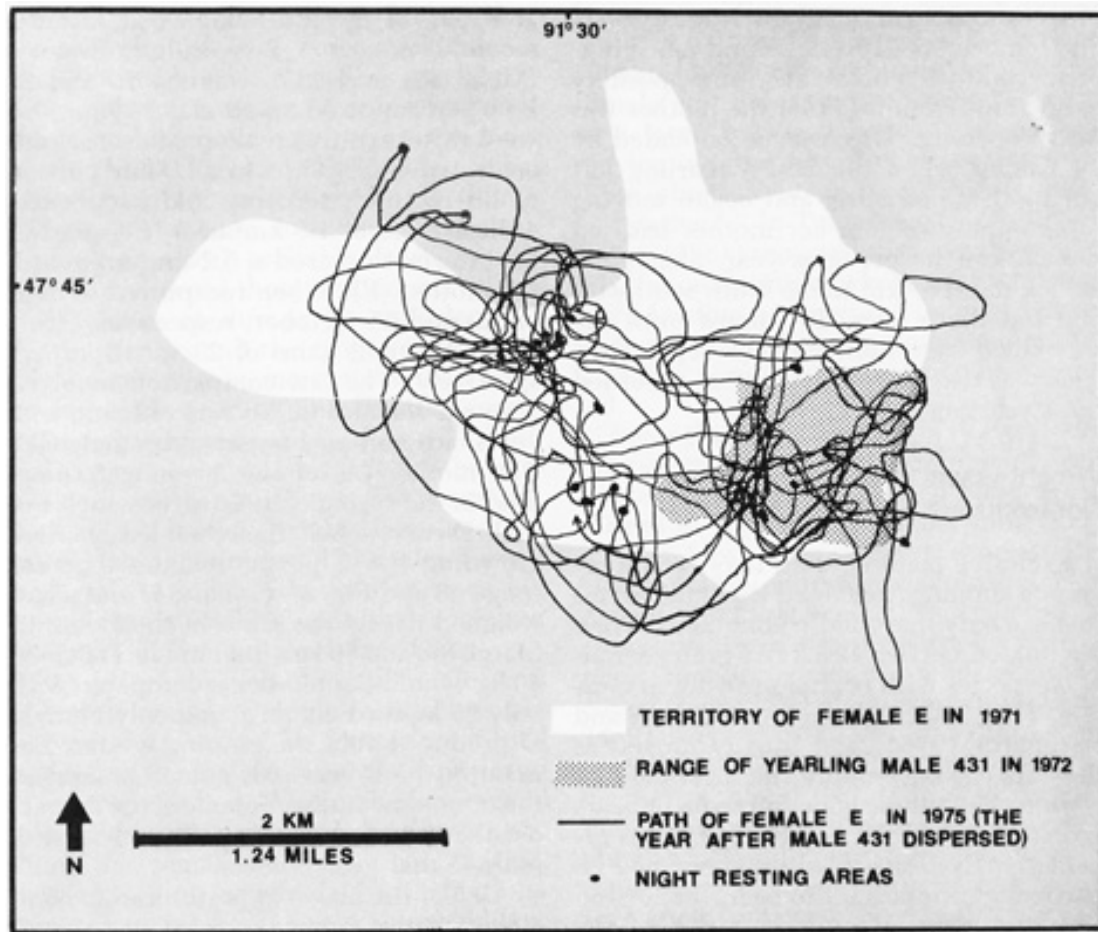
Fig. 10. Movements of 14-year-old Female E in 1975, the year after Male 431 dispersed, showing her reuse of his former range (compare with Fig. 9). Female E was radio tracked 482 hours between 30 June and 30 July 1975.

year after that, without cubs, she treed and fought with an unrelated yearling female, injuring the yearling's hind foot. While in estrus and accompanied by a male, the same female chased an unrelated estrous 3-year-old for >1.5 km with the male following.

The only observed interactions between a mother and her independent daughter also took place at the feeding station. On 20 June 1985, a lactating mother (403) chased her 2-year-old daughter, as she did all bears when with the cubs. However, when the daughter slipped while climbing a rock outcrop, the closely pursuing mother did not bite but merely slapped both paws on the ground a half meter behind the

daughter and continued the chase. Two additional chases of the daughter the following year, when the mother was without cubs, were <50 m and without vigor.

Mothers typically had no direct association with their offspring after family breakup. Mothers and yearlings were found <100 m apart on only 4 of 222 occasions when both were in the maternal territories (excluding locations for the family that reunited). Two of the 4 involved a yearling (Female 890) that had continued to use most of her mother's territory. The unusual behavior of this bear was determined in more detail through continuous radio tracking and occasional observations on

11 and 13 August 1976. She followed 50-150 m behind her mother for up to 3.5 hours at a time, possibly eating ants from logs that the mother was heard opening. This association ended by 14 August when the 20-kg yearling left her mother's territory and began moving south—the direction her mother had led her 32 km the previous year. She found an oak stand 89 km to the south-southwest and fed there from 26 August until she was killed by a hunter on 11 September. This was the longest movement recorded for a yearling.

Weight Gains in Exclusive Vs. Nonexclusive Feeding Areas

Exclusive feeding areas may be important to animals that feed on small items that are only marginally abundant. When feeding on berries, bears fed preferentially on species with berries growing in clusters. They fed partly by sight (Bacon and Burghardt 1976a) and usually moved as they ate, taking mainly the most evident clusters. With those gone, subsequent bears probably would not be able to feed as efficiently. Exclusive feeding areas may be particularly important to bears feeding on ants that were an important part of the diet in June and early July when the bears showed greatest fidelity to their territories. Ants exposed when bears turned over rocks or tore open stumps soon retreated to less accessible locations where subsequent bears would have more difficulty obtaining them.

Weight gains by bears with exclusive vs. nonexclusive feeding areas were compared in 3 cases. In each comparison the bear with the exclusive area gained more. In the first, Females d and e were of equal weight (30 kg) and body length (109 cm) when they left their mother (D) at 2.4 years of age in June 1972, but Female d obtained nearly exclusive use of a 5.2-km^2 area while Female e roamed an area twice as large, feeding in competition with her mother. By 11 September, Female d had gained 27.3 kg while Female e had gained only 13.6 kg. Female d produced her first cubs at 4 years of age and Female e at 7.

In the second comparison, 2 yearling littermates (Males 431 and 433) weighed 20 and 21 kg when captured on 18 and 19 June, 1.5 weeks after family breakup. Male 431 concentrated his activities in a 2.6-km^2 portion of his mother's territory and had nearly exclusive use of 1.8 km^2 of it (Fig. 9), but his littermate shared a 5.2-km^2 area with the mother (E). When recaptured in dens on 20 and 25 October, respectively, they showed weight gains of 23 vs. 15 kg, respectively. The last comparison involved 2 young females (a, 5 years old; and b, 2 years old) and an 11-year-old female (D). The mother (A) of the 2 young females died in the spring of 1972 after which Female D encroached upon their living areas, crowding the 2 young females together (page 43 and Fig. 3). Females D and a had weighed nearly the same in their dens in March (63 and 59 kg), but Female D gained 40 kg by mid-September as compared with only 25 kg for Female a, and only Female D produced cubs the ensuing winter. Female b, the 2-year-old, gained weight at the same slow rate as Female e, the 2-year-old that had fed in competition with Female D that year (above).

All 3 of the above opportunities to compare weight gains occurred in a year (1972) when nuts and berries were scarce and ants comprised 35% of the June-July diet rather than the average 18%. Results would be expected to differ with food supply. For example, where food was abundant and clumped at garbage dumps, 6 yearlings made superior weight gains despite competition. The 6 averaged 41.9 kg by fall, compared with 36.2 kg for 7 that fed only on natural foods.

Relationships Between Mothers and Older Daughters

Establishment of Territories.—Most females probably began to establish territories when they settled in their mothers' territories after family breakup. Of 22 subadult females radio-tracked during 1971-82, 15 expanded their yearling

ranges and continued to use them as they grew to maturity, 6 left their yearling ranges and established territories in adjacent areas, and 1 (Female d) dispersed 3 km as a 3-year-old and permanently usurped part of the territory of a 13-year-old female (C) (page 17). Two nonradio-collared females (656 and 812) dispersed 8 and 11 km. In all, only 3 of 31 females (including 9 nonradio-collared), whose birth places and adult ranges were known, dispersed. In addition, at least 3 females (P, S, and 704) immigrated to the study area from unknown areas at 3-4 years of age. No older female was known to disperse. Altogether, the data indicate that dispersal by females was uncommon, was typically of short distance, and involved females 3-4 years of age. Females apparently dispersed only to the nearest available area.

No injuries or strife were recorded for daughters that established territories adjacent to those of their mothers. However, of 3 immigrants, at least 2 had difficulties. Female S incurred injuries while establishing a territory (page 15), and Female P appeared unable to obtain a territory. Female P gave birth as a 4- or 5-year-old in the territory of a bear she had avoided the previous summer (page 17). She moved out in spring to an adjacent exclusive area of only 3 km^2 (Fig. 3), which was the smallest living area recorded for an adult that year (1972). She permanently left that area and moved beyond radio contact in late July.

Parental Investment and Female Philopatry.—The low dispersal rate among females may be explained in part by advantages mothers conferred on daughters that remained near their birthplaces. Nine mothers shifted their territories to include new areas away from ranges of 12 maturing daughters, and no mother shifted her territory toward a daughter. This shifting away may be an extension of the avoidance by mothers of yearling ranges (page 39) and/or may be due to mothers resolving crowding problems through conflict with nonkin rather than kin. The effect of this behavior was to aid daughters in establishing territories. The amount of territory mothers should give up to daughters or the effort mothers should put into range shifts should be governed by the average reproductive enhancement these behaviors confer on daughters vs. any cost to the future reproductive success of the mother herself (Hamilton 1964, Wilson 1975). Continued parental investment in daughters will be favored by natural selection if the resulting increase in FZ progeny averages more than twice any cost in future F; progeny. This ratio holds because sons or daughters carry twice as much of a mother's genetic material, on the average, as grandsons or granddaughters carry.

Black bears are similar to other polygamous species in that the sex most involved in resource defense is the more philopatric sex (Greenwood 1980, Dobson 1982, Waser and Jones 1983). In the black bear, the female is this sex. One explanation for the widely observed correlation between resource defense and philopatry may be that the sex most involved in resource defense tends to show differential aggression against nonkin with the result that same-sex offspring are aided in establishing living areas as was observed in this study.

