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Seasonal movements, home range utilization, and
denning habits of black bears (Ursus americanus)
in western Manitoba

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SEASONAL MOVEMENTS, HOME RANGE UTILIZATION, AND
DENNING HABITS OF BLACK BEARS (URSUS AMERICANUS)
IN WESTERN MANITOBA

BY

WALTER EDWARD KLENNER

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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ABSTRACT

Seasonal movements, home range, and den characteristics of black bears (Ursus americanus) were studied in western Manitoba using radio telemetry from June 1979 to November 1980. Subadult males utilized a significantly larger annual home range (506.4 sq. km) than subadult (35.2 sq. km) or adult females (29.1 sq. km). Similarly, males used larger seasonal ranges than females and showed high variability in utilization patterns. In general, annual home ranges of subadult males overlapped several or all female ranges in the study area. Adult and subadult females showed extensive overlap between and within cohorts ranging from 5 to 85 percent of the annual home range. Home ranges were stable from 1979 to 1980, showing no significant shift in the annual activity center. Seasonal range shifts were infrequent with subadult males moving greater distances and having a less stable seasonal range than other cohorts.

Subadult males travelled farther between locations than subadult or adult females in spring, summer, and fall. Adult females without cubs travelled farther between locations in summer (2.21 km) and were more mobile than adult females with cubs (1.35 km). Females did not undertake extensive movements away from their summer activity centers whereas subadult male movements were characterized by irregular and wide ranging movements into the Duck Mountain Provincial Forest.

Den sites were observed in all major habitat associations. Of the dens examined, ninety-three percent were excavated and all but one contained lining material. In 1979, yearling females entered dens later than subadult females ($P=0.02$). In 1980, adult females entered dens earlier than subadult males ($P=0.05$) with pregnant subadults showing a tendency to den earlier than females which did not have a litter in 1980. Females always constructed dens within the confines of their spring-summer home range. Subadult males often utilized remote den sites in the Duck Mountain Provincial Forest after an abrupt move (19.8-42.2 km) away from their summer activity center in mid-autumn.

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CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
	<u>page</u>
INTRODUCTION	1
STUDY AREA	4
Intensive Study Area	4
Duck Mountain Provincial Forest (DMPF)	7
Agricultural Zone	9
METHODS AND MATERIALS	12
Capture and Handling	12
Radio Telemetry	14
Monitoring Schedule	15
Data Analysis	16
Simulations	17
Area Calculations	20
Movement	21
Spatial use of home range	21
Den Sites	22
RESULTS	23
Capture and Aging	23
Simulations	24
Effect of Sample Size on the Area Estimate	24
Effect of Sample Size on Activity Center	25
Test for Normality	27
Effect of Data Distribution on the Jenrich and Turner Index.	28
Area Calculations	28
Effect of Sampling Period on Area	28
Home range comparisons	34
Spatial use of home range	42
Home range stability and overlap	47
Movement Patterns	55
Distance travelled per day	55
Distance between successive locations	57
Den Characteristics	59
Onset of denning and emergence	59
Relation between den site and home range	60

Entrance Aspect	64
Den reuse	66
Structural characteristics	66
DISCUSSION	68
Capture	68
Simulations	69
Home Range Utilization	72
Movement Patterns	84
Den Characteristics and Utilization	89
SUMMARY AND CONCLUSIONS	102
LITERATURE CITED	105

<u>Appendix</u>	<u>page</u>
1. MEAN MONTHLY PRECIPITATION AND TEMPERATURE RECORDED AT DAUPHIN AIRPORT, 60 KM SOUTHEAST OF THE STUDY AREA	116
2. PLANT SPECIES POSSIBLY USED AS FOOD ITEMS BY BLACK BEARS IN THE STUDY AREA	117
3. THE AGE AND AGE CLASS OF BLACK BEARS EQUIPPED WITH RADIO-TELEMETRY UNITS DURING 1979 AND 1980	120
4. TELEMETRY ERROR MEASUREMENTS USING A 14 ELEMENT DIRECTIONAL ANTENNA ON KNOWN TRANSMITTER LOCATIONS	122
5. BACKGROUND INFORMATION ON BLACK BEARS CAPTURED IN THE STUDY AREA, JUNE 1979 TO JULY 1980	123
6. INDIVIDUAL BLACK BEAR TOTAL AND SEASONAL HOME RANGE AREAS (SQ. KM) IN WESTERN MANITOBA DURING 1979 AND 1980	126
7. MEAN DISTANCE (KM) FROM THE SUMMER ACTIVITY CENTER FOR EACH BLACK BEAR AGE CLASS DURING 1980. MEAN AND STANDARD DEVIATION CALCULATED FOR BIWEEKLY PERIODS FROM 31 MARCH TO 31 OCTOBER	127
8. MEAN AND STANDARD DEVIATION OF DISTANCE MOVED PER DAY BY BLACK BEARS IN THE STUDY AREA DURING BIWEEKLY PERIODS FROM 1 JUNE TO 31 OCTOBER, 1980	128
9. MEAN AND STANDARD DEVIATION OF DISTANCE BETWEEN SUCCESSIVE LOCATIONS OF BLACK BEARS IN THE STUDY AREA DURING BIWEEKLY PERIODS FROM 31 MARCH TO 31 OCTOBER, 1980	129
10. INDIVIDUAL DEN SITE DESCRIPTIONS FOR BLACK BEARS MONITORED BY RADIO-TELEMETRY DURING 1979 AND 1980	130

11. INDIVIDUAL DISTANCES FROM THE SUMMER ACTIVITY CENTER TO THE DEN
SITE RECORDED FOR TELEMETRY MONITORED BLACK BEARS DURING
1980 134

LIST OF TABLES

<u>Table</u>	<u>page</u>
1. Periods used to characterize black bear seasonal home range utilization and movement patterns (based on phenology) . . .	18
2. Individual seasons and period of activity used to delineate black bear seasonal home range utilization and movement patterns during 1980	19
3. Kolmogorov-Smirnov test for normality of x and y coordinate data obtained during 1980	29
4. Effect of various distributions (normal, random, aggregated, perimeter) on the Jennrich and Turner home range index. 1000 coordinates in each array	30
5. Black bear seasonal home range areas in western Manitoba based on the Jennrich and Turner index and minimum polygon estimate.	37
6. Ratio of east-west to north-south dimensions of black bear home ranges in 1980. Measurements based on outermost points of the minimum polygon area	43
7. Dimensions (km) of major and minor axes of black bear home ranges (based on minimum polygon) in 1980	44
8. Distance between black bear seasonal home range activity centers. Shifts are considered significant if the change is greater than the radius of the minor summer home range axis .	51
9. Distance between the 1979 and 1980 annual activity centers for black bears surviving from June 1979 to August 1980	53
10. Denning and emergence chronology of black bears monitored by radio-telemetry during 1979 and 1980	61
11. Average summer home range radii (based on minimum polygon) of black bear ranges recorded during 1980 and mean distance from the summer activity center to the den site	65

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1. Location of the extensive and intensive study areas in western Manitoba	5
2. The intensive study area indicating trap site locations and the distribution of forested and agricultural lands	6
3. The effect of sample size (number of coordinate locations) on the Jennrich and Turner and minimum polygon home range estimate. A. 1000 random coordinates B. Actual dataset, M796, 1980	25
4. The effect of sample size (number of coordinate locations) on standard deviation of the home range activity center estimate. Distance indicated in arbitrary units	27
5. Scattergram of (a) normal (b) random (c) aggregated and (d) perimeter distributions used to test the effect of non-normality on the Jennrich and Turner index. 1000 coordinates in each array	31
6. The effect of cumulative coordinate locations obtained sequentially on the home range estimate. Database involves: A. 1000 random coordinates, B. data from F798, 1980	32
7. Increase in summer (16 June - 31 August) home range of M793 and F793 as increasing proportions of the season are included in the estimate	33
8. Decrease in home range of A: F798 and B: M793 as an increasing percentage of outermost coordinate locations are deleted. Inflection indicates the presence of a highly used "core area"	35
9. Home ranges of subadult female black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations	38
10. Home ranges of adult female black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations	39

11. Home ranges of subadult and adult male black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations	40
12. Relationship of subadult males and adult and subadult females to the summer activity center on an (A) annual and (B) biweekly basis	45
13. Distribution of representative female black bear locations recorded in the study area during 1980	47
14. The relationship between male black bear seasonal home ranges as recorded in western Manitoba during 1980	49
15. The relationship between female black bear seasonal home ranges as recorded in western Manitoba during 1980	50
16. Overlap of female black bear home ranges in the study area during 1980. Annual home ranges with peripheral locations joined are illustrated	54
17. Movement patterns of black bears in the study area during 1980. Distances are represented as (A) km moved per day and (B) distance in km between successive locations	56
18. Relationship of den sites used by subadult male black bears in 1979-1980 to the 1979 summer home range	62
19. Relationship of den sites used by adult and subadult female black bears to their respective annual range. Annual ranges with the outermost locations joined are illustrated	64

INTRODUCTION

The North American black bear (Ursus americanus Pallas) ranges over much of the continent from central Mexico north to the treeline in Alaska and Canada (Banfield 1974). The species is omnivorous (Bray and Barnes 1967, Hatler 1972, Beeman and Pelton 1980) and occurs in a wide variety of habitats ranging from temperate deciduous-coniferous forest associations to the tundra regions of northern Canada (Harlow 1961, Jonkel and Miller 1970, Jonkel and Cowan 1971, Kelleyhouse 1980).

Unlike the grizzly bear (Ursus arctos) whose populations have been decimated or extirpated in many areas (Cowan 1972, Craighead 1979, Craighead 1980), the black bear has not suffered the same fate and retains an extensive range in North America (Cowan 1972, Burk 1979, Herrero 1979). Because of its overall abundance, depredation problems in both agricultural and forested areas (Poelker and Hartwell 1973, Gunson 1979, Jorgenson 1979) and at park campsites (Merrill 1978, Singer and Power-Bratton 1980) have given impetus to management programs. In addition, the reduction of once widespread populations to remnants within refuges by human encroachment and hunting pressure (Lindzey et al. 1976, Pelton and Burkhardt 1976) has emphasized the need for more complete information on black bear ecology.

Logistic and technical difficulties encountered in studying a solitary and wide ranging forest carnivore (Mech 1974) have in the past restricted black bear investigations. Pioneering efforts emphasized

age-sex ratios, morphometric data, and reproductive information along with anecdotal descriptions on sociobiology, habitat selection and behavior (Black 1958, Erickson et al. 1964, Sauer et al. 1966). With the advent of biotelemetry and its widespread use by the late 1960's, animals could be followed through an entire life cycle, directly revealing aspects of their life history which formerly were inferred. Numerous studies were undertaken to determine various life history parameters which would form the basis of effective management policies (Poelker and Hartwell 1973, Rogers 1977, Alt et al. 1980, Hugie 1980).

Due to obscuring forest cover and the elusive nature of black bears, direct observations on behavior and intraspecific relationships (sociobiology) have been quite sparse. Several investigations have capitalized on unique habitat characteristics (i.e. forest clear cuts, garbage dumps, etc.) which permit direct observations (Jonkel and Cowan 1971, Rogers 1977). Reports by Getz (1972) and Slade (1976) demonstrate the use of capture statistics and activity indices to infer the social structure of nocturnal or secretive mammals. Further refinements of this procedure by Mazurkiewicz (1971), Voigt and Tinline (1980), and MacDonald et al. (1980) illustrate analyses to determine parameters from which interactions and sociobiology can be inferred.

With the increasing pressure from agriculture to secure new croplands and residential developments moving toward more aesthetically pleasing sites, ecotones between forests and developed areas are becoming increasingly common (Pelton and Burghardt 1976). Although numerous efforts have dealt with black bear ecology in what are essentially wilderness areas (Poelker and Hartwell 1973, Kemp 1976), information on

black bear ecology in a forest-agriculture ecotone is definitely lacking.

This report deals with an investigation of several life history parameters of a black bear population inhabiting a forest-agriculture ecotone. The study was initiated to realize three objectives:

1. Provide information on cohort differences in home range utilization and movement patterns.
2. Describe seasonal movement patterns with respect to forest and agricultural habitat.
3. Determine denning characteristics in this type of environment.

STUDY AREA

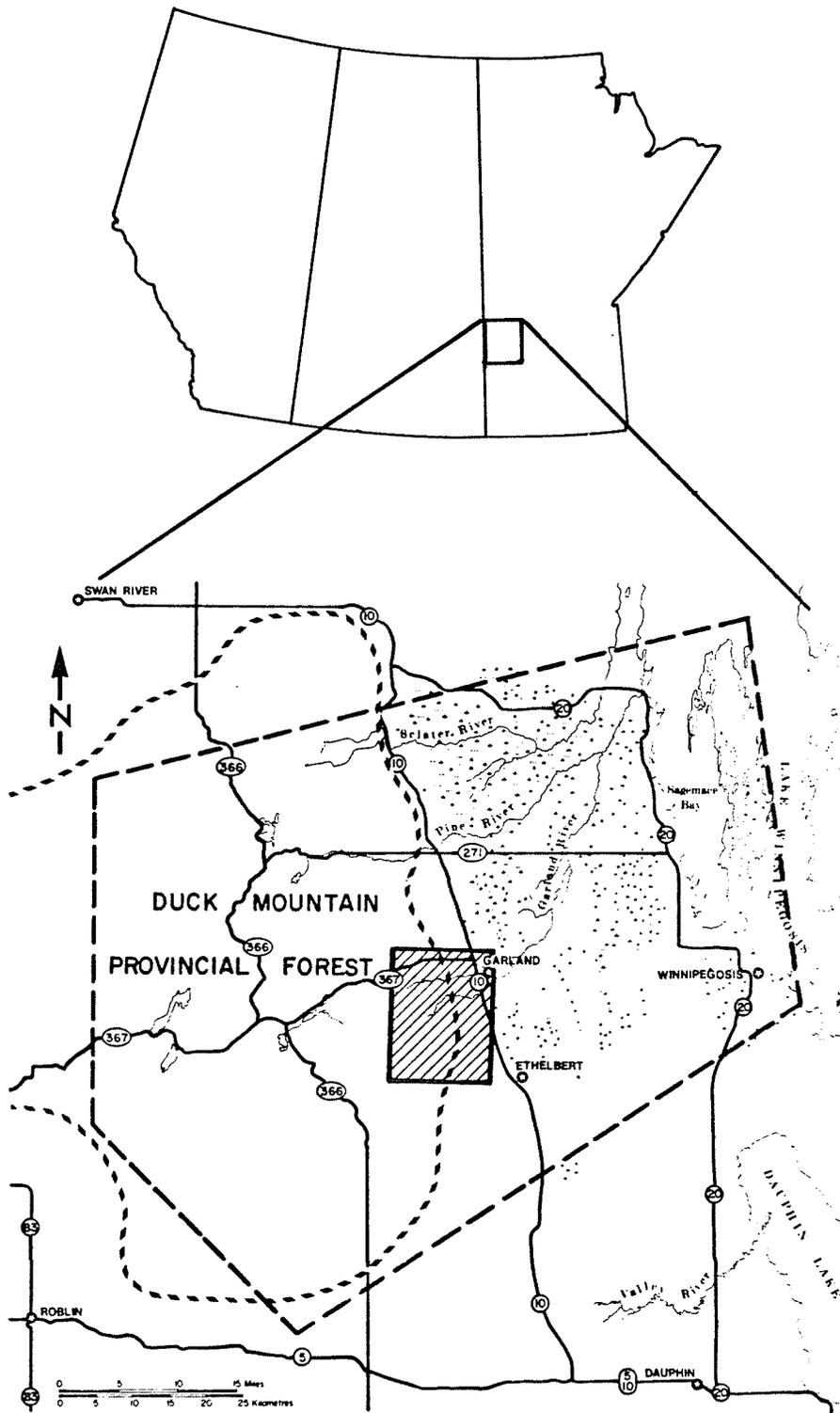
The intensive study area is situated in west-central Manitoba (Figure 1) and consists of a 250 sq. km quadrat bisected by the eastern boundary of Duck Mountain Provincial Forest (51°37' N. Lat.; 100°35' W. Long.). Trapping was restricted to the central portion of the study area (Figure 2), however, due to the wide ranging movements of several animals and a concurrent carcass collection program, monitoring activities were conducted up to 60 km away in the extensive study area. The area was chosen on the basis of accessibility through numerous roads and tracks, the presence of co-operative landowners, and its suitability as a representative forest-agriculture interface.

Intensive Study Area

Within the main study area, two major roads, PTH 367 and PTH 10 approximately delineate the northern and eastern boundaries respectively. An extensive network of dirt roads facilitate travel in the agricultural lands. Access to forested areas is restricted to abandoned logging roads and is largely dependent on road conditions.

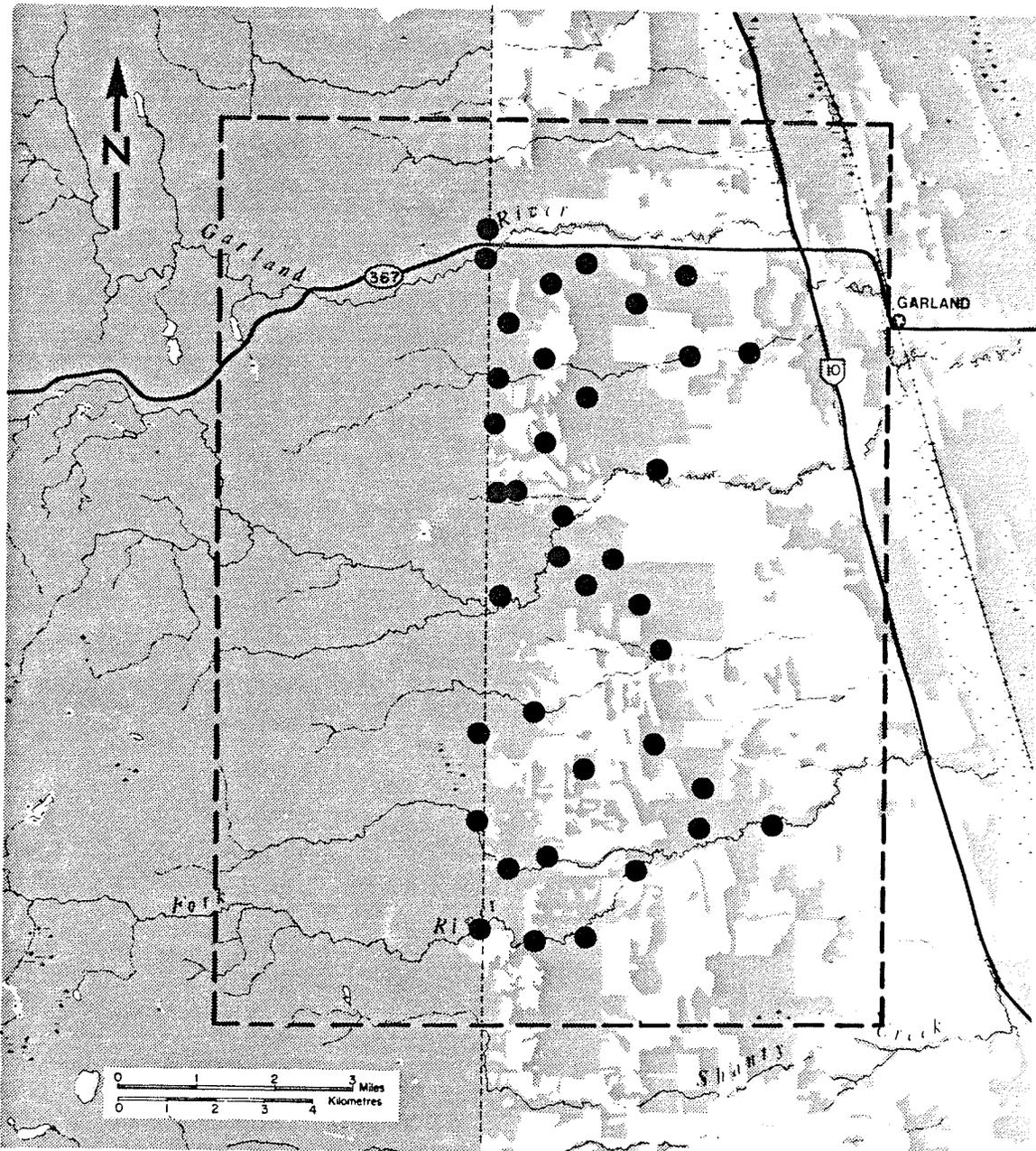
Climate is typically continental with wide seasonal fluctuations in temperature and little precipitation (see Appendix 1 for details). Mean January and July temperatures are -19°C and +19°C respectively (Barto and Vogel 1978). Upper regions of the Duck Mountain receive up to 50 percent more precipitation and are generally two to three degrees cooler

Figure 1: Location of the extensive and intensive study areas in western Manitoba



- EXTENSIVE STUDY AREA
- BOUNDARY BETWEEN FORESTED AREAS AND AGRICULTURAL LANDS
- ▨ INTENSIVE STUDY AREA

Figure 2: The intensive study area indicating trap site locations and the distribution of forested and agricultural lands



- FORESTED LANDS
 - AGRICULTURAL LANDS
 - TRAPSITE LOCATIONS
- EASTERN BOUNDARY, DUCK MOUNTAIN PROVINCIAL FOREST
 - INTENSIVE STUDY AREA

than the surrounding lowlands (Parks Branch 1971). This results in a decreased frost free period and a one to two week spring delay in upland phenology. Mean annual precipitation at lower elevations is approximately 43 cm with a mean annual snowfall of 120 cm. Although variable, the period 1 November to 15 April normally has snow accumulations exceeding 10 cm.

