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The Winter Activity and Movements, Winter Diet, and Breeding Biology of the Fisher (*Martes pennanti*) in Southeastern Manitoba

by

RICHARD D. LEONARD

A THESIS
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ABSTRACT

From May 1975 to June 1977 aspects of the ecology of the fisher were studied in the field by use of radio-telemetry, tracking, and track observations. Information on reproduction, food habits, age and sex distributions, and physical condition was gathered from analysis of 195 trapper-caught fisher carcasses collected from four areas during the winters of 1972-73 to 1977-78.

During the winters of 1975-76 and 1976-77 the upper levels of the snow cover affected fisher locomotion and extensiveness of activity. Changes in the use of gaits and cover types were qualitatively correlated with physical variations in the snow cover. An almost complete depression of fisher activity occurred in the intensive tracking unit during periods in January and February, 1975-76 and January, 1976-77 when the area was covered by extremely soft snow. Effects of temperature, prey availability, and social behavior could not be separated absolutely from the effects of snow cover, but application of snow factors into an established ecological energetics model developed to estimate energy requirements of free-ranging fishers indicated that soft snow could greatly increase energy expenditure of active fishers. The response of fishers to snow cover was believed to be unique for boreal *Martes*. Information from age class structure and radio-telemetry indicated that the juveniles moved more extensively than adults during winter.

Twenty-two genera and 20 species of prey and carrion were identified from alimentary tracts of 120 fishers that contained food items. Mammals, particularly snowshoe hares (*Lepus americanus*), and birds were the dominant food sources. Proportions of foods from scats collected in the intensive study area did not differ appreciably from proportions of foods from alimentary tracts. Porcupine was the only food that showed significant geographic and sex differences in the diet. Fishers responded functionally to increasing numbers of snowshoe hares. Use of other types of foods and the number of different foods declined as the proportion of snowshoe hares in alimentary tracts increased. Estimates of daily consumption rate of fishers also supported occurrence of a functional response and substantiated the importance of snowshoe hares in the winter diet. Use of small mammals, frequency of empty alimentary tracts, and standard deviations of condition indices were related to the proportion of hares in alimentary tracts.

Presence of pregnant females in the yearling age class, increased tract volume and follicular development of late-winter juveniles, and observation of a tract of a recently-bred juvenile indicated that first reproduction of females occurred at the end of the first year of the juvenile age class. Winter maturation of testes followed a similar pattern for juveniles and adults. All males tested in March were spermatic, but none were spermatic earlier in winter. By March bacula from juveniles approached the weight of bacula from adults. Estrus and parturition occurred in late March and April. Uniform development of early-winter juveniles suggested a restricted whelping period and possibly a restricted mating period occurred for all ages of reproducing females. The mean (3.5) and mode (3) corpora lutea counts for fertile females differed little from reports from other regions of the fisher's range. Age-related fertility rates appeared to exist, but indices of fertility and productivity remained relatively constant from 1972 to 1978, suggesting no time-specific changes in reproduction. Movements of a radio-collared adult female during active pregnancy were not extensive. It was believed that the reduction in activity was a strategy to conserve energy for growth of foetuses. The movements of this radio-collared adult female were monitored after she whelped kits in a tree den.

She spent more time away from her kits as time in the denning period progressed, but she did not travel progressively further each day. Movements of the female were extensive and covered most of her formerly-established home range. This behavior was attributed to the necessity of using a well-known home range for more successful foraging, maintaining non-breeding period patterns of social organization, and diverting male courtship activities from the den area. The diet of the female early in the denning period, as determined from analysis of scats, differed little from the winter diet. Radio-telemetry and tracking evidence during the breeding period suggested that adult females in estrus remained relatively sedentary, but males appeared to abandon non-breeding period territoriality to seek out females in estrus. No male-male physical interactions were observed in the field, but the presence of minor skull injuries in breeding-age implied that some form of interaction could occur.

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Dr. W. O. Pruitt, Jr., my supervisor, made available the Taiga Biological Station for research, suggested the present study of fisher ecology, and was a relentless, but important, fountain of advice and criticism. To him I offer my sincerest gratitude.

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INTRODUCTION

A feature that characterizes our understanding of the fisher (Martes pennanti) is the enigmatic quality that continues to shroud investigations of the species' ecology and natural history. This nearctic mustelid remains one of the least known mammals of North America as a result of its history of exploitation and the difficulty in conducting field studies on a frequently rare and sometimes elusive wilderness carnivore. The fisher was extirpated throughout much of its former geographic range due to the monetary value accredited to its pelt by the fur-trade industry, and if cessation of trapping had not been enforced this furbearer would surely be extinct today. Although population management and reintroductions rapidly and markedly improved the numerical status of the fisher, it was not until recently that sufficient numbers were available for study in most areas. Even when fishers were known to inhabit a particular region, logistic problems associated with research in remote forest, inability to locate sufficient numbers of study animals, and the difficulty of monitoring activities of fishers during snow free periods without use of radiotelemetry were nearly insurmountable problems that denied collection of copious amounts of meaningful data.

Much of the information available on fisher biology is limited in scope because of the rather narrow objectives of some management-oriented studies. Furthermore, most work was performed in eastern areas where man's impact on flora and fauna has been in effect for a long period of time and information generated may therefore be unrepresentative of the ecological relationships of the fisher in other regions of North America. Despite the importance of the fisher as a fur resource in many legislative districts, details relating to population regulation and social organization remain basically unknown parameters that are requisites for any management strategy that is the least amount more than simplistic in scope. In a strictly zoological vogue divorced from management schemes, the fisher should stimulate research because it is an atypically large and sexually dimorphic Martes that has no ecological vicariant in boreal regions of the Old World.

The above factors were paramount in influencing the rationale for the present study of the ecology of the fisher in Manitoba. Interpretation of geographic differences in biology of the fisher between Manitoba and eastern areas would aid in a more comprehensive understanding of the species. Additionally, the intensive and extensive study areas in Manitoba were believed to be more representative of the climate, flora and fauna of a greater proportion of the geographic range of the fisher than were eastern areas. Since the intensive study area possessed a relatively complete fauna and was comprised of mature forest that had escaped commercial logging, road construction, and development, it was believed that the observed ecological relationships of fisher in such a fundamentally pristine environment would closely reflect interactions that existed prior to the extensive human disturbance of boreal regions. In light of these facts I sought to fulfill four objectives:

(1) to ascertain which physical and biological factors affect activity, movements, and cover type selection of fishers during winter;

(2) to provide general information on the winter diet and test if fishers responded functionally to changes in snowshoe hare (*Lepus americanus*) numbers;

(3) to describe selected aspects of breeding biology;

(4) to relate applicable data to plausible patterns of social organization.

REVIEW OF THE LITERATURE

Anderson (1970) reviewed and analyzed the fossil record of *Martes* and found no evidence of fisher remains in regions other than North America. The extinct *Martes palaeosinensis* (Zdansky) 1924 of Eurasia was believed to be the progenitor of the contemporary fisher.

Three subspecies of fishers have been recognized (Goldman 1935; Miller and Kellogg 1955), but Hagmeier (1959) refuted their validity through a study of skeletal material and concluded that all forms were members of a single, variable species.

Seton (1909) summarized the known historical geographic distribution of the fisher. Hagmeier (1956) later re-examined present and past distribution of the fisher in greater detail. Rand (1944) and Banfield (1974) reviewed the status and distribution of the fisher in Canada. Hall (1942) and Rand (1944) recommended protection of the species from trapping to avoid extirpation. Regional population increases and changes in distribution were reported after protection was afforded the fisher over most of its range (Cook 1950; Hamilton and Cook 1955; Benson 1959; Coulter 1960; Balser and Longley 1966; Dodds and Martell 1971; Yocum and McCollum 1973; Dilworth 1975; Cottrell 1978). Reintroductions were undertaken in areas where the fisher was previously extirpated or reduced to extremely low numbers (Bradle 1957; Kebbe 1961; Morse 1961; Irvine et al. 1964; Weckwerth and Wright 1968; Brander and Books 1973).

Body size of fishers has been reported by deVos (1952), Coulter (1966), Powell (1977), and Kelly (1977). Blanchard (1964) reported a 20 lb. 2 oz. male from Maine and considered it to be a record weight for the species. Leach and Dagg (1976) and Leach (1977a, b) studied the post-cranial morphology of fishers and commented on the species' adaptations for arboreal locomotion. Parsons et al. (1978) described the sexual dimorphism in the measurement of lower canine teeth of fishers and indicated that root measurements could be used to segregate the sexes.

DeVos (1952) put forth a provisional scheme of age determination of winter-caught fishers. Eadie and Hamilton (1958) presented age determination data that differed from that of deVos (1952) and separated winter-caught fishers into juvenile and adult classes. Wright and Coulter (1967) refuted deVos' (1952) findings and confirmed the observations of Eadie and Hamilton (1958). Kelly (1977) sectioned and stained root portions of teeth from living and trapper-killed specimens and implied that counts of annuli were an adequate method of age determination. Strickland and Douglas (1974; unpublished manuscript) sectioned teeth from more than 1,500 individual fishers and demonstrated, through use of known-age specimens, that counts of cementum annuli were a reliable method for age determination.

The sole disease known for fishers was reported in Maine; O'Meara *et al*. (1960) and Coulter (1966) each reported a fisher that had sarcoptic mange, a contagious skin infection caused by a mite (*Sarcoptes scabei*). Helminth parasites of fishers have been listed in studies of ecology and management (deVos 1952; Hamilton and Cook 1955; Coulter 1966). Sprent (1952) described a new species of nematode from fishers and marten (*Martes americana*). Dick and Leonard (1979) reported seven species of helminths from 162 fishers from Manitoba. In other regions helminths of fishers have been reported in less detail (Chitwood 1932; Meyer and Chitwood 1951; Craig and Borecky 1976).

Most data on breeding biology of fishers stems from observations on fur-farms and analysis of trapper-caught carcasses. Hall (1942) used information from fur-farms to show that females entered estrus shortly after parturition and he attributed the long gestation to delayed implantation of blastocysts. Enders and Pearson (1943) positively demonstrated the occurrence of delayed implantation by describing blastocysts from winter-caught fishers.

Coulter (1966) and Wright and Coulter (1967) provided the most comprehensive information on reproduction and growth of fishers by studying male and female reproductive tracts and skeletons, growth of captive kits, changes of activity of fishers in the field during the breeding period, and other germane details. Other studies have dealt with measurement of fertility rates by counts of blastocysts and/or corpora lutea (Hamilton and Cook 1955; Eadie and Hamilton 1958; Kelly 1977; Strickland and Douglas 1979; van Nostrand 1979). Strickland and Douglas (1979) incorporated reproductive and age class data for computer simulation modelling of populations.

Reports of food habits of fishers in general texts have resulted from anecdotal accounts (Seton 1909; Grinnell _et al_. 1937). The diet is known almost exclusively from contents of trapper-caught specimens and scats collected near positively identified fisher tracks. Consequently, almost no data exist on the diet of the fisher during snow-free periods. The first quantitative study of food habits of fishers was in Ontario, where deVos (1952) analyzed 59 alimentary tracts and nine scats and spent about 17 days in the field tracking fishers during winter. Quick (1953a) stated that stomach and scat analysis of fishers from British

Columbia differed little from deVos' (1952) work, but no data were presented. Hamilton and Cook (1955) tabled food habits information from 60 fishers collected during winter in the Adirondack region of New York. Brown and Will (1979) extended this survey work in New York to include 405 alimentary tracts collected during early winter. Stevens (1968) and Kelly (1977) analyzed 178 and 40 digestive tracts, respectively, from New Hampshire. Grenfell (1979) reported on a limited sample of eight alimentary tracts from California. Coulter (1966) made a comprehensive study of 242 fisher carcasses and 127 scats collected from 1950 to 1964 in Maine; he tested his sample for geographic, temporal, and sex differences in the winter diet. Clem (1977a, 1977b) compared the winter diet of fishers and marten in Ontario and speculated on the possible existence of competitive exclusion. Powell (1977, 1978) extended previous food habit studies by comparing the foraging strategy of the fisher to another musteline, *Mustela erminea*.

The nutritional requirements of female fishers have been studied in laboratory conditions (Davison 1975; Davison *et al*. 1978). Powell (1977, 1979a) used laboratory and field methods to estimate the daily energy requirements of fishers during winter in Michigan.

The predator-prey relationship between fishers and porcupines (Erethizon dorsatum) has received special attention. Shoonmaker (1938), Quick (1953b), and Cook and Hamilton (1957) published brief accounts that first identified the relationship. Powell and Brander (1977) presented quantitative data from a long term study of sympatric porcupine and fisher populations and concluded that fishers were capable of regulating porcupine numbers. Powell (1977, 1979a) developed an ecological energetics model to test optimal foraging strategies of fishers that subsisted mainly on snowshoe hares and porcupines. Powell (1977, 1979b) also extended the foraging model to examine the predator-prey community stability of the fisher-porcupine relationship.

Winter activity and movements have been examined by tracking fishers in the snow in Maine (Coulter 1966) and by radio-telemetry in New Hampshire (Kelly 1977). Forest cover type selection was a major theme that these studies addressed, although Kelly (1977) presented additional information on distance travelled between relocations and characteristics of diurnal activity. Activity, movements, and cover type selection of fishers during snow free periods have been reported only by Kelly (1977). Powell (1980) reported a case of arboreal activity of a fisher, summarized the literature on fisher arboreal activity, and concluded that fishers were predominantly terrestrial during winter.

Patterns of social organization of fisher populations are basically unknown. DeVos (1951) presented highly speculative data on fisher dispersal from areas where trapping was illegal. In New Hampshire Kelly (1977) used radio-telemetry to show that fishers had overlapping yearly home ranges. Powell (1979c) reanalyzed Kelly's (1977) data and indicated that although yearly home ranges may overlap, individual fishers probably defended areas against members of the same sex during shorter time spans.

STUDY AREAS

Figure 1 shows the locations of the extensive study areas and the approximate location of the intensive study area.

Intensive study area

Figure 2 shows the intensive study area and the location of the Taiga Biological Station (51°02'41" N. Lat., 95°20'40" W. Long.). Pleistocene glaciation exposed irregular, parallel ridges of Precambrian granites and gneisses (Russell 1948). Dominant features between ridges are peat development, shallow lakes, glacial outwash sandplains, and sporadic glacial drift. The area is classed in the Northern Coniferous Section of the Boreal Forest Region (Rowe 1972). Relatively dry upland sites are dominated by jackpine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Thick black spruce and alder (*Alnus* spp.) stands are predominant in most lowland sites, but grade into scattered tamarack (*Larix laricina*) and

Figure 1. Location of extensive study areas, approximate location of the intensive study area, and the geographical distribution of fisher carcasses. Sample sizes are in parentheses. A. - East Lake Winnipeg, B. - Whiteshell, C. - Southeast, D. - West. Star denotes location of intensive study area.