The circumstances that prompted the few female dispersals were not determined. There was no evidence for aggression as a cause. The potential for aggression against young females appeared highest after mothers died and living areas were invaded by neighbors and immigrants. However, even in those cases, only 1 (Female 812) of 9 young females dispersed, which is similar to dispersal rates for females with living mothers (2 of 22 dispersed) (difference not significant, $x^2 = 0.03$, 1 df, $P > 0.5$). Females whose mothers died continued to show strong philopatry, which suggests that the mothers' vacant territories benefited the daughters despite problems with invading neighbors. For example, in 1972, 2 daughters (a, 5 years old; and b, 2 years old) that had been using separate portions of their dead mother's territory were forced together

Table 7. Numbers of captured immigrant black bears of various ages that became residents of the study area in northeastern Minnesota during 1969-77.

Age (years)	Immigrant males		Immigrant females	
	Captured w	Settling W	Captured[a] (N)	Settling W
1	*0*	*0*	0	0
2	20	*4*	4	0
3	24	*8*	5	2
4	5	*0*	4	1
5	3	2	0	0
6	1	0	1	0
7	2	1	1	0
8	1	0	1	0
9	0	0	1	0
10	0	0	1	0
13	0	0	2	0
14	1	0	1	0
15	0	0	1	0
22	0	0	1	0

[a] Not including 3 females of unknown age. These 3 had worn teeth, were probably ≥8 years old, and were not recaptured.

by an invading 11-year-old neighbor (Female D) (Fig. 3). However, during the next 2 years, the daughters regained use of the separate portions. They maintained them as territories through at least 1984, expanding them after 4 neighbors were killed in 1975 (D, E, and Q) and 1978 (q) and eventually abandoning their old yearling ranges to their own offspring (Yearlings 635 and 646 in 1975 and Yearling 200 in 1979). In another example, an orphaned cub (Female w) lived 1.5 years in a narrow (<l-km-wide) strip along the northeast edge of her mother's (h) former territory rather than dispersing after a female (y, 3 years old) from an adjacent area began encroaching. The natural outcome of this situation was not learned because the encroaching bear was killed. After that, Female w expanded her range as a 2-year-old (Fig. 6) and used approximately her mother's territory as a 3- to 5-year-old. The factors and circumstances that favor dispersal by female black bears are unknown.

Dispersal by Males and Establishment of Mating Ranges

Dispersal Age and Distance.—In contrast with the low dispersal rate among

females, all males born in the study area dispersed; 13 dispersed as 2-year-olds, 5 as 3-year-olds, and 2 as 4-year-olds. Strongly male-biased dispersal is common in species with polygynous mating systems and female defense of resources (Greenwood 1980, Dobson 1982, Waser and Jones 1983).

Dispersal distances were 13-219 km (mean 61 km, median 49 km) for 18 ear-tagged males that were born in the study area. Nineteen other males that were ear-tagged as they passed through the study area at 2, 3, or 4 years of age were recovered 20-224 km away (mean 75 km, median 60 km). One bear may have dispersed even farther because an unidentified radio-collared bear was seen by a wildlife biologist 324 km outside the study area. Excluding that movement, dispersal distances averaged <5 mating range diameters, which probably was not far enough to disrupt genetic adaptations to regional conditions (Shields 1982, 1983).

Most males established their adult ranges by 4 years of age (Table 7) and used those ranges for at least mating each year thereafter. During 1969-77, 4 immigrant males established ranges in the study area at 2 years of age, 8 did this at 3 years of age, and 3 as older bears although the latter 3 may only have expanded adjacent ranges. Two-year-olds appeared less successful than 3-year-olds in establishing ranges, but the difference was not significant ($x^2 = 0,02$ using Yates' correction, 1 df, $P > 0.1$). Four (20%) of 20 2-year-old immigrants obtained mating ranges in the study area compared with 8 (33%) of 24 3-year-olds.

Individual Accounts.—Four radio-collared males (401, 346, 306, and 569) that were born in the study area provided details of movements before, during, or immediately after dispersal. Two males (346 and 401) that were radio-tracked extensively before dispersal each showed increased travel immediately prior to dispersal. Male 346 was radio-tracked from 5.5 months of age until he dispersed at 28.5 months. During his first summer and fall, he was radio-tracked by his mother's (F) signals, and after that he wore

his own radio collar. During those 2 years, 102 of his 104 locations were in his mother's territory. The 2 times he was outside it, he was a cub accompanying his mother up to 13 km to the south. His first known independent movement outside the territory was on 25 May 1972 when he was a 2-year-old approaching dispersal. He moved 10 km east, returning 2 days later. On 2 June he moved 21 km northwest, returning within 5 days. The next day his signal was missing from his mother's territory, and he was not found again.

Male 401's first known movement outside his mother's territory after 9 months of radio tracking (63 locations) began on 3 June 1972 when he was a 2-year-old. He meandered 32 km east-northeast and returned by a nearly direct route, arriving on 29 June. Ten days later he left permanently. He moved 42 km west-south-west the first 5 days and 47 km west-southwest the next 55 days to the edge of a residential area where he fed on garbage, apples, and plums for 39 days. He left that place on 15 October, moving east, and radio contact was lost. In June 1977, nearly 5 years later, he was recaptured 133 km east-northeast of there. The place was 48 km east-northeast of his birthplace and 16 km beyond the area to which he had first moved in June 1972. Because adult males are usually in their mating ranges in June, it is likely that he settled approximately 48 km east-northeast of his birthplace after ranging widely as a sub-adult.

The third radio-collared male (306) dispersed farther than any other bear born in the study area. He was eartagged as a cub with his mother (H) on 23 August 1969 and was radio-collared as a 2-year-old in her territory on 9 August 1971. Ten days later he moved south out of her territory and radio contact was lost. A year later, on 19 August 1972, he was observed on the outskirts of Mahtowa, Minnesota, 145 km to the south-southwest, where he fed from garbage cans until 10 September. On 25 September, he was shot 74 km southeast of Mahtowa near Gordon, Wisconsin,

219 km from his mother's territory (as measured around Lake Superior). He had continued his long movements for more than a year, moving nearly 34% of his total distance in the last 15 days, which suggests that young males were capable of dispersing farther than they did.

The fourth bear. Male 569, dispersed the shortest distance recorded. He was eartagged as a cub with his mother (G) and was recaptured and radio-collared as a 2-year-old on 29 June 1974. The recapture location was 13 km northeast of his mother's territory in what would be his future mating range. He was radio-tracked for nearly the next 3 years as he grew to maturity, expanded his new range into a mating range of 13 x 9 km, and began pairing with females. However, as a 2-year-old, his new range was only 8x3 km (13 locations), and he remained there for little more than a month, returning in early August to the edge of his mother's territory where he fed at a garbage dump for 5-8 days until 14 August. Instead of then returning to his future mating range, he next moved 30 km east and then 24 km south to a portion of the loamy area where there were abundant hazelnuts, mountain-ash berries, gooseberries, hawthorns, and acorns. He foraged there from 23 August to 7 October in an area 5x2 km in size (9 locations) before traveling 65 km north-northwest through his future mating range and preparing a den 20 km beyond it in mid-October. The next 2 years he again used the 3 areas that he probably first used as a 2-year-old, arriving at his mating range each year by the beginning of the mating season but pairing with females only as a 4-year-old. In August each year he moved south to the food-rich area, moving directly to it rather than circuitously as he had as a 2-year-old. In October each year he moved north-northwest to the same denning area (page 37).

Proximal Effects of Food Shortage and Aggression on Dispersal.—Food shortage did not prompt early dispersal because males were no more likely to disperse at the minimum age of 2 years in years of

fruit and nut crop failures (7 of 11 2-year-olds dispersed) than in years of abundant food (6 of 9 2-year-olds dispersed). Five males that ate supplemental garbage all dispersed as 2-year-olds. In another part of Minnesota where natural food was more abundant and bears grew more rapidly, 4 of 7 males dispersed as yearlings and 3 dispersed as subadults **(D.** Garshelis and K. Noyce, pers. commun.). In Pennsylvania, where growth rates are the fastest reported for wild black bears (Alt 1980), the majority dispersed as yearlings (Alt 1978).

On Long Island, Washington, black bear density was >5 times that of northeastern Minnesota, and 3 of 4 males delayed dispersal until 4 years of age (Lindzey and Meslow 1977*a,b*). The fact that dispersal was delayed rather than hastened at high density suggests that aggression associated with high density may not initiate dispersal. Where there is differential aggression against nonkin, as in black bears, delayed dispersal might be expected at high population densities because risks associated with dispersing while body size is small may be relatively great. By the same logic, early dispersal by males might be expected where abundant food accelerates growth and sexual development. Thus, although aggression is known to deter immigration (page 47), aggression may not be effective in prompting the initial dispersal movements of young males from their mothers' territories.

Circumstances of dispersals from the study area further indicated that aggression was not a major factor prompting initial dispersal movements of males. Male 401 dispersed from his birthplace in spring 1972 at 2 years of age (page 45) even though his mother had died overwinter. His abandoned range and that of another 2-year-old that dispersed that spring (Male 346, page 44) were not immediately used by territorial neighbors or siblings, all or nearly all of which were radio-collared. Both males dispersed in a year (1972) when the potential for aggression from adult males was unusually low; 2 of 3 adult males that had overlapped the ranges of these subadults the year before were dead,

and the third was probably incapacitated after mid-June with injuries (including a 30-cm neck laceration) from a fight. The latter had been the dominant male in the ranges of the 2 subadult males but was not seen with females in 1972 after the fight. The loss of influence of those 3 adults opened the capture area to immigration by 7 subadult males, which was nearly as many as immigrated in all of the remaining 8 years in which immigration was assessed (8 bears, see below). Thus, although space was available locally in 1972, both males that reached 2 years of age that year dispersed. Further, movements of 32, 74, and 80 km were recorded for dispersing subadult males in September and October when aggression was an unlikely cause. At that time of year, aggression and testosterone levels are particularly low (McMillin et al. 1976), and bears of either sex are typically lethargic or in dens (page 37). Intraspecific aggression also cannot explain movements by 3 subadult males to points 75, 80, and 100 km outside the bear range in southern Minnesota. These movement data and the fact that all males dispersed led to a conclusion that initial dispersal movements and some subsequent movements by males were voluntary. Voluntary dispersal suggests that dispersal confers advantages on the dispersing individual.