The eastern boundary of the Duck Mountain Provincial Forest (Fig. 2) conveniently divides the primary study area into the broad categories of forest and agricultural land based on predominant landuse practices and vegetation cover. With the exception of occasional livestock grazing on the periphery, no agricultural activities are carried out within the provincial forest and natural vegetation predominates.

Duck Mountain Provincial Forest (DMPF).

Barto and Vogel (1978) classify the Duck Mountain region as Mesozoic in origin with underlying rocks consisting of grey bentonitic shale and hard grey siliceous shale of the Riding Mountain Formation. Elevation ranges from ca. 450 m a.s.l. along the DMPF eastern boundary to 831 m at Baldy Mountain in the central upper plateau. Physiography of the area consists of ice scoured or morainic uplands with numerous rock outcrops and a rolling to hilly topography. Surficial deposits are comprised of glacial till with end or ground moraines laid down during the Pleistocene glaciation (Parks Branch 1971, Barto and Vogel 1978). Soils are classified as medium to moderately fine grey luvisols which are somewhat calcareous and have developed over glacial till deposits (Ellis 1938, Barto and Vogel 1978). Ellis (1938) stated the soils have a well developed A and B horizon with a partially leached A horizon and an

accumulation of clay and humus in the B horizon. The glacial debris nature of parent materials has led to the presence of stones in all soil horizons and development under mixed coniferous-deciduous vegetation has resulted in acidic properties. Soil drainage is moderate to excellent in some regions due to the rolling topography and numerous streams or rivers. Poorly drained flat areas or depressions are common and often characterised by predominantly organic peat soils (Barto and Vogel 1978).

Vegetation in the DMPF is primarily of the mixed woods type with aspen (Populus tremuloides), balsam poplar (P. balsamifera), paper birch (Betula papyrifera), white spruce (Picea glauca), and balsam fir (Aibes balsamea) forming the dominant overstory associations. Jack pine (Pinus banksiana) and black spruce (P. mariana) or tamarack (Larix laricina) are common in sandy upland areas or poorly drained depressions respectively (Barto and Vogel 1978). Common shrub species include beaked hazel (Cornus cornuta), red-osier dogwood (C. stolonifera), willow (Salix spp.), alder (Alnus rugosa), high bush cranberry (Viburnum opulus var. americanum), saskatoon (Amelanchier alnifolia) and several cherry shrubs (Prunus spp.).

Characteristic understory plants include sarsaparilla (Aralia nudicaulis), dewberry (Rubus pubescens), wild strawberry (Fragaria virginiana), and numerous grasses (Graminae) and sedges (Cyperaceae). Schewe (1981) presented a comprehensive list of floral species and associations encountered in the study area. Plants known to occur in the study area and probably utilized by black bears are listed in Appendix 2.

Although most of the DMPF consists of mature or near mature stands of timber, diverse seral stages exist due to fires, clear-cut forestry operations, and to a limited extent, habitat manipulation projects (Schewe 1981). In combination, these factors result in significant areas where early seral stages support forbs and mast producing shrubs.

Much of the Duck Mountain uplands were burned by wildfires during the late 1800's, and in 1961, a large fire consumed approximately 200 sq. km in the central DMPF (Parks Branch 1971). Fires are now controlled whenever possible and no major burns have occurred since 1961.

Forest harvest operations and recreational activities within the central Duck Mountain Provincial Park are the only two forms of land use. Large scale timber harvesting dates back prior to 1882 and predates agricultural development in the surrounding lowlands (Welch 1979).

Agricultural Zone.

Like the Duck Mountain uplands, the geology of agricultural lands east of the DMPF is Mesozoic in origin but differs in that shale constitution varies from dark grey non-calcareous to carbonaceous or calcareous speckled shale. In addition, minor sand, silt, and bentonite deposits occur (Barto and Vogel 1978). Elevation in this region rises gradually from 350 m a.s.l. in the east to 450 m a.s.l. along the eastern DMPF boundary. The area is within the Interlake-Westlake Plain physiographic region and consists of a gently undulating till plain (Weir 1960). Surficial deposits include glacial drift limestone, shale, and granitic materials along with occasional lacustrine or marine strand lines (beach ridges).

Soils are primarily dark grey or black chernozemic of a coarse or medium loam texture. Most soils in the region are strongly calcareous and quite stony (Barto and Vogel 1978). Drainage varies from good to poor because of the flat or gently undulating relief.

Where undisturbed, natural vegetation is very similar to that in the adjacent DMPF. Dominant tree species include aspen, balsam poplar, paper birch and balsam fir. Coniferous species such as jack pine and white spruce are not widespread due to their commercial value and selective harvest. Understory shrubs and forbs are similar to those listed previously for the DMPF and include beaked hazelnut, red-osier dogwood, various cherry shrubs, high-bush cranberry, currants (Ribes spp.), sarsaparilla, and wild strawberry. Of particular importance to bears are the numerous mast-producing shrubs along ravines and watercourses where natural vegetation persists.

The percentage of cleared farmland is highly variable, ranging from 90+ to less than 5 on farms used for pasture or as woodlots. On the average, pasture and cropland involve 40 and 30 percent of total farm area respectively (Barto and Vogel 1978). Predominant agricultural practices include livestock raising (primarily beef cattle) and the production of forage or grains for consumption by livestock or sale. Crops include oats, wheat, barley, legume crops for forage or seed, and oilseed crops such as rapeseed. Honey production is of importance due to the abundance of native flowering species and large areas of legume crops or flowering oilseeds.

Several cereal and legume crops appear to be widely utilized by bears. Legumes (ie. clover) were common in scats during the early

summer before native mast crops matured. Cereals (grains) were utilized from early August to late September or until harvesting was complete as evidenced by the occurrence of numerous grainfilled scats and depredation complaints from farmers. Early summer utilization of the green vegetative parts of cereals was not documented but may have occurred along with utilization of native forbs and grasses.

Landclearing activities were noticed in agricultural lands throughout both the primary and extensive study areas during 1979 and 1980. An accurate estimate of hectares cleared per year is not available, however, the 1.2 percent average annual increase in improved lands cited by Barto and Vogel (1978) appears conservative.

METHODS AND MATERIALS

Capture and Handling

Bears were captured with Aldrich leg snares (Aldrich Animal Trap Co., Clallam Bay, Washington) at trapsites placed along ravines or in forested areas showing signs of bear activity. Possible capture bias resulting from subjective trapsite placement was avoided by employing additional baitsites in a modified grid pattern. Slight modifications to trapping techniques outlined in Johnson and Pelton (1980a) were incorporated and included utilizing larger quantities of bait consisting of livestock carcasses obtained from the Provincial Veterinary Laboratory (Winnipeg, Manitoba). Standard cubby (Jonkel and Cowan 1971, Poelker and Hartwell 1973, Johnson and Pelton 1980) or trail sets were employed for all captures. Trapping continued throughout much of 1979 but was restricted to spring in 1980 due to the potential influence of baitsites on movement and foraging patterns.

All bears were immobilized using a combination of ketamine hydrochloride (Ketaset [100 mg/cc]; Rogar/STB) and xylazine hydrochloride (Rompun [100 mg/cc]; Bayvet). An initial dosage of 4.5 mg per kg Ketaset and 2.5 mg per kg Rompun (Haigh 1978; Addison and Kolenosky 1979) was administered by a jab-pole syringe equipped with a 14 gauge, 4 cm needle (Nasco Supply Co., Guelph, Ontario). Intramuscular injections to the hindquarters or front shoulder-neck region were preferred. In cases where initial injections did not induce complete tractability, a second injection was applied to the hindquarters using a hand syringe.

Standard measurements including weight, length, girth, and foot dimensions were taken on all bears. General condition was evaluated through a subcutaneous fat index as well as anecdotal comments on injuries, ectoparasites, or anomalies.

Upper and lower first premolars were extracted for aging. In 1980, an intramuscular injection of tetracycline (tetracycline hydrochloride; Reverin [100 mg/cc], Hoescht) was administered at 7 to 14 mg per kg (decreasing dosage in older animals) as a cementum labelling agent (Cleall et al. 1964, Demers et al. 1968, Ellenton and Johnston 1975). Teeth were prepared for aging by a commercial process (Matsons; Milltown, Montana) or through the Ontario Ministry of Natural Resources (Wildlife Research Station, Maple, Ontario) and assessed using cementum annuli counts (Willey 1974, Rogers 1978, Hensel and Sorensen 1980).

Animals were assigned to four age classes: cub, yearling, subadult, and adult. Bears less than one year and from one to two years of age were classified as cubs and yearlings respectively. Females were designated subadults from age two until first parturition after which they were considered adults. Males from two to four years were recorded as subadults. Males five years or older had a burly appearance (attributed to the development of secondary sex characteristics) and were classified as adults. The estimated age of all animals equipped with radio telemetry units is listed in Appendix 3.

All bears were fitted with numbered metal ear tags (Kurl-lock cattle tags; Ketchum Manufacturing, Ottawa) to permit future identification. Selected animals were equipped with neck-collar radio telemetry units fitted to ensure minimal restriction yet tight enough to prevent removal.

During the handling procedure, all animals were bound to prevent premature departure and hooded to protect the eyes from sunlight or debris. Wounds inflicted during the capture process were cleaned and treated with an antibiotic. In all cases, bears were kept under surveillance until fully mobile or until they had partially recovered from the anesthetic and were respiring normally.

Radio Telemetry

Twenty-eight animals were equipped with Telonics model 5B (Telonics; Mesa, Arizona) or AVM model SB2 (AVM Instrument Co.; Champaign, Illinois) transmitters which weighed from 300 to 600 gms when fully assembled on collars. Use of rubberized canvas belting collar material was discontinued in 1979 due to chafing and replaced with a smooth butyl rubber collar which proved satisfactory. Collars were color coded in 1979 to permit visual identification. Lack of observations and a possible effect on hunter selection resulted in the choice of black collars in 1980.

An AVM model LA12 receiver was used to monitor transmitters emitting a discontinuous signal in the 150.860 to 151.375 MHz range. Transmitter frequencies were spaced at 2500 Hz intervals to permit individual recognition. Telonics transmitters incorporated an "inverse mode" activity sensing option which indicated active/inactive status through signal pulse rate (90+ pulses/min. active, 60 pulses/min. inactive). A delay time (time required to switch from active to inactive once movement ceased) of five minutes was incorporated into the first ten units. In 1980, a delay time of 1.20 minutes was chosen to evaluate a possible bias toward activity in the five minute delay transmitters.

Standard telemetry triangulation and monitoring techniques were employed throughout the study (Brander and Cochran 1969, Mech 1974). Most ground tracking was conducted from a vehicle equipped with a collapsible 14 element yagi (directional) antenna. Accuracy of the monitoring system was generally within five degrees of the true azimuth (determined from 20 tests on known transmitter locations [Appendix 4]). Hand held two or three element directional antennas were used when tracking nearby animals or during den searches. Aircraft monitoring involved a 172 Cessna equipped with two four element directional antennas connected through a left-right switching mechanism.

Reception range was variable due to the hilly topography but in general ranged from 2-3 km for the hand held yagi, 5-8 km for the 14 element antenna, and 15-30 km during aerial monitoring at 1500 m.

Monitoring Schedule

In 1979, 15 animals were monitored opportunistically once or twice a week. Restrictions on aerial survey support, defective transmitter units, and a prolonged trapping/baiting program combined to restrict the data's usefulness. In 1980, these shortcomings were avoided by confining the trapping period to spring and increasing the monitoring effort. Each triangulation series resulted in an x y coordinate location which was recorded along with information on climatic variables. From early June to late September, an attempt was made to locate each of the 18 transmitter-equipped animals on a daily basis. When not feasible, a minimum of four to ten sequential daily locations were obtained as often as possible to represent movements. To delineate

spatial utilization accurately, all animals were located when searched for regardless of their location. On two occasions, wide-ranging individuals were not detected on the first day of searching but were located early the next day from aircraft. Bears which moved to and remained at locations greater than 30 km from the intensive study area were monitored less frequently due to logistic constraints. In addition to representing spatial utilization more accurately, frequent monitoring decreased the need for aerial surveys since long range movements could often be predicted.

Data Analysis

Home range and movement analyses were processed through the University of Manitoba computing services facility using APL algorithms developed specifically for this investigation (available from the author). Some preliminary calculations and plotting involved a Hewlett Packard model 9830A digital computer, 9862A calculator-plotter, and a 9864A digitizer (Manitoba Dept. Mines and Natural Resources; Wildlife Research Branch). Algorithms and analyses were confirmed for accuracy with manual calculations.

Where information was sufficient, annual data were separated into seasons based on phenology (Table 1). Spring was characterised by the absence of ripe mast or berry crops and began with emergence from the winter den. During this period, green vegetation, roots, and tubers made up the available food supply. The presence of ripe mast and berry crops was used to delineate summer. The fall period was marked by a decreasing availability of both green vegetation and mast crops. Data

from 1979 were not classified into seasons due to insufficient locations per season. As indicated in Table 2, season dates show annual variability, primarily the result of climatic fluctuations. Since all animals did not react simultaneously to changing food sources, season dates are not absolute. Season dates for several animals were adjusted using marked changes in behavior as the criteria. To prevent bias, repeated observations at the den site were omitted once inactivity was established.

Simulations

Computer simulations were used to investigate the effect of varying sample size (number of location points) and deviation from normality on the minimum convex polygon (MP) estimate and Jennrich and Turner (JT) index. To determine if the assumption of normality as required by the JT index was being violated, x and y coordinate data from each animal were tested using the Kolmogorov-Smirnov test (Univariate procedure, SAS 1979).

Using data from a representative animal or coordinates generated randomly to represent the total area, the effect of using an increasing number of data points (drawn at random and independently from the total) to estimate home range area was established. For each sample size (i.e. 3, 5, 7... 50), 200 determinations were completed to minimize bias, giving a mean home range area and standard error for each sample size. By interchanging bivariate normal, aggregated, perimeter, and randomly generated coordinate arrays, JT index area calculations were used to determine to what extent violating the assumption of normality affected the JT index.

Table 1. Periods used to characterize black bear seasonal home range utilization and movement patterns (based on phenology).

1979

Spring	10 May - 10 July
Summer	11 July - 15 September
Fall	16 September - 15 November

1980

Spring	10 April - 15 June
Summer	16 June - 31 August
Fall	1 September - 10 November

* Breeding season	26 May - 5 July
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* Approximate: Based on the period when females in estrous were captured \pm 15 days.

Table 2. Individual seasons and period of activity used to delineate black bear seasonal home range utilization and movement patterns during 1980.

Animal #	Spring	Summer	Fall	Onset of Inactivity
F792	+ - June 15	June 16 - Aug. 31	Sept. 1 - Sept. 29	Sept. 30
F793	Apr. 15 - June 15	June 16 - Aug. 31	Sept. 1 - Sept. 25	Sept. 26
F795	+ - +	June 22 - Aug. 22	+	+
F796	Apr. 5 - June 15	June 16 - Aug. 31	*	
F798	Apr. 15 - June 15	June 16 - Aug. 31	Sept. 1 - Nov. 11	Nov. 12
F799	Apr. 9 - *			
F801	+ - June 15	June 16 - Sept. 2	Sept. 3 - Sept. 23	Sept. 23
F802	+ - June 15	June 16 - Aug. 31	Sept. 1 - Sept. 30	Oct. 1
F807	+ - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 5	Oct. 6
F809	+ - June 15	June 16 - Aug. 31	Sept. 1 - Sept. 30	Oct. 1
F8010	+ - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 10	Oct. 11
F8011	+ - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 26	Oct. 27
F8012	+ - +	June 16 - Aug. 31	Sept. 1 - Oct. 19	Sept. 26
M793	Apr. 15 - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 11	Oct. 12
M794	Apr. 7 - *			
M795	Apr. 15 - June 15	June 16 - Sept. 20	Sept. 21 - Oct. 10	Oct. 11
M796	Apr. 20 - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 27	Oct. 28
M804	+ - June 15	June 16 - Aug. 31	Sept. 1 - Oct. 24	Oct. 25
M807	+ - +	June 19 - Oct. 1	Oct. 2 - Oct. 20	Oct. 21

+ Dates unavailable.

* Terminated

A comparable simulation was used to investigate the effect of sample size on the activity center (mean x, mean y coordinate). For various sample sizes (2, 3, 5, 7...50), 200 determinations were used to calculate the activity center and standard deviation of both the x and y coordinate. Data points were drawn at random without replacement from the total dataset for each computation. In addition (using the same simulation procedure), the mean shift in activity center and its standard deviation was calculated as sample size increased.

Area Calculations

Home range area was determined using both the minimum convex polygon (Mohr 1947) and Jenrich and Turner index (Jenrich and Turner 1969, [95% utilization ellipse]). Modification of annual data sets allowed for seasonal comparisons and the elimination of outlying data points to delete excursions from the area estimate (Burt 1943). Comparisons between cohorts and seasons were computed using the JT index based on a minimum of 15 locations (13-14 locations for several spring ranges) and Duncan's multiple range test (SAS 1979). Complete datasets (without outer points deleted) were used for all animals since the JT index evaluates the smallest area enclosing 95 percent of the utilized habitat. The reliability of data collected over part of a season as an indicator of total area was investigated using cumulative totals from increasing proportions of a season with known total area.

Using annual data sets, an increasing percentage of outermost locations (furthest from the activity center) were deleted to determine the effect on area. Using the above trials, a percent deletion level

was established to exclude infrequent forays and estimate a home range "core" area.

Movement

Two analyses were used to test for cohort and seasonal differences in movement patterns. Distance per day analyses calculated linear distance travelled on a per day basis ($[\text{distance}/\text{hours between locations}] \times 24$) when successive locations were less than 48 hours apart. To include infrequent observations during low intensity spring monitoring, the distance between sequential locations was determined. Since each location involved some measurement error, movements of less than 0.5 km per day or between successive locations must be interpreted with caution. A one way (by season or cohort) analysis of variance and a two way factorial (by season and cohort) analysis of variance along with Duncan's multiple range test (GLM Procedure, SAS 1979) was used to test for cohort and seasonal differences.

Spatial use of home range

Home range utilization was assessed by comparing the spatial distribution of locations for each individual and cohort. In addition to evaluating the actual locations, distance from the activity center on an annual and biweekly basis was used to quantify cohort and seasonal utilization differences. A one way (by season or cohort) analysis of variance and a two way factorial (by season and cohort) analysis of variance along with Duncan's multiple range test (GLM Procedure, SAS 1979) was used to compare biweekly differences.

Individual home range stability between years and seasons was compared using the distance between activity centers. A shift was considered significant if the distance was greater than the radius of the minor summer home range axis.

Home range overlap was subjectively evaluated within and between cohorts and based on overlap of the annual minimum polygon area.

Den Sites

An attempt was made to locate and investigate all den sites. In 1979, dens were initially inferred from weak radio-telemetry signals or lack of movement and later verified with ground checks in winter. Several incidents involving harassment or mortality of denned animals by landowners after dens had been located and marked led to a modified program. Subsequently, dens were not approached and site descriptions are limited due to difficulties encountered in locating dens once the transmitter-equipped bear had departed in spring.

Onset of denning was inferred from several variables including telemetry signal strength, active-inactive status and lack of movement. Visual confirmation of denned animals was avoided until late fall to reduce the possibility of investigator-related disturbances.

When dens were located, habitat characteristics, den location and a general description of the den was recorded.

RESULTS

Capture and Aging

Summary information on animals captured during the study is given in Appendix 5. In total, 23 females and 16 males were secured. Adult, subadult, and yearling females represent 21.5, 21.5, and 15.5 percent of all captures respectively. Adult males were uncommon, making up only eight percent of the total. Subadult, yearling, and cub males represent 18, 13, and 2.5 percent of the total respectively.

At least three animals (M794, M796, F798) suffered lesions and tissue necrosis following capture in the leg-hold snare. If pulled too tight, circulation was restricted and tissue damage resulted. The injuries were not noticed until two recaptured animals (M794, F798) were examined. Injured bears did not exhibit abnormal movement or home range utilization patterns when compared to uninjured animals. When recaptured in mid-October 1979, F798 and M794 (both with injured front paws) were in good physical condition and had gained 14 and 18 kg respectively since initial capture on 1 August.