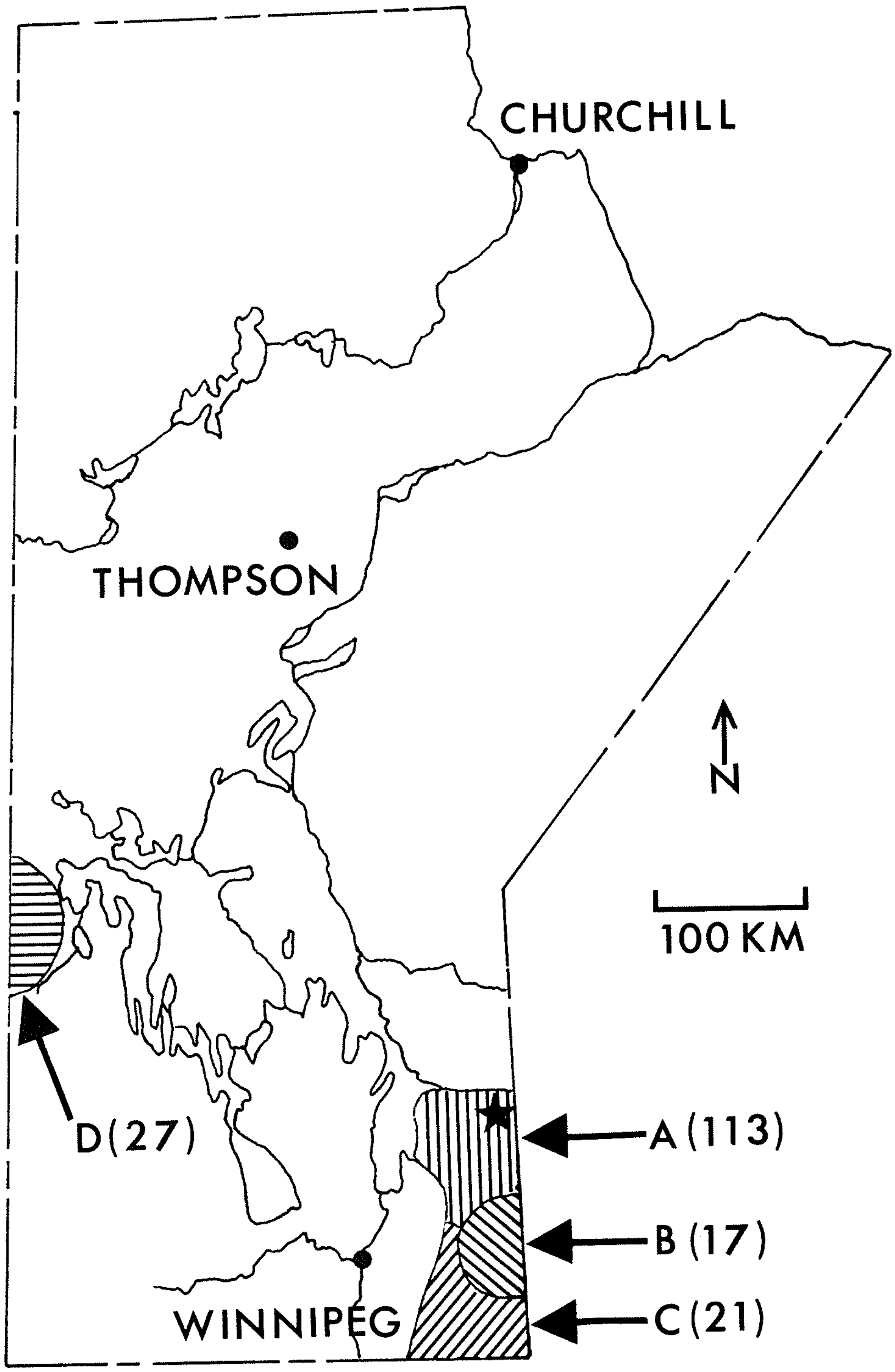
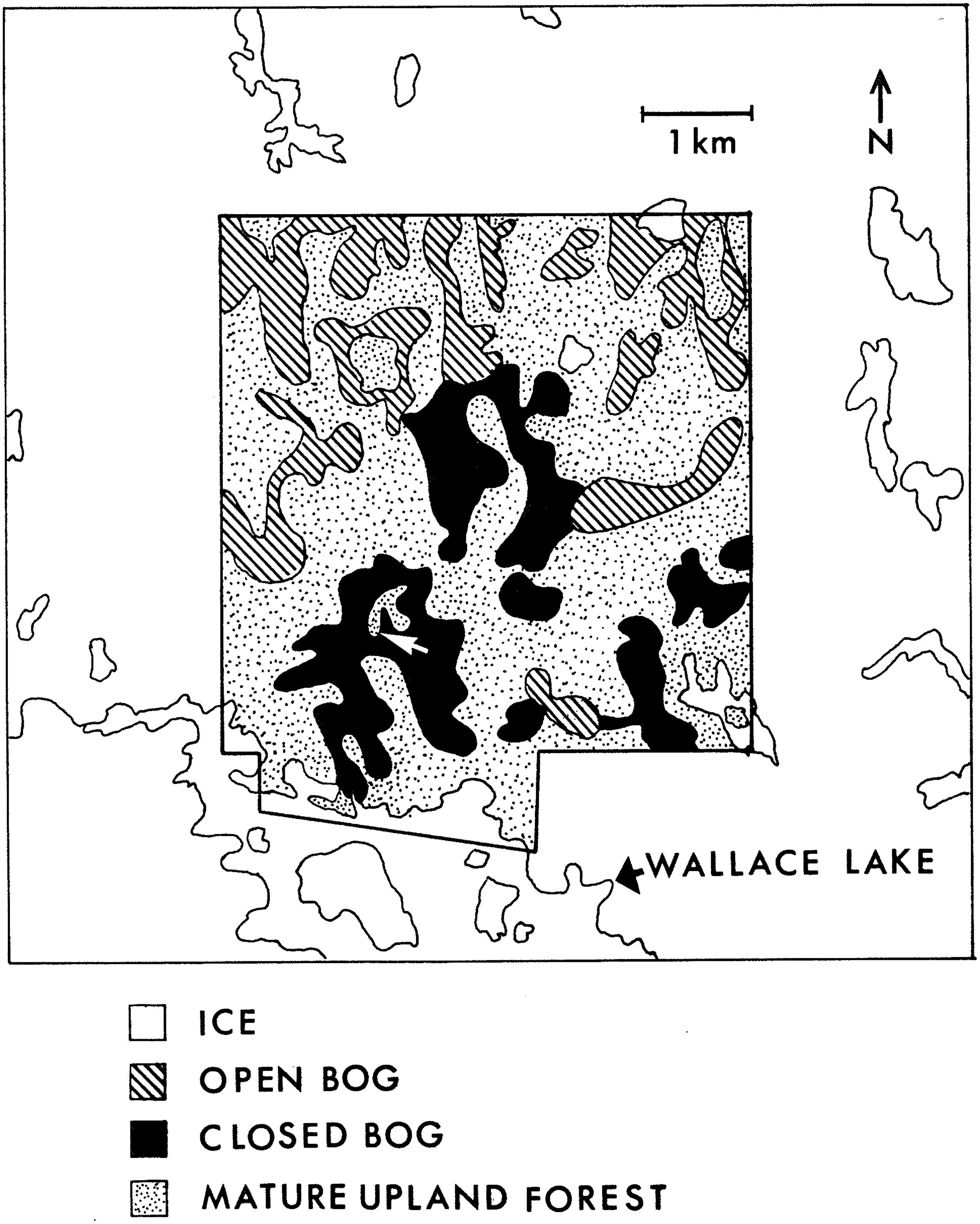

CHURCHILL
THOMPSON
N
100 KM
D(27)
A(113)
B(17)
C(21)
WINNIPEG

Figure 2. The intensive study area and the cover types of the intensive tracking unit. Arrow points to location of Taiga Biological Station.


1 km
N
WALLACE LAKE
ICE
OPEN BOG
CLOSED BOG
MATURE UPLAND FOREST

stunted black spruce where the water table is particularly high. With the exception of regeneration from a 1928 burn, most of the region is covered by mature forest.

Beaver (*Castor canadensis*) have flooded most available areas. Abandoned beaver ponds are in varying stages of secondary succession. The mammalian fauna has remained relatively intact since contact with European man. The extirpation of wolverines (*Gulo gulo*) and the northward spread of negligible numbers of white-tailed deer (*Odocoileus virginianus*) have been the most significant faunal changes. Recent impact of man on the intensive study area has been minimal. There has never been commercial logging operations or motor vehicle roads.

I established an intensive tracking unit of 26.8 km^2 to determine temporal changes in winter activity of fishers (Fig. 2). In order to divide the unit into cover types I used the following criteria: species composition of tree stands, degree of crown closure of tree stands, elevation, and edaphic factors. Interdigitation of numerous small blocks of distinct habitats within the larger cover types negated the possibility of using a more finely divided system without the results of an intensive mapping study. The tracking unit was comprised of four cover types: (1) upland forest (42.6%), (2) closed bog (31.2%), (3) open bog (17.8%), and (4) lake, beaver pond, and river ice (8.4%). Upland forest consisted of a varied mixture of the aforementioned tree species of relatively dry upland sites growing on ridges and shorelines. Small pockets of lowland species such as black spruce and alders were present in topographic depressions within larger ridge complexes. Crown closure ranged from completely closed to small areas of completely open. Closed bog was composed of thick stands of black spruce and alders growing on peat. In many closed bogs, rock outcrops covered by upland species were common. Open bog consisted primarily of stunted tamarack and black spruce growing in stands typified by a low density of trees.

Extensive study areas

A. East Lake Winnipeg: This study area lies in the Boreal Forest Region and is composed of Northern Coniferous, Manitoba Lowlands, and Lower English River Forest Sections (Rowe 1972). Relief in the northern portion is rugged due to intense glacial action, but grades southward into stratified sand and clay deposits with occasional morainic ridges, rock outcrops, and fluvial terraces (Rowe 1972). Trapping formerly reduced but did not extirpate fishers in this region. Fisher populations have increased in number and are harvested without quota by trappers on registered traplines.

B. Whiteshell: This area is similar to area A but with the exception that the Lower English River Forest Section is dominant (Rowe 1972). Much more human use and disturbance has also occurred, mainly because the area is a Provincial Park and has been developed for recreation. Fishers were extirpated or reduced to an extremely low level but have exhibited increases in distribution and number during the last 10 years. Trappers on registered traplines harvest fishers without quota.

C. Southeast: Most of this area lies in the Rainy River and Quetico Forest Sections of the Great Lakes - St. Lawrence Forest Region (Rowe 1972). The area is mainly covered by lacustrine and modified glacial deposits. Logging operations and fires have led to the replacement of red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) by jackpine. Changing land use practices have left much of the region in various stages of secondary succession. Fishers were extirpated in the area but are now becoming more common, presumably as a result of immigration and reproduction. Trapping of fishers is done only under special permit.

D. West: Most specimens from this area were taken from the Porcupine Forest Reserve, part of the Manitoba Escarpment. Glacial till covers extensive shale deposits in much of the area. Most of the region lies in the Mixedwood Forest Section of the Boreal Forest Region (Rowe 1972). Fishers were reduced or extirpated in the region because of exploitation and the effects of extensive logging, but have recently increased in numbers. They are now taken only on registered traplines under special permit.

MATERIALS AND METHODS

I Field Research

Trapping and handling of fishers

Fishers were trapped in the intensive study area with standard wire-mesh box-traps baited with carrion and/or scent (Table 1). One fisher was cut from a tree, chased, and pinned to the ground with forked sticks. Fentanyl citrate-droperidol (Innovar-Vet)[1] mixed with atropine sulphate[2] was administered intramuscularly to immobilize all captured fishers. Fishers were usually handled and drugged twice: once for general examination, ear-tagging, age determination, and measurements, and once for fitting a radio-collar. Between handling periods fishers were either kept in a trap or placed in a larger holding pen. An effort was made to minimize disturbance of the captives at all times. Live fishers were sexed and placed in juvenile or adult age classes (Wright and Coulter 1967). Presence or absence of a palpable sagittal crest, body size, and condition of teeth were used as criteria in age determination of eight fishers (including four dead, unskinned specimens). Ages of five of these fishers were

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[1] Pitman-Moore Company, P.O. Box 344, Washington Crossing, New Jersey, 08560.

[2] Moore Kirk Laboratories Inc., Worcester, Massachusetts, 01600.

Table 1. Relevant background information about radio-tagged fishers.

Number of ear tags	Sex	Age	Weight (kg)	Period tracked	Number of locations	Number of observations	Reproduction	Fate
1812 1825	female	adult	2.4	9 April/76- 21 Sept./76	318		Whelped litter on 28 March, all kits (4) died, female released in estrus on 9 April.	lost radio contact on 21 Sept.
			2.9	10 March/77- 27 May/77	346	3	Captured in active pregnancy, whelped litter of at least 2 in April.	Lost radio contact on 27 May.
		3 annuli in cementum	2.4				4 corpora lutea 4 placental scars	killed by trapper in December/77.
1801 1802	female	juvenile	2.2	24 Feb./77- 29 March/77	99			travelled out of radio reception
1810 1822	male	juvenile	4.3	1 Nov./76- 4 Nov./76	21		Testes not easily palpable.	Travelled out of radio reception
	male	adult	5.0	21 March/77- 25 March/77	39		Palpable, well developed testes.	Travelled out radio reception

later determined using dental, skull, and skeletal criteria. All were placed in the correct age class when first examined in an unskinned condition.

Radio-telemetry

In March 1976, when I first captured a fisher in the intensive study area, there were no published records describing use of radio-collars on wild-caught fishers. This first fisher was held in a large, three-tiered, wire pen with two nest boxes. I observed her movements both prior to and after a radio-collar was attached. During both observation periods her movements were characterized by a displacement type of pacing as she ran a systematic pattern among different levels and used specific openings in the nest boxes. Based on observations from 24 March 1976 to 8 April 1976, I could detect no change in activity of the penned fisher due to attachment of the radio-collar.

An AVM model LA12 portable receiver (AVM Instrument Co., Champaign, Illinois, U.S.A.) and a four-element yagi antenna were used to locate AVM model SB-2 transmitters powered by individual lithium batteries. The transmitter, battery, and brass antenna were encapsulated with dental acrylic (Mech *et al*. 1965). Transmitter packages emitted a discontinuous signal from 150.850 mHz to 151.150 mHz and they weighed between 80 and 120 g.

Standard triangulation techniques (Brander and Cochran 1969) were used to locate transmitters. If possible, more than two azimuths were obtained to verify a location. Attempts to use fluctuations in signal strength to determine activity were generally unsuccessful because transmitters sometimes produced an erratic signal even when stationary.

During April and May 1977 I monitored the movements of an adult female that had whelped kits in a hollow tree. Because the den was high off the ground and in close proximity (1.2 km) to the Taiga Biological Station, the signal received when the female was in the den was extremely powerful. Consequently, I could determine periods when the female was out of the den solely by signal strength. It was usually not possible to determine the exact time the female returned to the den. The mean time between the last fix out of the den and the first fix in the den was used to estimate the female's time of return. The female demonstrated two distinctly different types of movements. (1) Linear routes were characterized by movements from and to the den in the same general line of travel. If I was able to determine only the terminal position and general direction of the movement, I estimated the distance travelled by measuring the map distance and then I applied a correction factor (X 1.4) calculated from the best-known linear movements. (2) Circuitous routes were characterized by movement in a broad loop to and from the den. The total distance travelled was estimated by measuring map distance of connected relocation points.