Inbreeding Avoidance.—One advantage of dispersing is avoidance of inbreeding (Packer 1979). The facts that all males in this study dispersed before mating and that all males dispersed farther than any female support that idea. However, any suggestion that inbreeding avoidance is a major factor promoting dispersal in black bears is weakened by 3 observations. First, dispersal was mainly by males even though this sex would stand to lose less with inbreeding than would females in a polygynous system, due to males' smaller parental investment and larger reproductive potential (Dawkins 1979, Smith 1979). Second, the few females that dispersed probably did not move outside their fathers' mating ranges. Third, males did not disperse a second time when daughters

began to mature in their mating ranges. None of 10 radio-collared adult males dispersed while being radio-tracked for more than 22 bear-years, and none of 9 eartag returns from adult males indicated dispersal. Thus, father-daughter matings were possible. Males did not avoid pairing with females young enough to be their daughters; 2 of 4 observed pairs involving males > 10 years of age included females young enough to be daughters. Father-daughter matings would be possible for males at 10 years of age if males began mating at the usual age of 4.5 years and their daughters first mated successfully at 5.5 years, which is approximately the average of successful mating for females in northeastern Minnesota (range 3.5-7.5 years, page 51). In areas of unusually high nutrition, both sexes may mature at 3.5 years (Erickson et al. 1964, Rogers 1976), making father-daughter matings possible for 7-year-old males. Approximately 15% of the adult males were > 10 years of age, and 33% were >7 years (Table 3).

For females, the benefits of remaining in or adjacent to their mothers' territories (page 43) apparently outweighed any potential inbreeding disadvantages of remaining in their fathers' ranges. No deleterious effects of inbreeding were noted when a sibling pair was mated in captivity. They produced 38 cubs in 12 litters of normal number (2-4 cubs) with no mortality or obvious birth defects (0. Eg-gleston, pers. commun.). This could imply that bears may be at least mildly inbred in nature (Shields 1982). Avoidance of close inbreeding is logically a factor promoting dispersal, but it may be of limited importance relative to other factors influencing reproductive success and dispersal in black bears (see below).

Influences of Dominant Males, Females, and Food on Dispersing Young Males.— Mating privileges appear to be obtained by males primarily through male-male competition rather than as an obvious result of female choice. Successful competition depends greatly on body size (page 29). Consequently, dispersing males might be expected to establish mating ranges in areas with few dominant males, many mature females, and sufficient food for rapid attainment of large body size. Costs of dispersing to find such areas might be small for black bears for 3 reasons—(1) mating ranges are so much larger than natal ranges that most of the mating range would initially be unfamiliar whether males dispersed or not, (2) the large size of mating ranges precludes young males from obtaining meaningful amounts of space from their mothers (as young females do), and (3) black bears have few predators (Rogers and Mech 1981).

Evidence that dispersing males tended to establish mating ranges in areas with reduced numbers of dominant males was obtained in this study and in Alberta. In this study, the loss of influence of the 3 adult males in the study area resulted in a great increase in immigration in 1972. In that year, 12 new males remained in the study area long enough to be caught, and 7 of them established permanent ranges there. By comparison, in the 8 other years of intensive trapping (1969-77), an average of only 5 new males/year remained in the study area long enough to be caught and only 1 new male established a range there per year. In Alberta, 26 adult males were experimentally removed from a population during 1971-72 with the result that 95 new bears, mostly subadult males, immigrated by 1973 (Kemp 1976, Ruff et al. 1976).

However, areas with few or no dominant males may not be attractive to dispersing males if the areas lack females. Such areas may be the wooded vicinities of towns where there are few bears of either sex due to people shooting them (Rogers 1976). Two dispersing radio-collared males (306 and 401) fed in such areas for 23 and 39 days, respectively, and left (page 45). The fact that they remained so long in those areas is an indication of the influence of food on movements. Food influenced movements to the extent that dispersing males stopped to feed at garbage dumps for up to 72 days despite the presence of numerous dominant males. Conversely, food, females, and reduced

numbers of dominant males did not induce young males to remain in their natal ranges (page 46). Possible explanations for their leaving, in addition to avoidance of inbreeding, are presented below.

Enhancing Inclusive Fitness Through Dispersal.—The majority of males dispersed 2 years before reaching sexual maturity, typically dispersing as 2-year-olds and mating at age 4. Most probably were not sexually mature before 4 years according to comparisons of testicle sizes and body sizes of Minnesota bears with those of males studied for sexual maturity in Michigan (Erickson et al. 1964). By dispersing prior to maturity, males might increase the time available for finding areas favorable to reproductive success. Alternatively, the fact that the males were immature suggests that dispersal was not directly related to obtaining mates. Early dispersal may increase inclusive fitness by reducing competition among the kin left behind (Rogers 1977, Shields 1983). Males in Minnesota dispersed when they weighed 29-59 kg (N = 17). At that size, due to sexual dimorphism, they usually outweighed their sisters and were approaching the weights of their mothers. If they remained, they probably could displace female kin from preferred feeding sites, which might interfere with the females' growth and reproductive success. If males remained and deferred to female kin at feeding sites, they might reduce their own growth, which could reduce their potential for winning future mating fights. What occurred was that males dispersed to areas where competitors were nonkin, and they did so the earliest where they shared the maternal territory with their sisters. Nine of 10 males that had living sisters dispersed at 2 years of age, whereas only 4 of 9 without living sisters dispersed that early (difference significant, $x^2 = 4.55$, 1 df, $P < 0.05$).

Dispersal by young males can reduce competition among the kin left behind only if the latter can prevent or reduce immigration. The effectiveness of resident adult males in deterring immigrants was discussed above.

Territorial females may also deter immigration; during 1,480 hours of radio tracking a territorial female (E), 3 transient subadults (males by circumstantial evidence, page 19) were observed fleeing from her.

If resident adults can prevent or reduce immigration, and if dispersing males establish mating ranges where chances of mating are no worse, on the average, than in their fathers' ranges, dispersal may further improve the inclusive fitness of young males by reducing mate competition with fathers and brothers. Males benefit more by taking matings away from nonkin than from kin. Where a young male's competitors on the natal range share half his genes (e.g., father, brothers), a young male can achieve up to a 50% increase in gene copies passed to the next generation if, by dispersing and mating elsewhere, he enables one of his close kin to mate with a female with whom the young male otherwise would have mated. In this way, more of the young male's gene copies (those shared with the father or brother) are passed to the next generation than if he had remained and taken the mating away from his kin. Underlying assumptions are that mating success is not reduced as a result of dispersal and that the male : female ratio is high enough to promote competition among males. Again, young males would realize an increase in inclusive fitness through dispersal only if their nondispersing kin were successful in preventing immigration. All males dispersed at least 1 mating range diameter from their birthplaces.

INFLUENCES OF FOOD SUPPLY ON SOCIAL RELATIONSHIPS Evolution of Solitary Behavior

Black bears are generally solitary even though they have the visual acuity, vocalizations, and body signals necessary for close social communication (Henry and Herrero 1974, Bacon and Burghardt 1976fo, Jordan 1976, Pruitt 1976, Pruitt and Burghardt 1977). Two reasons for their solitary habits probably are that they have

little need for group protection and that the foods most important to fattening and reproductive success (fruit, nuts, and insects) are usually too scattered for group feeding by such large animals. Social aggregations probably have been limited by dispersed food throughout the black bear's existence, inasmuch as this species evolved from another omnivorous species of bear (Erdbrink 1953, Kurten 1976). Thus, there has been little selective pressure for black bears to develop the herding tendencies typical of large, open-country herbivores and some of the smaller omnivores (Wilson 1975). Being omnivores, black bears also have not evolved the cooperative behavior found in cooperative hunters (Schaller 1972).

Effects of Food Supply on Home Range Overlap

Although feeding interactions between bears in northeastern Minnesota appeared competitive rather than cooperative under all circumstances, the bears showed some social flexibility, as might be expected for animals that adapt in part through learning. The degree to which bears aggregated varied with food distribution, as has been shown for other carnivores (Bekoff et al. 1984). Where food was dispersed, as was typical for fruit, nuts, and insects, bears were dispersed. Males were solitary, and females were territorial as was described. Where food was clumped, as at garbage dumps, bears of both sexes integrated into an hierarchy, as has been reported for grizzly and brown bears *(Ursus arctos)* at dumps and salmon streams (Hornocker 1962, Stonorov and Stokes 1972, Egbert and Stokes 1976). Thus, social organization as a whole was governed by the distribution and abundance of food, although some social relationships were influenced by kinship as was described.

Females that lived adjacent to garbage dumps competed with each other for access. As a result, their territories overlapped slightly at the dumps, and all dumps were located at the edges of 2 or

more territories (Figs. 2-6). Females from the different territories fed at separate times in small dumps but often fed simultaneously in large municipal dumps. Territories that overlapped at dumps were separate away from them (Figs. 2-6) where the bears fed on wild foods. Females whose territories were not adjacent to dumps seldom or never visited them. Females with access to dumps were as prone to move to distant natural feeding areas as were females without dumps in their territories (page 34).

Home range overlap may be influenced not only by food distribution but by food abundance and its effect on bear density. Where food is more abundant than in northeastern Minnesota, reproductive rates and bear densities may be higher, with increases in overlap being especially likely among closely related females. Further overlap would be expected where the abundant food is distributed in unreliable patches. Overlap was common under such conditions in Tennessee (Conley 1979, Garshelis and Pelton 1981) and Idaho (Beecham 1980, Reynolds and Beecham 1980) and also occurred on Long Island, Washington, where population density was >**5** times that of northeastern Minnesota (Lindzey and Meslow *1977a,b).*

Food and Play

The only play observed among bears older than 7 months was near concentrated, abundant food sources. At garbage dumps and at a feeding station operated in 1984-85, bears <4.7 years old commonly engaged in gentle pawing and inhibited biting with no vocalizations or agonistic behavior. This play was done in standing, sitting, or lying positions as has been described for captive black bear cubs (Burghardt and Burghardt 1972, Henry and Herrero 1974, Burghardt 1975, Pruitt 1976) and for wild brown bears at salmon streams (Egbert and Stokes 1976). Play partners associated from time to time over periods of 6-22 days, wrestling and sparring for up to approximately 2 hours at a time and traveling together for up to 5

days. Of 11 sets of partners observed at the feeding station, none involved litter-mates or other close kin. The 11 sets included 7 pairs of males 1.5-4.7 years old, 1 pair of 2-year-old females, and 3 mixed pairs consisting of young adult males with 2-year-old females. Three young males that attempted to play with 4- and 5-year-old males desisted after getting no playful response. No bears playfully approached mothers with cubs.

Where several bears were receptive to play advances, fidelity between partners was weak. A subadult male played with at least 4 males, 2-4 years of age, during 14 June-11 July 1985. However, in July 1984, few or no potential play partners were available, and a pair of subadult males traveled together for 5 days (20-24 Jul), playing frequently the first 2 days, infrequently the next 2 days, and not at all on the fifth day. They reassociated 12 days later but were not observed playing. They traveled separately after that.