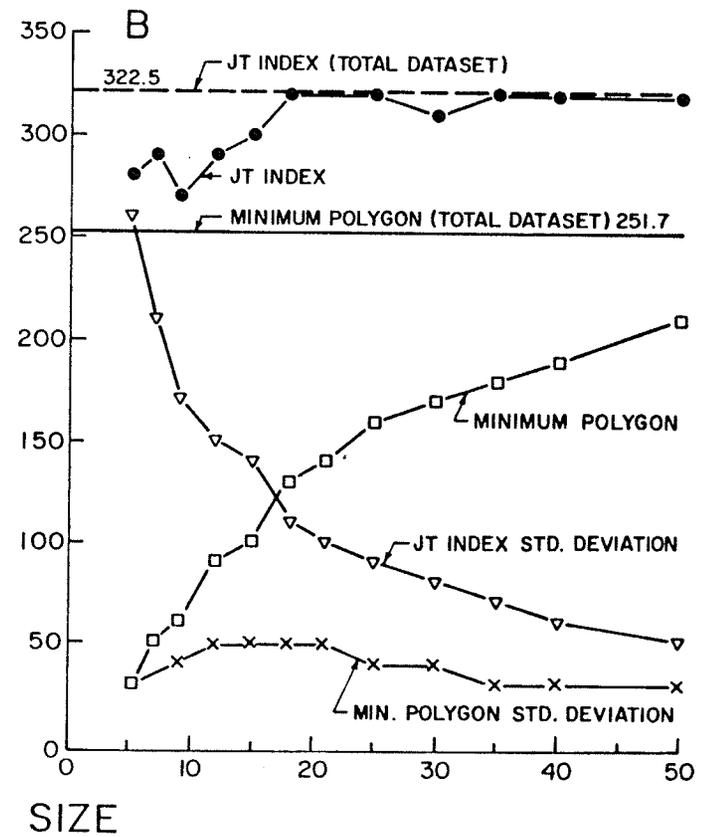
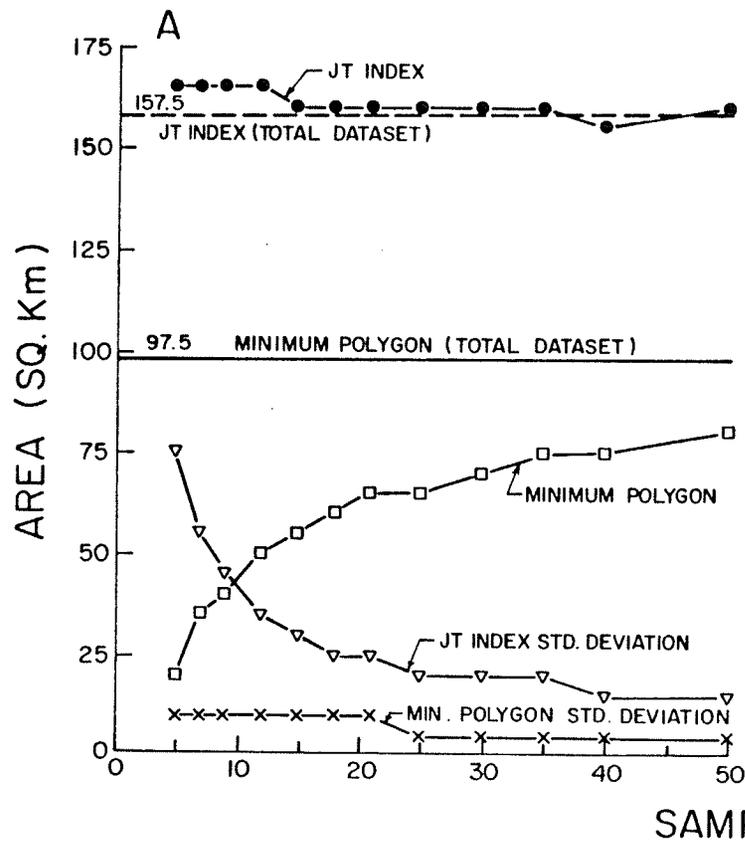
During the initial capture and termination phase of the project, two adult females were lost. One sustained a serious injury during capture and was dispatched. The second mortality occurred during den site investigations in March 1981 after a female with cubs (F801) was immobilized and did not recover. Both animals were in good physical condition and did not suffer from any apparent anomalies.

Simulations

Effect of Sample Size on the Area Estimate.

Figure 3A illustrates the effect of increasing sample size (number of locations) on both the minimum polygon estimate and the Jennrich and Turner index. The data base involves 1000 randomly generated coordinates. Simulations using 100 random coordinates follow a similar trend. A comparable analysis on actual data is shown in Figure 3B (M796, 1980). With increasing sample size, the JT index stabilizes whereas the minimum polygon estimate does not reach an asymptote. Standard deviation of both the JT index and MP estimate drop rapidly with increasing sample size. Similar analyses were conducted on additional datasets with results not unlike those illustrated. At sample size greater than 15 or 20, the JT index shows only minor fluctuations. Similarly, standard deviation of the JT index at greater than 20 locations remains relatively constant with only a minor decrease to sample size 50. In contrast, the MP estimate continues to increase throughout the sample size range. At 25 or greater, the increase in MP area shows a gradual decrease in slope (Figure 3A). Although apparent in Figure 3A, this trend is not evident in Figure 3B and relates to differences in data distribution. In contrast to the 1000 uniformly distributed coordinates, actual data are often aggregated and may enclose large empty areas. The trend observed in Figure 3B is therefore not due entirely to sample size effects but includes effects of the underlying data distribution as well.

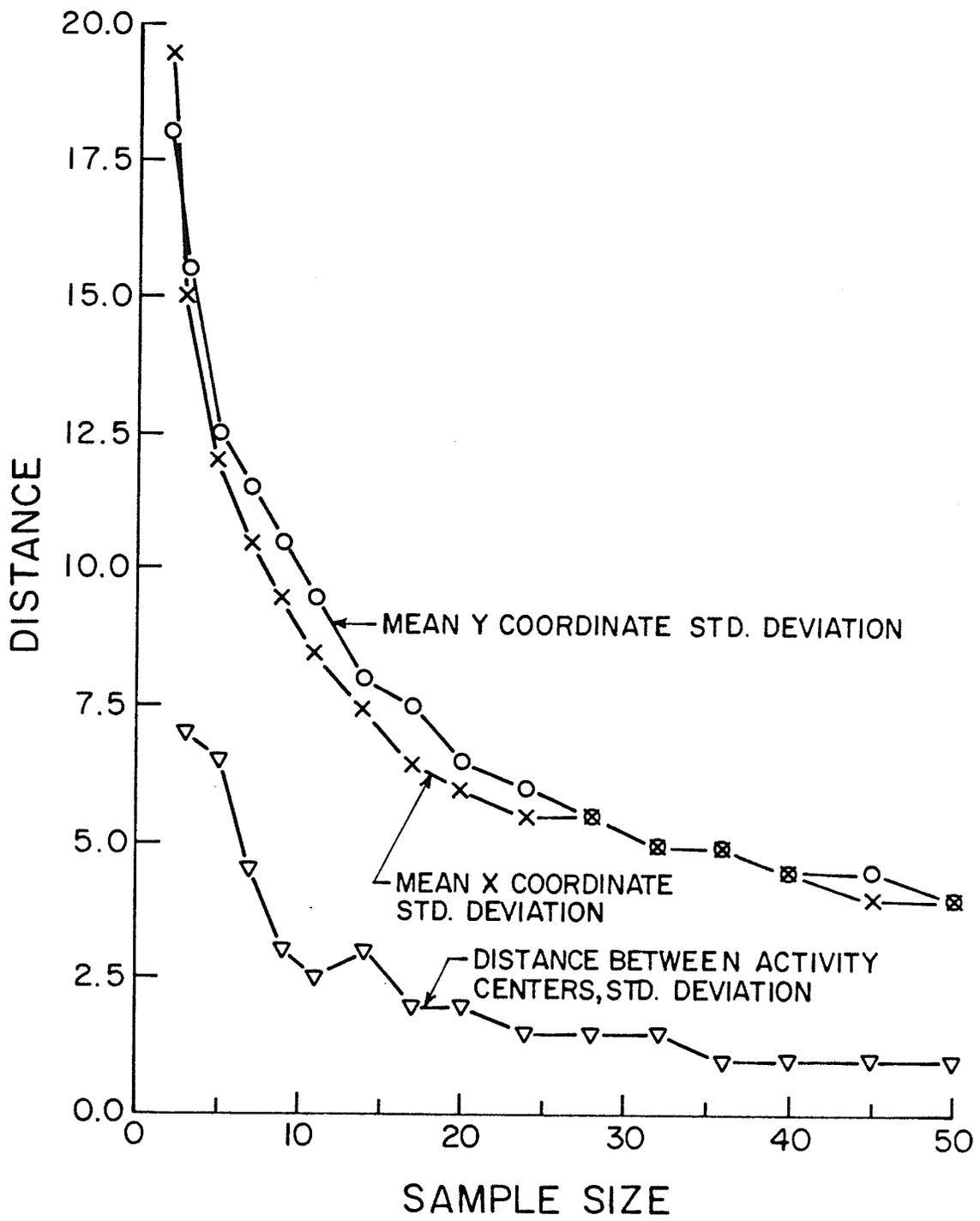
Figure 3: The effect of sample size (number of coordinate locations) on the Jennrich and Turner and minimum polygon home range estimate. A. 1000 random coordinates B. Actual dataset, M796,1980



Effect of Sample Size on Activity Center.

A simulation comparable to testing the effect of sample size on area was conducted to determine the influence of sample size on the activity center estimate. The result of varying sample size on standard deviation of the mean x , mean y coordinate is outlined in Figure 4. In addition, the standard deviation of the change in activity center as sample size increases is shown. The data base involves 1000 randomly generated coordinates within a ten by ten unit quadrat. Analyses conducted on actual datasets (F793, F802, M795, M796) gave similar results. The mean activity center for each sample size tested is not presented since multiple computations (200) result in a similar value regardless of sample size. Of interest however is the standard error of the mean coordinate since it provides a measure of how variable the activity center estimate is. In all cases, standard error of the mean x and y coordinates decreased rapidly with increasing sample size and began to stabilize at approximately 20. The distance between mean activity centers with increasing sample size was minimal and is related to the averaging effect of multiple computations cited previously. However, standard deviation of the shift in activity center indicates how variable the estimate can be with few locations. Variability begins to stabilize at approximately 15 observations after which only a small decrease occurs. These results are consistent with the central limit theorem (ie. standard error of the mean decreases inversely as the square root of the sample size).

Figure 4: The effect of sample size (number of coordinate locations) on standard deviation of the home range activity center estimate. Distance indicated in arbitrary units



Test for Normality.

Using the Kolmogorov-Smirnov test for normality and a significance level of .05, data from one abscissa (east-west) and seven ordinate (north-south) axes were normally distributed. Rejection or acceptance of the null hypothesis that the data are a random sample from the normal distribution is indicated in Table 3. No animals had data from both axes normally distributed.

Effect of Data Distribution on the Jennrich and Turner Index.

To determine how the data distribution effects the JT index, four different distributions of known area were tested. Table 4 indicates the JT index overestimates the true area by varying degrees, depending on how much the distribution deviates from normality. It is most accurate on a bivariate normal distribution and overestimates by 3.5 times when all data points are located on the perimeter. The random and aggregated distributions were overestimated by 1.5 and 1.3 respectively. Scattergrams of each distribution tested are illustrated in Figure 5. The results in Table 4 are based on a single replication with 1000 (x,y) points. Therefore, a standard error is not available, but replicate to replicate variation was less than five percent (results not shown).

Area Calculations

Effect of Sampling Period on Area.

The increase in area as larger proportions of a season are included is illustrated in Figures 6b and Figure 7. The area increase during a

Table 3. Kolmogorov-Smirnov test for normality of x and y coordinate data obtained during 1980.

° Animal	X Coordinate		Y Coordinate	
	PROB >D	Result	PROB >D	Result
+F792	< .01	*R	.095	*A
F793	< .01	R	.04	R
F795	> .15	A	.01	R
F796	.037	R	> .15	A
F798	< .01	R	.032	R
F801	< .01	R	< .01	R
F802	< .01	R	> .15	A
F807	< .01	R	> .05	A
F809	< .01	R	.047	R
F8010	< .01	R	.037	R
F8011	< .01	R	> .15	A
F8012	< .01	R	.09	A
M793	< .01	R	< .01	R
M795	< .01	R	< .01	R
M796	.025	R	< .01	R
M807	< .01	R	.147	A

+ 'F' specifies female, 'M' specifies male (80-100 locations per data set)

* 'R' indicates rejection of the hypothesis that the data are normally distributed, 'A' indicates acceptance of the hypothesis. $\alpha = .05$

° Each test involves 80-95 coordinate locations

Table 4. Effect of various distributions (normal, random, aggregated, perimeter) on the Jennrich and Turner home range index. 1000 coordinates in each array.

% Outermost Points Deleted	*DISTRIBUTION TYPE			
	+ Bivariate Normal	°Random	°Aggregated	°Perimeter
0	19.42	27.80	24.40	56.63
5	16.54	26.31	22.59	56.22
10	14.49	24.87	20.91	55.20

* All distributions consist of 1000 points

+ 95% of the data points within two standard deviations of the mean.
Minimum polygon area (5% outermost points deleted) = ca. 18.50

° Minimum polygon area = ca. 18.50

Figure 5: Scattergram of (a) normal (b) random (c) aggregated and (d) perimeter distributions used to test the effect of non-normality on the Jennrich and Turner index. 1000 coordinates in each array

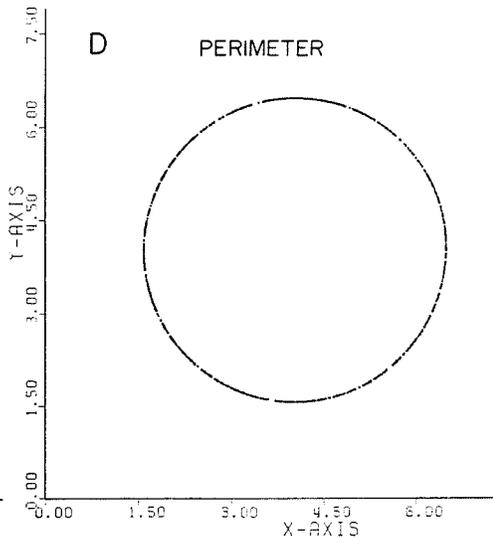
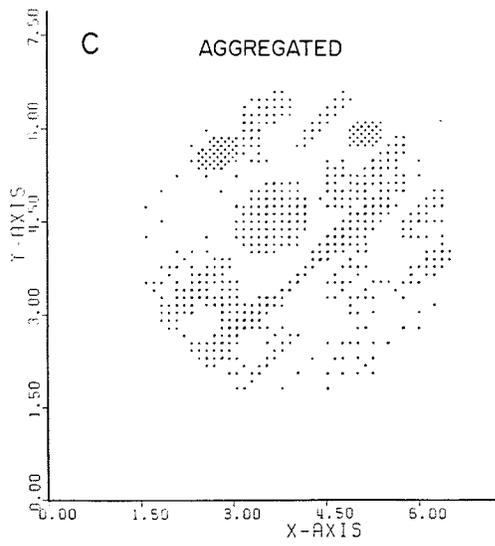
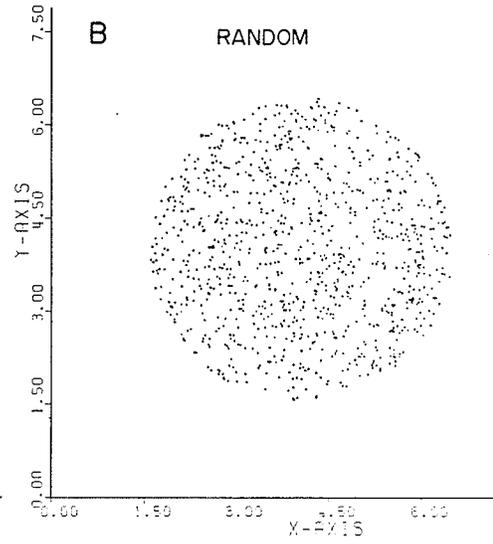
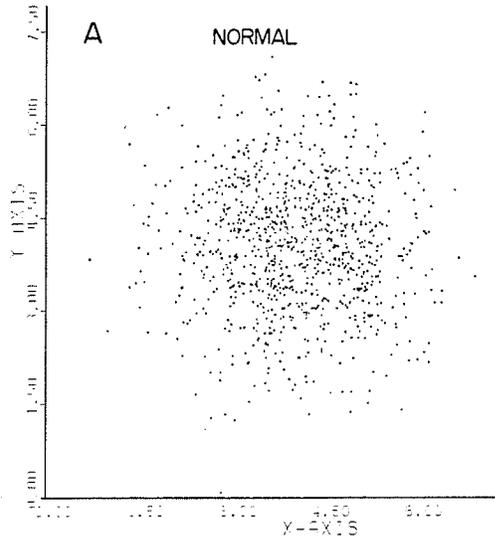


Figure 6: The effect of cumulative coordinate locations obtained sequentially on the home range estimate. Database involves:
A. 1000 random coordinates, B. data from F798, 1980

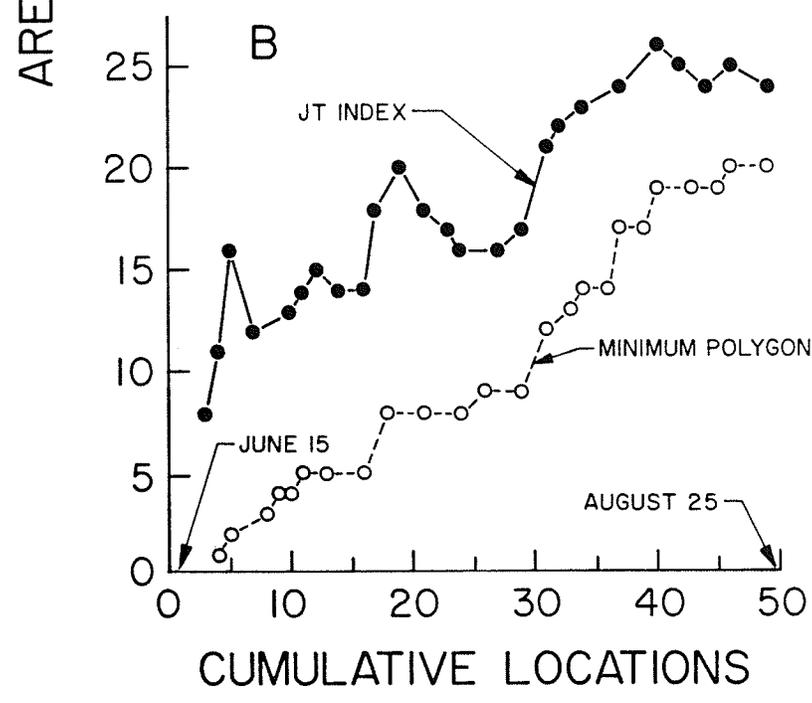
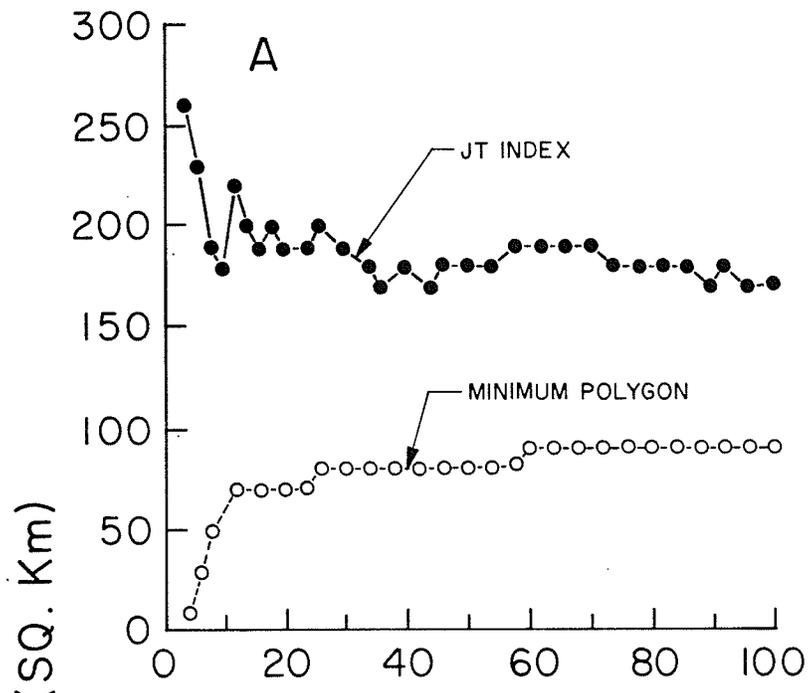
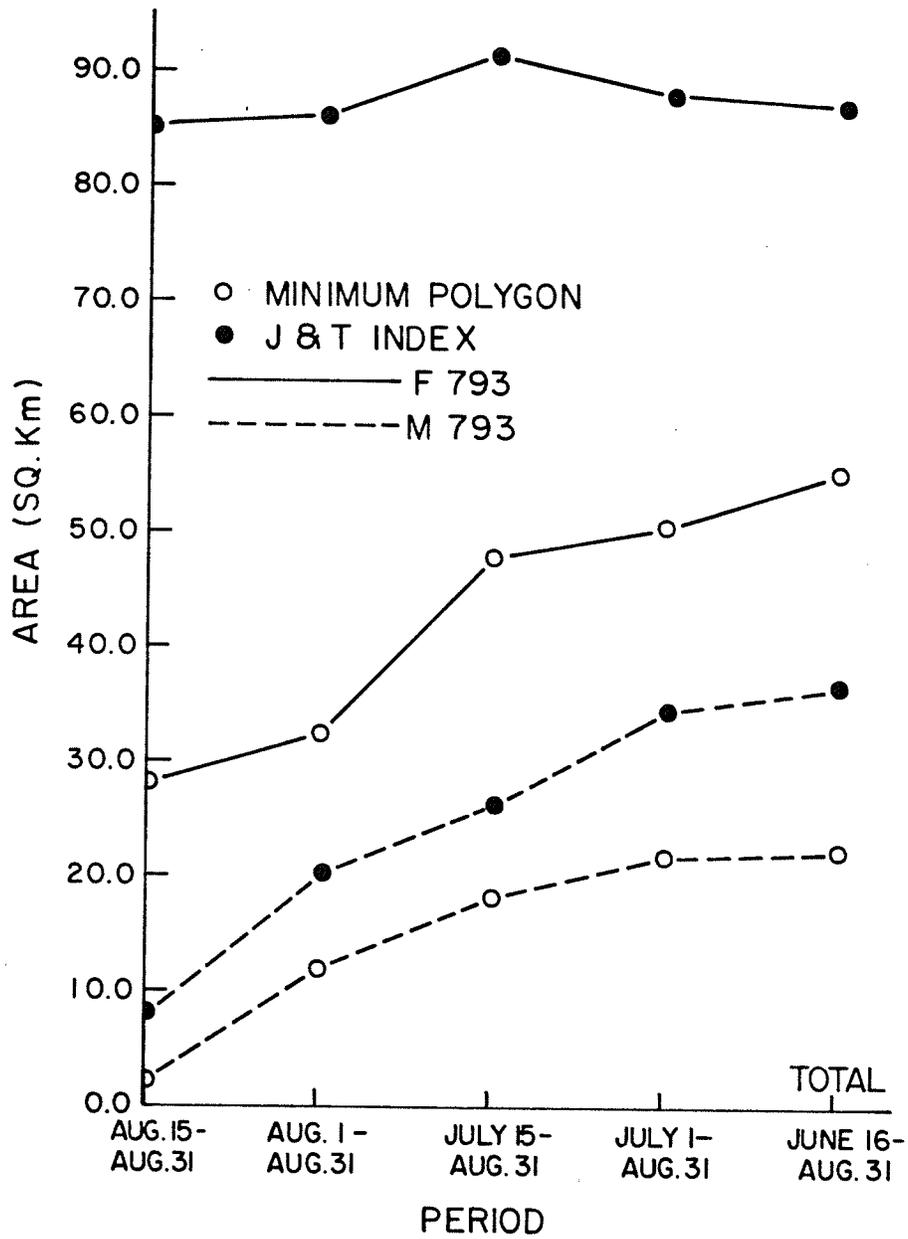