Tracking and track records

Two different types of snow tracking were performed in the intensive study area. First, individual fisher trails were followed on foot, snowshoe, or skis. Data were collected on cover type selection, hunting behavior, reaction to snow conditions, and inter and intraspecific behavior. I collected scats, recorded kills or scavenges, and studied specific behaviors such as scent marking and use of sub-nivean dens. A combination of ground pacing and examination of aerial photographs was used to measure the total distance travelled along fisher trails.

The second method of snow tracking involved use of track records in the intensive tracking unit (Fig. 2). A network of trails linked all cover types described in the previous section. These trails were systematically scrutinized for fisher tracks on a regular basis during the winters of 1975-76 and 1976-77. I used temporal and spatial partitioning of effort to ensure cover types were examined in proportion to their availability in the intensive tracking unit. Several types of data were recorded when a fisher track was intercepted. The age of the track was estimated in light of known snowfalls and thaws. A note was made of the general snow conditions, particularly of the upper 20 cm, and the type of gait the fisher used was recorded. The cover type in which the track was observed was recorded. If a clear foot imprint was available, I determined the sex of the fisher that made the track. This technique was verified by ground tracking radio-tagged individuals of known sex.

A cover type selection index (SI) was calculated for each winter month of the study. Total tracks observed for a respective month were multiplied by the percent occurrence of each cover type to give the expected number of track observations for each cover type. The observed number of tracks was divided by the expected number to yield the cover type selection index (SI). An index equal to one meant that the cover type was selected in proportion to its availability for the respective month.

Food availability

Snowshoe hares: Two indices of hare availability were used. First, notes on the general distribution and abundance were made in conjunction with tracking, track counts, and general activities. Second, Dr. W. O. Pruitt, Jr. made available data from an annual winter hare drive performed in relation to teaching activities in the intensive study area (Appendix 1).

Other prey species: Availability of small mammals was known in a general sense, due to research on microtines that was carried out in the intensive study area until May 1976 (Penny 1978). Track records and observations of other mammalian and avian prey species were made during field activities.

Carrion: A concurrent ungulate study (Darby 1979) made available information on presence of ungulate carrion. My own observations, coupled with tracking in the intensive study area, provided supplementary data. To test further the effect of carrion on fisher behavior, I transported eight white-tailed deer carcasses from southern Manitoba and placed them in the intensive study area in regions that fishers frequented. In these localities I observed frequency of fisher visits and the amount of feeding.

Measurement of physical factors

Wind: A portable, rotating-cup anemometer was used to measure wind speed in various cover types. It failed to measure wind speed on the ground or snow surface even when strong winds were evident in the overstory. I believe low wind speeds at ground level and insensitivity of the instrument were reasons for the failure. After December 1976 all wind measurements were discontinued.

Snow cover: Measurement of various parameters of snow cover and their relation to fisher locomotion and activity proved to be difficult during the study. The ultimate analysis was dependent on a variety of techniques. During 1975-76 standard api-profile stations (Pruitt 1959) were established in a variety of cover types in connection with microtine studies (Penny 1978). By November 1976 it became obvious that standard profile measurements were too time consuming for the amount of data obtained. During 1976-77 most snow profile work was done in the vicinity of fisher tracks to determine parameters affecting locomotion. I also concentrated in describing the upper 20 cm of snow cover in greater detail than in 1975-76 by using qualitative descriptions and vertical hardness measurements. During both winters I qualitatively catalogued changes in snow cover on a cover type basis after most snowfalls and thaws. Along fisher trails and at track intercepts I recorded how the snow cover apparently affected fisher locomotion.

In outlining a general snow cover description for the intensive study area I combined all cover types and used hardness values of the upper 20 cm of api. However, it was difficult to obtain a mean hardness value that was feasible to calculate, but yet effective in describing the relationship between upper level hardness and fisher locomotion. Fishers responded to subtle changes in upper level hardness that could not be described, with the available sample size, in terms of snow cover-activity models (Pruitt 1966, 1979). Another problem in interpreting data was the time disparity between hardness measurements and track observations; between observations temperature shifts and snowfalls undoubtedly affected upper levels of the snow cover and fisher locomotion. This problem became acute in February and March during both winters. Daytime thaws softened the snowcover in some or all cover types, but nocturnal freezing temperatures frequently created an extremely hard crust. Under these circumstances it was difficult to determine a mean hardness value for a particular time period. Therefore, I used the data solely to show the considerable differences in snow cover between early and late winter, rather than as a predictive model of fisher activity. I estimated the mean hardness for two-week periods by using the location, thickness and hardness of layers in the upper 20 cm, as well as qualitative observations on snow cover and fisher tracks. Data were presented in graphical form and no statistics were applied to test relationships between snow cover and fisher activity.

Data analysis

Data collected on fisher activity and physical factors were categorized into two-week periods for each winter month that had a snowcover (December to March 1975-76; November to March 1976-77). Each period divided the month evenly in number of days. The first period of each month was termed "early" (e.g., early January) and the second period termed "late" (e.g., late January).

II Laboratory analysis of carcasses

Carcass collection

Carcasses were collected from trappers in the extensive study area from 1972-73 to 1977-78 (Fig. 1; Table 2). Staff of the Department of Natural Resources, Government of Manitoba, obtained carcasses from the Whiteshell, Southeast and West regions. I collected most carcasses in the East Lake Winnipeg area. Most specimens were placed in plastic bags and a label including date of capture, location, and sometimes type of set and/or bait was attached. Trappers that I personally interviewed usually provided information on the set and type of bait used. Prior to collection, carcasses were exposed to a wide variety of weather conditions; some were thawed and refrozen several times and others were frozen quickly at low temperatures. I was able to examine five specimens that were previously unfrozen.

General handling

Each carcass was thawed at room temperature, examined for anomalies and missing parts, and assigned a catalogue number that followed the specimen through all processing steps. Individual specimens were weighed,

Table 2. Distribution of trapper-caught fisher specimens by year and month.

Winter	November	December	January	February	March	Unknown	Totals
1972-73			1	1		10	12
1973-74		1	1	1	3	7	13
1974-75	7	12	6		2	15	42
1975-76	12	7	6	13	3	11	52
1976-77	17	15	11	8	3	7	61
1977-78	2	2	1	5			10
Unknown						5	5
Totals	38	37	26	28	11	55	195

measured (L., T., H.F.) and eviscerated. Lungs, heart, liver, kidneys, mesentaries, and body cavity of most carcasses were examined for helminths (Dick and Leonard 1979). Female reproductive tracts were removed and trimmed of excess fat and connective tissue. After volumes were recorded, tracts were preserved in 10% formalin or Bouin's fixative. The tunica vaginalis was stripped free and the combined volumes of testes and epididymides were recorded. If only a testis and epididymis were present, their combined volume was doubled to maintain comparability. Testes and epididymides from fishers taken in January, February, and March were stored in Bouin's fixative. Alimentary tracts that could not be immediately examined for food habits analysis or parasitism were either refrozen or stored in 10% formalin.

Condition indices

Qualitative observations on the fat distribution of 25 fishers were recorded. A kidney fat index (KFI) and a mesentary fat index (MFI) were developed:

$$\text{KFI} = \frac{\text{Weight of kidney and attached fat}}{\text{Weight of kidney}} \times 100$$

MFI = Weight of greater omentum and attached fat

Both indices were performed on 34 specimens. KFI and MFI were significantly correlated ($r = .631$, $p < .01$). MFI was chosen for the remaining specimens because it appeared to give a better index of extremely fat individuals.

Skeletal material

Each eviscerated carcass was stripped of excess fat and muscle. The skull, baculum, innominate bones, scapulum, and one set of fore and hind long bones were boiled in water for approximately 20 minutes. All loose teeth (usually all canines, incisors, and some premolars and molars) were extracted and stored in labeled vials of 70% ethanol. The remaining material was processed in an enzyme bath (E. Drescher's method, University of Manitoba, Department of Zoology, teaching handout), washed, air dried, and stored in plastic bags. Residue from the enzyme bath was washed over a sieve and examined for presence of porcupine quills.

Age determination

The criteria of Wright and Coulter (1967) were used to segregate specimens into four classes: adult male, adult female, juvenile male, and juvenile female. Juveniles were all less than one year of age. Teeth were shipped to C. Douglas and M. Strickland[1], who have sectioned over 1,500 fisher teeth and have well developed techniques. Lower teeth (canines, and if necessary, first and second premolars) were decalcified in 5% nitric acid and the root portions were embedded in paraffin. Roots were sectioned longitudinally at 10 microns. Sections were stained with hematoxylin (8-15 min) and eosin (2 min) and were examined under a light microscope at 40 and 100 power. Strickland and Douglas identified and counted annuli for each submitted specimen. I repeated the counts using their methods (Strickland and Douglas, unpublished manuscript).

Reproduction

Female reproductive tracts were examined for gross signs of physiological activity. Ovaries were cut from the tract, dissected from the bursa, washed in 90% ethanol,

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[1] Wildlife Biologists, Ministry of Natural Resources, 7 Bay Street, Parry Sound, Ontario.

lightly blotted, and were slightly air dried. Each ovary was glued (Permabond, Lepage's Limited, Bramalea, Ontario) to a glass slide that was fastened by a metal block to the chuck of an Oxford vibratome (Model G, Cat. # 501,502). Slow vibratome speed and high amplitude were used to section ovaries at thicknesses varying from 10 to 175 microns. Sections were placed in order on a glass slide and examined under a dissecting microscope (20 and 40 power). Follicles and corpora lutea were examined, counted, and usually measured.

Testes were removed from fixative and a portion of epididymis was excised, smeared on a glass slide, air dried, and examined under a light microscope (150 power) for presence of mature sperm (after Flook 1970). Bacula were air dried and weighed to the nearest .01 g.

Fishers captured in the field were examined for reproductive condition. Testes were palpated and measured with a plastic rule. The criteria of Enders and Leekley (1941) were used to assess the degree of estrus exhibited by females.

Food Habit Analysis

Alimentary tracts were divided into stomach, small intestine (four sections), and large intestine. Contents were analyzed separately. Each portion of tract was opened and distinct food items were separated with forceps and washed over a 1.0 mm mesh sieve until relatively clean. Scats were soaked for several hours, gently separated, and individual segments or food items were washed. Food items were identified to as low a taxonomic level as was practical. Bones, teeth, hair, and claws were compared to similar material from a reference collection of potential mammalian prey. If size and color comparisons of hair were ambiguous, then acetate slides (van Zyll de Jong 1966) were used to compare unknown material with reference material. The key of Adorjan and Kolenosky (1969) was useful to determine initially the most logical prey species for comparison. The taxon, portion identified, and an estimate of percent volume were recorded. Avian remains that were not readily identifiable were shipped to Henri Ouellet[1] for proper identification.

Bait could be separated from legitimate food items in most cases. If bait was not shown on the original label, it could usually be identified because it differed from typical prey species. Fish was the most common bait

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[1] Chief, Vertebrate Zoology Division, National Museum of Canada, Ottawa, Ontario.

because of trapper access to the Lake Winnipeg commercial fishery. Beaver remains were next in importance. Trappers marketed beaver pelts, so large quantities of meat (usually tail) and the absence of hair indicated use of beaver for bait. If masses of hair were present, the beaver was considered to be carrion from natural sources. A high frequency of waterfowl (Anatidae) feathers in some tracts suggested that trappers were using feathers from fall-shot waterfowl for bait. However, the presence of anatid feathers in some carcasses in which the bait was known, and in one of 55 scats, suggests that there was a natural source of waterfowl in the fisher's diet. I had no method of detecting whether ungulate remains were naturally scavenged or taken as bait. Since trappers had no source of ungulate remains except from a limited hunting season (December 1-14, Alces alces), I believe fishers scavenged much of the observed ungulate food items. Even if trappers set traps near gut piles from hunter-kills, the sample would remain meaningful because fishers would use the carrion in the presence or absence of traps.

Calculation of consumption rate

Modification of a model developed by Diana (1979) to estimate the daily ration of a top carnivore (Esox lucius) was used to estimate the daily consumption rate (in kilojoules) of East Lake Winnipeg fishers during the winters of 1974-75, 1975-76, and 1976-77. The basic data fed into the model were occurrence figures from analysis of alimentary tracts and meal size and percent metabolizable energy of gross energy per unit meal from the feeding trials Davison (1975) performed on captive fishers.

The model: Diana (1979) discussed the theoretical considerations of the consumption rate model and its application to top level carnivores that are asynchronous in feeding patterns. The two variables necessary to calculate daily consumption rate are meal frequency and meal size. I considered a winter collection of alimentary tracts to be a time-specific sample (N) that was subdivided into two classes: tracts containing food (F) and empty tracts (E). Davison (1975) determined that the gastric evacuation rate (G) of female fishers was 16 h. Meal frequency (X) may therefore be calculated from Diana's (1979) formula:

$$X = \frac{G}{F/N} = \frac{G \times N}{F} \qquad (1)$$

Consumption rate (CR) equals mean meal size ($\bar{M}$) ÷ meal frequency:

$$CR = \frac{\bar{M}}{X} = \frac{\bar{M}}{\left(\frac{G \times N}{F}\right)} = \frac{\bar{M} \times F}{G \times N} \times 24^{1} \qquad (2)$$

^{1}to convert to daily rate.

The main discrepancy between use of the model for piscivores and for fishers is the calculation of mean meal size ($\bar{M}$). Piscivores ingest all prey whole; weight of prey may then be "back-calculated" by fitting length or an estimate of length (from age class) into a weight-length regression. Fishers ingest small prey whole, but are only capable of taking separate meals from large prey or some types of carrion. Therefore, it was necessary to estimate unit meal size for some food items.

Davison (1975) fed female fishers individual, *ad libitum* meals of snowshoe hares, small mammals, white-tailed deer, and coturnix quail. I assumed that the amounts consumed in feeding trials were good estimates of mean meal size for each food type. This assumption was supported by the fact that there were no statistical differences in meal size among food types (Davison 1975). From general comparisons of the amount of food consumed by two female and two male fishers that I held captive, I estimated the weight of a male's meal to be twice that of a female's meal. A meal of muskrat (*Ondatra zibethicus*) was estimated to be the same weight as a meal of hare. A meal of unidentified mammal was given a value that was the mean weight of a single shrew and a meal of deer. Ducks and grouse were allotted the same meal size as coturnix quail. Unidentified birds were given a composite meal weight dictated by the proportion that identified birds were represented in alimentary tracts during the winters of 1974-75, 1975-76, and 1976-77 (gray jays (*Perisoreus canadensis*) 17%, grouse 50%, and ducks 33%).

Weights of prey that could be ingested in a single meal were taken from Banfield (1974). Cricetids were given a mean of 28 g calculated from the mean weights of species represented in alimentary tracts. Mean weight of red squirrels (*Tamiasciurus hudsonicus*) was 190 g. Shrews were not frequently identified to the specific level. Therefore, weights of *Blarina brevicauda* and *Sorex cinereus*, the only identified shrews, were averaged in the 3:1 ratio in which they were represented in alimentary tracts to give a mean value of 16 g for unidentified shrews. The mean weight of gray jays was 73 g, calculated from weights of 13 male and nine female winter-killed jays from the University of Manitoba Zoology Museum.