Partners appeared attracted to each other mainly to spar and wrestle. Partners did not aid each other in competing for food and did not defend each other against other bears. A male and a 2-year-old female wrestled on the fourth day before they copulated and during the 2 hours afterward, but the play involved no mounting or sniffing of genitalia and probably was only coincidental to the copulation. No sexual activity was observed between members of the other 10 pairs at the feeding station or between males and females observed playing at dumps. Play was common at the feeding station when abundant food was provided in late May and June 1985. Play became less common when less food was provided in early July; play partners threatened each other and sometimes fought briefly over food. All partners separated by mid-July when wild foods ripened and most bears ceased using the feeding station. Egbert and Stokes (1976) reported that play was common among brown bears at a salmon stream when salmon were abundant but infrequent when salmon were scarce.

FACTORS INFLUENCING POPULATION GROWTH

Food Shortage

Feeding Adaptations and Limitations.— Black bears are highly adapted for living on small items that are high in nutrients, low in cellulose, and available only part of the year. Fruit, nuts, acorns, and colonial insects are primary foods throughout their range, and buds, flowers, and young plants are eaten in seasons when the primary foods are scarce (Pelton 1982; Rogers, unpubl. data). However, adaptations for living on these foods reduce the black bear's ability to capture prey or to digest vegetation that is high in cellulose. Consequently black bears are poorly able to turn to foods other than their primary ones in the event of crop failures. For example, they are poor predators. In order to survive through cold seasons when food is unavailable, black bears have evolved blocky bodies that can carry large amounts of fat and minimize heat loss during hibernation. This body lacks the agility needed for efficient predation. Further, their legs and feet are adapted for climbing, tearing apart logs, and bending fruit-laden branches rather than for speed. Their short, tightly curved claws are well suited for climbing but, unlike the long claws of the grizzly bear, not for digging out fossorial animals. They have color vision and the ability to distinguish fine details at close range (Bacon and Burghardt 1976&), but there is a question as to whether their distance vision is sufficient for stalking distant prey. Altogether, these limitations prevent black bears from capturing most prey other than newborns (Rowan 1928, Chatelain 1950, Ozoga and Verme 1982) and animals whose escape is hampered by injury, deep snow, confinement, or other unusual circumstances (Barmore and Stradley 1971, Cardoza 1976:70). Spawning fish may be captured where escape is hampered by shallow water, but those are available only during spawning and in few locations (Frame

1974). Only a few areas have ungulate populations high enough and scavenger populations low enough to make winterkilled ungulate carcasses still available when black bears emerge from hibernation. Sixteen of 17 deer and moose carcasses observed in northeastern Minnesota were consumed by ravens, wolves, maggots, and other scavengers rather than by bears. Black bears typically obtain little meat, and they generally cannot turn to predation or scavenging when their primary foods are scarce.

Black bears also cannot efficiently turn to herbivory in the event of crop failures. Although they increase their consumption of vegetation when the primary foods are scarce (Rogers, unpubl. data), digestion of vegetation is low relative to digestion of fruit and nuts (Mealey 1975, Dierenfeld et al. 1982), and they lose weight or only slowly gain weight on a diet largely of vegetation (Jonkel and Cowan 1971). Black bear digestive tracts are shorter and less complex than those of specialized herbivores, which enables more rapid passage of food but allows less time for microbial digestion (Davis 1964, Mealey 1975, Dierenfeld et al. 1982). The rapid passage compensates somewhat for low digestibility, but digestion is limited primarily to cell contents rather than cell wall constituents (Mealey 1975, Dierenfeld et al. 1982). The bunodont teeth of black bears lack the elaborate grinding surfaces needed for fine mastication of vegetation, although they are well suited for crushing hard-shelled nuts. Soft items such as berries and insects are generally swallowed whole and ground up in the muscular pyloric compartment of the stomach (Cottam et al. 1939, Rogers and Applegate1983). The grinding action of the pylorus reduces the need for chewing, which increases ingestion rate and avoids breakage of seeds that contain cyanogenetic substances (Kingsbury 1964). The grinding action of the pylorus, together with the highly acid stomach (pH < 3.5), also aids in the digestion of protein and sugar and in the breakage of certain linkages in

hemicellulose (Bell et al. 1965, Dierenfeld et al. 1982). In short, the digestive systems of black bears seem better adapted for digesting fruit, nuts, insects, and succulent vegetation than for digesting mature, non-succulent vegetation, which is the major vegetation available in summer and fall when fruit and nut crop failures occur.

Other abilities that help black bears survive on foods subject to crop failures are memory, navigational ability, and learning ability. Hungry black bears may revisit distant feeding areas (page 33) or may forage beyond familiar areas (Schorger 1946, 1949), using orientation and navigational abilities to return home (Rogers 1987). They also may learn to exploit new foods such as garbage or campers' food (Rogers 1976, Steinhart 1978). Their learning ability, curiosity, memory, and ability to form concepts compare favorably with those of dogs, wolves, and nonhuman primates (Bacon 1973, 1980; Bacon and Burghardt 1976fo), However, where food shortages are widespread, the effects become apparent on even the most dominant bears (Rogers 1976).

Effects of Food Shortage on Reproduction.—Reproduction in black bears is controlled mainly in a density independent manner by fruit and mast supplies that fluctuate in abundance from year to year (Rogers 1976, 1983; Bunnell and Tait 1981). Access to food is influenced to some extent by dominance and territoriality (see above), but overall food supply is generally of overriding importance. For example, even the most dominant females living at relatively low population densities in northeastern Minnesota showed reproductive rates less than half those of females living at higher densities in Pennsylvania where there is more food. Minnesota females without access to garbage produced their first litters at 6.3 years of age, on the average (range 4-8 years) (Table 8), and produced subsequent litters at intervals averaging 2.28 years (Table 9). Litter size averaged 2.38 cubs (Table 10). In Pennsylvania, females usually reproduced by 4 years of age (38% at 3, 88% by 4) and

Table 8. Ages at which female black bears produced their first litters in northeastern Minnesota during 1969-80.[a]

Age	No. Producing first litter	
	Natural food only[b]	With supplemental garbage[c]
3	0	1
4	2	5
5	2	5
6	4	0
7	7	0
8	2	0

[a] Excluding Female P, background unknown, who gave birth at 4 or 5 years of age.
[b] Mean age 6.3 years.
[c] Mean age 4.4 years,

Table 9. Intervals between litters born to black bear females in northeastern Minnesota during 1969-80.[a]

Diet of mothers	No. years between litters	N
Natural	2	27
	3	8
	4	1
Mean	2.28	36
With supplemental garbage	2	8

[a] Excluded are 6 intervals of 1 year that occurred when mothers lost litters before mating seasons. Three of those mothers were on natural diets and 3 ate at least some supplemental garbage.

reproduced at 2-year intervals after that (Alt 1980, Kordek and Lindzey 1980). Litters averaged 3.0 cubs (Alt 1980). Using these data, the average Minnesota female at age 6.6 years, the average age at death for females that reached at least 2.4 years of age (calculated from Table 3), would be accompanied by her first litter containing 1.2 female cubs, whereas the average Pennsylvania female of that age would have produced 2 litters containing a total of 3 female cubs, and the offspring from the first litter would already be pregnant. The differences are probably due primarily to food supply rather than genetics because a Minnesota female raised in captivity began reproducing at 3 years of age and averaged 3.2 cubs/litter *(N = 12 litters)* (0. Eggleston, pers. cummun.). Wild females that supplemented their diets with garbage in Minnesota also approached this high reproductive rate despite the high competition among bears at garbage dumps. These produced their first litters at 4.4 years of age, on the average (Table 8), and produced all subsequent litters at the minimum interval of 2 years (Table 9). Litter size averaged 3.0 cubs (Table 10).

Variations in food supply during 1969-79 provided an additional means of assessing the importance of food supply to reproductive success of females that ate only natural foods. Food was relatively abundant in 6 of those years (1969-71, 1973, 1977, 1979) and relatively scarce in the other 5 (1972, 1974-76, 1978). Fifteen

of 17 females produced their first litters after years of relatively abundant fruit and nuts, and only 2 (Females n and e) produced their first litters after years of scarce food (difference significant, $x^2 = 8.4$, 1 df, $P < 0.005$). Reproduction in all years may have been enhanced slightly by bait used for live trapping.

Effects of Food Shortage on Survival.— Survival of cubs and yearlings also appeared to be controlled mainly in a density independent manner by food supply. First-year survival of cubs without access to garbage averaged 88% (N = 40) when fruit and nuts were abundant in both the year of conception and the year of birth, but survival averaged only 59% (N = 37) when food was scarce in both those years (difference significant, $x^2 = 7.86$, 1 df, $P < 0.01$) (Table 11). Survival averaged 75% (N = 104) when food was scarce in 1 or the other of those years (Table 11).

Starvation deaths of cubs and yearlings occurred either before or after hibernation rather than during it. Each of 68 cubs that survived to be weighed around the beginning of hibernation survived until spring regardless of prehibernation weight. However, 9 of 15 that weighed <10 kg at the end of hibernation died as yearlings within 4 months. Two of 13 yearlings that weighed 10-13 kg also died, but none of 16 heavier ones died. Of 28 2-year-olds that were radio-tracked from the time they left their dens in spring, only 1 (Female 295) died. She died in late spring or early summer 1982 after having weighed 12.7 kg in spring as a yearling and 17 kg in

Table 10. Number of cubs per litter for black bears in northeastern Minnesota during 1970-80.

Diet	First litters		Subsequent litters	
	No. per litter	No. of litters	No. per litter	No. of litters
Natural	1	1	1	3
	2	13	2	11
	3	3	3	21
	4	0	4	0
Mean	2.12	17	2.51	35
With supplemental	1	1	1	0
garbage	2	2	2	0
	3	5	3	6
	4	0	4	4
Mean	2.50	8	3.4	10

Table 11. Effects of fruit and nut supply on first-year survival of black bear cubs in northeastern Minnesota during 1970-80.[a]

Fruit and nut supply		Cub survival		
In year of conception	In year of birth	Percent survival	N	Years of birth
Good	Good	88	40	1970, 1971, 1980
Good	Poor	78	68	1972, 1974, 1978
Poor	Good	69	36[b]	1973, 1977, 1979
Poor	Poor	59	37	1975, 1976
All years		75	181	1970-80

[a] Excluding cubs of mothers that ate garbage.
[b] Excluding a newborn litter eaten by wolves in mid-February 1977.

spring as a 2-year-old. Her bone marrow was nonfatty, indicating starvation.