Figure 7: Increase in summer (16 June - 31 August) home range of M793 and F793 as increasing proportions of the season are included in the estimate



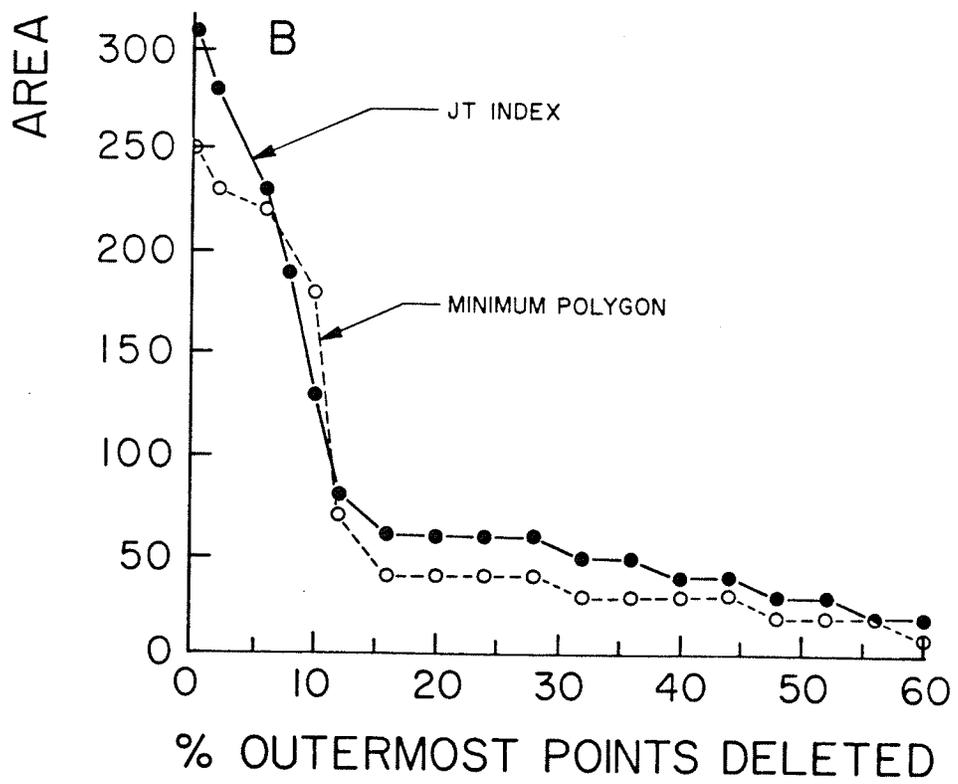
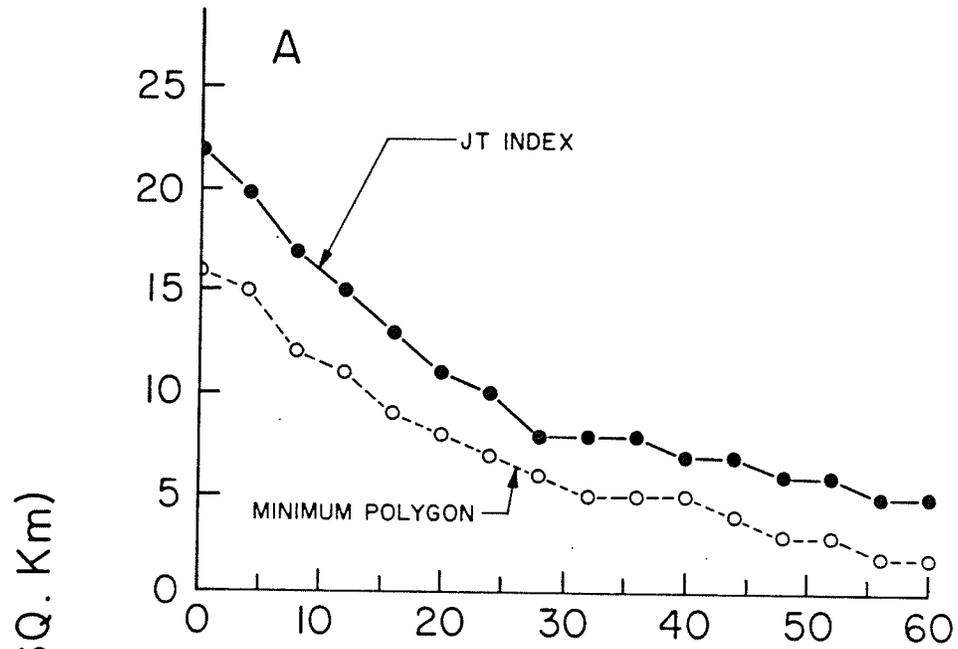
season is partially due to the increase in sample size (number of locations) plus the cumulative effect of utilizing additional area as the season progresses. When cumulative locations are chosen at random from a fixed area the trend shown in Figure 6A results. Both the JT index and MP estimate stabilize by 15 observations. Cumulative sequential locations often follow the trend outlined in Figure 6B and Figure 7. Neither the JT index or MP estimate stabilize. From a previous simulation investigating the effect of sample size on area, the JT index can be expected to stabilize by sample size 20. The continued increase in JT area for M793 (Fig. 7) and F798 (Fig. 6B) indicate the area utilized is increasing over the season. The JT index stability shown by F793 (Fig. 7) indicates the area used has remained relatively constant and the increase in F793 MP area can be attributed primarily to increasing sample size. These results suggest an animal must be monitored for a large part (i.e., greater than three-quarters) of the season before a reliable and unbiased estimate of seasonal area can be made.

Home range comparisons.

In 1979, 15 telemetry equipped bears were monitored opportunistically to yield ca. 350 locations, in 1980 a more intensive schedule on 18 animals resulted in 1500 locations.

Trials were run to determine if a natural "percent deletion" existed which would eliminate occasional sallies. Home range decreased log linearly as an increasing percentage of outermost locations were deleted (Figure 8). At 25 to 30 percent deleted, a reduction in the rate indicated the presence of an inner "core area" with a higher density of

Figure 8: Decrease in home range of A: F798 and B: M793 as an increasing percentage of outermost coordinate locations are deleted. Inflection indicates the presence of a highly used "core area"



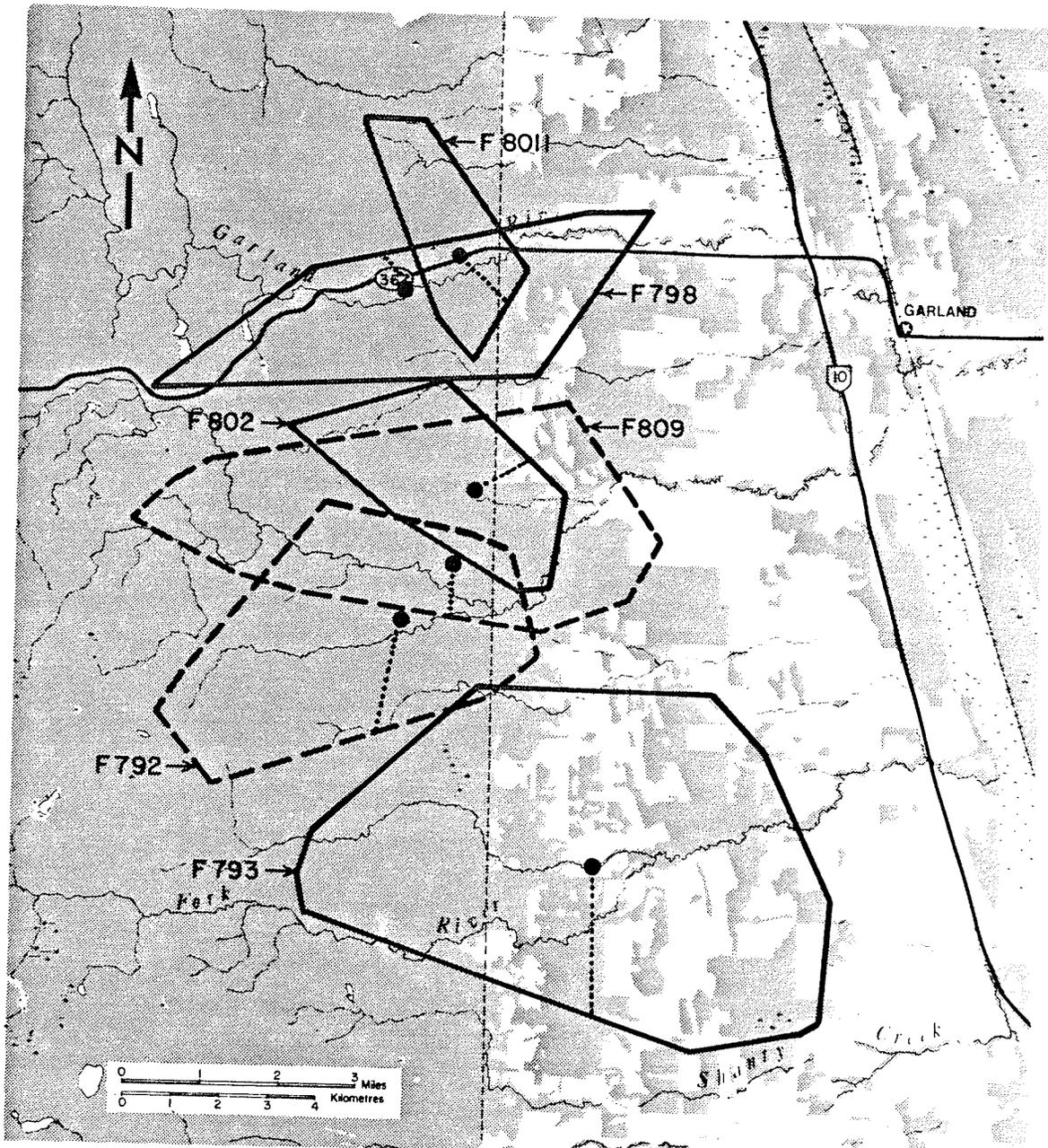
data points than peripheral areas. The marked inflection in Figure 6B at 15 percent deleted is partially an artifact resulting from reduced monitoring while M795 was in peripheral areas. If monitoring in all areas were equally intensive, the inflection point would be shifted to the right by 10 to 15 percent.

To test for cohort differences in seasonal home range utilization, the JT index based on a minimum of 15 locations was used in most analyses (several spring comparisons involved 13 or 14 locations). Seasonal areas for all cohorts are listed in Table 5 which includes the MP area for comparison. Individual home ranges are presented in Appendix 6. Representative subadult and adult female home ranges are illustrated in Figures 9 and 10 respectively. Both cohorts had portions of their home range in forest and agricultural land and moved freely between the two areas. In contrast to the small home ranges occupied by females, subadult males ranged over very large regions in both agricultural lands and the DMPF (Figure 11).

When cohort effects were eliminated and seasonal differences compared, spring home ranges (425.41 sq. km) were significantly larger than summer (68.78 sq. km) or fall (68.80 sq. km).

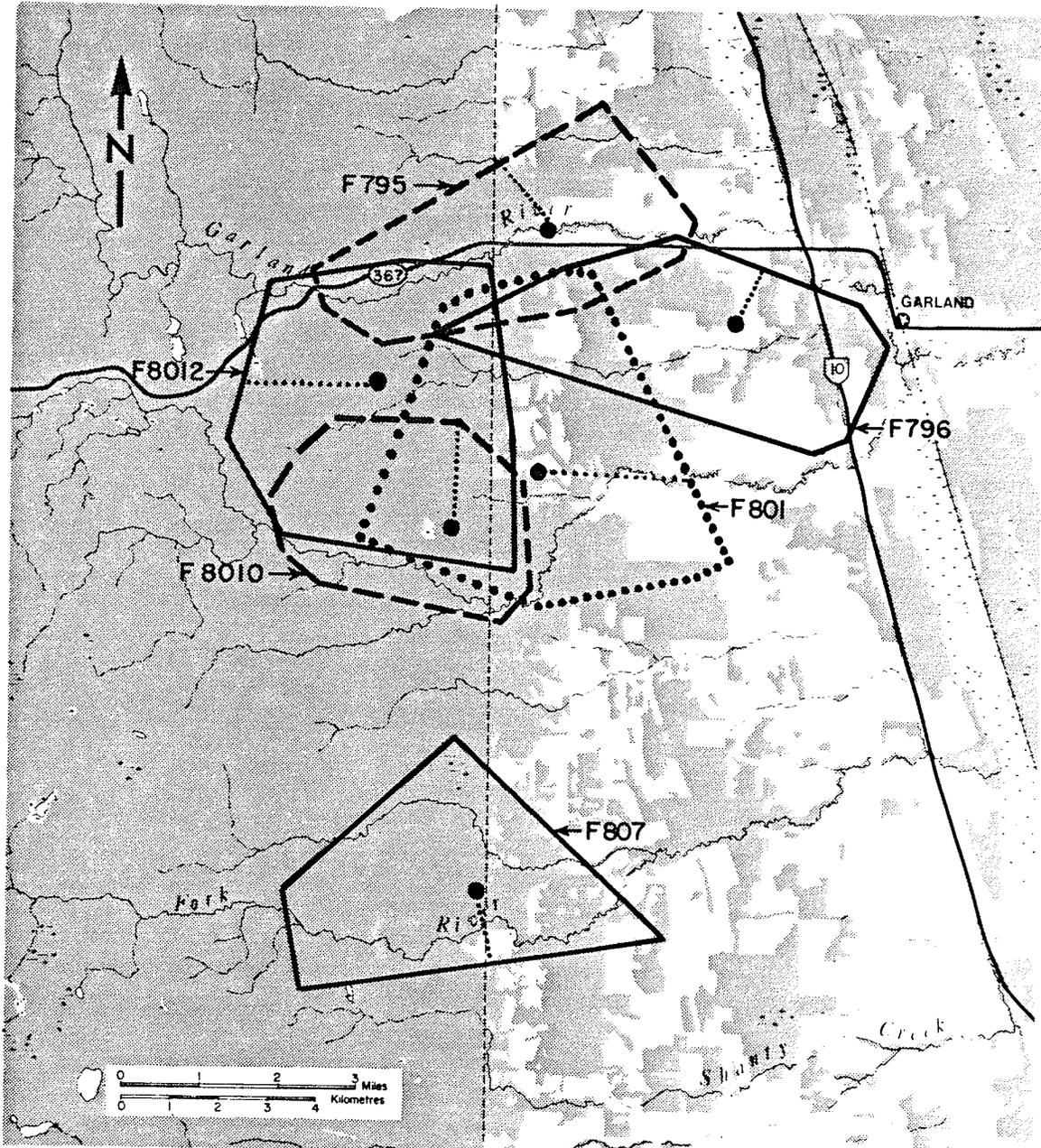
Annual subadult male home ranges were larger than subadult or adult female home ranges (506.44 vs. 35.19 and 29.12 sq. km respectively). Subadult male spring (807.39 sq. km) and summer (189.25 sq. km) ranges were larger than subadult and adult female ranges but the difference was not significant. In fall, subadult males occupied significantly larger areas (213.83 sq. km) than subadult or adult females (22.98, 15.43 sq. km). These results indicate subadult males range over larger areas than

Figure 9: Home ranges of subadult female black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations



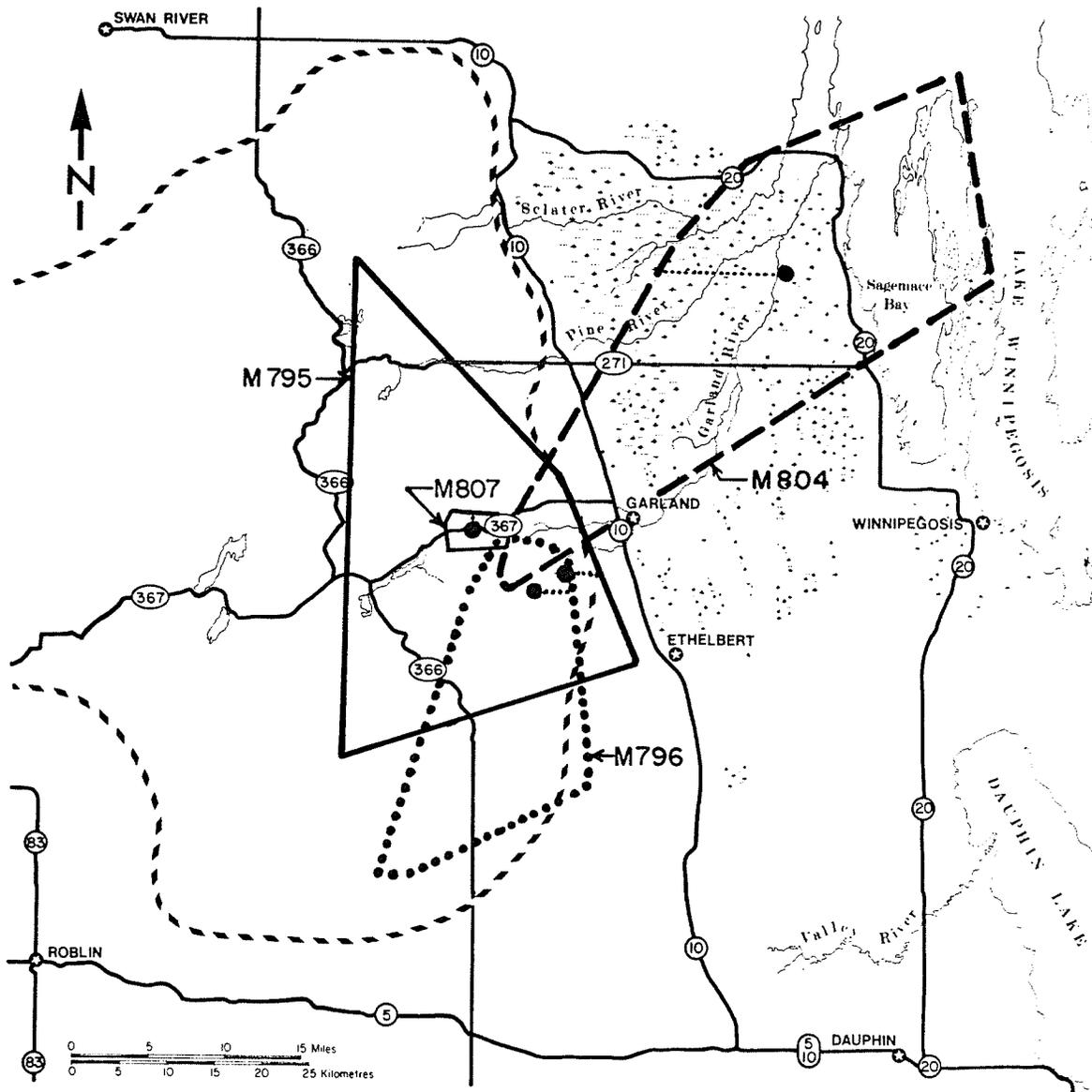
- ACTIVITY CENTER
- INDICATES RELATION OF ACTIVITY CENTER TO SPECIFIC HOME RANGE

Figure 10: Home ranges of adult female black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations



- ACTIVITY CENTER
- INDICATES RELATION OF ACTIVITY CENTER TO SPECIFIC HOME RANGE

Figure 11: Home ranges of subadult and adult male black bears in western Manitoba monitored during 1980. Outer boundary determined by joining peripheral locations



- ACTIVITY CENTER
- INDICATES RELATION OF ACTIVITY CENTER TO SPECIFIC HOME RANGE

other cohorts during all seasons. Lack of significant differences in spring and summer between males and females results from high subadult male variability (see standard deviations in Table 5), which itself is a characteristic typical of this cohort. On the average, subadult females occupied larger areas than adult females during all seasons but the differences were not significant. In contrast to both subadult males and females, adult females utilized ranges which showed little variability between individuals (Table 5).