I used the energy value of a meal, rather than weight, to calculate consumption rate. Davison (1975) tabled data on digestive efficiency (percent metabolizable energy of gross energy) of female fishers fed four different diets of deer, coturnix quail, small mammals, and snowshoe hares. I estimated the percent metabolizable energy of gross energy for taxa not included in Davison's (1975) feeding trials. The estimates probably show limited error because known digestive efficiency was within a fairly restricted range for four diets (Davison 1975). Golley (1961) also commented on the markedly uniform energy values of animal tissues. I estimated the metabolizable energy (ME) available in red squirrels to be the mean ME available in hares and mice (after Powell 1979a), that of muskrats to be the mean of hares and deer, and that of unidentified mammals to be the mean of mice and deer. All birds were considered to have the same ME as coturnix quail. The same logic and estimates were used to obtain values of gross energy/unit weight (GE/g) of food items.

Field evidence from this study and others (Coulter 1966; Powell 1978, 1979a) indicated that fishers did not frequently obtain large meals from sources of carrion, even though alimentary tracts often possessed circumstantial evidence of scavenging. Consequently, I classed meals from carrion into three groups that were defined by the type and amounts of remains found in the tracts. Significant scavenges were typified by large amounts of undigested meat (with or without large amounts of hair and bone) and were estimated to yield the same number of kilojoules as an average meal of deer eaten by captive fishers (Davison 1975). An intermediate scavenge was characterized by a tract with $<50\%$ volume of meat, hair, or bone, and was given an energy value of 50% of an average meal of deer. Tracts containing only trace amounts of scavenged material, such as hair or bone, were classed as insignificant with a nil energy intake.

Application of the model: Consumption rates were calculated separately for the winters of 1974-75, 1975-76, and 1976-77. For each fisher captured with food in its tract, the estimated mean meal weight of individual contents was calculated. The energy value was calculated by multiplying food item weight by gross energy (GE) content per gram. This product was multiplied by the percent metabolizable energy of gross energy to give the energy value of each individual food item. These values were summed for each fisher and divided by the sample size (N) to give $\bar{M}$, mean meal energy value for each winter. $\bar{M}$ was then applied with other variables into equation (2) to calculate the estimated consumption rate (CR).

RESULTS

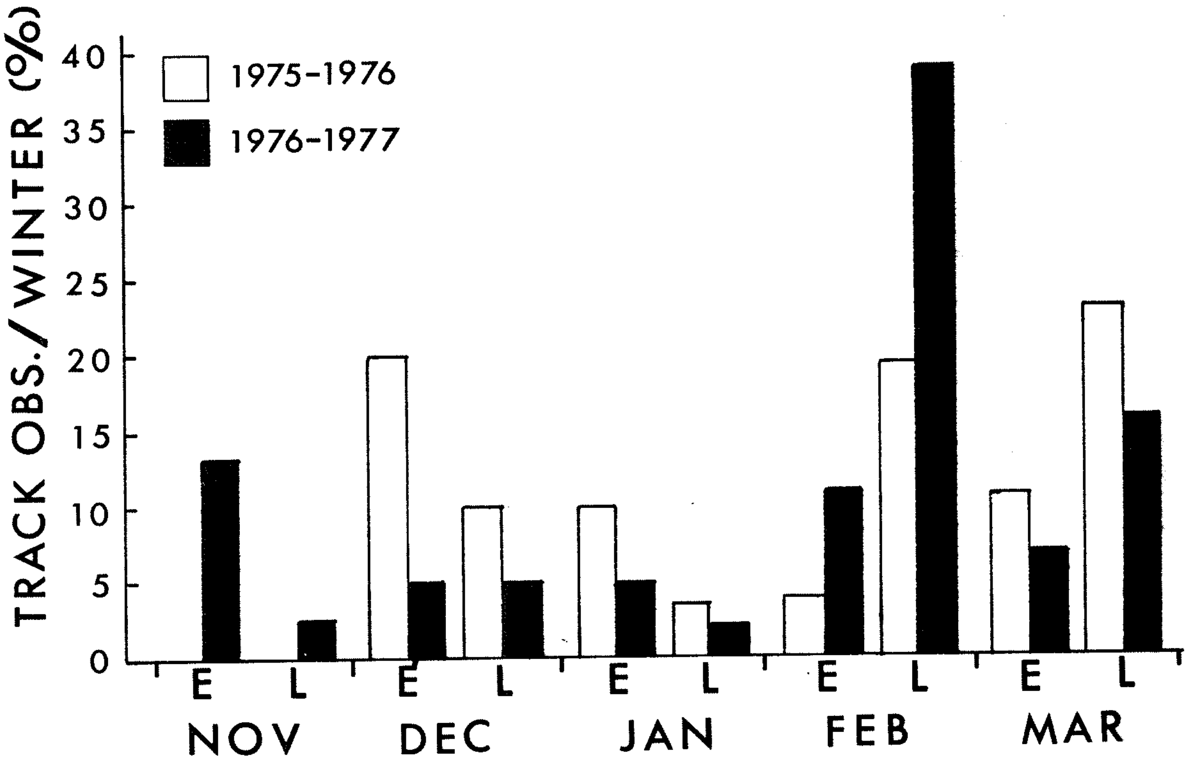
I Winter Activity and Movements

Activity patterns and cover type selection

Figure 3 shows the temporal distribution of track observations during the winters of 1975-76 and 1976-77. For the winter of 1976-77, a highly significant difference existed between a hypothesized numerically-even distribution of tracks in time and the observed distribution ($X^2 = 98.0$, d.f. = 9, $p < .001$). Data from 1975-76 were not testable because expected values were less than five in all cells, but the pattern of distribution was similar to that of 1976-77. When data from 1975-76 and 1976-77 were combined, the difference between the hypothesized and observed values remained highly significant ($X^2 = 76.4$, d.f. = 7, $p < .001$). The significant differences were mainly attributable to a mid-winter depression in track observations: only two tracks (6.5%) were recorded in late January and early February 1975-76,and only five tracks (5.8%) were observed in early and late January 1976-77.

Radio-telemetry data on an adult female (Table 1) also supported the occurrence of decreased winter activity of fishers in the intensive study area. The female's movements during a snow free period indicated that she

Figure 3. Distribution of winter track observations from 1975-76 (n = 31) and 1976-77 (n = 86) in the intensive tracking unit. E - early (see text), L - late (see text).


TRACK OBS./WINTER (%)
0
5
10
15
20
25
30
35
40
1975-1976
1976-1977
E
L
NOV
DEC
JAN
FEB
MAR

crossed a portion of the trail system at least once per day (Fig. 4). Her movements in March 1977 were less extensive than in the snow free period but she crossed a portion of the trail system frequently. Since this female appeared to have a well established home range in which she whelped two litters (see Section III; Breeding Biology), I had no reason to suspect that she left the area between radio-tracking periods. If this female was present and did not reduce the extent of her movements during the winter of 1976-77 the expected number of tracks in the intensive study area would have been far greater than the observed number.

Tables 3 and 4 summarize cover type selection for the winters of 1975-76 and 1976-77, respectively. During both winters the observed selection differed significantly from the expected selection based on cover type availability (1975-76: $X^2 = 20.0$, d.f. = 3, $p < .005$; 1976-77: $X^2 = 17.7$, d.f. = 3, $p < .005$). Cover type preferences, determined from following fisher trails 31.4 km in 1975-76 and 22.1 km in 1976-77, deviated little from the selection indices (Tables 3 & 4). The single major exception was the use of closed bog, which appeared to be selected during all months of 1975-76. Within cover types fishers frequently selected ecotones between homogeneous forest stands. Open bogs were usually crossed in a relatively straight line of travel.

Figure 4. Stationary relocations and range of an adult female fisher during a snow free period, April 1976 to September 1976.

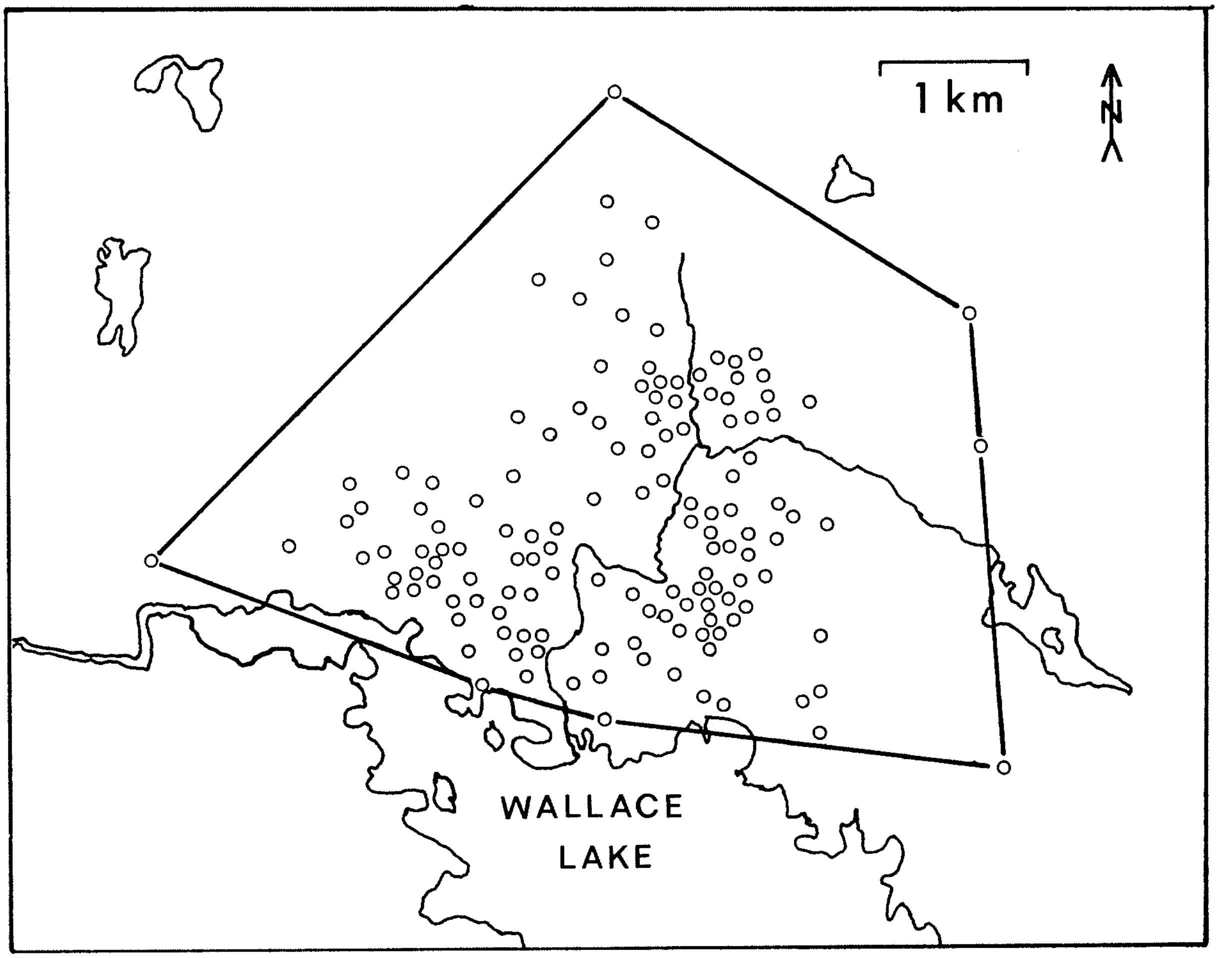

1 km
N
WALLACE
LAKE

Table 3. Cover type selection by fishers in the intensive tracking unit during winter 1975-76 (N=31). Figures are selection index (SI)+; 1.0 = selection in proportion to availability of cover type.

	Cover Type			
Month	Ice	Closed Bog	Open Bog	Mature Upland Forest
December				2.3
January		0.8		1.8
February			1.6	1.7
March		0.3	1.0	1.7

+ see text for calculation.

Table 4. Cover type selection by fishers in the intense tracking unit during winter 1976-77 (N=86). Figures are selection index (SI)+; 1.0 = selection in proportion to availability of cover type.

	Cover Type			
Month	Ice	Closed Bog	Open Bog	Mature Upland Forest
November	5.5	0.5		0.9
December		0.4		2.1
January		0.6	1.1	1.4
February		0.5	3.1	0.7
March		0.9	1.3	1.1

+ see text for calculations.

Factors affecting activity and cover type selection

Snow cover: Fishers used three distinctly different gaits for travelling on snow (Fig. 5). On relatively hard surfaces, such as thinly snowed bare ground, ice, or crusted snow, fishers utilized the lope more often than other gaits. Fishers shifted to the double bound when 4-5 cm of little-changed snow accumulated on hard surfaces. Continued accumulation of soft snow made use of the double bound more difficult; the floating phase of this gait was hampered by contact of the ventral surface of the body on the snow cover. When about 25 cm of soft snow (<10 gm/cm^2 hardness) was present, fishers used a walking gait that left a body-drag imprint in the snow cover.

Tracking data from 53.5 km of fisher trails revealed two details: individuals were capable of rapidly sensing subtle differences in snow cover, and they could react by changing gaits in mid-stride. When a fisher using a lope broke through a snow cover crust, the individual immediately shifted to a double bound until the softer area was negotiated, and then reverted to a lope (Fig. 5C). Fishers that encountered a micro-habitat of thinner snow, such as a qaminiq, frequently changed gaits for two or three strides; walking fishers shifted to a bound and bounding fishers changed to a lope. Fishers that traversed more than one cover type often switched gaits to negotiate different snow conditions.

Figure 5. Track imprints of two gaits used by fishers during winter. a. - double bound, b. - lope, c. - transition in mid-stride from lope to double bound to compensate for differences in snow cover.