The yearling deaths most closely documented were those of 3 littermates that weighed 3.9, 5.0, and 6.8 kg at 14 months of age on 19 March 1977. They had been conceived and raised in consecutive years of scarce fruit and nuts (1975 and 1976) and had survived a year when 10 of 20 cubs had died (1976). As yearlings, they died in order from lightest to heaviest in weight. They left their den with their mother (d) on 13 April 1977. The first yearling died 14 days later, 5.6 km from the den. He was skinned and eaten by the mother, whose weight of 44 kg was only 56% of her peak. Six days later the family was seen 1.3 km away from there. The mother and largest yearling were feeding on catkins in an aspen tree, but the smaller yearling was by then too weak to climb trees or run. He died 3-6 days later, and the remaining yearling died in late June. Neither of those was eaten. Their red, jellylike marrow again indicated starvation as the cause of death.

Reproductive failure by adult females and deaths of cubs and yearlings contributed to a population decline when food was scarce for 3 consecutive years (1974-76). During that time, the study area population (including cubs) declined 35% from 1 bear/4.1 km^2 in June 1974 to 1 bear/6.3 km^2 in June 1977. Jonkel and Cowan (1971) found that reproduction declined nearly to zero in Montana when huckleberries *(Gaylussacia* spp.) were scarce for 3 successive years.

Predation, Cannibalism, and Aggression

Nine wolves killed a presumably healthy mother and her newborn cubs at a den in mid-February 1977. The 16-year-old mother (C) weighed approximately 72 kg. This was the only predation among the occupants of 206 dens, although the den of a wounded bear was visited by wolves (Rogers and Mech 1981). In summer, a wolf scat with cub remains was found in an area where a well-nourished cub of Female 271 had disappeared. In addition, an orphaned cub was killed or scavenged by wolves or bears in October 1975. Some predation on cubs could have been missed because cubs did not usually wear radio collars. However, the 88% survival of cubs in years of abundant food (page 52) indicates that predation on cubs was <12% in years of good nutrition. Information on how food shortage affects both the vulnerability of cubs and the cannibalistic tendencies of older bears is needed.

Cannibalism has been documented in other studies (Table 12), but there was no clear documentation of intraspecific predation on free-ranging bears in this study. Of 11 yearlings and 1 2-year-old that died, 4 yearlings were eaten, including the yearling eaten by its mother. Whether these 4 were killed or scavenged, their deaths could have been nutrition-related because their spring

Table 12. Free-ranging black bears killed by other black bears.

Victim	Attacker and/or situation	Date	Location	Source
Cub	A mother of another litter killed and ate the cub.	Late summer 1930	Yellowstone National Park	Arnold 1930
Cub	A male killed and ate a treed cub.	14 Jul 1959	Yellowstone National Park	M. Hornocker, pers. commun.
Cub	A bear killed a radio-collared cub that was with its mother		Arizona	A. LeCount, pers. commun.
Cub	A cub was killed during or after a fight between 2 adults.	17 Jul 1955	Yosemite National Park	Hartesveldt 1955
Mother and 2 cubs	A large bear killed and ate the family at their den.	Mid-Apr 1963	Michigan Arizona	D. Wenzel, pers. commun.
Yearling female	A medium-sized bear killed a radio-collared yearling that was with its mother.			A. LeCount, pers. commun.
Yearling male	A 5-year-old male killed a radio-collared yearling.	Early fall 1976	Alberta	W. D. Tietje, B. Pelchat, and R. L. Ruff; pers. Commun.
Yearling male	An adult male killed a radio-collared yearling.	1977	Alberta	W. D. Tietje, B. Pelchat, and R. L. Ruff; pers. commun.
Subadult male	The victim died of infected bite wounds to the head.	Winter	Arizona	LeCount 1982
16-year-old female	A large bear, probably a male, killed and ate the female at her den.	October 1976	Alberta	W. D. Tietje, B. Pelchat, and R. L. Ruff; pers. commun.

weights were all below average. Starving young bears too weak to run or climb would be vulnerable to a variety of predators.

Bears of either sex can benefit from killing nonkin. Carcasses may be eaten; the killings may reduce competition for food, space, and mates; and some of the benefits may extend to offspring. However, injuries to attackers could reduce fitness; therefore, attacks would be expected mainly on bears too small or vulnerable to inflict serious injury. Accordingly, small bears that behave abnormally because they are drugged or in traps are fairly commonly cannibalized (Jonkel and Cowan 1971, Kemp 1976, Payne 1978, Johnson and Pelton 1980). In this study, a trapped 28-kg, 3-year-old female was killed and partially eaten by a medium-sized bear on 11 June 1983. In natural situations, too, reported victims have been young bears or bears that were unusually vulnerable because of their reduced metabolisms in dens (Table 12). Victims included 6 cubs, 2 yearling males, a yearling

female, a sub-adult male, and 2 adult denning females (Table 12). In addition, cub remains were found in a bear scat on Long Island, Washington (Lindzey and Meslow 1977a). In unsuccessful cannibalism attempts, a male attempted to catch a cub in Yellowstone National Park (Barnes and Bray 1967), and a bear in Alberta wounded a 5-year-old radio-collared male in a den in mid-October 1976 (W. D. Tietje, B. Pelchat, and R. L. Ruff, pers. commun.). In Minnesota, an adult male at a garbage dump leaped up a tree, caught a retreating yearling, and tried to pull it down on 22 May 1984. The yearling bawled, the mother came running, and the male leaped off the trunk and was pursued 10 m.

Killings by black bears are by both sexes (Table 12), as also has been reported for brown bears (Troyer and Hensel 1962), but probably are mainly by large males. Because of their size, these are the bears that have the best chance of killing small bears without injuries to themselves.

Whether or not males in their mating ranges kill young bears that may be their offspring is unknown. In other species, the males most likely to be cannibalistic are new immigrants (Mohnot 1971, Eisenberg et al. 1972, Schaller 1972). Cannibalistic females can recognize close kin and avoid harming them (page 40).

Cannibalism is infrequently documented even in national parks and at garbage dumps where black bears are concentrated and visible. A question remains as to whether cannibalism rates are sufficiently density dependent to significantly regulate population growth. The scant evidence available suggests they are not. Probably the densest black bear population intensively studied to date is the one on Long Island, Washington, where Lindzey and Meslow (1977a) found 1.2-1.5 bears/km^2, excluding cubs. During 3 years of study, the researchers observed no agonistic encounters that included physical contact, nor did they find scars that would suggest attacks were common (Lindzey and Meslow *1977b)*. They found cub remains in 1 bear scat (Lindzey and Meslow 1977a). Cannibalism may have been more common in a population in Alberta where population density (approximately 0.6 bears/km^2) was less than half that of Long Island (Young and Ruff 1982). Four of the 14 cannibalism or attempted cannibalism incidents mentioned above or in Table 12 occurred there. The 2 populations differed in that the Long Island bears probably had a high degree of genetic relatedness with a low proportion of immigrant males (Lindzey and Meslow 1977&:421), whereas the Alberta population had been heavily exploited with resulting ingress of large numbers of new males (Kemp 1976, Young and Ruff 1982). The number of new males may influence cannibalism rates more than does overall population density, as has been found for other species (above). Although the possibility remains that cannibalism is a density dependent regulatory factor, it also may be an additional cause of mortality where heavy local exploitation has resulted in increased ingress of new males.

Additional information is needed to determine the role of cannibalism in black bear population dynamics. Information is particularly needed on causes and rates of mortality among cubs and dispersing subadults—the 2 age classes most likely to be cannibalized.

How often males are killed rather than evicted by resident adults is unknown. The only report of a free-ranging male of dispersal age being killed by a bear is that of LeCount (1982) in which a subadult male with bear bite wounds on his head was captured in June and monitored until infection killed him the following winter. Whether or not dispersing males are killed directly, aggression might reduce access to preferred food patches and force dispersing males into suboptimal habitat (Rogers 1976, Bunnell and Tait 1981). However, occasional deaths or slowed growth among subadult males probably has little effect on population growth due to the polygamous mating system. Effects on population growth can be properly assessed only if detriments to subadult males are considered in conjunction with any resulting gains in the survival and reproductive success of females due to the decreased competition.

Territoriality

There was no indication that the territorial system of females was effective in limiting population growth or density. The system seemed mainly to influence which bears, rather than how many bears, obtained easiest access to food, and it was not entirely effective in that. No territorial female was able to maintain sole access to any unusually important feeding site such as a garbage dump, and many females fed far outside their territories in late summer and fall. The territorial system probably increased the feeding efficiency of territorial females and their offspring (page 42) and probably enabled daughters to more easily obtain living space (page 43). This could work to the disadvantage of neighbors or immigrants, but effects of crowding were not adequately assessed due to human-caused deaths.

Parasites, Disease, and Other Health Problems

Deaths from parasites are rare in black bears despite the fact that many or most individuals are parasitized (Rogers and Rogers 1976). No radio-collared bear in this study died due to parasites, but any slowing of growth due to parasites was not assessed.

A variety of diseases have been reported for black bears (reviewed in Rogers 1983), but no serious disease has been found to be common, and no decimation of a wild population by disease has been reported. However, at least 28 of 148 black bears in a game park in South Dakota contracted canine adenovirus type 1 infection, and 24 of them died (Collins et al. 1984). In Minnesota, the only death of a radio-collared bear that could have been disease-related was that of 21-year-old Female A, the oldest bear studied. She appeared well in fall but died of unknown causes in her den in late March 1972 after having lost a third of her weight in 5 months of denning. A day or 2 before she died she bit the head off 1 of her newborn cubs and killed the other, probably by accidentally stepping on its head.

There were few natural injuries aside from the punctures and lacerations from fighting mentioned earlier (pages 29 and 35). Deformed penis bones with bone calluses indicating mended fractures were found in 4 of 30 adult males but in none of 53 subadult males. These breaks probably did not result from tree-climbing because similar breaks occurred among cave bears *(Ursus spelaeus),* which probably did not climb trees (Kurten 1976:27, 113).

The most common and serious injuries were from gunshot, arrows, steel jaw traps, and necksnares, as has been reported from other areas (King et al. 1960, Rausch 1961). A radio-collared female (263) died in November 1970 approximately 4 months after being gutshot. Another (Female 892) lived at least 3 years after having the distal third of her lower jaw shot off. Three had unuseable, deformed legs from gunshot. Others received massive bullet wounds that took up to a year to close.

Two nonradio-collared males lost testicles to birdshot.

Thirty-two (91%) of 35 deaths of radio-collared bears >1.5 years of age were from gunshot. The remaining 3 were from natural causes (wolves, starvation, and unknown) described above. Additional causes of death were observed among nonradio-collared bears: a cub was strangled by the cover of a garbage cannister, 2 orphaned cubs traveling together were struck by a train, a yearling was electrocuted atop a power pole, and 2 older bears were struck by cars.