Subadult males utilized significantly larger ranges in spring (807.39 sq. km) than during summer (189.25 sq. km) or fall (213.83 sq. km). Subadult females showed a similar trend with spring ranges slightly larger than summer or fall. Adult females with and without cubs occupied ranges of approximately equal size during all seasons. Only one adult male with a home range of 2921.9 sq. km was monitored in 1980. Comparisons to other cohorts were not made since the representativeness of this individual is not known.

Although 1979 and 1980 data are not directly comparable due to sampling differences, the following trends are suggested. Subadult male ranges were smaller in 1979 (224.56 vs 506.42 sq. km) but are not significantly different. Subadult females utilized larger areas in 1979 (60.15 vs 35.19 sq. km) but high variance does not permit definite conclusions. Adult females utilized smaller areas in 1979, however the difference may result from insufficient sample size in 1979 and a shorter monitoring period.

To determine if home ranges had a characteristic orientation or shape, the ratio of east-west to north-south dimensions was calculated. Average ratios for summer and the annual home range are presented in

Table 6. Subadult females had a greater (but not significantly different) annual east-west to north-south ratio (1.79) than adult females (1.40) or subadult males (1.12). Summer ratios were similar to those derived from annual home ranges.

Spatial use of home range.

Home range utilization was quantified on both an annual (Figure 12A) and biweekly basis (Figure 12B). Females had greater than 65 percent of total locations within two km of the summer activity center. Conversely, subadult males had fewer than 30 percent of total locations within two km of the summer activity center. Female utilization dropped off sharply at greater than two km while subadult males showed a gradual decline to the home range periphery. Major-minor axis dimensions which partially explain the absolute difference in distance from the activity center are outlined in Table 7. Subadult males spent much (70%) of their time within five km of the activity center but undertook long movements to peripheral regions. If the time spent in remote areas was equally represented, males would show an even greater tendency towards uniform home range utilization.

Mean distance from the summer activity center during biweekly periods from 10 April to 20 October 1980 is portrayed in Figure 12B. Descriptive statistics for each cohort are outlined in Appendix 7. In spring, distance to the summer activity center was greater for subadult males (14.23 km) than subadult females (2.40 km) or adult females with (2.80 km) or without cubs (2.07 km). Subadult males show a similar trend in summer and fall when mean distance from the activity center (4.07 and

Table 6. Ratio of east-west to north-south dimensions of black bear home ranges in 1980. Measurements based on outermost points of the minimum polygon area.

Cohort	+n	Annual Home Range		n	Summer Home Range	
		Mean	Std. Dev.		Mean	Std. Dev.
Adult Female	5	1.40	0.54	6	1.24	0.25
Subadult Female	6	1.79	0.85	6	1.71	1.04
Adult Male	1	0.95		1	0.95	
Subadult Male	4	1.12	0.68	4	1.23	0.52

* Ratios calculated only for animals with greater than 20 locations.

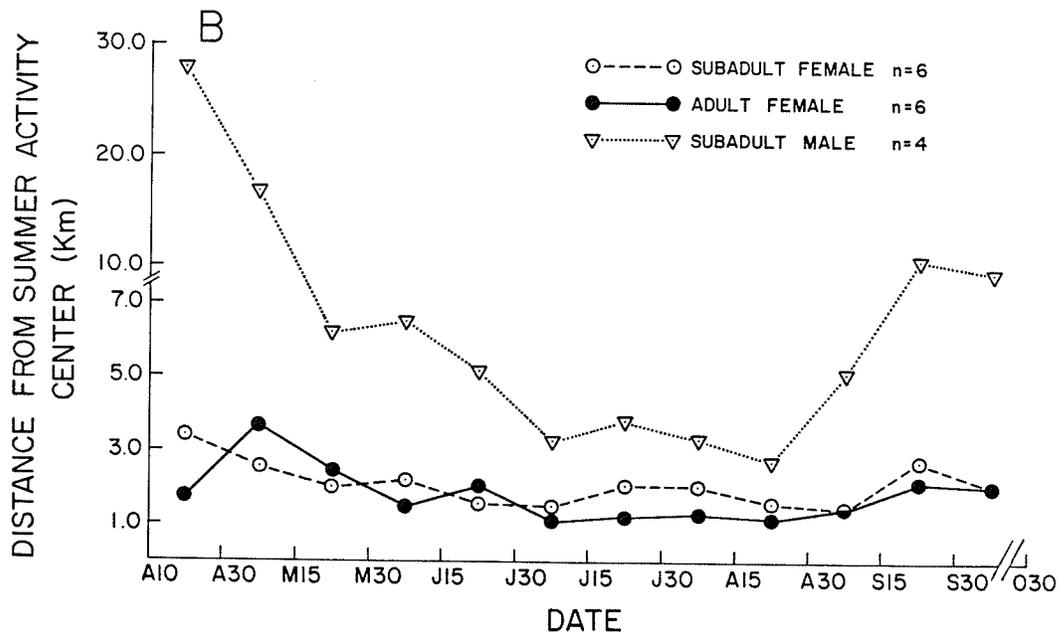
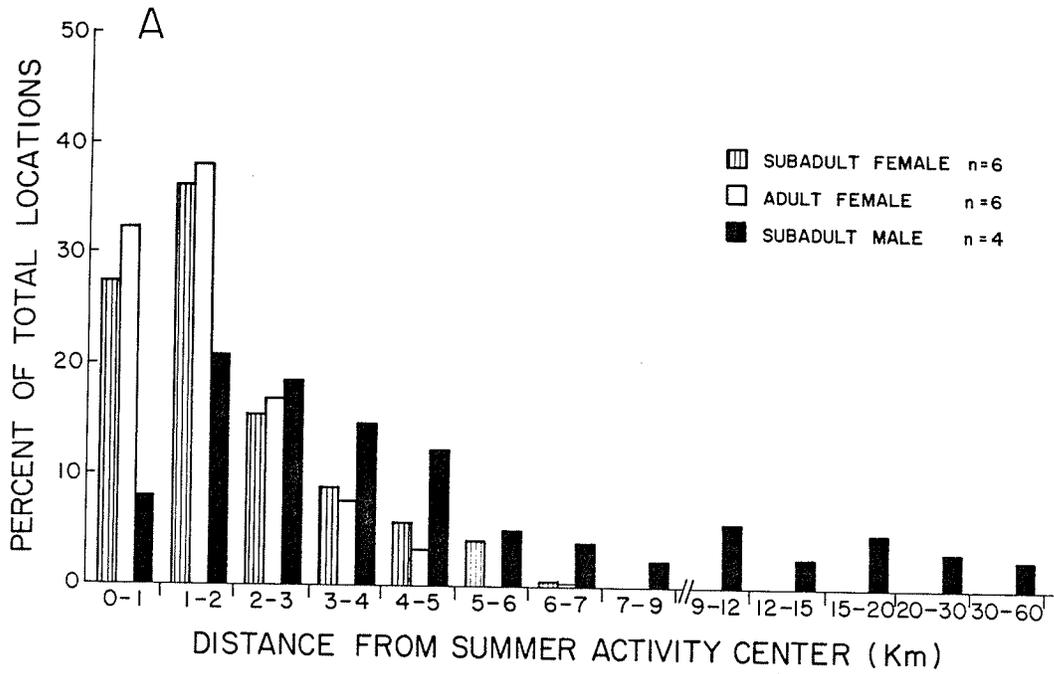
+ Indicates sample size (number of animals).

Table 7. °Dimensions (km) of major and minor home range axes of black bear home ranges (based on minimum polygon) in 1980.

Cohort	n	Annual Home Range				Summer Home Range				
		Mean Major	Std. Dev.	Mean Minor	Std. Dev.	n	Mean Major	Std. Dev.	Mean Minor	Std. Dev.
Adult Female	5	7.48	1.17	5.43	1.54	6	6.88	1.52	5.11	1.62
Subadult Female	6	8.81	2.56	4.08	1.79	6	7.55	2.90	3.57	1.91
Adult Male	1	72.75		32.25		1	72.75		32.25	
Subadult Male	4	25.21	17.76	14.53	12.56	4	16.69	13.90	10.09	9.49

° Dimensions calculated only for animals with greater than 20 data points.

Figure 12: Relationship of subadult males and adult and subadult females to the summer activity center on an (A) annual and (B) biweekly basis

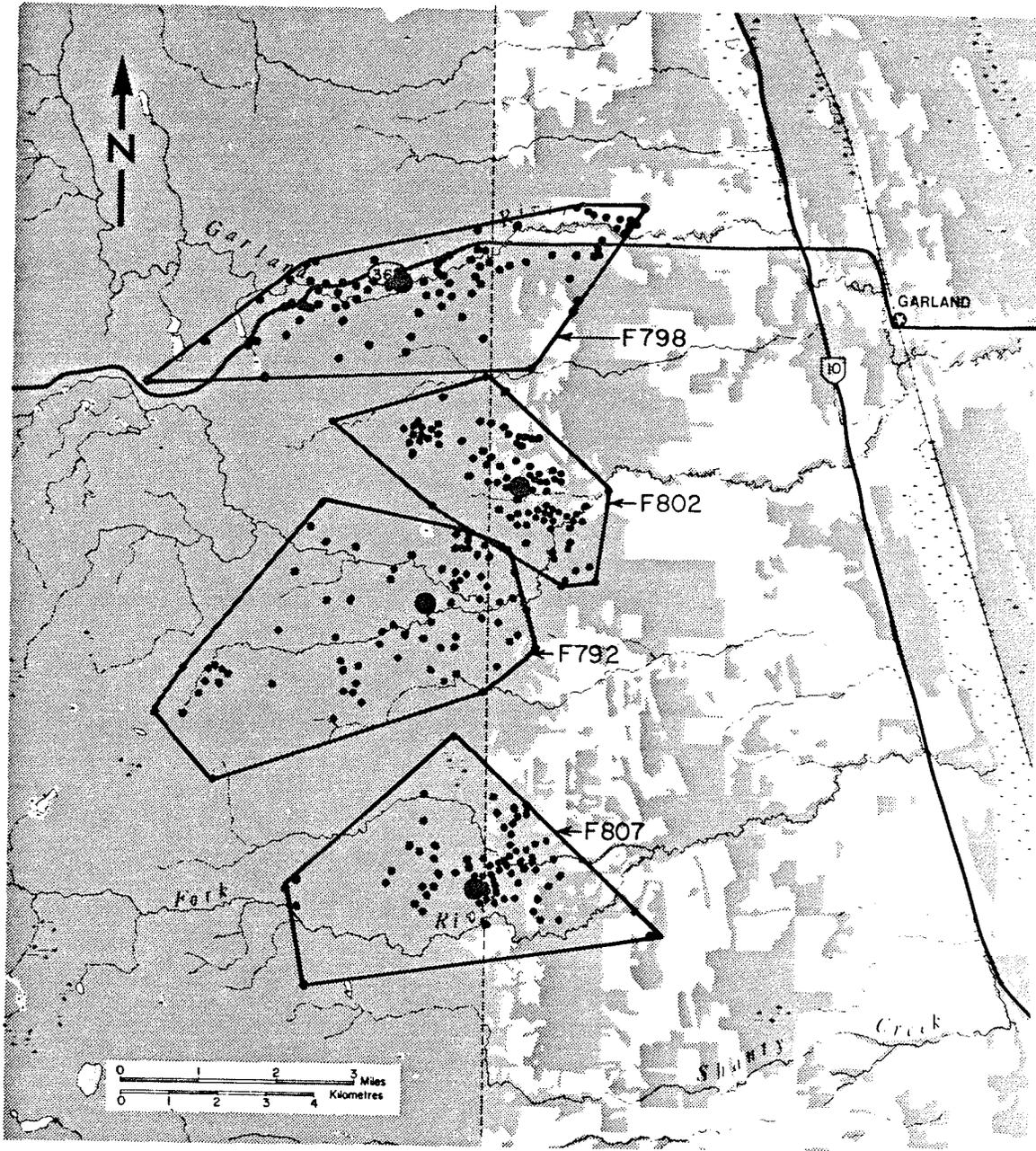


5.46 km respectively) was significantly greater than for other cohorts. There was no difference between subadult or adult females with and without cubs.

Within cohorts, subadult females were farther from the activity center in spring (2.40 km) than summer (1.78 km). Subadult males showed a similar trend with greater distances from the activity center in spring (14.23 km) than summer (4.07 km) or fall (4.07 km). Adult females with cubs were farther from the activity center in spring (2.80 km) than summer (1.39 km) or fall (1.38 km) while adult females without cubs showed no difference.

Subadult male distance from the activity center was greatest in spring and reflects use of a remote den site by all subadult males. In fall only two of four animals made extensive movements to remote den sites. Subadult male forays to peripheral areas account for greater summer distances than those observed in female cohorts. High standard deviations (Appendex 7) reflect the variability characteristic of subadult males. Several males (M795, M796) made numerous excursions during summer while others (M793, M807) were very sedentary. The general pattern of home range utilization (distribution of locations) by females is shown in Figure 13. While some females show a tendency towards random home range utilization (F792), others demonstrate a contagious pattern. Within the intensive study area males did not use their summer ranges uniformly, tending to restrict their activities in smaller areas which received intensive use. The paucity of locations (approximately 100 per animal) does not allow definite conclusions about the utilization distribution or factors which influence the dispersion of locations.

Figure 13: Distribution of representative female black bear locations recorded in the study area during 1980



- INDICATES INDIVIDUAL LOCATIONS
- ACTIVITY CENTER

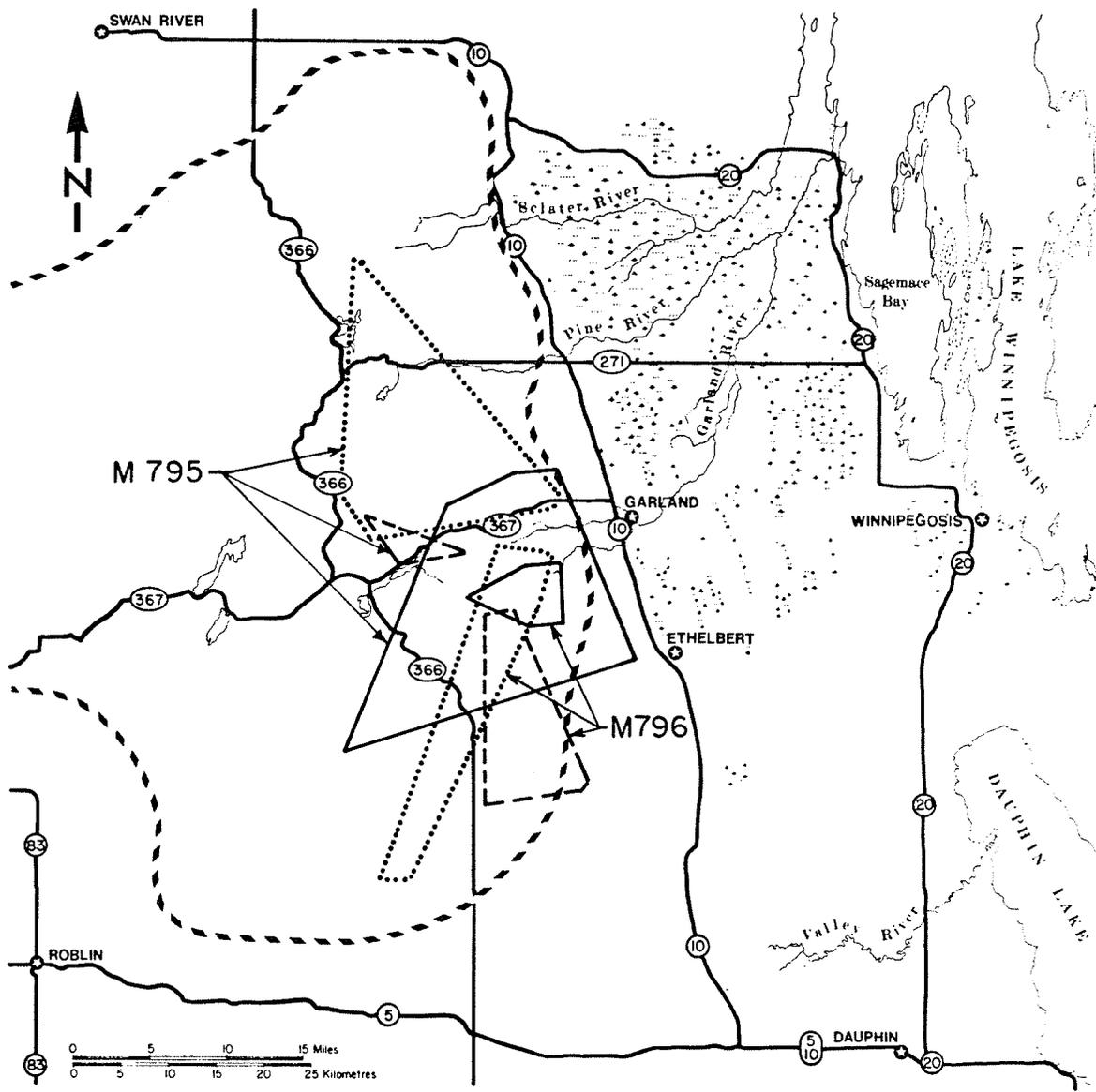
Home range stability and overlap.

Seasonal range shifts (changes in the activity center) were considered significant if the shift was greater than the radius of the summer home range minor axis. The relationship between seasonal ranges of several representative males and females is illustrated in Figures 14 and 15 respectively. Two subadult females and two subadult males showed significant shifts from spring to summer (Table 8). Two females (F798, F801) and one male (M793) made significant changes from spring to fall. One female and three subadult males demonstrated range shifts from summer to fall.

A comparison of seasonal range shifts indicates no difference in distance moved between adult and subadult females. Females showed similar shifts from spring to summer, spring to fall, and summer to fall ($P > 0.5$ in all cases). Subadult males showed a greater change from summer to fall (17.25 km) than spring to summer (9.50 km) or spring to fall (8.02 km) but the difference was not significant. The small spring to summer shift may be the result of infrequent monitoring during early spring, thereby biasing the spring activity center estimate. Since all subadult males spent late spring (20 May to 15 June) near their summer range, the activity center shift from spring to summer may be underestimated.

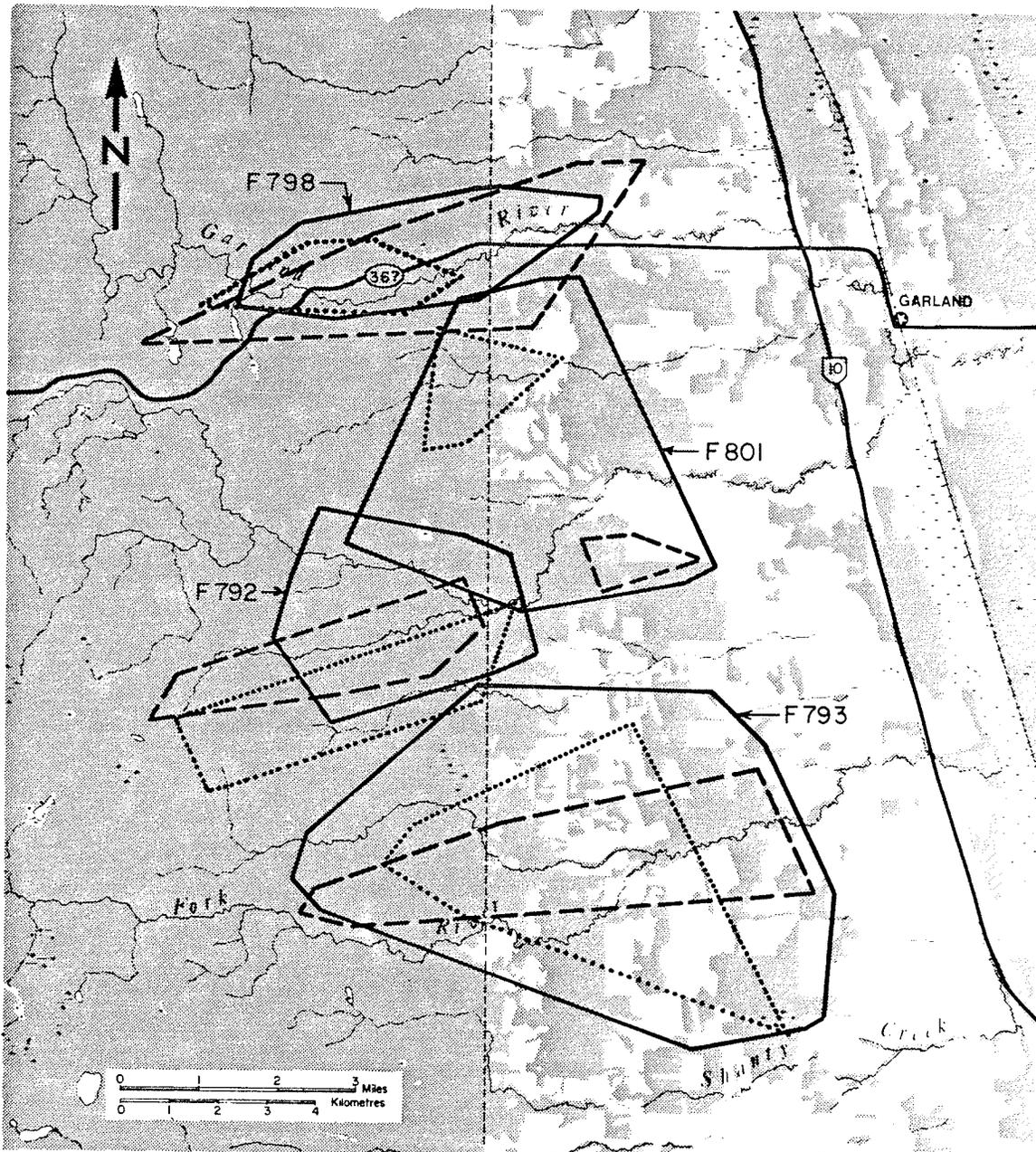
During the spring to summer period subadult males demonstrated a greater shift in their range (9.50 km) than either subadult (1.55 km) or adult (1.56 km) females ($t = 5.75$, $P = .002$; $t = 5.13$, $P = .030$ respectively). Similarly, females were more stable and showed less change than subadult males from spring to fall ($t = 3.66$, $P = .008$).