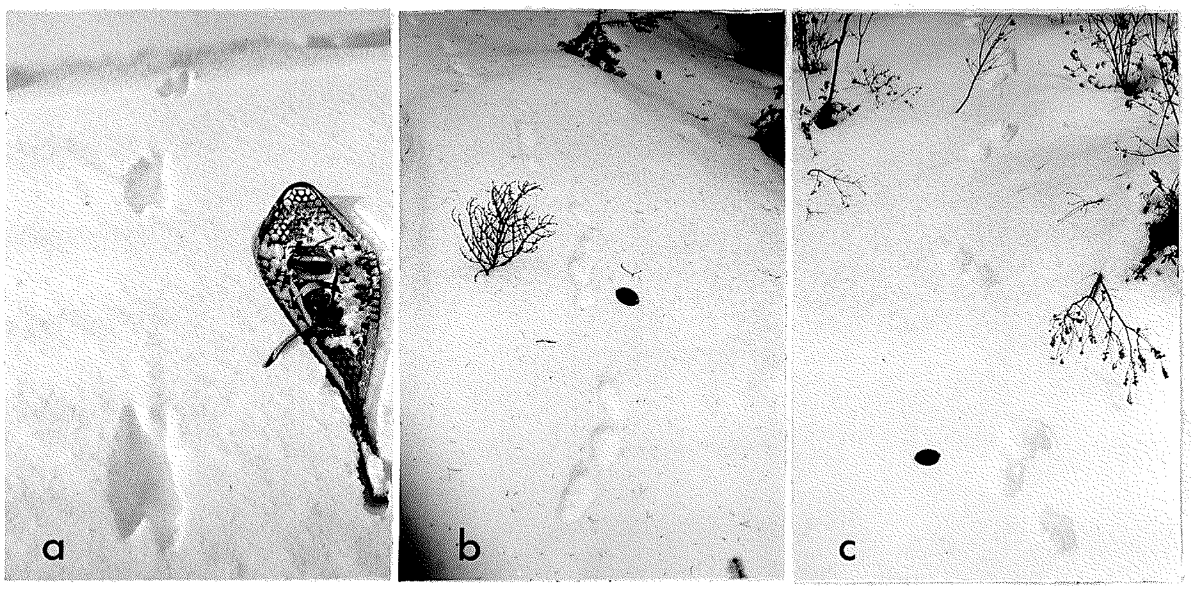
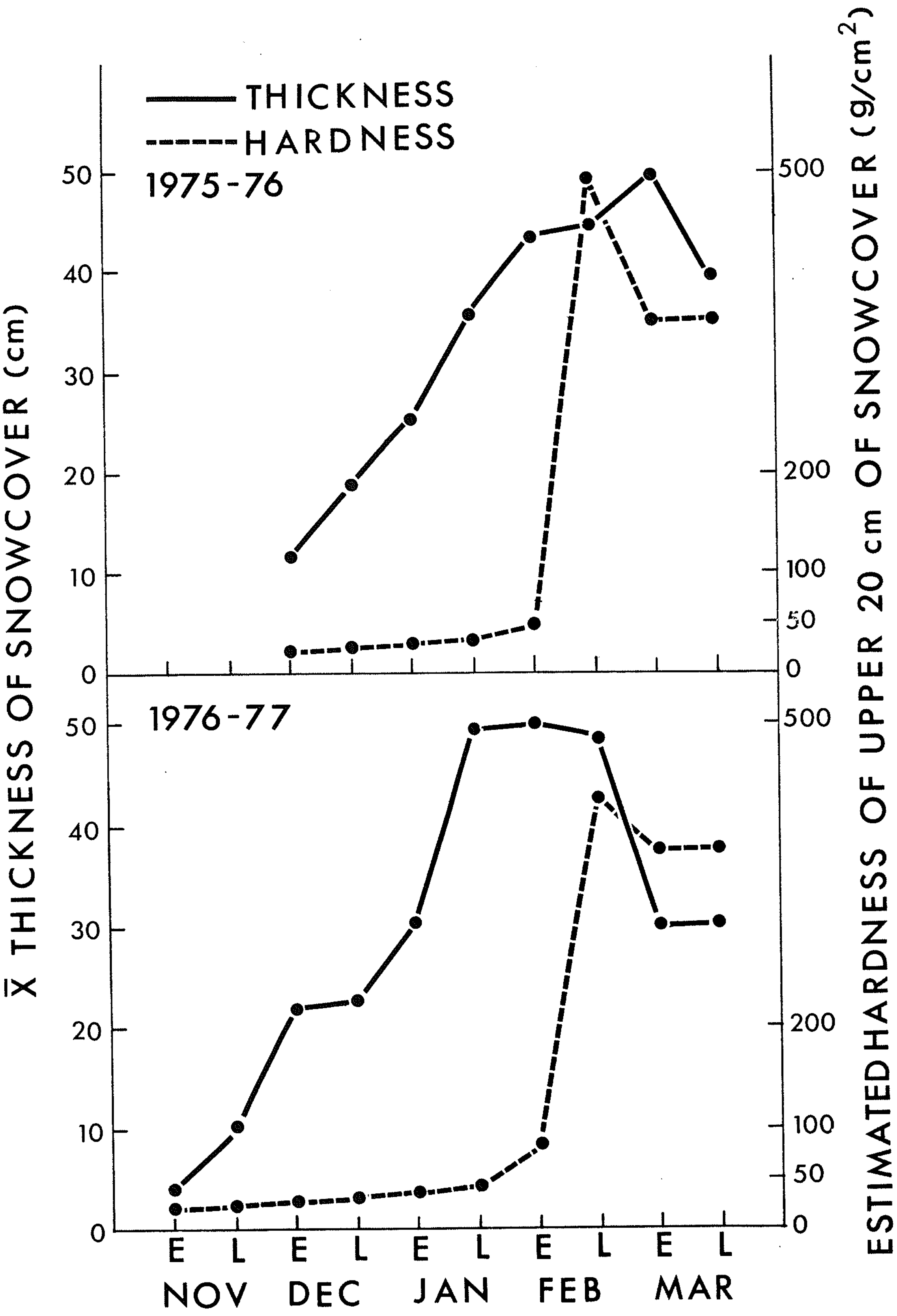

a
b
c

Figure 6 shows the thickness and hardness (relevant to fisher locomotion) of the snow cover during the winters of 1975-76 and 1976-77. Figure 7 depicts a conceptual representation of major events of formation of the snow cover for each winter. Both winters exhibited a markedly similar pattern, particularly with respect to details that could affect fisher locomotion.

Changes in cover type selection, gaits, and amount of track activity occurred concomitantly with changes in the snow cover. Each winter began with a period of relatively frequent track observations (Fig. 3). Snow cover was thin and soft (Fig. 6) and fishers used the lope and double bound (Table 5). In early November 1976 much of the activity was on ice near shorelines (Table 4). When snow accumulation reached 4-5 cm in the intensive study area, fishers confined activity to forested areas and used the double bound.

As each winter progressed, snow thickness increased (Fig. 6) and the number of track observations decreased (Fig. 3). Snow was soft in all cover types and fishers used the double bound (Table 5). In late January and early February 1976 snow conditions were particularly adverse and only two fisher tracks were recorded. On 30 January 1976, I tracked a fisher that was confined to a walking gait in most cover types. This individual left a deep body-drag furrow in the snow cover and its mobility

Figure 6. Thickness and hardness of snow cover in the intensive study area during the winters of 1975-76 and 1976-77.



THICKNESS
HARDNESS
1975-76
1976-77
X̄ THICKNESS OF SNOWCOVER (cm)
ESTIMATED HARDNESS OF UPPER 20 cm OF SNOWCOVER (g/cm²)
0
10
20
30
40
50
0
50
100
200
500
E
L
NOV
DEC
JAN
FEB
MAR

Figure 7. Conceptual representation of major events of formation of the snow cover in the intensive study area during the winters of 1975-76 and 1976-77.

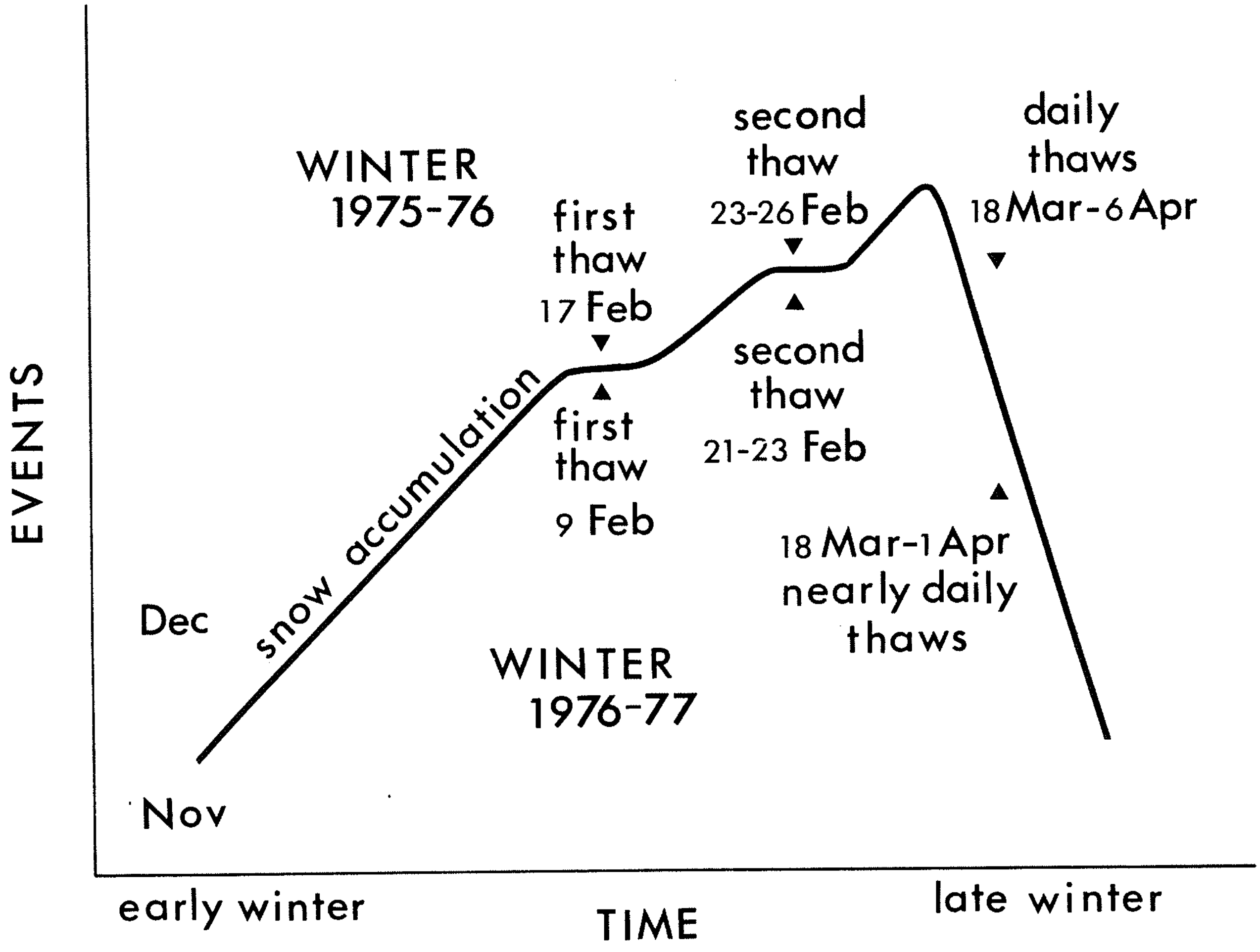

EVENTS
TIME
early winter
late winter
Nov
Dec
snow accumulation
WINTER 1975-76
first thaw 17 Feb
second thaw 23-26 Feb
daily thaws 18 Mar-6 Apr
WINTER 1976-77
first thaw 9 Feb
second thaw 21-23 Feb
18 Mar-1 Apr nearly daily thaws

Table 5. Fisher gaits recorded in the intensive tracking unit during winter.

	1975-76			1976-77		
Period	Bound	Lope	Walk	Bound	Lope	Walk
November E*				1	10	
November L+				2		
December E	4	2		4		
December L	3			4		
January E	3			4		
January L			1	1		
February E			1	9		
February L	2	4		7	27	
March E	3	1		3	2	
March L	2	5		2	10	

E - Early (see text)

L - Late (see text)

appeared to be greatly affected by soft snow. The fisher later intercepted a hard (approximately 1000 gm/cm^2) otter (Lutra canadensis) trail, followed it for 2 km using a lope, and apparently abandoned the trail only because the otter made a radical change of direction.

The first thaw of each winter (Fig. 7) caused notable changes in fisher activity. In 1975-76 the thaw formed a supportive crust in all cover types. Fisher track records increased six-fold over the prior two-week period and four of six tracks were the lope (Table 5). Open bogs were used in proportion to their availability. In 1976-77 the thaw formed a supportive crust only in the open bogs. Fisher activity increased four-fold and 27 of 34 tracks were the lope (Table 5). Open bogs, the only cover type possessing the crust, were the site of much of the increase in activity (Table 4).

During both winters the second series of thaws (Fig. 7) affected all cover types and the relatively high plane of activity continued (Fig. 3).

Soft snow accumulated in all cover types during early March in 1976 and 1977. Snow conditions resembled those of early winter because the crust had supporting characteristics similar to those of bare ground. Figure 3 indicates that activity declined to the respective levels observed in early winter. The double bound was recorded more frequently than the lope during this period (Table 5).

The daily and almost daily thaws of late March 1976 and 1977, respectively, softened the snow cover during daylight hours. Freezing nocturnal temperatures hardened the snow surface (1000 to 4000 gm/cm^2 surface hardness). Confirmed cases of activity of two radio-tagged female fishers (Table 1) were shared evenly between diurnal and nocturnal periods during much of early March 1977. In late March 1977 both individuals almost simultaneously reduced diurnal activity on days when thaws softened the snow cover. Examination of tracks showed that radio-tagged fishers sank deeply in the snow cover during mid-day, but at night were supported by a crust.

Temperature: Mean temperatures for each two-week period were inversely related to the number of track observations; however, regressions of mean temperatures on track observations could explain little of the variance in total activity in 1975-76 (r^2 = .387) and less in 1976-77 (r^2 = .104). Table 6 shows the frequency of days during each two-week winter period that had a minimum temperature below the estimated Tc of fishers (Powell 1979a). A regression of the percent occurrence of days with minimum temperature below Tc (lower critical temperature) on number of track observations was not significant for either 1975-76 or 1976-77. The relationship between

Table 6. Percent occurrence of days that had minimum temperatures below estimated+ Tc for male (-30°C) and female (-20°C) fishers during 1975-76 and 1976-77.

Period	1975-76		1976-77	
	Males	Females	Males	Females
November E[1]			0	0
November L*			13	33
December E	50	87	53	93
December L	13	38	44	81
January E	40	80	53	100
January L	19	75	50	100
February E	47	67	36	71
February L	7	29	7	71
March E	20	73	33	67
March L	6	25	0	25

[1] E = Early (see text)

+ from Powell (1979a)

* L - Late (see text)

Tc and track observations explained little of the variance in total activity in 1975-76 ($r^2 = .287$) or 1976-77 ($r^2 = .247$). Wind speeds did not appear to be an important factor affecting fishers.

Moonlight: I could detect no moonlight-related changes in activity of two female and two male fishers radio-tracked during winter. Different phases of the moon with a variety of cloud cover could not explain the pattern of track observations depicted in Figure 3.

Interspecific relationships: Presence of other mammalian predators (*Canis lupus*, *Vulpes fulva*, *Lynx canadensis*, *Lutra canadensis*, and *Mustela* spp.) in areas where fishers were present did not appear to influence fisher activity. Except for the previously mentioned case of a fisher following an otter trail, fishers seldom displayed interest in tracks of other predators. On one occasion a female fisher in active pregnancy scent-marked a fox trail that was located 15 m from the fisher's sub-nivean den.

Staple prey species (see Section II; Winter Diet) did not change in number, distribution or availability in a fashion that was related to fisher activity depicted in Figure 3. In one case prey did appear to be partially responsible for affecting fisher activity during a short period of the study. In November 1976 tracking evidence indicated that fishers hunted muskrats that were apparently frozen out of their winter push-ups. Cessation of fisher activity on shore ice, disappearance of muskrats, and a change of snow conditions (described previously) all occurred during the same time span.