HABITAT AND MANAGEMENT CONSIDERATIONS

Habitat loss, gunshot, and nutritional deficiencies limit black bear populations over much of the black bear range. The first 2 of these are human related and continue to increase due to an expanding human population. State and national forests and parks are the ultimate refuge for future bear populations, but public lands are commonly of low soil fertility, which increases the chances of food shortages and nutritional deficiencies. The Superior National Forest has low fertility and relatively few food species. Management to maintain or increase important fruit, nut, and acorn species in this and similar areas may be more critically important to bears than similar management in regions where food shortages are less frequent and severe.

Mature stands of oak *(Quercus rubra, Q. macrocarpa)* constitute <0.05% of the Superior National Forest (E. Lindquist, pers. commun.) but are disproportionately important to bears as was evidenced by long, traditional movements of bears to certain stands and by the superior reproductive success of these bears (page 34). The 2 species of oak each requires 25-50 years to begin producing acorns but then produces them for the next 100-300 years (Elias 1980). However, mature oaks in northeastern Minnesota are threatened by demands for firewood. Protection is needed to preserve this component of the forest. Mountain-ash trees also are uncommon

and heavily used by bears and also should be given special consideration in forest management.

The other fruit or mast producing species of the region are shrubs or forbs. Shade intolerant species such as blueberries, cherries, raspberries, serviceberries, and strawberries produced significantly more fruit in natural openings or where the forest canopy was thinned to <800 trees/ha than they did under denser tree canopies (Arimond 1979; Rogers, unpubl. data). A burned area produced 356 kg of blueberries/ha, on the average, during a 4-year period compared to an average of only 3.74 kg/ha over the same period in 29 unburned areas (range 0-57 kg/ha) (Arimond 1979). Wild sarsaparilla was the only extensively eaten fruit more productive in dense (> 1,000 trees/ha), mature stands than in more open stands (Arimond 1979). Hazelnuts were produced under both dense and sparse canopies, with highest production in the midrange densities (Arimond 1979). All of the fruit and nut producing species eaten by bears are susceptible to herbicides. Aerial application of herbicide to 2 stands ended blueberry, cherry, and hazelnut production for at least the 3 and 4 years the stands were subsequently observed (Arimond 1979). Rotting logs of trees killed by herbicides became sources of ants. Restricting herbicide treatment to individual trees and avoiding treatment of preferred fruit and nut producing species would benefit bears and other omnivores.

The value of forest openings to bears may be enhanced by plantings of legumes *(Trifolium* spp., *View* spp., *Lathyrus* spp.) or fruit-producing species (Jonkel and Cowan 1971:21, Irwin and Hammond 1985). Large clear-cuts may be further improved by leaving islands or peninsulas of standing trees for escape and shade. Black bears are reluctant to move far from forest cover, especially with cubs (Jonkel and Cowan 1971; Rogers, unpubl. data), and they are easily heat-stressed on warm, sunny days (Rogers 1980 and unpubl. data).

Hollow trees provide superior insulation and protection in winter and are preferred den sites throughout the black bear's range (Bromlei 1965; Johnson et al. 1978; Johnson and Pelton 1979, 1981). Only 2 large, hollow trees *(Pinus* spp.) were found in the mainly second growth forests of the study area, and both were used as dens (1 twice). However, hollow trees were not necessary for winter survival because bears survived and raised newborn litters approximately as well in other types of dens, including surface nests. At present low levels of human disturbance in winter and early spring, den sites are not a critical component of the habitat. However, elevated and secure den sites such as hollow trees may be a more important habitat component in regions where flooding and human disturbance are more common problems (Smith 1946, Johnson and Pelton 1980, Alt 1984).

Gunshot accounts for the great majority of adult deaths in northeastern Minnesota (page 56), with nuisance kills and hunter kills being largely additive, rather than compensatory, according to kill records of the Minnesota Department of Natural Resources. Unusually high levels of nuisance activity occur in years of widespread food shortage (Rogers 1976), and many wide-ranging bears are shot in and around towns, resorts, and residences (page 34). The nuisance kill and the low reproductive rate reduce the allowable hunter kill below that of better habitats such as northern Wisconsin (Kohn 1982) and northeastern Pennsylvania (Alt 1980, Kordek and Lindzey 1980). The slow maturation of females (6.3 years to first reproduction, on the average) could necessitate special measures to aid survival of females through at least 1 reproductive cycle if the population should decline. One available measure is the closing of logging roads after timber removal in order to create areas of reduced human accessibility. This should differentially aid females because females use smaller ranges than males. Nuisance problems in wilderness camping areas can be minimized by use of bear-proof food containers (Dalle-Molle et al. 1986) and capsaicin spray repellents (Miller 1980, Rogers 1984).

Reduction and fragmentation of bear

habitat due to the expanding human population have become major problems for black bear populations in parts of the eastern United States, with some populations having been extirpated recently (Cowan 1972, Maehr 1984). The bear population in northeastern Minnesota is not threatened by excessive habitat loss at present. However, bears of that region may be unusually sensitive to such problems because food conditions there induce bears to forage farther than has been reported for any other region (Rogers 1987). Bears in northeastern Minnesota may require a larger area of unbroken habitat to maintain a viable population than is required where bears range less widely. Nevertheless, the future appears bright for bears there due to their being protected as game animals and due to over 12,000 km^2 of bear habitat within the Superior National Forest and various state forests.

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Appendix 1.   Summary of telemetry data for male black bears in northeastern Minnesota, 1971-76.

Year	Age (years)	Bear no.	Period monitored	No. of locations[a]	Movements outside usual range[b]	Remarks
1971						
	1	346	Entire year	63 (1)[a]	Mid-Jul, area unknown.[c]	Son of F. Signal range <2 km. No signal in mother's territory 18 Jul. ^
	1	401	28 Aug-31 Dec	38 (0)	None.[d]	
	2	346	9 Aug-19 Aug	5 (2)		Son of H. Dispersed 19 Aug.
	4	295	23 Jun-31 Dec	46 (16)	Late Jun-early Jul, area unknown. Early Aug, area unknown. Mid-Aug-late Oct, 28 km south-southeast and area unknown.	
	5	353	1 Jan-1 Nov	24 (23)	Mid-Sep-late Oct, area unknown.	Transmitter range of <2 km resulted in 12 unsuccessful attempts to locate bear in spring and summer. No signal after 1 Nov 1971. Shot in study area 22 Sep 1973.
	6	338	23 Jun-17 Oct	42 (8)	4 movements to unknown areas in Sep and early Oct.	Found dead, cause unknown, 17 Oct.
	6	225	28 Jun-21 Aug	23 (0)		Transmitter failed after 21 Aug.
	6	215	1 Jan-22 Sep	51 (17)	Late Apr, area unknown. Mid-Aug-mid-Sep, area unknown.	Not found after 22 Sep 1971. Never recaptured.
	10	224	1 Jan-12 May, 19 Sep-31 Dec	23 (0)		Transmitter failed after 12 May and was replaced 19 Sep.
1972						
	Cub	459	23 Aug-25 Sep	11 (0)		Orphan. Killed by train 25 Sep.
	1	440	1 Jan-19 Nov	73 (1)	Mid-Aug, area unknown.	Son of B. Not found 16 Aug. Collar was removed 19 Nov.
	1	506	1 Jan-20 Jun	7 (0)		Son of 222. No signal heard after 20 Jun 1972. Shot 22 Sep 1974.
	1	433	Entire year	90 (1)	Mid-Jul-early Aug, 9 km south-southwest and area unknown.	Son of E.
	1	431	Entire year	79 (16)	Late Jul-mid-Aug, area unknown.	Son of E.
	2	346	1 Jan-7 Jun	31 (0)		Son of F. Dispersed 7 Jun 1972.
	2	401	1 Jan-18 Oct	58 (0)		Son of A. Dispersed 3 Jun 1972.

Appendix 1.   Continued.

Year	Age (years)	Bear no.	Period monitored	No. of locations[3]	Movements outside usual range^	Remarks
	5	295	Entire year	103 (0)	Late Aug-early Oct, 24 km south-southeast	
	7	453	29Jun-ll Nov	57 (0)	Usual range unknown. Bear moved 43 km south southeast from study area to a dump in mid-Jul and returned 25 km to a den early Oct.	
	11	224	1 Jan-20 Jun	56 (0)		Lost collar in a fight on 20 Jun.
1973						
	Cub	503	14 Aug-31 Dec	15 (1)	Late Oct, area unknown.	Orphaned son of h. Not found 28 Oct.
	2	431	1 Jan-6 Apr, 11 Oct-31 Dec	10 (0)		Collar removed 6 Apr, replaced 11 Oct.
	6	295	1 Jan-14 Aug	12 (1)	Not found 9 May.	Transmitter failed after 14 Aug.
1974						
	1	503	1 Jan-1 Jul	17 (0)		Orphaned son of h. Collar was removed, and bear was located on 1 Jul.
	1	601	Entire year	28 (0)	None.	Son of D.
	1	628	Entire year	53 (0)	None.	Son of E.
	2	569	29 Jun-31 Dec	31 (0)	Mid-Aug-mid-Oct, 20 km south-southeast. Denned 20 km north in late Oct.	Son of G. Dispersed within study area in Jun.
	3	431	1 Jan-30 May	11 (0)		Bear removed collar, dispersed.
	4	442	8 Jun-31 Dec	21 (1)	Mid-Aug, area unknown.	
	7	295	Entire year	51 (1)	Mid-Jul, 9 km east-southeast. Late Jul, area unknown. Mid-Aug-late Sep, 33 km south-southeast.	
	7	445	3 Jun-31 Dec	27 (0)	None.	
	13	224	3 May-12 Jun	8 (0)		Bear lost collar in another fight.
1975						
	Cub	869	20 Aug-31 Dec	29 (0)	None.	Orphaned son of E.
	Cub	872	17 Aug-31 Dec	28 (0)	None.	Orphaned son of E.
	1	816	1 Jan-22 Jun	10 (0)		Son of L. Died of natural causes.
	1	818	Entire year	36 (0)	None.	Son of L.
	1	646	Entire year	34 (0)	Late Aug-late Sep, 15 km south-southeast	Son of a.