Figure 14: The relationship between male black bear seasonal home ranges as recorded in western Manitoba during 1980



- INDICATES SPRING HOMERANGE
- INDICATES SUMMER HOMERANGE
- - - - - INDICATES FALL HOMERANGE

Figure 15: The relationship between female black bear seasonal home ranges as recorded in western Manitoba during 1980



- INDICATES SPRING HOMERANGE
- INDICATES SUMMER HOMERANGE
- INDICATES FALL HOMERANGE

Table 8. Distance (km) between black bear seasonal home range activity centers. Shifts are considered significant if the change is greater than the radius of the minor summer home range axis.

Animal #	SEASON		
	Spring to Summer	Spring to Fall	Summer to Fall
+F792	*2.54	0.60	2.26
F793	2.16	0.43	1.75
F796	*1.67		
F798	0.89	*3.21	*2.39
F801	2.09	*4.80	2.86
F802	0.59	0.27	0.61
F807	0.92	0.25	0.72
F809			0.82
F8010			1.11
F8011			1.06
F8012			1.93
M793	*7.42	*8.40	1.09
M795	12.44	11.31	*19.84
M796	*8.65	4.36	*10.26
M804			*24.16
M807			*37.97

+ 'F' indicates female, 'M' denotes male.

* Indicates a significant shift.

Subadult males also showed a greater shift between the summer and fall range than females ($t = 3.36$, $P = .006$ with equal variance, $t = 1.99$, $P = .140$ with unequal variance).

From 1979 to 1980, all cohorts had stable annual ranges (Table 9). Observed shifts were insignificant in relation to the annual home range radius.

In 1980, overlap between subadult male and female home ranges was extensive. Since an unknown number of unmarked animals was present in the study area, overlap was evaluated qualitatively and based on static overlap of the annual minimum polygon home range. Data from 1979 were not evaluated for overlap because of insufficient observations and the possible influence of a concurrent trapping/baiting program. The extensive home range of male M795 completely overlapped all females being monitored in the study area. Another subadult male (M793) with a smaller home range than M795 overlapped the ranges of three adult and three subadult females. Avoidance by males of areas intensively used by females was not observed.

Overlap between adult and subadult female ranges was also widespread. An example of the extensive overlap between females is outlined in Figure 16. Several animals have not been included in this figure to promote clarity. Overlap between subadult females ranged from almost total (F802:F809, 85%) to marginal overlap of peripheral areas (F792:F793, 5%). Overlap between adult females was equally variable, ranging from 15% (F795:F796) to 75% (F8012:F8010). Similarly, adult-subadult female overlap was often extensive. F802 shared 80% of her range with adult female F801 and 85% with another adult female (F8012).

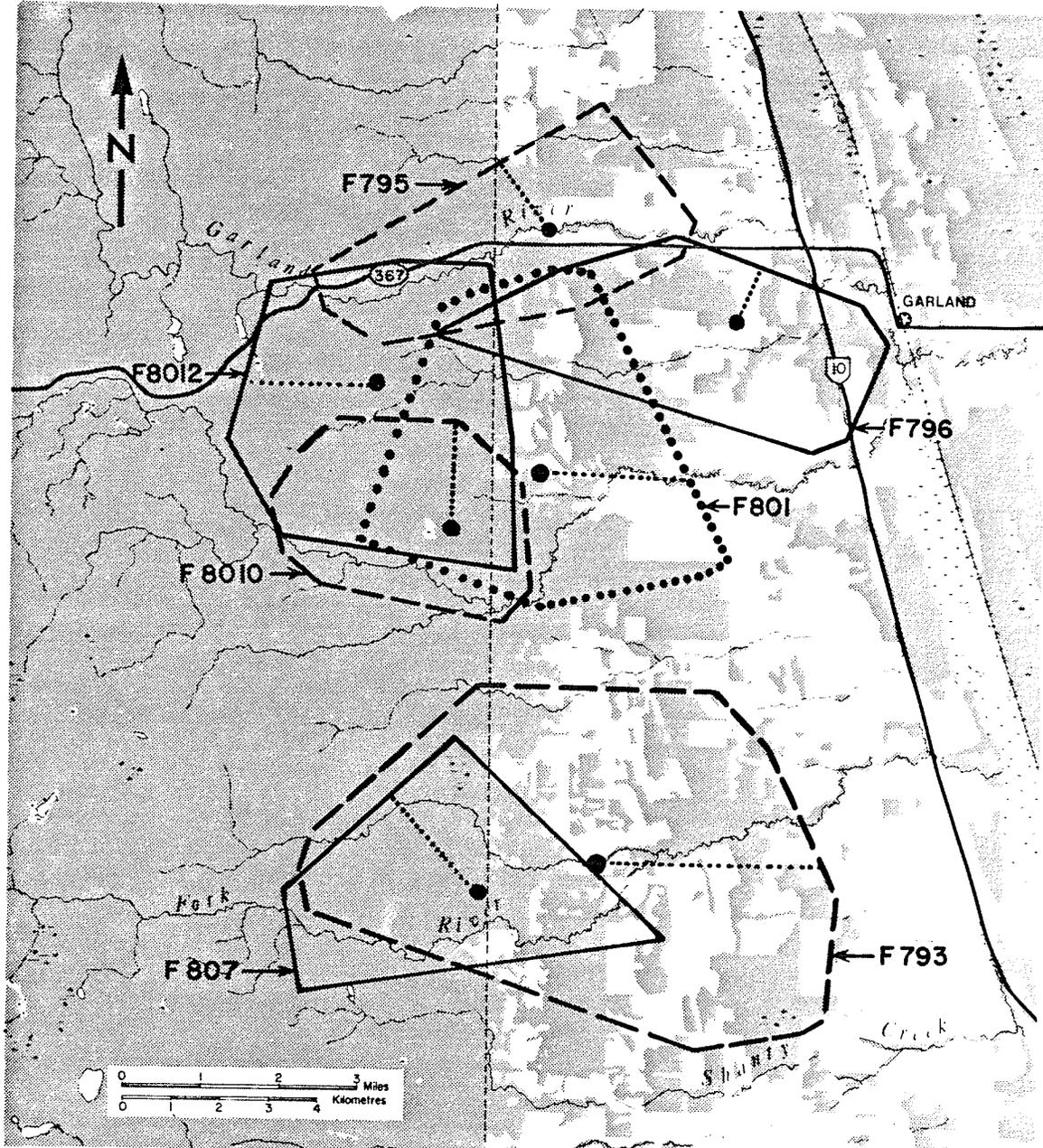
Table 9. Distance between the 1979 and 1980 *annual activity centers for black bears surviving from June 1979 to August 1980.

Animal #	Distance, 1979 to 1980 Annual Activity Center (km)
+F792	0.20
F793	0.58
F796	0.22
F798	0.74
M793	0.08
M795	2.23
M796	3.64

+ 'F' indicates female, 'M' denotes male.

* Annual activity center based on all locations with outermost 10% deleted.

Figure 16: Overlap of female black bear home ranges in the study area during 1980. Annual home ranges with peripheral locations joined are illustrated



- ACTIVITY CENTER
- INDICATES RELATION OF ACTIVITY CENTER TO SPECIFIC HOME RANGE

Multiple overlap was common with three to five adult and subadult females all showing greater than 25% overlap in a certain area.

A subjective evaluation of overlap during the annual cycle indicated overlap was not constant but appeared to peak in mid-July. During a three week period, up to eight animals were located each day in a small two sq. km area. When examined, the area proved to have an extreme abundance of saskatoons.

Movement Patterns

Distance travelled per day.

Movement data from four subadult males, six subadult females and six adult females were analyzed. The single adult male (M804) was not included since cohort movement patterns cannot be inferred from a single animal.

Mean distance moved per day for each cohort on a biweekly basis is illustrated in Figure 17A. Descriptive statistics for each category are listed in Appendix 8. With seasons combined, subadult males moved significantly farther per day (2.85 km) than subadult or adult females (1.85, 1.75 km).

Subadult females showed no difference between spring, summer, or fall movements while adult females travelled significantly farther in summer (2.31 km) than fall (1.75 km). When evaluated as distance travelled per day, subadult males exhibit no significant seasonal differences.

In summer, subadult males travelled farther per day (3.14 km) than adult females without cubs (2.31 km) which also moved more than subadult

Figure 17: Movement patterns of black bears in the study area during 1980. Distances are represented as (A) km moved per day and (B) distance in km between successive locations

females (1.86 km) or females with cubs (1.32 km). In fall, subadult males travelled farther (2.58 km) than subadult females (1.84 km) or adult females without cubs (1.75 km). Information from spring was not analyzed due to insufficient data. Further analyses based on 12 biweekly periods did not yield additional information.

Distance between successive locations.

Figure 17B illustrates the mean biweekly distance between successive locations for each age class. Descriptive statistics for each cohort and period are outlined in Appendix 9. Seasonally, subadult males travel farther in spring (6.67 km) than summer (3.44 km) or fall (2.92 km). Similarly, adult females move farther between successive locations in summer (2.21 km) than fall (1.45 km) with spring comparisons omitted due to insufficient data. Subadult females showed greater movements in spring (2.77 km) than summer (1.78 km) or fall (1.70 km).

Biweekly analyses indicate the period 1 May to 15 May has significantly greater movements than other periods. This corresponds to the interval during which all three subadult males being monitored returned to their late spring/early summer range from a remote den site. These results indicate a trend towards decreasing movement as the season progresses. Spring subadult male movements may be exaggerated by the return from a remote den site. In fall, decreased overall movements may be confounded by one or two long range movements to a remote den site.

In spring, subadult males travelled significantly farther between locations (6.47 km) than subadult (2.77 km) or adult females with (1.49 km) or without cubs (1.70 km). Similarly, subadult males moved greater distances in summer (3.44 km) and fall (2.92 km) than other cohorts. In

summer, adult females without cubs moved farther than adult females with cubs (2.21 vs 1.35 km). Subadult females did not differ from adult females during any season. Overall, subadult males exhibit greater and more variable movement than other cohorts.

In addition to the above systematic observations on movement patterns, incidental observations were recorded whenever possible. During two years of observation, only one female undertook a sally away from her home range. Subadult female F796 left the summer home range on 8 September 1979 and travelled a minimum of seven km westward into the DMPF. After several days, she returned to the summer range where a den was constructed in October.

During both years, subadult males exhibited irregular and wide ranging movements. In 1979, travel to peripheral regions often went undetected since the animals could not be monitored by ground vehicle. In light of 1980 information, the periodic absence of subadult males during 1979 was interpreted as evidence for movements similar to those recorded in 1980. Two subadult males (M791, M798) which were not monitored regularly in 1979 provided some information on male dispersal. After being captured as a 2.5 year old in June 1979, M791 remained close to the capture site until mid-July after which he could no longer be located. In early September, he was shot in a farmyard approximately 30 km to the northwest. Subadult male M798 was captured in early October 1979 and monitored for only a week. He was sighted in a farmer's yard (identified by collar) in May 1980 approximately 30 km to the southwest and was killed by a trapper in mid-October 1981 several km to the west of where he was sighted last.

During a long range movement, the total distance travelled (including meanderings) and rate of travel remain unknown. The return of M793 to his 1980 summer range from the 1979 den site (40+ km) illustrates the potential distance travelled per day. On 2 May M793 was still near his den site while on 4 May he was located five km west of his 1980 summer range. When calculated as direct linear distance between the two locations, M793 travelled approximately 18 km each day. The return movement was through a densely forested area with numerous lakes which would make direct travel unfeasible. The actual distance covered was probably much greater. Similar movements by M796 (return to summer range from a remote den site) and M795 during frequent mid-summer wanderings substantiate these findings.

Den Characteristics

Through 1979 and 1980, 28 dens were located with on-site descriptions recorded for 26 (Appendix 10). Dens were found in all major habitat types including black spruce bogs, coniferous-deciduous uplands, riparian associations, early seral stages (both deciduous and coniferous), and open fields. Subjectively, selection or avoidance of a particular cover type was not observed. Habitat selection-availability analysis was not employed due to insufficient information on availability and small sample size.

Onset of denning and emergence.

In 1979, subadult females entered dens prior to yearling females ($t = 4.47$, $P = .021$). Subadult females denned earlier than subadult males (19 Oct. vs 28 Oct.) but the difference was not significant. Denning

chronology during 1979 and 1980 is summarized in Table 10. Insufficient sample size precludes comparisons involving adult males and females. Emergence in the spring of 1980 ranged from 5 April to 20 April. One adult female with cubs emerged earlier (5 April) than other animals, however, this difference was probably the result of milder temperatures and less snow in the agricultural lands where this den was located. There was no difference between the mean emergence dates of subadult males and females. The synchronous emergence in spring 1980 may have been a function of the past mild winter and an unusually warm spring.

In autumn 1980, adult females entered dens earlier than subadult males ($t = 2.45$, $P = .05$). There was no significant difference between subadult females and adult females or subadult males. Subadult females which gave birth to cubs in 1981 on the average denned earlier than animals of the same cohort which did not have a litter in 1981 (29 Sept. vs 23 Oct.). Subadult and adult females denned earlier in 1980 compared to 1979 (10 Oct. vs 19 Oct, 4 Oct. vs 20 Oct. respectively) but the difference was not significant.

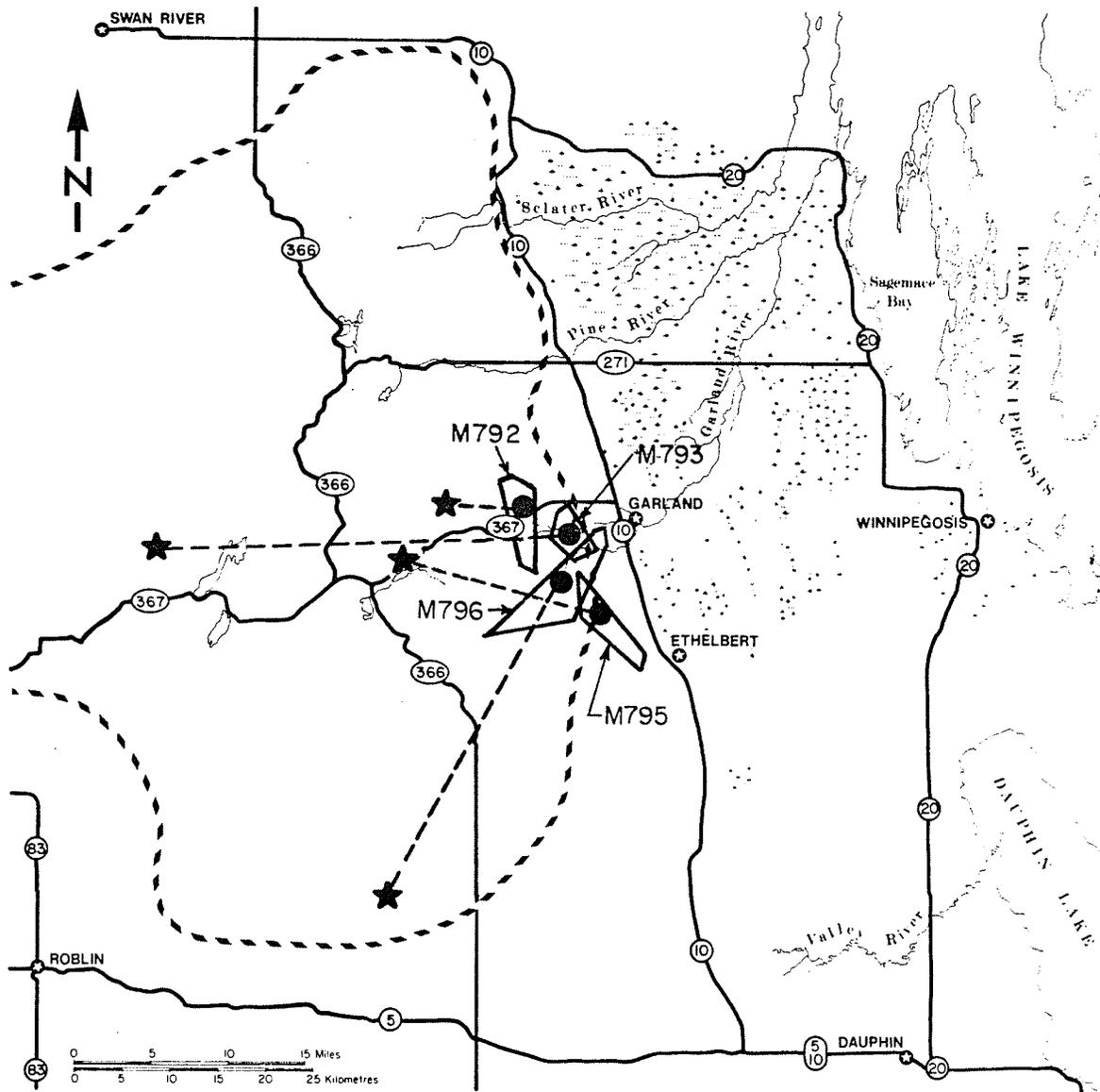
Relation between den site and home range.

In 1979, movement to den sites by subadult males was characterised by an abrupt movement (range 19.80-42.23 km) away from the summer activity center (Figure 18). A single adult male and a yearling male constructed dens 7.26 and 0.75 km respectively from their summer activity centers. In 1980, one subadult male which moved to a remote den location in 1979 followed a similar pattern while two denned close to their 1980 summer activity center. A subadult male (M807) monitored since June 1980 denned 38.5 km from the summer activity center.

Table 10. Denning and emergence chronology of black bears monitored by radio-telemetry during 1979 and 1980.

1979 Denning				
	Sample Size	Mean Date	Std. Dev.	Range
Females				
All ages	6	Oct. 28	14.50	Oct. 10 - Nov. 15
Subadults	5	Oct. 30	15.60	Oct. 10 - Nov. 15
Adults	1	Oct. 20		
Males				
All ages	3	Oct. 31	4.36	Oct. 28 - Nov. 5
Subadults	2	Oct. 28	0.70	Oct. 28 - Oct. 29
Adults	1	Nov. 5		
1980 Emergence				
Females				
All ages	4	April 11	4.90	April 5 - April 15
Subadults	3	April 13	3.46	April 9 - April 15
Adults	1	April 5		
Males				
Subadults	4	April 14	5.38	April 7 - April 20
1980 Denning				
Females				
All ages	10	Oct. 5	16.59	Sept. 23 - Nov. 12
Subadults	6	Oct. 11	18.78	Sept. 26 - Nov. 12
Adults	4	Oct. 4	7.81	Sept. 23 - Oct. 7
With cubs in 1981	7	Sept. 27	7.39	Sept. 16 - Oct. 27
Barren in 1981	3	Oct. 23	20.70	Oct. 1 - Nov. 12
Males				
All ages	5	Oct. 12	9.18	Oct. 7 - Oct. 28
Subadults	4	Oct. 13	10.18	Oct. 7 - Oct. 28
Adults	1	Oct. 7		

Figure 18: Relationship of den sites used by subadult male black bears in 1979-1980 to the 1979 summer home range



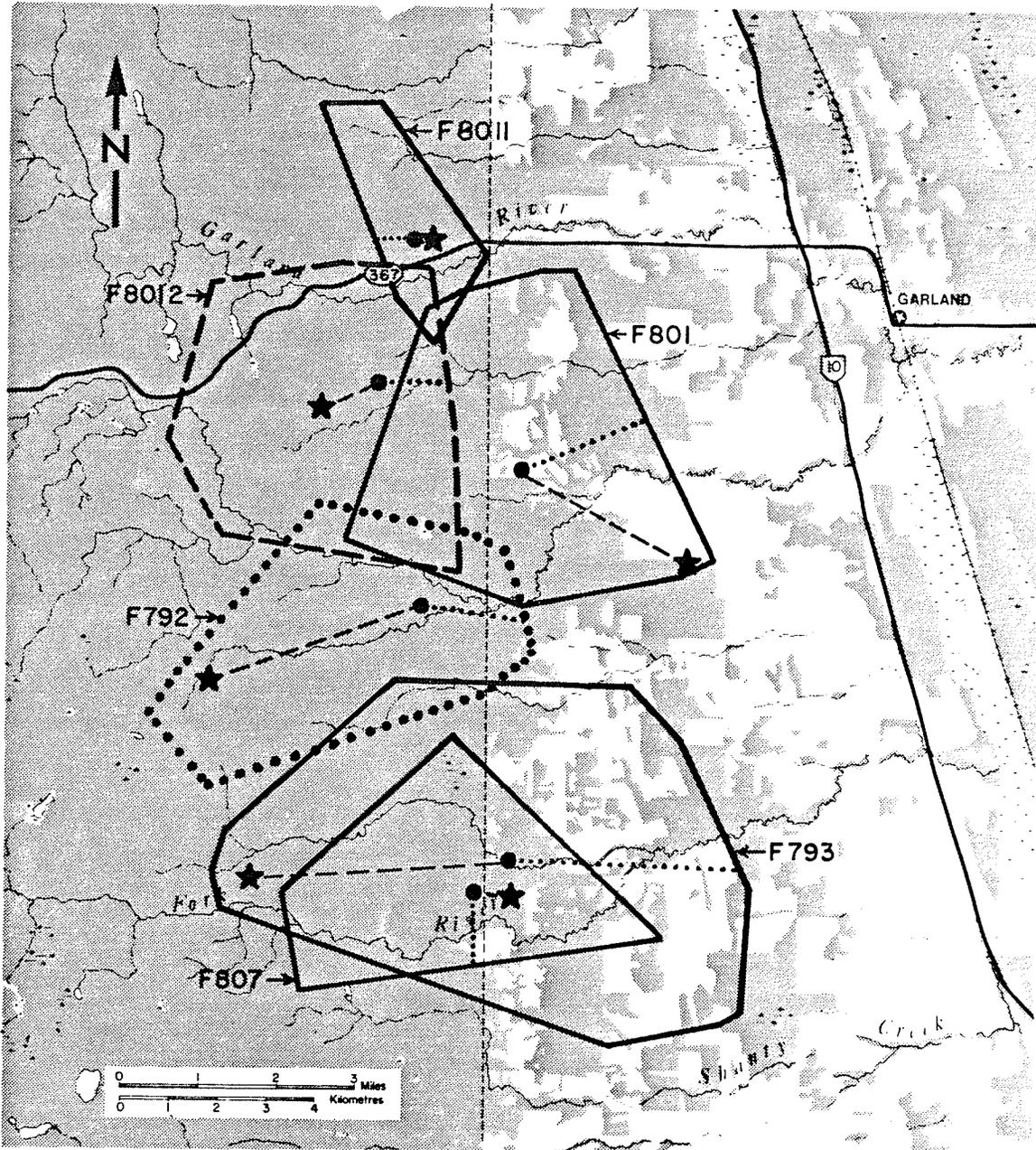
- HOME RANGE BOUNDARY
- - - - DEN SITE ASSOCIATED WITH ACTIVITY CENTER
- ACTIVITY CENTER
- ★ DEN SITE

In most cases, females did not exhibit an abrupt movement away from the summer activity center prior to denning. In 1979 and 1980, F792 and F793 moved to the western extreme of their summer range before denning (Figure 19). No females constructed dens beyond the periphery of their spring and summer home range.