Intraspecific relationships: The general increase in fisher track observations in late winter could be partially attributed to changes in social behavior of fishers (see Section III; Breeding Biology).

Movements in relation to age class

Age class distribution of a sample of fishers trapped within 75 km of the intensive study area serves as an index of age-related movements and susceptibility to trapping (Table 7). The ratio of juveniles to adult females older than two years (those adult females old enough to have produced the juvenile increment) was 10.3:1, at least three-fold greater than expected from the known reproductive potential (see Section III; Breeding Biology). Radio-telemetry data also substantiated that during winter juveniles may move more extensively than adults. A radio-tagged juvenile male was released on 1 November 1976.

Table 7. Age and sex composition of sample of fishers trapped within 75 km of the intensive study area during winters of 1972-73 to 1976-77.

Age Class	Males	Females	Total
Juvenile	39	54	93
1	1	1	2
2	1	4	5
3	3		3
4	1	1	2
5	1	1	2
6	2		2
7	1	1	2
8		1	1
9		1	1
Totals	49	64	113

It remained within the study area until 4 November 1976. On 27 November 1976 this male was killed 60 km west of the release site. A post-mortem examination revealed that this juvenile was in excellent physical condition with mesentary fat, no physical anomalies, and normal size adrenal glands. A juvenile female was captured, radio-tagged, and released on 24 February 1977. Although this female remained in the general region, she used a larger area and moved greater daily distances than an adult female that was radio-tracked during the same winter period. The adult female was not known to have left a 20 km^2 home range during any radio-tracking sessions from 9 April 1976 to 27 May 1977. However, the juvenile female exhibited progressively longer range movements during late March 1977. By 1 April 1977 this juvenile had expanded her range from 16 km^2 to 24 km^2 and continued southerly movements had taken her out of reception range.

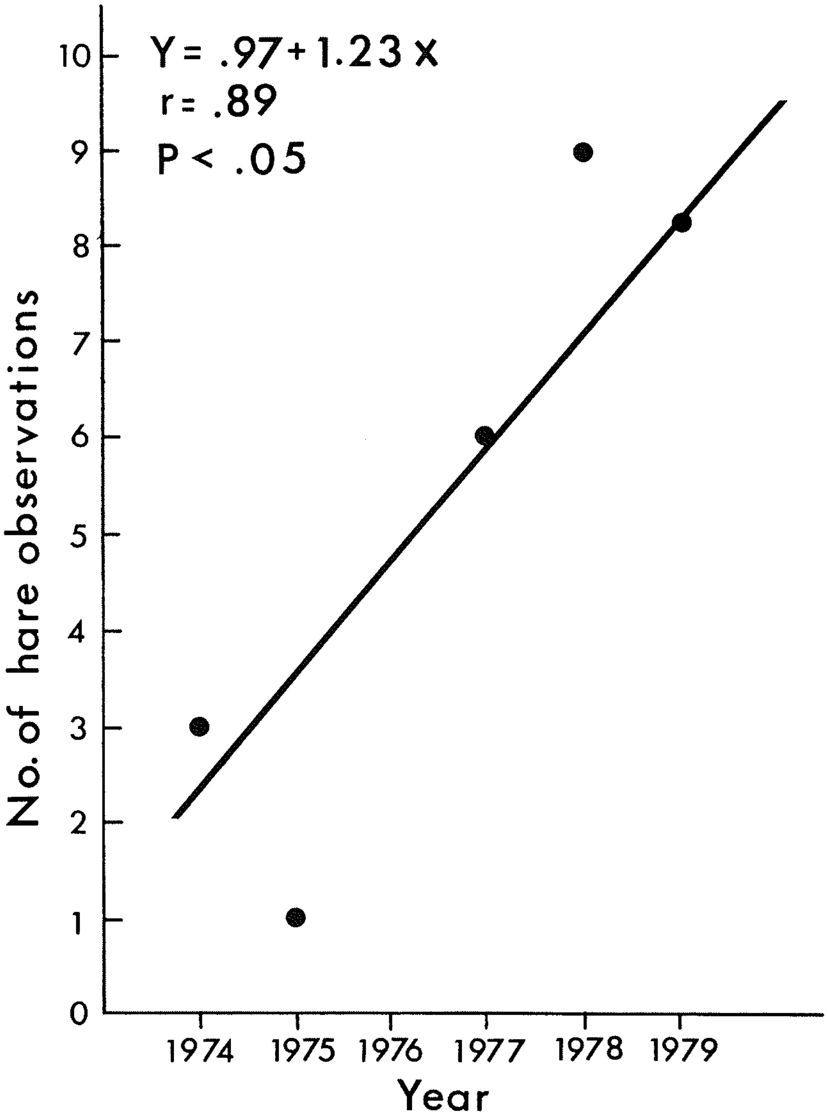
II Winter Diet

Availability of prey and carrion in the intensive study area during winter

Figure 8 shows the regression of number of hare observations made during hare drives (Appendix 1) on individual years. Much of the variance in hare observations (79%) could be attributed to regression on time. Changes in the distribution of hares in the intensive study area also supported the occurrence of an increase in hare numbers. In 1974-75 hare tracks and sign were contagiously distributed, mainly in areas of dense mixed-wood cover on islands and along lakeshores. In 1975-76 hares broadened their general distribution and by 1976-77 hare sign was recorded in all cover types.

No evidence of porcupines was recorded during winter in the intensive study area, although one individual was observed in October 1975. The detrimental snow cover and weather conditions of the winter of 1974-75 reduced the numbers of small mammals (Penny 1978). Red squirrels and flying squirrels (*Glaucomys sabrinus*) were present in the study area, but both species limited supra-nivean activity in cold weather. Woodland caribou (*Rangifer tarandus caribou*) and moose did not exhibit a substantial mortality within the intensive study area. Tracks of white-tailed deer were observed only once during winter in the study area. Therefore ungulate carrion was rare. Muskrats frozen out of winter push-ups were observed in November 1976 and December 1977. Beaver travelled from their ponds in 1976-77, and if mortality occurred, were a potential source of carrion.

Figure 8. Increasing index of hare numbers determined from a hare drive performed in December in the intensive study area.


Y = .97 + 1.23 X
r = .89
P < .05
No. of hare observations
0
1
2
3
4
5
6
7
8
9
10
1974
1975
1976
1977
1978
1979
Year

Ravens (*Corvus corax*), gray jays, ruffed grouse (*Bonasa umbellus*), spruce grouse (*Conachites canadensis*), boreal chickadees (*Parus hudsonicus*), and black-capped chickadees (*Parus atricapillus*) were the birds most often observed in the intensive study area during winter.

Foraging behavior

Foraging behavior was recorded from following fisher trails 31.4 km from December to March 1975-76 and 22.1 km from November to March 1976-77. The majority of trails were characterized by either: (1) unidirectional long distance (>1 km) travel, or (2) intensive use of a restricted area (usually <2 km^2). Foraging appeared to be the sole purpose for the latter type of activity. Fishers hunted opportunistically and used overturned tree roots, qaminiqs of coniferous trees, and piles of brush to facilitate attacks on prey. A dominant feature of fisher travel was the use of fallen logs. Fishers travelled upon most logs they encountered; if more than about 30 cm of snow had accumulated on a log, fishers travelled alongside or under it. All activity, except for two records of brief arboreal excursions, was terrestrial.

A total of 53.5 km of tracking revealed two kills (red squirrel and ruffed grouse) and three insignificant scavenges. The mean distance between kills or scavenges was 10.7 km.

Ungulate carrion that was experimentally introduced into the intensive study area elicited a varied response from different fishers. One individual, probably the radio-tagged adult female, investigated but consumed little carrion. At least one other fisher consumed considerable amounts of carrion during a three day period. In general, the introduced carrion did not appear to affect the dispersion of fishers in the area. Fisher tracks and resting forms were observed near a woodland caribou that had been killed by wolves (*Canis lupus*) northeast of the intensive study area.

Composition of the winter diet

Table 8 lists the percent occurrence of food items from fishers collected from November to March during the winters of 1972-73 to 1977-78. Twenty-two genera and 20 species were identified. Mammals and birds dominated as winter food sources. The most frequently taken mammal was snowshoe hare (35.8%). The birds most often recorded were grouse (10.0%). Table 9 shows the percent occurrence of food items from scats collected in the intensive study area during winter.

Table 8. Frequency of occurrence of food items in alimentary tracts of fishers collected in Manitoba during the winters of 1972-73 to 1977-78. (N=120).

Taxon	No.			% Occurrence		
MAMMALIA	95			79.2		
Unidentified large mammal[1]		8			6.7	
Unidentified small mammal		14			11.7	
Lagomorpha						
Leporidae						
Lepus americanus			43			35.8
Rodentia						
Cricetidae		24			20.0	
unidentified cricetid			8			6.7
Ondatra zibethicus			5			4.2
Clethrionomys gapperi			4			3.3
Microtus pennsylvanicus			5			4.2
Peromyscus maniculatus			2			1.7
Sciuridae		16			13.3	
unidentified sciurid			1			0.8
Sciurus carolinensis			2			1.7
Tamiasciurus hudsonicus			10			8.3
Glaucomys sabrinus			2			1.7
Marmota monax			1			0.8
Castoridae						
Castor canadensis			5			4.2
Erethizontidae						
Erethizon dorsatum			5			4.2

cont'd....

Table 8. cont'd

Taxon	No.	% Occurrence
Zapodidae		
Zapus hudsonius	1	0.8
Insectivora		
Soricidae	9	7.5
unidentified soricid	5	4.2
Sorex cinereus	1	1.7
Blarina brevicauda	3	2.5
Carnivora		
Mustelidae	3	2.5
Mustela vison	1	0.8
Mustela sp.	2	1.7
Artiodactyla		
Cervidae	9	7.5
AVES	58	48.3
Unidentified aves	29	24.2
Anatidae	9	7.5
unidentified anatid	8	6.7
Anas platyrhynchos	1	0.8
Accipitridae		
Buteo jamaicensis	1	0.8
Tetraonidae	12	10.0
unidentified tetraonid	7	5.8
Bonasa umbellus	3	2.5

cont'd .....

Table 8. cont'd

Taxon	No.		% Occurrence	
Conachites canadensis		2		1.7
Corvidae	7		5.8	
Corvus sp.		3		2.5
Perisoreus canadensis		4		3.3
REPTILIA	1		0.8	
Thamnophis sp.		1		0.8

---

[1] Large mammal is larger than a gray squirrel (*Sciurus carolinensis*).

Table 9. Percent occurrence of food items from scats collected from fisher trails in the intensive study area.

Food Item	Winter 1975-76 (N = 32)	Winter 1976-77 (N = 19)
Lepus americanus	65.6	63.2
Small mammals	40.6	5.3
unidentified	9.3	
Clethrionomys gapperi	6.3	5.3
Microtus pennsylvanicus	25.0	
Ondatra zibethicus	6.3	
Cervids		5.3
Birds	12.5	21.1
Anatids	3.1	
Egg	3.1	

Geographic variation in diet

Table 10 shows the percent frequency of occurrence of major food groups from fishers collected during three successive winters. There were no significant ($p > .10$) geographic differences in proportions of food groups during individual winters. Samples too small in number to test showed the same trend as larger samples of the respective food groups. Occurrence of porcupines, detected from remains in alimentary tracts and from quills recovered from body musculature, revealed marked geographic differences: 14.3%, 11.1%, 2.7%, and 0.0% were recorded from Southeast, West, East Lake Winnipeg, and Whiteshell areas, respectively.

Sex differences in diet

Females showed a greater frequency of hares than did males in 1974-75 (30% versus 8%) and 1975-76 (27.8% versus 16.7%), but males displayed a greater frequency than did females in 1976-77 (55% versus 43.5%). These differences were not significant ($p > .10$). When the entire sample was combined, females showed insignificantly ($p > .10$) greater frequencies of sciurids (12.9% versus 8.0%), small mammals (27.4% versus 22.4%), and >1 small mammals (8.1% versus 5.2%). Carrion, muskrats, and birds were present

Table 10. Variation in percent occurrence of major food types during the winters of 1974-75, 1975-76, and 1976-77. Sample sizes are in parentheses.

	East Lake Winnipeg			Whiteshell			Southeast			West			All Areas Combined		
Category	1974-1975 (26)	1975-1976 (27)	1976-1977 (41)	1974-1975	1975-1976 (10)	1976-1977 (5)	1974-1975	1975-1976 (6)	1976-1977 (8)	1974-1975 (15)	1975-1976 (9)	1976-1977 (2)	1974-1975 (41)	1975-1976 (52)	1976-1977 (56)
Empty[1]	46.2	29.6	22.0		30.0	60.0		33.3	12.5	40.0	44.4	50.0	43.9	32.7	25.0
Snowshoe hares	11.5	18.5	39.0		10.0	20.0			50.0	6.7	11.1	50.0	9.7	13.5	39.3
Squirrels	11.5	3.8	14.6					16.7	37.5		11.1	50.0	7.3	5.8	17.9
Small mammals[2]	23.1	14.8	17.1		10.0			16.7	37.5	40.0	11.1		29.0	17.3	17.9
>1 Small mammal	7.7	7.4								20.0	22.2		12.2	7.7	
Other mammals[3]	15.4	11.1	12.2							20.0	22.2		17.1	9.6	8.9
Birds	19.2	44.4	31.7		40.0	40.0		33.3	25.0	40.0	33.3	50.0	26.8	40.4	32.1
Carrion	11.5	3.8	7.3		20.0			33.3			11.1		7.3	11.5	5.4

[1] includes specimens with bait, [2] mammals smaller than squirrels, [3] includes porcupines, muskrats, and unidentified mammals.

in similar frequencies for both sexes. A significantly greater proportion of porcupine quills was found in body musculature of males than in females ($X^2 = 6.43$, d.f. = 1, $p < .025$).

Temporal variations in diet, condition index, and frequency of empty tracts

Table 10 presents the temporal variation in proportion of major food items from fishers taken in the four study areas. Table 11 lists the results of tests of difference in proportions and ordering of proportions of major food items for the three successive winters of 1974-75, 1975-76, and 1976-77. Two null hypotheses were tested: (1) no significant difference in proportions of major food items existed among years (Chi-squared test), and (2) no significant difference in ordering of proportions of major food items existed among years (Bartholomew's test, Fleiss 1973). Yearly changes in the number of food items recorded per individual are shown in Table 12. The relationship between percent frequency of hares and percent frequency of >1 small mammal for the winters of 1974-75, 1975-76, and 1976-77 is shown in Figure 9.

Figure 9. Regression of percent frequency of >1 small mammal on percent frequency of snowshoe hare.