Year	Age (years)	Bear no.	Period monitored	No. of location[a]	Movements outside usual range[b]	Remarks
	3	569	Entire year	22 (0)	Mid-Aug-late Sep, 35 km south-southeast	Son of G. Denned about 3 Oct.20 km north of usual range
	5	442	1 Jan-30 Sep	22 (1)	Late Aug-early Sep, area unknown.	Shot 30 Sep 1975.
	8	445	Entire year	19(3)	Mid-Jun, area unknown. Mid-Aug-late Sep, area unknown.	Only 2 attempts to locate during mid-Aug-late Sep.
		295	1 Jan-21 Aug	22 (0)	Mid-Jul, 8 km east-southeast. Early Aug-mid-Aug, 24 km south-southeast.	Shot 21 Aug.
1976						
	1	869	1 Jan-24 Mar	12 (0)	None.	Son of E. Transmitter failed after 24 Mar and was replaced 9 Aug.
	1	872	Entire year	12 (0)	None.	Son of E.
	1	937	1 Jan-8 May	11 (0)		Son of d. Weighed 5.2 kg on 19 Mar; died of starvation 7-8 May.
	1	939	1 Jan-3 May	9 (0)		Son of d. Weighed 3.9 km on 28 Mar; died of starvation 24 Apr-3 May.
	2	646	Entire year	20 (0)	Early Aug-late Sep, 42 km south-southeast.	Son of a.
	2	818	Entire year	16 (0)	Mid-Aug-mid-Sep, 10 km south-southwest.	Son of L.
	4	569	Entire year	24 (0)	Mid-Aug-early Oct, 42 km south-southeast.	Son of G. Denned 20 km north of usual range.
	9	445	Entire year	12 (1)	Jul-Oct, 42 km south-southeast.	
	11	450	5 Jun-31 Dec	35 (5)	Late Jul-late Oct, 201'km southwest.	

[a] Parentheses enclose number of unsuccessful attempts to locate bears wearing functional radio collars.

[b] Dates of movements >7 km outside usual ranges are noted. Months are divided into thirds: early, mid-, and late. Distances and directions are to the farthest known locations. Usual ranges of adult males were considered to be their mating ranges. Usual ranges of young males prior to dispersal were considered to be their mothers' territories. For Male 569, the only subadult radio-tracked intensively after dispersing to a new area, usual range was considered to be the area used through July that eventually became his mating range,

[c] Area unknown indicates a bear was not found by aerial radio tracking during the period stated.

[d] None indicates a bear was not found >7 km outside his usual range despite his being radio-tracked through much or all of the July-October period when most long movements occurred.

Appendix 2.   Summary of telemetry data for female black bears in northeastern Minnesota, 1971-76.

Year	Age (years)	Bear no.[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	Remarks
1971						
	1	f	1 Jan-2 Sep	66 (0)[b]	None.[d]	Daughter of F. Transmitter failed after 2 Sep.
	1	g	1 Jan-13 Sep	73 (0)	None.	Daughter of F. Transmitter failed after 2 Sep.
	1	b	20 Aug-31 Dec	33 (0)		Daughter of A.
	1	d	7 Sep-31 Dec	29 (0)		Daughter of D.
	2	308	30 Jun-31 Dec	44 (0)	None.	Daughter of H.
	3	Q	1 Jan-4 Dec	79 (2)	Late Aug-early Sep, 23 km southeast.	Denned 21 km northwest of territory in winter of 1970-71. Returned by 13 May 1971. Transmitter failed in Dec 1971.
	4	a	Entire year	77 (7)	Late Aug, area unknown." Early Sep, area unknown.	Probably a daughter of A.[f]
	4	L	1 Jan-14 Aug	56 (0)		Transmitter failed after 14 Aug.
	4	K	1 Jan-11 Jul, 22 Aug-31 Dec	50 (4)	Late May, area unknown.	Transmitter failed after 11 Jul and was replaced 22 Aug.
	4	389	1 Jan-9 Aug	32 (0)		No signal heard after 9 Aug 1971. Nonfunctional radio collar replaced in Aug 1972. Territory was outside the study area.
	4	P	5 Aug-31 Dec	49 (0)	None.	Immigrant.
	6	222	Entire year	75 (2)	Late Jul, area unknown. Late Aug, 24 km north-northwest. Early Sep, 20 km north-northwest.	With 2 cubs. Territory outside study area.
	6	G	23 Jun-31 Dec	41 (2)	Late Jun, area unknown. Early Sep, 20 km south-southeast.	
	6	F	Entire year	82 (3)	Early Aug, area unknown. Late Aug-early Sep, 17 km south	With 3 yearlings until Jun.
	6	M	1 Jan-1 May	14 (0)		Transmitter failed after 1 May.
	6	419	30 Jul-26 Aug	10 (3)		Territory was outside study area.
	9	B	18 Aug-31 Dec	42 (2)	Late May, seen 9 km east. Sep, seen 41 km east.	With 4 cubs.
	10	D	3 Jul-31 Dec	64 (0)	None.	With 2 yearlings that rejoined her.
	10	C	Entire year	117(0)	Mid-Aug, 27 km south-southeast. 26 Aug to 2-3 Nov, 45 km south-southeast	With 3 cubs. Outside territory 69 days.
	10	E	25 Jun-31 Dec	65 (0)	7-9 Sep, 16 km south-southeast.	With 3 cubs. Moved 14.9 km in 25.25 hours.
	10	J	3 Jul-31 Dec	52 (0)	None.	
	20	A	9 Jul-31 Dec	48 (2)	Mid-Jul, area unknown. 17-24 Aug, area unknown. 25 Aug-21 Sep, 19 km north.	Seen with yearlings b and 401 in spring.

Year	Age (years)	Bear no.[a]	Period monitored	No. of location[b]	Movements outside territories[c]	Remarks
1972						
	Cub	460	23 Aug-25 Sep	10 (0)		Orphan. Killed by train 25 Sep.
	Cub	472	10 Oct-15 Nov	17 (1)		Orphan. Shot by hunter 17 Nov.
	1	n	Entire year	67 (16)	Late Aug-early Oct, area unknown.	Daughter of C. Not found in all 16 telemetry attempts 22 Aug-3 Oct.
	1	q	Entire year	74 (1)	Late Jul, area unknown.	Daughter of B.
	1	r	Entire year	67 (4)	Mid-Jul, area unknown. Late Jul, area unknown. Mid-Aug, area unknown.	Daughter of B.
	2	f	28 May-31 Dec	69 (0)	None.	Daughter of F.
	2	b	Entire year	79 (0)	None.	Daughter of A.
	2	d	Entire year	73 (0)	None.	Daughter of D.
	2	e	Entire year	76 (5)	Early Jul, area unknown. Mid-Jul, area unknown. Late Jul, area unknown	Daughter of D.
	3	308	1 Jan-17 Jul	37 (0)		Daughter of H. Translocated 17 Jul.
	3	h	31 May-31 Dec	81 (0)	None.	Daughter of H.
	5	a	Entire year	93 (1)	Late Jun, area unknown.	Probably a daughter of A.' Not found in territory 26 Jun. No wider search conducted.
	5	L	8 Jul-31 Dec	53 (0)	None.	
	5	K	Entire year	81 (0)	None.	With 3 cubs.
	5	389	20-28 Aug	9 (0)		Captured and radio-collared as nuisance outside study area. No signal heard after 28 Aug. Presumed shot as nuisance.
	5	P	1 Jan-25 Jul	53 (0)		Immigrated in 1971. Produced a cub. No signal heard after 25 Jul. Probably left study area.
	7	222	Entire year	21 (0)	None.	With 1 yearling in spring. Territory outside study area.
	7	G	Entire year	77 (0)	None.	With 3 cubs.
	7	F	Entire year	87 (1)	Mid-Jun, area unknown.	With 3 cubs. Not found in territory 11 Jun.
	7	419	22 Jun-12 Aug	20 (2)		Territory outside study area.
	10	B	Entire year except 8-29 Jun	81 (0)	None.	With 4 yearlings./
	11	D	Entire year	75 (0)	None.	With 2 2-year-olds in spring.
	1	C	Entire year	99 (1)	Late Jul-late Aug, 5 movements 8-15 km to north-northwest and area un known. 24 Aug-mid Oct, 42 km south-southeast.	With 2 yearlings in spring.

Year	Age (years)	Bear no.[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	Remarks
	11	E	Entire year	93 (9)	Late Jul-early Aug, area unknown.	With 2 yearlings in spring.
	11	J	Entire year	69 (0)	None.	With 3 cubs.
	15	H	8 Aug-26 Aug	17 (0)		Shot by poacher on 26 Aug.
	21	A	1 Jan-22 Mar	1 (0)	Died in den on 21-22 Mar. With 2 dead cubs.	
1973						
	Cub	w	14 Aug-31 Dec	15 (0)	None.	Daughter of h. Orphaned 13 Aug.
	2	n	Entire year	27 (2)	Mid-May, 16 km south-southeast. Aug,12 km south-southeast and area unknown. Late Sep-early Nov, 18 km south-southeast.	Daughter of C.
	2	q	Entire year	32 (0)	None.	Daughter of B.
	2	r	1 Jan-22 Jul	18 (1)	Mid-May, area unknown.	Daughter of B. Not found 17 May. Transmitter failed after 22 Jul.
	3	f	1 Jan-7 Sep	21 (0)	None.	Shot by hunter on 7 Sep.
	3	b	Entire year	26 (0)	None.	Daughter of A.
	3	d	*See* remarks	14 (4)		Transmitter weak. Not found on 4 of 6 attempts16 May-7 Sep. New transmitter given 22 Sep. Daughter of D.
	3	e	Entire year	23 (1)	Mid-May, area unknown.	Daughter of D.
	3	S	6 Jun-31 Dec	11 (0)	None.	Immigrant.
	4	h	1 Jan-17 Aug	25 (0)		Daughter of H. Translocated as nuisance 13 Aug. Signal lost 17 Aug. Probably shot.
	6	a	Entire year	27 (0)	None.	Probably a daughter of A.[f]
	6	L	Entire year	22 (0)	None.	
	6	K	Entire year	32 (0)	None.	With 3 yearlings in spring.
	8	222	1 Jan-23 Apr	5 (0)		Signal lost after 23 Apr. Not recaptured. Territory outside study area.
	8	G	Entire year	21 (1)	Mid-Jul, area unknown.	With 3 yearlings in spring. Not found on 16 Jul.
	8	F	1 Jan-7 Sep	21 (1)	Early Jul, area unknown.	Not found on 5 Jul. Shot 7 Sep.
	8	M	24 Jul-31 Dec	15 (1)	Early Aug, area unknown.	Not found on 9 Aug.
	8	419	1 Jun-31 Dec	22 (2)	Late Jul-early Aug, area unknown.	With 2 cubs. Territory outside study area.
	11	B	1 Jan-27 May	11 (0)		With 4 cubs. Shed collar 27 May.
	12	C	Entire year	35 (0)	Mid-Aug-early Nov, 28 km south-southeast.	With 3 cubs.
	12	D	Entire year	25 (0)	None.	With 3 cubs.
	12	E	Entire year	22 (1)	Late Aug, area unknown.	With 2 cubs. Not found 29 Aug.
	12	J	Entire year	21 (0)	None.	With 3 yearlings in spring.