In 1980, subadult and adult female dens were approximately equidistant (2.75 vs 2.13 km) from the activity center (Table 11). Individual distances from the activity center are listed in Appendix 11. Subadult males denned farther from the activity center than subadult females (16.36 vs 2.75 km) but the difference was not significant. When used to test if den sites were located far beyond the summer home range periphery, the ratio: [distance from summer activity center to den site : average radius of the summer home range] indicates adult females, subadult females, and adult males on the average do not den far beyond the summer home range boundary (Table 11). On the contrary, average subadult male dens are 2.44 summer home range radii from the activity center. This trend indicates subadult males utilize den sites isolated from the area occupied in summer.

Males selected den sites to the west of summer activity centers ($\chi^2 = 3.84$, $P < .05$) whereas females showed no directional preference. By moving westward to a den site, subadult males denned within the DMPF on all occasions. One adult male (M804) monitored in 1980 moved eastward, denning in a remote forested area on a peninsula in Lake Winnipegosis. One yearling male (M794) monitored in 1979 denned near the summer activity center in agricultural lands.

Figure 19: Relationship of den sites used by adult and subadult female black bears to their respective annual range. Annual ranges with the outermost locations joined are illustrated



- INDICATES RELATION OF ACTIVITY CENTER TO SPECIFIC HOME RANGE
- - - - - DEN SITE ASSOCIATED WITH ACTIVITY CENTER
- ACTIVITY CENTER
- ★ DEN SITE

Table 11. Average summer home range radii (based on minimum polygon) of black bear ranges recorded during 1980 and mean distance from the summer activity center to the den site.

Cohort	Sample Size	Mean Major Axis (km)	Mean Minor Axis (km)	* A Average Summer Home Range Radius	B Distance from Activity Centre to Den (km)	Ratio B:A
Adult female	5	6.88	5.11	2.99	2.13	0.71
Subadult female	6	7.55	3.57	2.78	2.75	0.99
Adult Male	1	72.75	32.25	26.25	26.54	1.01
Subadult Male	4	16.69	10.09	6.70	16.36	2.44

* Calculated as the radius of $(\frac{\text{major axis} + \text{minor axis}}{2})$.

Entrance Aspect.

Two dens faced north, four east, three southeast, three south, four southwest, three west, and two northwest. Chi-square tests for preferred direction indicate there was no selection ($P > 0.1$ in all tests).

Den reuse.

No instances of den reuse were recorded. Of the six animals monitored in 1979 which survived to the winter of 1980, only one subadult female (M793) denned within 0.5 km of the 1979 den. During field observations, numerous dens dating back several years were located, many of which appeared servicable. Reports by local residents indicate den reuse does occur but no specific information was available regarding frequency of reutilization or cohort involved.

Structural characteristics.

Only 2 of 26 dens were constructed without excavation. Forty-two percent were dug under the roots of standing or partially blown down trees, 23 percent were excavated into hillsides and 23 percent were dug in areas with no relief. Eight percent were located in bulldozed brush-piles. Of the two dens not excavated, one was located under some logs in a bulldozed brush-pile while the other (F807, 1980: adult female, cubs born in February 1981) consisted of a shallow grass lined depression under some overhanging shrubs. Individual den descriptions are listed in Appendix 10.

Internal dimensions were quantified for only a few dens and the remainder were subjectively evaluated. Den chambers were approximately

1.0 m in diameter and 0.6 m high. Entrance tunnels were characteristically 1.0 to 1.5 m long and 0.5 to 0.7 in diameter. F801 (1980) had an unusually long entrance tunnel (2.5 m) which sloped downward into a typical nest chamber. Dimensions of the nest chamber and the entrance tunnel appeared to be correlated with animal weight. Yearling females (F799, F798; 1979) had especially small entrances. All except one nest chamber was lined with grass, moss, leaf litter, or twigs. Lining material appeared representative of items available in the immediate vicinity. One subadult female which made an abrupt move to the den site shortly before permanent snowfall did not have lining material in the den.

DISCUSSION

Capture

The Aldrich leg snare was used throughout the capture program to minimize bias relating to trap avoidance by certain segments of the population. In addition to being expensive and cumbersome, culvert traps may be avoided by some bears (Erickson 1957, Stickley 1961). Unlike steel leg hold traps, the leg snare causes fewer injuries when monitored frequently and is effective in capturing all age classes (Jonkel and Cowan 1971, Johnson and Pelton 1980a).

Bears captured throughout the study appeared representative of each cohort and were in good physical condition. The behavioral variability recorded throughout the monitoring period (behavior at capture, movement patterns, home range area, den characteristics) suggests the animals were a random sample from the population.

Overt behavioral changes resulting from the capture and handling operation were not observed. The traumatic effects of capture and handling on an ungulate have been documented by MacArthur et al. (1979) and illustrate long term physiologic effects which may influence behavior for several days. After being released, bears often showed signs of reduced activity, a situation which may relate to the cumulative effects of handling and the anesthetic used. Animals frequently moved a short distance (0.5-1.0 km) away from the capture site and then remained stationary and inactive for one to three days. Subsequently,

bears resumed movement patterns comparable to those recorded several weeks later. Profound long term effects were not observed but are hard to evaluate since previous life histories remain unknown.

To minimize the effect of transmitter units on behavior, collars were kept loose to allow for future growth and fat deposition. Rogers (1977) reported bears showed initial irritation and attempted to remove the collar. However, after several weeks, behavior returned to normal and no ill effects were recorded. Similar observations during the present study concur with these results. Hamley and Falls (1975) and Webster and Brooks (1980) observed initial depressed activity patterns in voles fitted with radio transmitters. After several days, activity and movements returned to normal except for a somewhat higher predation rate on instrumented animals. Erlinge (1977a) reported no obvious behavioral changes after attaching telemetry units to a small carnivore which actively pursues prey. Bears being monitored in the study area gained weight, produced litters and showed no aversion to the trap site: indicating no detrimental long term effects resulted from the capture or instrumentation procedure.

Simulations

In a report describing the influence of sample size (number of captures) on home range area, Mares et al. (1980) observed an asymptotic relationship between sample size and home range. Using data on the eastern chipmunk (Tamias striatus) and the minimum area estimate (Stickel 1954), a minimum of twenty locations were required to represent the home range accurately. The relationship between sample size and

area is not a recent concept and dates back to previous studies by Blair (1942) and Heezen and Tester (1967). More recently, Voigt and Tinline (1980) presented an extensive evaluation concerning the effects of sample size on several area estimators. Jennrich and Turner (1969) reported similar findings and introduced a new home range estimate based on the variance of locations about the activity center (Hayne 1949). Unlike other home range estimates including capture radii (Hayne 1949, Calhoun and Casby 1958), minimum area, and the convex polygon, the Jennrich and Turner index is unbiased at all sample sizes provided the assumption of bivariate normality is satisfied. Van Winkle (1975) compared several probabilistic home range models and concluded the estimators proposed by Jennrich and Turner (1969), Mazurkiewicz (1971), and Van Winkle et al. (1973) are unbiased with respect to both sample size and home range shape. Koepl et al. (1975) reported a modified version of the JT index which also provides a confidence region about the area estimate.

Simulations based on either actual data or randomly generated coordinates were carried out and illustrate the above trend, indicating the convex polygon estimate is not asymptotically unbiased within the sample size range tested. The minimum polygon estimate showed significant bias at all sample sizes with a trend toward decreasing bias at higher sample size. Since numerous seasonal and annual comparisons involved data sets with few locations or unequal sample sizes, the JT index based on a minimum of 15 data points was chosen as an unbiased and reasonably precise estimate of home range area. If all animals were represented by numerous locations (ie. in excess of several hundred or

a thousand), the minimum polygon would be equally appropriate. In cases where the data base is sufficient, a subjective evaluation of area (Rogers 1977) may be preferable since mathematical models are often based on a theoretical distribution and can not properly evaluate behavioral influences (MacDonald et al. 1980).

The activity centre (mean x, mean y coordinate) estimate is also influenced by sample size (Mazurkiewicz 1971). Since the activity center is used to describe various spatial utilization and movement patterns, an accurate estimate of the true center is essential. The observed high standard error of the mean distance between activity centers at small sample size indicates an imprecise estimate. Metzgar (1972), Koepl et al. (1975), and Mares et al. (1980) have also described analyses of known circular home ranges which yield spuriously noncircular dimensions when fewer than 20 locations are used in the evaluation. Based on these results, home range dimensions and in most cases activity centers were calculated only for animals with greater than 20 locations (several spring activity centers estimated using 12-15 locations).

One shortcoming of most statistical home range models involves the assumption that locations are independent and random samples from a multivariate normal distribution (Jennrich and Turner 1969, Mazurkiewicz 1971, Koepl et al. 1975). Independence and randomness can be achieved by allowing sufficient time between locations which are taken periodically throughout the sampling period. Normality is often assumed (Alt et al. 1980, Garshelis and Pelton 1981) or moderate deviations from normality are considered insignificant (Maza et al. 1973). Since

analysis of the present data indicated a significant deviation from normality in the majority of animals tested, simulations were carried out to determine how non-normality affected the JT estimate. The resulting over-estimates for random and aggregated distributions were not considered large enough to warrant selecting another method.

Since most animals showed only marginal deviations from normality, the overestimate was probably less than for the random or aggregated distributions tested (ie. less than 30 percent). In a situation where the utilization distribution approached a "peripheral ring" (ie. a defended territory) with few internal locations, the JT index would not be appropriate.

Home Range Utilization

The concept of home range in mammals has long been accepted and stems from evidence that terrestrial vertebrates do not wander aimlessly but restrict their activities to a particular area (Seton 1909). Burt (1943) defined home range as the area "traversed by the individual in its normal activities of food gathering, mating, and caring for young". Occasional sallies outside the area should not be considered part of the home range. Although somewhat subjective with respect to what constitutes a "normal" activity or where regular movements become sallies, this definition outlines one basic form of land tenure which mammals use to ensure access to adequate resources. In contrast to the home range, territories involve a certain degree of exclusive use, enforced by aggression or some other form of defense (Noble 1939, Brown and Orians 1970).

Although not included as part of the home range, excursions and dispersal movements are often mechanisms by which an animal extends, maintains, or initially acquires a home range (Jewell 1966). The often extensive region over which an animal ranges in its lifetime, including all movements, has been termed the "total range" (Goin and Goin 1962, in Wilson 1975). In many cases, the home range is not used uniformly and consists of a single or numerous intensively utilized areas, reflecting a heterogeneous environment. Where much of an individual's activities are concentrated in a restricted area within the home range, the term "core area" (Kaufman 1962) is often used to describe this region.

Since the nutritional requirements of an organism are largely fulfilled within the home range, productivity of the environment is a crucial determinant of the area utilized (Jewell 1966). Studies by Simon (1975) and Mares et al. (1976) using artificial food sources support this contention and demonstrate an inverse relationship between the area utilized and food availability. Erlinge (1977a) noted wide variations in the area used by individual stoats from year to year and concluded a similar inverse correlation between home range size and prey availability exists.

McNab (1963) indicated that although large mammals are highly mobile and able to exploit larger areas, they also have greater energy requirements. In addition to being a function of body size, the required home range area of "hunters" is approximately four times the area of "cropping" species of equal weight. Sanderson (1966) and Maza et al. (1973) emphasized the dynamic nature of home ranges which were shown to vary with population density and behavioral changes such as

occur during the breeding season. Since the data from the present study are restricted primarily to one annual cycle, information on individual variability between years is lacking. Under modified conditions of food availability and population density, different home ranges would be expected.

Annual home ranges recorded for all females in both 1979 and 1980 are within the range of values reported from other studies. Some care must be taken when comparing results since different methods of data collection (capture locations vs. telemetry) or area calculation (minimum area, convex polygon, capture radii) are not always directly comparable. In Washington, Poelker and Hartwell (1973) reported females utilize approximately 5.2 sq. km ranges while on a small coastal island home ranges averaged 2.35 sq. km (Lindzey and Meslow 1977). Rogers (1977) noted female territories averaged 9.6 sq. km in northeastern Minnesota while in Idaho, Amstrup and Beecham (1976) reported 48.9 sq. km home ranges. In northern Alberta, Fuller and Keith (1980) reported ranges of 7.5 sq. km with somewhat larger home ranges (20.5 sq. km) noted in the Cold Lake area by Young (1976, in Fuller and Keith 1980). Using capture locations, Jonkel and Cowan (1971) reported an estimate of 5.2 sq. km for female black bears in Montana. The average 1980 female home range in western Manitoba (32.2 sq. km) falls within the range reported for other areas, indicating the results are representative of the cohort.

In addition to occupying much larger home ranges on an annual basis, subadult males also showed greater variability. The wide ranging movements recorded for several males did not conform to the standard definition of home range, but at the same time, were too frequent to

delete. Although the number of peripheral locations would in some cases justify deletion, infrequent monitoring of animals in isolated areas resulted in fewer locations. Therefore, the time spent in remote area is often underrepresented if only the number of locations is referenced.

In Idaho, Reynolds and Beecham (1980) observed average adult and subadult male home ranges of 60 and 46 sq. km respectively. Alt et al. (1980) reported an average male home range of 173 sq. km with high variability between animals, while on Long Island, Lindzey and Meslow (1977) noted restricted ranges of approximately five sq. km. The differences in reported male home ranges and those observed in western Manitoba (506 sq. km) are substantial and probably reflect both habitat and social status differences (Lindzey and Meslow 1977, Reynolds and Beecham 1980).

Numerous factors including habitat, social status, and population density can interact to influence home range size. Rogers (1976) indicated differences in food availability and productivity affected home range size in Minnesota while Jonkel and Cowan (1971) and Lindzey and Meslow (1977) felt diverse habitats within their study area contributed to the small home ranges. Reynolds and Beecham (1980) cited differences in social status which probably accounted for the large variation in subadult male ranges between two comparable areas. Dispersing subadults without a stable home range would be expected to wander over larger areas than residents.

Despite the variation in home range area reported from different regions, a general trend is evident. In all cases, female black bears utilize smaller home ranges than males. Craighead (1976), Berns et al.

(1980), and Glenn and Miller (1980) reported a similar pattern for grizzly bears in Yellowstone National Park and Alaska.

In the present study, adult females with cubs did not use significantly larger areas than females without cubs as has been reported by Alt et al. (1977). Although females with offspring need larger foraging areas (since they require nutrients for themselves and their offspring), the limited mobility of young cubs may restrict foraging in spring when food is scarce (Alt et al. 1980). If the habitat is productive and sufficient food sources are available in mid-summer (as was noted in 1980), larger home ranges would not be required. Alt et al. (1980) noted a gradual increase and late autumn peak in the area utilized by females with offspring. During this period, home ranges were largest and may reflect a combination of increased mobility and decreasing or scattered food sources. No comparable data are available from western Manitoba since both females with cubs were not monitored after 1 September.

Rogers (1977) indicated the large size of male home ranges are the result of social pressures and do not accurately reflect the area required to fulfill nutritional requirements. Males increase their inclusive fitness by patrolling larger areas during the breeding season and mating with a larger number of females than would be possible on a restricted home range. In addition, competition for food resources between father and offspring is reduced by foraging over a larger area. During the non-breeding season, Rogers observed males utilizing habitat between female territories, thereby further reducing competition for food resources. With mobility restricted by their offspring, females have evolved an alternate strategy. By ranging over a small area which

they are able to explore intensively and with which they become familiar, search time, movement, and energy expenditure during foraging are reduced.

Over the annual cycle, females showed a general trend towards decreasing home range size from spring to fall. Although not significant, this trend may reflect changes in food availability or social status. Rogers (1977) indicated the early spring period involved active territorial defense by females, contributing to wide ranging movements and exploratory behavior over the entire range. The absence of concentrated food sources (ie. mast crops) would also lead to wide ranging movements. In summer, concentrated food sources may contribute to decreased movements and restricted home ranges (Beeman 1975, in Beeman and Pelton 1980). Limited food sources in fall result in decreased movements and smaller home ranges if adequate fat reserves have been accumulated. During years of food scarcity, the fall range would probably expand as animals forage widely to increase adipose reserves.

Subadult males show a similar trend with very large spring ranges and smaller ranges in summer and autumn. These trends reflect the influence of utilizing a remote den site in 1979 and circuitous wanderings while returning to the summer range in late spring. During summer, the generally smaller ranges and wide variation in movements is characteristic of animals with an insecure home range (Rogers 1977, Reynolds and Beecham 1980). The slight increase in fall home range reflects a tendency towards greater movements by some animals and travel to a remote den site in others. Whether social pressure or an innate

dispersal tendency (Rogers 1977) initiated the observed wanderings remains unknown. Only a sample of animals from the study area were monitored and unmarked individuals were observed on occasion. The influence of resident adult males (Kemp 1976) on subadults may have triggered the frequent wanderings, or as Rogers (1977) suggested, the tendency to search for unoccupied areas may be innate and not always the result of aggression.

The inclination towards greater east-west home range dimensions, especially in the subadult female cohort, correlates with topography in the region. Numerous rivers flow out of the Duck Mountain towards the surrounding farmland in the east. In most cases a wide belt of natural vegetation persists along ravines, resulting in a natural travel corridor (Wegner and Merriam 1979). Subadult females in the process of obtaining or expanding a home range would probably use protected travel corridors instead of moving across open fields. In addition, these sheltered ravines are used as foraging areas because of numerous mast producing shrubs and sedge meadows. After becoming familiar with their range, adult females may rely on alternate travel corridors and utilize other habitats to feed in, resulting in a more circular home range. Garshelis and Pelton (1981) noted a similar trend in the Great Smoky Mountains National Park where black bear home ranges often conform to the shape of watersheds and are usually elongate. The extreme wanderings of subadult males often occurred within the Duck Mountain Provincial Forest where protective cover was total and movements exceeded the length of drainage systems. These factors may have contributed to the circularity of observed ranges.

Spatial use of the home range, measured as distance from the activity center, reflects the sedentary nature of females and wide ranging male utilization pattern. The tendency amongst subadult males to use peripheral areas more frequently in spring and early summer may relate to foraging, social interactions, or exploratory activities. Kelleyhouse (1980) observed subadult males were at times excluded from prime foraging areas by intraspecific intolerance, especially during periods of limited food availability. Scarcity of food sources with high nutrient value in spring may lead to increased levels of aggression and displacement of subadults to peripheral areas. Exploratory movements in early summer would be advantageous in locating unoccupied ranges resulting from overwinter mortality or predation (Boyer 1949, Rogers 1977).

The difference in home range utilization patterns (distribution of locations) observed between females probably reflects differences in habitat and availability of food sources within individual ranges. Black bear activities are closely related to the phenologic condition of preferred food items (Stickley 1961, Jonkel and Cowan 1971, Kelleyhouse 1980), resulting in contagious utilization patterns in heterogeneous environments. Erlinge (1977a) noted a similar habitat utilization pattern in the stoat and concluded the observed pattern resulted from heterogeneous prey density. Habitat within the study area consisted of numerous plant associations which matured and became available as food sources at different times. Maximum foraging efficiency in this environment would involve wide ranging movements with subsequent area restricted searching once a suitable patch was located (Krebs 1978).