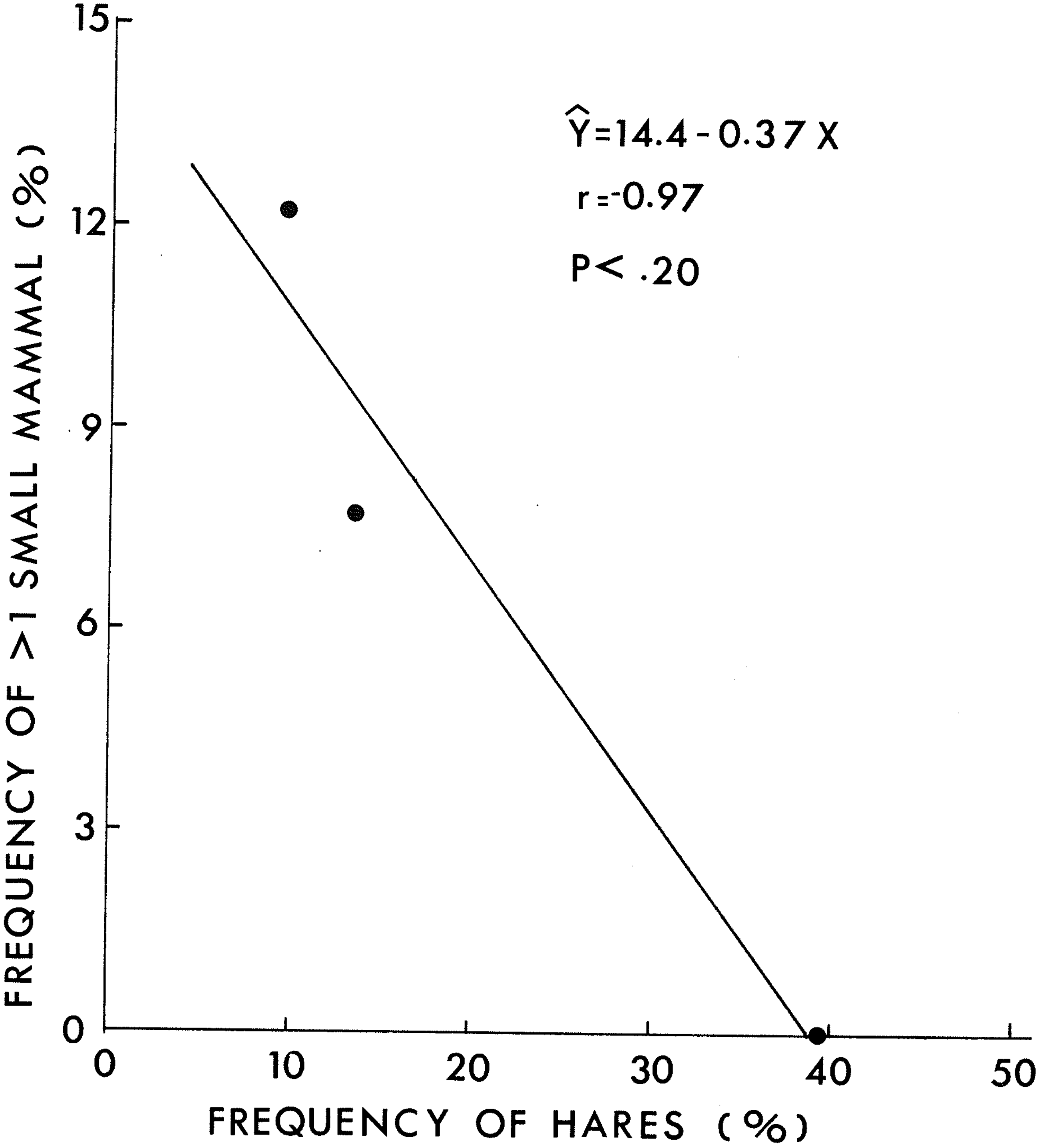

$\hat{Y}$=14.4 - 0.37 X
r =-0.97
P< .20
15
12
9
6
3
0
0
10
20
30
40
50
FREQUENCY OF >1 SMALL MAMMAL (%)
FREQUENCY OF HARES (%)

Table 11. Tests for among-year differences and trends in proportions of food items from fishers collected during the winters of 1974-75, 1975-76 and 1976-77. * denotes significance at $p < .10$ or lesser p.

Food Item	Test of difference in proportions		Test of trend in proportions		
	X^2_{2df}	P<	c	P<	Trend
Snowshoe hares (ELW[1], with empty[2])	7.32*	.05	.5439*	.01	increase
Snowshoe hares (ELW, without empty)	4.71*	.10	.5159*	.05	increase
Snowshoe hares (all areas, with empty)	15.5*	.001	.4781*	.005	increase
Snowshoe hares (all areas, without empty)	23.5*	.001	.4650*	.001	increase
Squirrels (with empty)	11.9*	.005			
Squirrels (without empty)	2.26	.25			
Small mammals (with empty)	3.04	.25			
Small mammals (without empty)	7.43*	.025	.4700*	.01	decrease
> 1 Small mammal (with empty)	7.99*	.025	.4780*	.005	decrease
>1 Small mammal (without empty)	11.5*	.005	.4700*	.005	decrease
Birds (with empty)	1.99	.5			
Birds (without empty)	2.86	.25			
Carrion (with empty)	2.41	.5			
Carrion (without empty)	2.05	.5			

---

[1] East Lake Winnipeg

[2] Tracts containing bait or no food

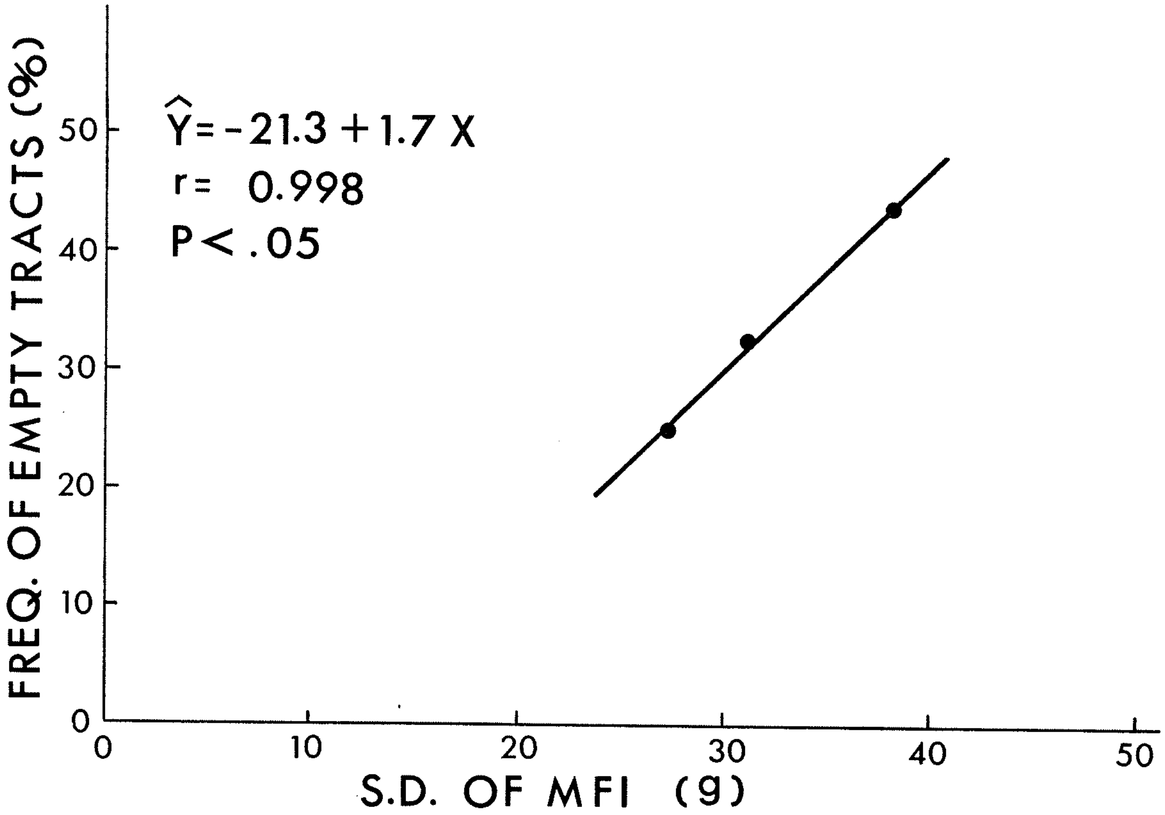
Table 12. Winter variation in number of food items per individual trapper-caught fisher carcass.

No. of food items per individual	1974-75		1975-76		1976-77	
	No.	Percent	No.	Percent	No.	Percent
1	12	50.0	19	52.8	25	54.3
2	5	20.8	15	41.6	15	32.6
3	2	8.3	1	2.8	6	13.0
4	3	12.5	1	2.8		
5	1	4.2				
6	1	4.2				

Fishers collected during the winters of 1974-75, 1975-76, and 1976-77 had similar mean condition indices of 53.5 g, 50.1 g, and 51.8 g, respectively. The standard deviations of condition indices followed a decreasing trend from 1974-75 to 1976-77 (38.1 g, 31.1 g, 27.2 g), but no significant differences existed between variances (Levene's test, Levene 1960). The proportion of empty tracts did not exhibit a significant difference among years, but a significant ordering of proportions (proportion 1 > proportion 2 > proportion 3) was evident for the East Lake Winnipeg area ($X^2 = 4.40$, $c = .5439$, $p < .10$) and all areas combined ($X^2 = 3.83$, $c = .4781$, $p < .10$). Ten of 19 tracts collected during the winters of 1972-73 and 1973-74 were empty. Figure 10 shows the regression of percent frequency of alimentary tracts on the standard deviations of condition indices for the winters of 1974-75, 1975-76, and 1976-77.

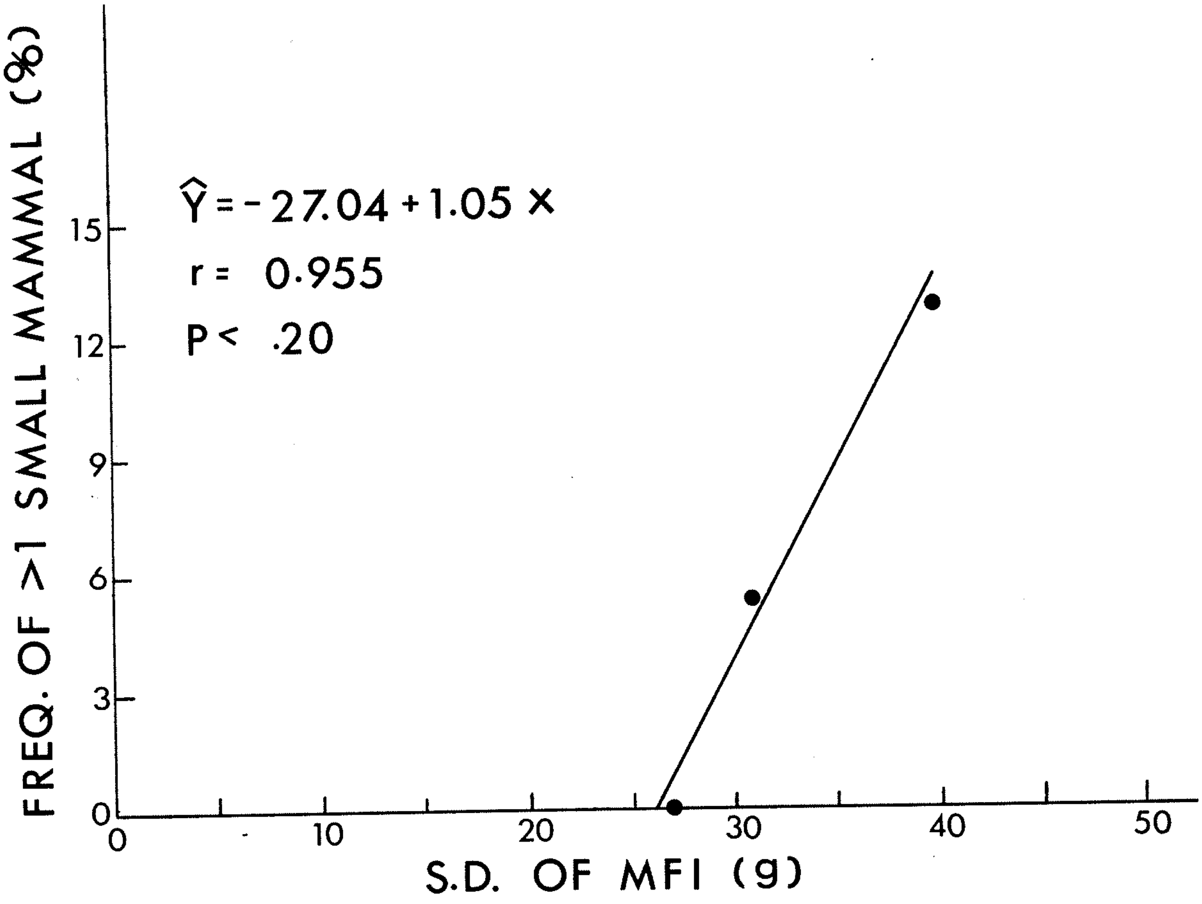
Figures 11 and 12 depict the relationship between food categories that showed a significant ordering of proportions; namely, hares and >1 small mammal, and standard deviations of the condition indices for the winters of 1974-75, 1975-76, and 1976-77.

Figure 10. Regression of percent frequency of empty alimentary tracts on standard deviations of condition indices. S.D. - standard deviation, MFI - mesentary fat index. Error in S.D. is small due to large samples each year.



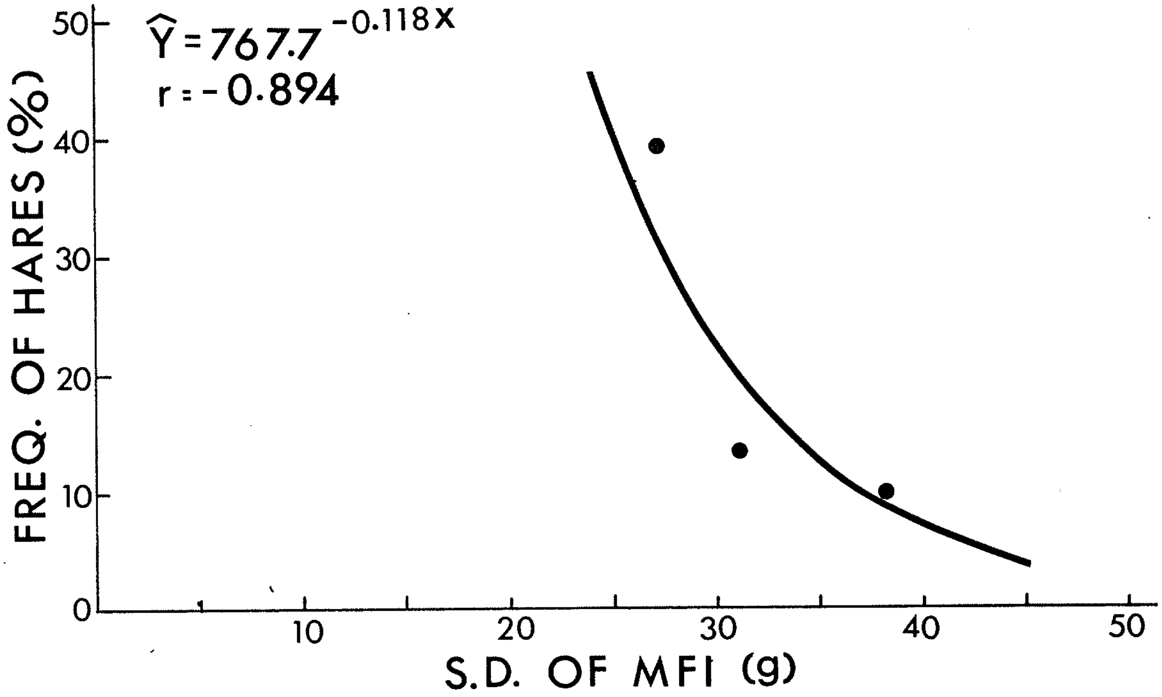
$\hat{Y} = -21.3 + 1.7X$
r = 0.998
P < .05
FREQ. OF EMPTY TRACTS (%)
0
10
20
30
40
50
S.D. OF MFI (g)
0
10
20
30
40
50

Figure 11. Regression of percent frequency of >1 small mammal on standard deviations of condition indices.