Year	Age (years)	Bear no.[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	Remarks
1974						
	1	w	Entire year	35 (0)	None.	Daughter of h. Orphaned.
	1	626	Entire year	44 (0)	None.	Daughter of E. In addition to the 44 locations, the bear was radio-tracked nearly continu-ously 8-14 Apr, 15-17 Jul, and 10-14 Sep.
	1	855	12 Jul-31 Dec	13 (0)	None.	Probably a daughter of 851.' Territory outside study area.
	2	t	13 Aug-9 Sep	5 (0)		Daughter of F. Shot 9 Sep.
	3	n	Entire year	51 (0)	Early May, 13 km south-southeast. Late Aug-early Nov, 14 km south-southeast.	Daughter of C.
	3	q	Entire year	47 (0)	Mid-Jun, 7 km north-northwest.	Daughter of B.
	3	r	10 May-30 Jun	11 (0)		Daughter of B. Shot 30 Jun.
	3	y	2 Jul-31 Dec	24 (0)	Sep, 17 km south-southeast. Early Oct, 7 km south-southeast.	Daughter of B.
	3	507	27 Jul-31 Dec	17 (0)	Sep, 24 km south-southeast.	Territory outside study area.
	4	g	2 Jun-20 Sep	32 (0)	Early Aug, 18 km south-southeast.	Daughter of F. Shot 20 Sep.
	4	b	Entire year	34 (0)	Late Aug-early Oct, 38 km south-southeast.	Daughter of A.
	4	d	Entire year	37 (0)	None.	Daughter of D.
	4	e	Entire year	36 (0)	None.	Daughter of D.
	4	S	1 Jan-17 Oct	31 (0)	None.	With 1 cub. Shot by hunter 17 Oct.
	4	U	8 Jun-31 Dec	26 (0)	None.	
	4	859	25 Jul-31 Dec	18 (0)	Mid-Aug-mid-Sep, 9 km east.	Probably a daughter of 851.[f] Territory outside study area.
	7	a	Entire year	46 (0)	None.	Probably a daughter of A.' With 2 cubs.
	7	L	Entire year	36 (0)	None.	With 2 cubs.
	7	K	Entire year	46 (0)	None.	With 3 cubs.
	9	G	1 Jan-15 Aug, 28 Sep-31 Dec	29 (0)	Oct, 2 movements 10-13 km south-southeast.	With 3 cubs. Shed collar mid-Aug. New radio collar 28 Sep.
	9	M	Entire year	40 (0)	Late Aug-mid-Oct, 24 km southeast.	With 3 cubs.
	9	419	Entire year	34 (2)	Jul, 26 km north-northwest. Mid-Aug- late Sep, 27 km south-southwest.	With 1 yearling in spring. Territory outside study area.
	9	T	23 Jun-31 Dec	30 (0)	Mid-Aug, 7 km southeast. Late Aug, 14 km east-southeast. Early Sep, 7 km northeast.	

Year	Age (years)	Bear no[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	
	12	B	3 Jul-31 Dec	27 (0)	Late Aug, 14 km southeast. Early Sep-early Oct, 13 km southeast.	
	13	D	1 Jan-10 Dec	44 (0)	Mid-Aug-mid Sep. 7 km northeast.	With 3 yearlings in spring. Killed 10 Dec.
	13	C	Entire year	46 (0)	Sep. 26 km south-southeast.	With 3 yearlings in spring.
	13	E	Entire year	72 (0)	None.	With 2 yearlings in spring
	13	J	Entire year	36 (0)	Mid-Aug-late Oct, 34 km south-south-east.	With 3 cubs.
	13	v	25 Sep-31 Dec	13 (0)		With 1 cub.
	13	841	6 Aug-31 Dec	26 (0)	Aug-mid-Sep, 56 km south-southeast.	Territory outside study area. With 3 cubs.
1975						
	Cub	874	15 Aug-Oct	5 (0)	None.	Orphan of E. Died or was killed in Oct. Eaten by bear or wolves.
	1	511	1 Jan-17 Aug	16 (0)		Daughter of v. Died or was killed.
	1	635	Entire year	46 (0)	None.	Daughter of a.
	2	855	Entire year	20 (0)	Late Aug-mid-Sep, 7 km southeast.	Probably a daughter of 851.[f] Territory outside study area.
	2	w	Entire year	21 (0)	None.	Orphaned daughter of h.
	4	n	Entire year	21 (0)	Early Aug-early Sep, 32 km south.	Daughter of C. With 2 cubs.
	4	q	Entire year	33 (0)	None.	Daughter of B. 3 cubs died in spring.
	4	50	1 Jan-3 Oct	20 (0)	Aug, 15 km south-southeast. Early Sep-early Oct, 39 km south-southeast.	Territory outside study area. Was shot or shed collar about 3 Oct, 39 km outside territory.
	4	704	29 Jun-31 Dec	12 (0)	Mid-Aug-late Sep, 18 km east-south-east.	Immigrant.
	4	706	17 Jul-31 Dec	8 (0)	Mid-July, 20 km west.	Territory outside study area.
	5	b	Entire year	30 (0)	Early Sep-mid-Sep, 23 km south-south-east.	Daughter of A.
	5	d	Entire year	22 (0)	Mid-Aug-early Sep, 36 km southeast.	Daughter of D. With 3 cubs.
	5	e	Entire year	33 (0)	None.	Daughter of D.
	5	U	1 Jan-4 Jun	4 (0)		
	5	859	Entire year	19 (0)	Late Aug-mid-Sep, 9 km east-south-east.	Territory outside study area. Probably a daughter of 851.[f]

Appendix 2. Continued.

Year	Age (years)	Bear no.[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	Remarks
	8	*a*	Entire year	37 (0)	Late Aug-late Sep, 29 km southeast.	Probably a daughter of A.[f] With 2 yearlings in spring.
	8	L	Entire year	32 (0)	Early Sep-early Oct. 31 km southeast.	With 2 yearlings in spring.
	8	K	Entire year	19 (0)	Early Sep-early Oct. 16 km south-southeast.	With 2 yearlings in spring.
	10	G	1 Jan-3 Aug	14 (0)		Transmitter failed after 3 Aug
	10	T	Entire year	21 (0)	Late Aug-early Oct, 27 km south-southwest.	
	11	502	23 Jul-31 Dec	9 (0)	Late Jul, 18 km northwest.	Territory outside study area.
	13	B	Entire year	22 (0)	Late Aug-early Sep, 25 km southeast.	With 4 cubs.
	14	C	Entire year	23 (0)	Mid-Aug-early Oct, 20 km south-southeast.	With 3 cubs.
	14	E	1 Jan-10 Aug	21 (0)		Killed 10 Aug. 3 orphaned cubs.
	14	J	Entire year	20 (0)	Late Aug-late Sep, 28 km south-southeast.	With 2 yearlings in spring.
	14	v	Entire year	32 (0)	Early Sep-early Oct, 8 km southeast.	With 1 yearling in spring,
	14	841	Entire year	15 (0)	None.	With 3 yearlings in spring. Territory outside study area.
	14	851	Entire year	19 (0)	None.	Territory outside study area.
1976						
	1	890	1 Jan-11 Sep	21 (0)	14 Aug-11 Sep, 89 km south-southwest.	Daughter of n. Continuously radio-tracked 11, 13 Aug. Shot 11 Sep.
	1	892	Entire year	28 (0)	None.	Daughter of n.
	1	936	1 Jan-28 Jun	16 (0)		Daughter of d. Weighed 7.8 kg on 19 Mar. Died 12-28 Jun.
	2	635	Entire year	30 (0)	None.	Daughter of a.
	3	w	Entire year	13 (0)	None.	Daughter of h.
	3	855	Entire year	19 (0)	None.	Probably a daughter of 851.[f] Territory outside study area.
	4	475	21 May-7 Sep	17 (0)	None.	Daughter of K.
	5	n	1 Jan-7 Sep	25 (0)	20 Aug-7 Sep, 34 km south-southeast.	Daughter of C. With 2 yearlings in spring. Shot 7 Sep.

Appendix 2. Continued.

Year	Age (years)	Bear no.[a]	Period monitored	No. of locations[b]	Movements outside territories[c]	Remarks
	5	q	Entire year	29 (0)	None.	Daughter of B. 3 cubs died in spring.
	5	704	Entire year	27 (0)	None.	
	5	706	1 Jan-29 Sep	5 (0)		Territory outside study area. Transmitter failed after 29 Sep.
	6	b	Entire year	20 (0)	None.	Daughter of A.
	6	d	1 Jan-29 Sep	41 (0)	None.	Daughter of D. Transmitter failed after 29 Sep.
	6	e	Entire year	27 (0)	None.	Daughter of D.
	6	859	Entire year	22 (0)	None.	Probably a daughter of 851.[f] Territory outside study area.
	9	a	Entire year	36 (0)	None.	Probably a daughter of A.[f]
	9	K	Entire year	21 (0)	None.	With 3 cubs.
	9	L	Entire year	28 (0)	None.	With 3 cubs.
	11	M	4 Jun-31 Dec	21 (0)	Mid-Aug-late Aug, 24 km southeast.	
	11	T	Entire year	19 (0)	None.	With 2 cubs.
	11	419	6 Jul-31 Dec	12 (0)	Jul-Aug, 30 km north-northwest. Sep, 9 km south.	With 1-3 yearlings in spring. Territory outside study area.
	12	502	1 Jan-29 Jul	5 (0)		Territory outside study area.
	14	B	Entire year	30 (0)	None.	With 2 yearlings in spring.
	15	C	Entire year	28 (0)	20 Aug-late Oct, 36 km south-southeast	With 2 yearlings in spring. Killed by wolves the following Feb (1977).
	15	J	Entire year	20 (0)	None.	With 2 cubs.
	15	841	Entire year	8 (0)	With 3 cubs. Territory outside study area.	
	15	851	Entire year	19 (0)	None.	With 2 cubs. Territory outside study area.
	Adult	5438	28 May-31 Dec	16 (0)	None.	Lost litter in spring.

[a] Females identified by letters are included in Figures 2-6. Females identified by numbers either held territories outside the study area or were too young (<3 years old) for inclusion in Figures 2-6.
[b] Parentheses enclose number of unsuccessful attempts to locate bears wearing functional radio collars.
[c] Dates of movements >7 km outside territories are noted. Months are divided into thirds: early, mid-, and late. Distances and directions are to the farthest known locations.
[d] None indicates a bear was not found >7 km outside her territory despite her being radio-tracked through much or all of the July-October period when most long movements occurred.
[e] Area unknown indicates a bear was not found by aerial radio tracking during the period stated.
[f] Mother-daughter relationship was not determined before family breakup but is assumed on the basis of territorial tolerance otherwise observed only between mothers and daughters.