The observed stability in annual ranges between 1979 and 1980 for all cohorts supports similar findings by Jonkel and Cowan (1971), Amstrup and Beecham (1976), and Garshelis and Pelton (1981). Of the seven (4 female, 3 male) bears monitored during both years, none showed a substantial shift in their annual activity center. The observed stability in subadult male ranges is somewhat surprising since members of this cohort are often in a dispersal phase and would be expected to show changes in the area utilized (Rogers 1977). The removal of several large males from the study area by hunters in spring 1980 may have created unoccupied areas which subadult males returning from remote den sites could occupy (Kemp 1976). Fritzell (1978) indicated male raccoons respond quickly to the removal of other males by appropriating the available area or shifting their original range. In addition, all males which returned were in their fourth year, an age when most subadult males establish a home range (Rogers 1977). Reynolds and Beecham (1980) reported similar annual stability in females but noted an almost total change in ranges occupied by adult males between years. Rogers (1977) observed a comparable situation in Minnesota where adult females held exclusive territories from year to year with little change. As adults, males usually had stable annual ranges but did occasionally shift the area utilized. Reynolds and Beecham (1980) indicated food availability was not a factor influencing the home range shifts observed in their study. They concurred with Sauer et al. (1969) that one year may not be sufficient to delineate accurately the male home range. Rogers (1977) indicated the absence of estrous females in certain years may cause males to concentrate their activities elsewhere.

The low proportion of females which undertook a seasonal home range shift contrasts with the extensive seasonal changes reported by Garshelis and Pelton (1981) and indicates the habitat was heterogeneous enough to support seasonal foraging across the entire range. Seasonal changes would be expected where large areas of uniform habitat provide seasonally available food sources. Also, changes in behavior (ie. the breeding season) may lead to specialized habitat requirements which would initiate a shift. Reynolds and Beecham (1980) observed a correlation between seasonal or daily use of home ranges and food availability (phenologic development). Studies by Jonkel and Cowan (1971) and Amstrup and Beecham (1976) have shown similar utilization patterns with bears more likely to be observed in areas where mast or berry crops are available. Within the study area, information on specific habitat characteristics was not available, making it difficult to determine if the observed changes were in response to social pressure or changing food supplies.

Subadult male changes from spring to summer and summer to fall ranges were related to the use of den sites located in peripheral regions. The adult male monitored in 1980 undertook a particularly long movement in mid-July to an area which supports numerous oak trees (Quercus macrocarpa). Rogers (1977) and Pelton et al. (1980) reported similar movements and utilization patterns in areas where highly desired food sources become available outside the normally occupied range. Unlike their studies, the adult male did not return to his pre-July range and denned in the peripheral area which was considered his late summer-autumn home range.

The extensive overlap between male and female ranges supports similar findings by Jonkel and Cowan (1971), Lindzey and Meslow (1977), and Rogers (1977). Rogers observed that adult males often range over numerous (7 to 15) adult female territories, presumably to gain access to as many females as possible during the mating season. By utilizing a larger area and preventing dispersing subadults from settling (Kemp 1976), males could also decrease competition for food resources between their offspring and other bears.

The large degree of overlap amongst adult males reported by Amstrup and Beecham (1976) and Garshelis and Pelton (1981) is comparable to the widespread overlap between males in the present study. Even though all males in the area were not being monitored, overlap was extensive in most cases. Since very large areas are involved (over 100 sq. km), males may not be able to defend their ranges against intruders (Rogers 1977). Erlinge (1977b) also commented on the high energetic cost of defending a large area exclusively, possibly leading to the breakdown of normal male territories during the breeding season.

Overlap between adult females was often extensive. Conversely, Jonkel and Cowan (1971) and Rogers (1977) observed very little overlap of female ranges due to aggressive defense of individual territories. To calculate overlap, Rogers used a subjective delineation of utilized habitat which did not include areas where there was no evidence of use. When applied to the present data, overlap between several adult females remained extensive, indicating the initial result was not merely an artifact of the methodology. Lindzey and Meslow (1977) observed comparable widespread overlap between all female cohorts on a small

offshore island. They concluded the entire population may have stemmed from one or two original colonizers and the resulting high degree of relatedness between all animals explained the observed tolerance. Although possibly of consequence in adult-subadult female overlap, close kinship would not be expected amongst most adult females in the study area because of contact and free interchange between neighboring areas. During studies on a solitary ungulate, Waser (1975) noted a comparable degree of overlap without apparent aggression between individuals.

The extensive overlap observed between adult and subadult females is advantageous since by tolerating female offspring and increasing their chances of survival by sharing part of their range, adult females can increase their inclusive fitness (Rogers 1977). Erlinge (1977b) reported a similar trend in the stoat where maturing female offspring usually established home ranges close to their natal range. Since mother-offspring relationships remain unknown, this hypothesis can not be refuted.

The increased overlap observed in mid-July is probably the result of abundant food sources. Amstrup and Beecham (1976) concluded the extensive overlap observed in Idaho resulted from the sporadic availability of patchy food resources. Although somewhat unpredictable in occurrence, food sources (ie. berry patches) were a temporary and superabundant source when available. A similar situation involving increased intraspecific tolerance occurs at artificial food sites such as garbage dumps (Rogers et al. 1976, Rogers 1977). In an environment where temporary, scattered, and somewhat unpredictable food sources predominate, tolerance and home range overlap would be expected (Brown

and Orians 1970). Observations on black bears in western Manitoba support this hypothesis.

Movement Patterns

Black bear movement patterns observed during this study reflect the high mobility of subadult and adult males and sedentary nature of all female cohorts. The linear distance travelled per day remains a conservative estimate since meanderings between the two locations are not included. With reference to daily foraging patterns in grizzly bears, Craighead (1976) summed up most activities as "considerable roaming without going very far". A more general estimate of movement used in this and other investigations involves an index based on the distance between successive locations.

Across North America, several authors have noted similar trends in black bear movement patterns. Rutherglen and Herbison (1977) and Zytaruk and Cartwright (1978) both reported more extensive movements by adult males than females in British Columbia and New Brunswick respectively. In Idaho, Amstrup and Beecham (1976) reported adult males on an annual basis travel 1.3 km per day while adult females average 0.9 km per day. Alt et al. (1977) noted a somewhat greater distance travelled per day with peak movements by adult males and females occurring during the July breeding season (7.05 and 3.29 km per day respectively). In western Manitoba, daily distances travelled by females were comparable, however, there was no definite mid-summer peak in movement by breeding females.

More extensive movement by subadult versus adult females in spring may result from a lower level of fat reserves (Jonkel and Cowan 1971, Hamilton and Marchinton 1980) and the need to forage over larger areas to find sufficient food. Also, it would be advantageous for subadult females to emerge earlier and explore the area for possible unoccupied ranges left vacant by bears dying during the winter (Rogers 1977). The observed similarity between adult and subadult females during summer possibly reflects abundant food resources which are available locally.

Alt et al. (1980) indicated adult females with cubs often show depressed movements in early summer but become the most active group by late fall. Although autumn data are unavailable, this trend is supported by summer data which indicates females with cubs travelled significantly less than females without cubs. In Idaho, black bears with cubs did not follow this trend, showing little difference in movement over the annual cycle and indicating cubs do not necessarily hinder female movements (Reynolds and Beecham 1980). The greater mobility of breeding females reported in Pennsylvania during the mating season by Alt et al. (1977, 1980) is not supported by the present study. Adult and subadult females which were bred in 1980 (cubs in 1981) did not show increased movements during the midsummer breeding season. Pelton and Burghardt (1976) and Reynolds and Beecham (1980) reported similar findings which indicate the increase in midsummer movements observed by Alt et al. (1977, 1980) may be related to forage availability in addition to behavioral changes associated with the mating season.

The extensive movements in early spring and late fall recorded for subadult males (related to utilizing a remote den site) contrast with

the low level of activity reported for adult males in other regions (Alt et al. 1977, 1980, Reynolds and Beecham 1980). Tietje and Ruff (1980) reported a tendency to use remote den sites amongst black bears in Alberta. Although no data on annual movement patterns are presented, increased spring and late autumn movements would be expected. The often rapid and direct return movements observed in some cases indicate the animal is either familiar with the area being traversed or has a particular homing ability (Beeman and Pelton 1976). Craighead (1976) used several criteria to establish eight movement categories for grizzly bears, one of which involved rapid and direct movement to or from a remote den site. Return movements by subadult males (and several females) from den sites within the DMPF results in an increased density of animals in the forest-agriculture zone in late spring. These findings may explain reports from local residents that there is a regular spring movement of black bears out of the DMPF into the forest-agriculture zone.

Alt et al. (1977, 1980) reported adult males exhibit only short range movements in spring and fall with a definite peak in movement (7.05 km between successive locations) during the mid-summer breeding season. Reynolds and Beecham (1980) noted adult males in Idaho did not show marked variations in movement patterns while Pelton and Burghardt (1976) observed restricted male movements during the summer period except for several adults in search of females. Neither of these studies reported annual movement patterns for subadult males. In their study, Pelton and Burghardt made brief reference to a small midsummer peak in movement by subadults making exploratory probes into new habitat. This trend was

also observed in western Manitoba during late July when several extensive movements by subadult males increased the average distance moved. Niewold (1974) observed similar irregular movements in the red fox (Vulpes vulpes) and concluded they were motivated by food sources or in the case of dog foxes, were sexually oriented.

The only adult male monitored in 1980 supports movement data presented by Alt et al. (1977, 1980). Information on early spring movements by male M804 is lacking but during July, travel was extensive. By early August, activity decreased and movements were confined to a small peninsula in Lake Winnipegosis.

Extensive travel away from the home range "core area" was restricted to the subadult male cohort with only one subadult female exhibiting a similar movement. Numerous authors have reported long excursions away from the late summer activity center by all cohorts. Piekielek and Burton (1975), Pelton and Burghardt (1976), and Rogers (1976, 1977) have reported extensive early autumn forays by both sexes. All attribute these movements to exploitation of seasonally abundant food sources outside the normal home range when local foods were scarce. In Minnesota, Rogers (1977) recorded all age classes except yearling females involved in extraterritorial foraging. Alt et al. (1977) observed late autumn foraging trips by females with cubs which at times led animals up to 35 km from their normal range. Contrary to results from Minnesota, Alt et al. did not observe excursions by solitary females. Rogers (1977) and Garshelis and Pelton (1981) indicated extraterritorial movements are influenced by local food abundance, social status of the individual, and learned behavior. In Minnesota,

only females which held well defined territories participated in extraterritorial foraging. Rogers also noted that family tradition and learning appeared to influence foraging movements. Only offspring whose mothers had undertaken foraging excursions utilized remote food sources. Pelton and Burghardt (1976) and Garshelis and Pelton (1981) attributed the "fall shuffle" to lack of local food sources and indicate an inverse relationship between food abundance and the extent of wanderings. The absence of comparable movements in western Manitoba in both 1979 and 1980 may be related to abundant food resources during both years. In addition, diverse habitat within the study area and lack of remote but abundant food sources (ie. acorns) may favor localized foraging.

Conclusive information on black bear dispersal from the study area is lacking since background information on individuals prior to capture was not available. Subadult males appeared to be the only cohort in a transient or dispersal phase. The yearling male monitored in 1979 did not show dispersal tendencies. These results concur with other reports indicating males begin dispersing at approximately two years of age and almost invariably leave their natal range (Rogers 1977, Alt 1978, Reynolds and Beecham 1980). In Pennsylvania where maturation occurs rapidly, males may undertake excursions and show dispersal tendencies as yearlings (Alt 1978).

Jonkel and Cowan (1971) noted comparable results but report some subadult females established permanent ranges several km away from their natal range, indicating limited dispersal amongst females as well. Reynolds and Beecham (1980) reported similar findings from Idaho where dispersing subadult males make up greater than 90 percent of the animals

classified as transients. The wide ranging movements exhibited by subadult males in this study are suggestive of exploratory wanderings which may be related to dispersal. The departure of two subadult males in mid-July and October 1979 without subsequent return follows a trend noted by Rogers (1977) where dispersing males seldom return to their natal range.

While the advantages of dispersal in terms of survival and reproduction have been reported (Murray 1967, Bekoff 1977), the mechanisms which initiate dispersal in black bears are difficult to determine. Although aggression by adult males may often discourage dispersing subadults from settling (Kemp 1976), Bekoff (1977) and Rogers (1977) indicated dispersal tendencies are often innate and not necessarily the result of direct aggression.

Den Characteristics and Utilization

Throughout the two years of observation, all bears monitored by telemetry utilized dens and became inactive during winter months. In temperate regions, dens help reduce energy loss when food is inadequate or inaccessible and weather conditions are most severe (Johnson and Pelton 1980b, Tietje and Ruff 1980). During the period of "winter dormancy", black bears do not urinate, defecate or require food and water (Brown et al. 1971, Nelson et al. 1973). In addition, a stable physiologic condition is maintained (Lundberg et al. 1976, Folk et al. 1980). In contrast to "deep hibernators" such as ground squirrels (Lyman and Chatfield 1955), the black bear undergoes only a minimal decrease in body temperature (39°C to 34°C) and is easily aroused

(Nelson 1973). A similar pattern of winter lethargy is described for several other species (ie. the striped skunk [Mephitis mephitis], and raccoon [Procyon lotor]) and has been termed "carnivorean lethargy", "heavy sleep", or "dormancy" (Lyman and Chatfield 1955). While dormant, bears lose between 15 and 37 percent of their late fall adipose reserves, depending on body size, reproductive condition, the period of dormancy and disturbances (Erickson and Youatt 1961, Nelson et al. 1973, Tietje and Ruff 1980). Mutch and Alexiuk (1977) reported a similar overwinter weight loss in the striped skunk and concluded the depressed metabolic state was crucial to survival at northern latitudes where intermittent foraging is not possible.

Den entry dates for different cohorts in 1979 and 1980 concur with reports from other authors. Johnson and Pelton (1980) reported that adult females den prior to subadults, with adult males entering last. Tietje and Ruff (1980) indicated bears in east-central Alberta exhibit a similar trend with significant differences occurring in some years. Studies in North Carolina and Arizona by Hamilton and Marchinton (1980) and Le Count (1980) have both shown a comparable tendency. High variability by both sexes in Idaho resulted in males denning earlier in 1975 but later than females in 1976 (Reynolds and Beecham 1980).

In the present study, data on adult male entry dates were inconclusive since only one animal was monitored each year. Reports in 1979 of several large males (which were still active) being taken by hunters after other telemetry equipped bears had denned suggests that some adult males remain active into early winter.

Early den entry may provide a mechanism to conserve energy in late fall, especially when food is scarce. Adult males are under a lesser energetic constraint through heat loss because of their favorable volume to surface area ratio. In addition, pregnant females need to conserve fat reserves which are used to produce and nourish offspring. Earlier den entry by pregnant subadult females compared to non-pregnant females of similar age supports this hypothesis. Lindzey and Meslow (1976a) noted that although embryonic development does not begin until several weeks after the onset of dormancy, physiologic condition may influence the time of entry. Reynolds and Beecham (1980) concurred and stated that pregnancy may be a more important factor in determining date of entry than age or sex.

In contrast to the synchronous emergence recorded in spring 1980, Tietje and Ruff (1980) reported asynchronous emergence with males and subadults leaving the winter den before adult females. Earlier activity by males and subadults was also recorded in Washington and North Carolina by Lindzey and Meslow (1976) and Hamilton and Marchinton (1980). Since dens within the study area were located at widely differing elevations, climatic factors at individual den sites probably influenced emergence. Rogers (1974) observed emergence by most bears once the ambient temperature reached 10 °C and snow began to melt rapidly. Subadult males with dens at higher elevations experienced thick snow cover and cool temperatures persisting into mid-April. Bears occupying dens at lower elevations were exposed to milder temperatures and, in at least one case, were forced to leave by meltwater in early April. The climatic differences at individual den sites preclude

further conclusions regarding a typical emergence pattern. Under uniform conditions, large males would be expected to emerge prior to other cohorts since their efficient surface area to volume ratio would result in less energy lost at cool temperatures. In addition, the early spring period may involve active territorial defense and home range exploration (Rogers 1977). Because subadults are often in poorer condition than adults (Jonkel and Cowan 1971, Hamilton and Marchinton 1980), this cohort would be expected to emerge before adult females to utilize early spring vegetation and carrion. Adult females are often hindered by small cubs and do not emerge until the cubs are mobile and able to withstand precipitation and cool temperatures. It is possible that females with cubs avoid aggressive encounters with adult males by remaining inactive and emerging only after cubs are able to climb trees.

In 1979, animals were dormant from early November to early April (5 months), whereas in 1980, dormancy lasted from early October to late March (6 months). Across North America, black bears show high variability in the period of winter inactivity (Johnson and Pelton 1980). In regions where snow or adverse weather is seldom encountered, bears often utilize dens during the period from late October or November to early April (Lindzey and Meslow 1976, Hamilton and Marchinton 1980, Le Count 1980). In North Carolina, Hamilton and Marchinton observed periods of dormancy ranging from 85 to 113 days (mean=102), with den entry occurring in mid-December and emergence in early April. Rogers (1977) reported a longer period of dormancy in northeastern Minnesota, lasting from September to April in some years; a period exceeding six months. Black bears in Washington entered dens in November and emerged in early

March despite the absence of snow and continued mild temperatures (Lindzey and Meslow 1976). Even during mild weather and potential forage availability, Johnson and Pelton (1980) observed no mid-winter activity or excursions. They concluded the complex physiological adaptations for dormancy precluded foraging or intermittent activity during the period of dormancy. In addition to physiologic changes, Matson (1946) described shrinkage and hardening of the stomach which may physically inhibit foraging once dormancy has begun.

Although not significant, the earlier den entry dates recorded in 1980 indicate a degree of flexibility in denning behaviour. Rausch (1961) felt that bears in poor physical condition will not attempt to den but remain active until starvation occurs. In contrast, Jonkel and Cowan (1971) observed bears denning regardless of their nutritional state, often after an abrupt change in weather (ie. a snowfall). Lindzey and Meslow (1976) interpreted the onset of dormancy as a combination of proximate (climatic) and ultimate (physical condition) factors. Johnson and Pelton (1980) agreed with the above rationale but indicate physical condition is closely related to climatic factors and is therefore too variable or unstable to be considered an ultimate factor. Instead, they proposed an ultimate circannual (endogenous) rhythm as observed in true hibernators which prepares the animal both physiologically and behaviorally for hibernation. The lethargy observed in bears several days prior to entering the den (Armstrup and Beecham 1976, Craighed 1979) supports this contention and indicates a definite physiological and behavioral change has occurred. Proximate factors including food supply, physical condition, and weather combine to

provide the final stimulus to den. The high degree of activity observed in late summer may reflect intensive foraging in an attempt to maximize fat deposition. The rapid decrease in activity noted in mid-September probably indicates a cessation of activity to conserve fat reserves.

In 1979, mast crops (primarily high-bush cranberry) were very abundant into early winter and consequently, bears did not enter dens until late October. Early phenologic development and lack of mast crops after mid-September in 1980 led to earlier den entry by all cohorts. Tietje and Ruff (1980) indicated the presence of blueberries in late autumn (October) resulted in later den entry than recorded during other years. Jonkel and Cowan (1971) noted a comparable trend during a year when mountain ash (Sorbus scopulina) berries became available in late fall and were utilized extensively by bears. In Idaho, Reynolds and Beecham (1980) reported a similar situation where active foraging continued until after the first snowfall during a year with delayed phenologic development. Early maturation of mast crops and lack of food after mid-autumn the following year resulted in earlier denning. Captive bears reacted in a comparable manner, remaining active while food was available but denning shortly after feeding was terminated (Erickson and Youatt 1961).

Although possibly a contributing factor in 1979, climatic conditions did not appear to initiate dormancy in 1980. Several females constructed and entered dens in mid-September, two months before adverse weather and snowfall.

Physical condition may have contributed to the early onset of dormancy in 1980. The widespread abundance of saskatoons in late June

led to early fat deposition. One lactating female autopsied in mid-July had extensive fat reserves (approx. 10 cm dorsally) and other cohorts were in good condition also. In the northeastern United States, bears often "disappeared" in early autumn (presumably entered dens) during years when food was abundant (Matson 1946). When located and autopsied, such animals were invariably fat and had empty digestive tracts, indicating a cessation in feeding once adequate physical condition was attained. Lindzey and Meslow (1976) and Hamilton and Marchinton (1980) indicated physical condition may directly influence den entry, especially where climate is not severe. However, sudden adverse weather (ie. a snowstorm) may override physical condition and stimulate den entry (Jonkel and Cowan 1971). In North Carolina, subadult males did not den on some occasions, possibly because of poor physical condition and relatively mild weather which permitted foraging (Hamilton and Marchinton 1980). These observations are supported by the late den entry of two yearling females in 1979. One became active very early in 1980, and upon examination in early May (hunter kill), was in poor physical condition. Since subadults are often in poorer condition than adults (Jonkel and Cowan 1971, Hamilton and Marchinton 1980), late foraging by subadults may be an effective strategy to build up adequate fat reserves for dormancy.

Pelton et al. 1980) and Rogers(1977) noted that almost all bears returned to their mating or summer ranges to construct dens. Although adult males and females often utilized foraging areas up to 174 km away, these animals usually returned to their early summer range to den. Rogers observed only one male which utilized a den outside the summer

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