$\hat{Y} = -27.04 + 1.05X$
r = 0.955
P < .20
FREQ. OF >1 SMALL MAMMAL (%)
15
12
9
6
3
0
0
10
20
30
40
50
S.D. OF MFI (g)

Figure 12. Regression of percent frequency of snowshoe hares on standard deviations of condition indices.


$\hat{Y} = 767.7^{-0.118X}$
r = -0.894
FREQ. OF HARES (%)
0
10
20
30
40
50
10
20
30
40
50
S.D. OF MFI (g)

Changes in estimates of consumption rate

Table 13 shows the gross energy (GE) values and weights of meals estimated for male and female fishers. Data include only food types that Davison (1975) fed to captive fishers. Table 14 lists the estimated weight per unit meal and energy values of all food types found in alimentary tracts of fishers taken in the East Lake Winnipeg region during the winters of 1974-75, 1975-76, and 1976-77. For these fishers, the estimated mean metabolizable energy available from scavenges is shown in Table 15. Table 16 shows the partitioning of consumption rate in time for individual food types taken by fishers from East Lake Winnipeg during winter. Table 17 summarizes metabolizable energy (ME) intake for each winter sample and an estimate of the daily consumption rate of individual fishers for each winter. Estimated consumption rate increased 42 percent from 1974-75 to 1975-76, and increased 16 percent from 1975-76 to 1976-77.

Table 13. Estimated meal sizes of four food types eaten by fishers. Meal size of females and subsequent estimates are based on feeding trials of captive female fishers (Davison 1975). GE = Gross energy.

Food Type	Meal size of females[1]		Estimated meal size of males[2]		Mean of female meal size and estimated male meal size	
	GE kJ	Weight (g)	GE kJ	Weight (g)	GE kJ	Weight (g)
Snowshoe hare	1403	238	2806	476	2105	358
Deer carrion	1949	244	3898	488	2924	366
Small mammal[3]	1585	245	3170	489	2378	369
Bird[4]	2024	249	4048	498	3054	375

[1] Calculated directly from results of feeding trials (Davison 1975).

[2] See text for explanation of estimates.

[3] 73% meadow vole, 16% short-tailed shrew, 11% white-footed mouse (from Davison 1975).

[4] Coturnix quail.

Table 14. Estimated energetic values of food items eaten by fishers in the East Lake Winnipeg area during winter. ME = metabolizable energy, GE = gross energy.

Food Type	ME/GE %	ME/kg kJ	Weight/ unit meal kg	ME/ unit meal kJ
Snowshoe hare[1]	76.7	4512	.358	1615
Mouse[1]	73.9	4789	.028	134
Shrew[1]	73.9	4402	.016	70
Squirrel[+]	75.2	4650	.190	884
Muskrat[+]	81.0	5648	.358	2022
Unidentified Mammal[+]	77.6	5593	.191	1068
Grouse[+]	86.9	7068	.375	2651
Jay[+]	86.9	7068	.073	516
Duck[+]	86.9	7068	.375	2651
Unidentified bird[+]	86.9	7068	.325	2295

[1] from Davison (1975).

[+] See text for explanation of estimate.

Table 15. Estimated mean metabolizable energy (kJ) available from scavenges known from analysis of alimentary tracts. Number of fisher carcasses analyzed is in parentheses.

Scavenge class[1]	Winter 1974-75 (26)	 1975-76 (27)	 1976-77 (41)
Insignificant	0.0		0.0
Intermediate	22.9	22.1	14.5
Significant	127	61.4	40.4
Totals	150	83.5	54.9

[1] See text for explanation of class.

Table 16. Partitioning of estimated consumption rate for fishers collected in the East Lake Winnipeg area during winter. CR = estimated consumption rate[1] in metabolizable energy/day.

Winter	1974-75		1975-76		1976-77	
	CR		CR		CR	
Food Type	kJ/day	%	kJ/day	%	kJ/day	%
Snowshoe hares	151	15.5	316	18.7	738	36.5
Small mammals	34	3.5	37	2.2	25	1.2
Squirrels	55	5.6	35	2.1	151	7.5
Muskrats	63	6.5	79	4.6	58	2.9
Carrion[2]	121	12.4	88	5.2	64	3.2
Unidentified mammals	100	10.3	42	2.5	122	6.0
Birds	450	46.2	1091	64.6	862	42.7

---

[1] See text for estimation of consumption rate.

[2] From Table 15.

Table 17. Estimates of metabolizable energy intake for fishers from the East Lake Winnipeg area during winter. ME = metabolizable energy.

	Winter		
Metabolizable Energy	1974-75 (N=26)	1975-76 (N=27)	1976-77 (N=41)
Total ME intake (kJ)	31299	43139	70754
ME intake/fisher (kJ/individual)	1204	1598	1726
ME intake/fisher containing food (kJ/individual)	2236	2270	2211
Consumption rate[1] ME/day (kJ/day)	974	1688	2020

---

[1] See text for estimation of consumption rate.

III Breeding Biology

Age of sexual maturity and timing of reproduction

Eighty-one juvenile females collected during November, December, January, and early February had reproductive tracts that showed no gross signs of increased physiological activity ($\bar{x}$ tract volume = 0.7 ml). All 41 pairs of ovaries that were sectioned had relatively small developing follicles ($\bar{x}$ diameter = 0.1 mm). Two juvenile females killed on 1 and 8 March had large Graafian follicles ($\bar{x}$ diameter = 0.6 mm) and each tract was engorged to a volume of 2 ml. A post-estrus tract from a juvenile female collected in late March had increased in volume to 4 ml. The right ovary contained two recently formed corpora lutea and the left ovary had two Graafian follicles that each displayed an oöcyst on an antrum. The corpora lutea in the ovaries of yearling females (one cementum annulus) indicated that ovulation occurred when these females were in the juvenile age class.

Estimated dates of parturition, based on development of embryos from three adult females in active pregnancy, were late March and early April. Periods of estrus of these females were estimated to occur in early April. The adult female (Table 1) whelped a litter in captivity on 28 March 1976. Between 3 and 5 April 1976 at least one male approached within 25 m of her cage. On 8 April 1976, one day prior to release, her vulvular region displayed external signs of estrus. She whelped a litter in the wild in early (1-3) April 1977. The presence of corpora lutea in her ovaries in December 1977 indicated that she underwent a period of estrus after parturition.

Juvenile testes development paralleled that of adults. Figure 13 shows the maturation of testes of a combined sample of juveniles and adults taken during winter. Only juvenile and adult males taken in March were spermatic. Figure 14 compares juvenile and adult bacula weights. The wide range of adult bacula weights is probably due to the presence of several adult age classes; however, small samples preclude further segregation.

Termination of breeding activity, the length of time a female would remain in estrus if not impregnated, and dates of recrudescence of testes were unknown because of the paucity of observations and specimens after early April. Juveniles collected in November and December exhibited uniform degrees of suture closure and skull and skeletal development, implying that termination of reproductive activity may closely follow the observed onset in late March and early April and that timing of parturition is similar for all age classes.

Figure 13. Maturation of testes of juveniles and adults during winter (n = 31).

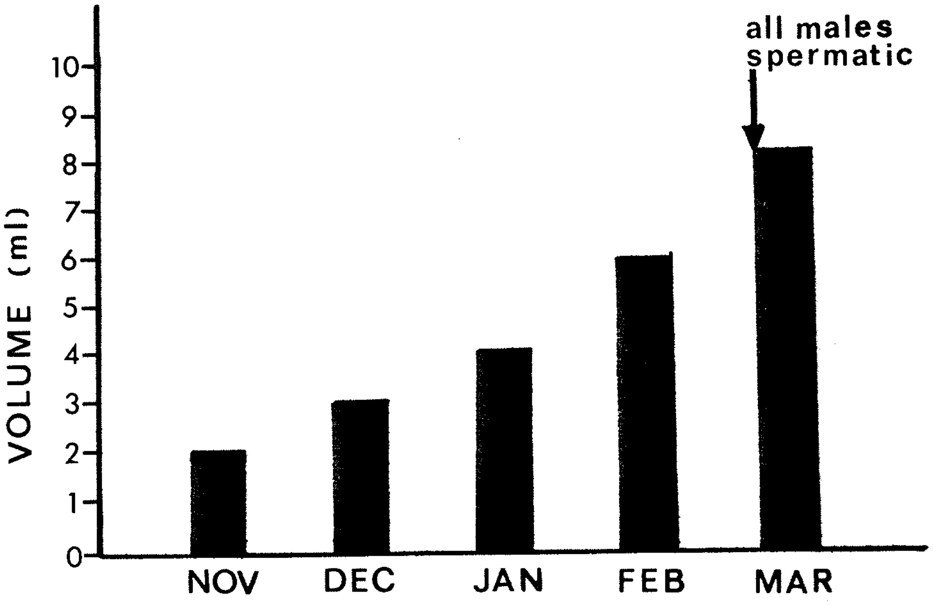
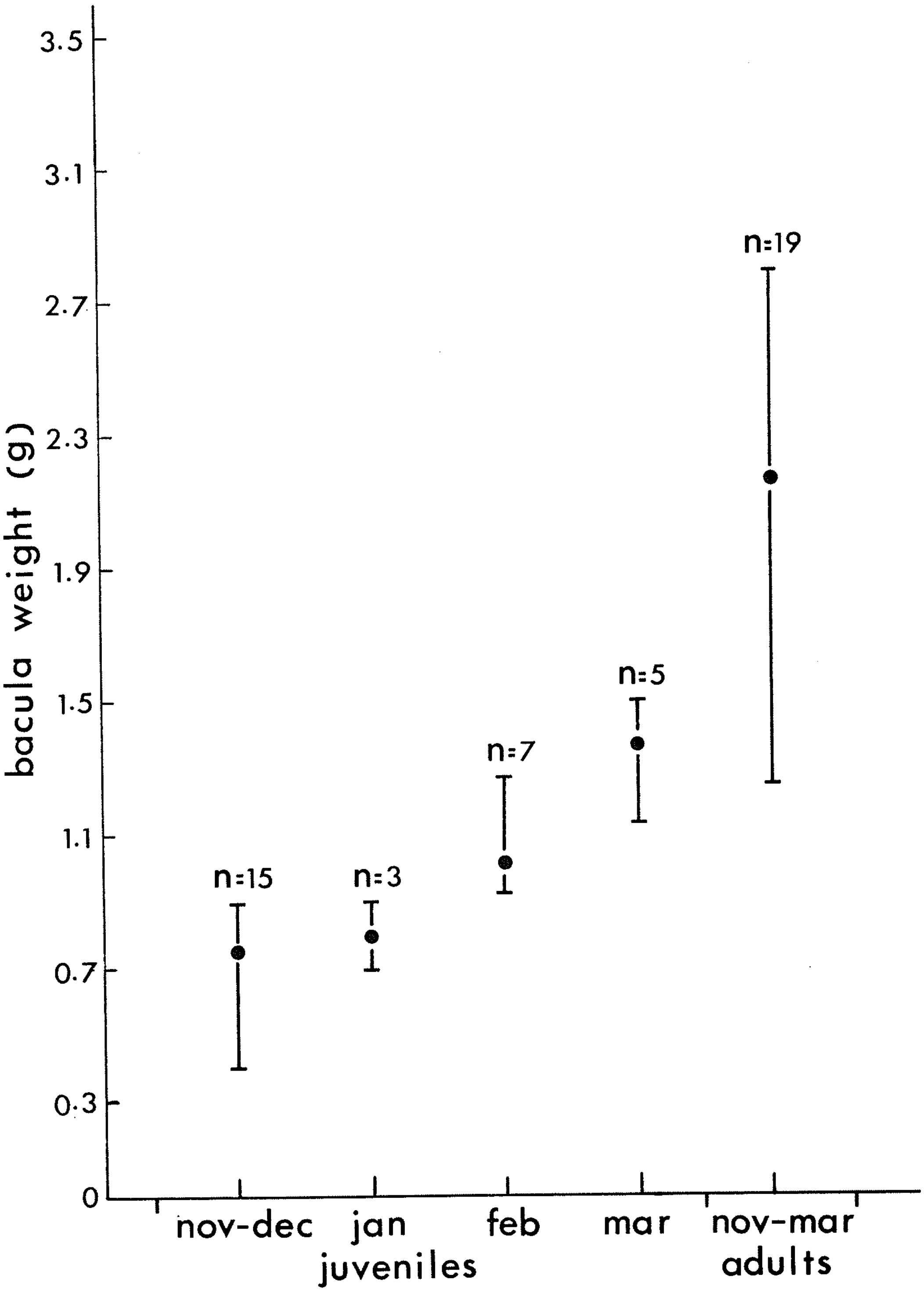

all males spermatic
VOLUME (ml)
0
1
2
3
4
5
6
7
8
9
10
NOV
DEC
JAN
FEB
MAR

Figure 14. Comparison of juvenile and adult bacula weights during winter. Vertical bar denotes range. Dot denotes mean.



bacula weight (g)
3.5
3.1
2.7
2.3
1.9
1.5
1.1
0.7
0.3
0
n=15
n=3
n=7
n=5
n=19
nov-dec
jan
feb
mar
nov-mar
juveniles
adults

During late February and March of two successive winters track records revealed an increase in fisher activity in the intensive study area (see Section I; Winter Activity and Movements). Data from tracking individual fishers a total of 17.7 km in March indicated the change in activity was related to reproductive behavior.

Description of reproductive activity

Much of the increase in activity during March appeared to be due to movements of males; 14 of 18 tracks that could be assigned to sex were made by males. This proportion differed significantly from a 50:50 distribution ($X^2 = 11.8$, d.f. = 1, $p < .005$). In March 1977 a radio-tagged adult male (Table 1) and at least one other male of unknown age moved into the immediate area occupied by the radio-tagged female in active pregnancy. Earlier in winter males had not been known to frequent the general area. Tracking evidence indicated that males did not approach closer than 0.5 km from the adult female in her resting den. Both sexes were apparently aware of the opposite sex in the area, investigated other fisher tracks, and frequently marked elevated surfaces such as rocks and stumps with combinations of urine, musk, and scats. The adult female investigated the site where the male was live-trapped and approached within 150 m of the Taiga Biological Station where the male was being radio-tagged. Four days after I initially detected the adult male in the area, it moved out of radio reception in less than 8 h.

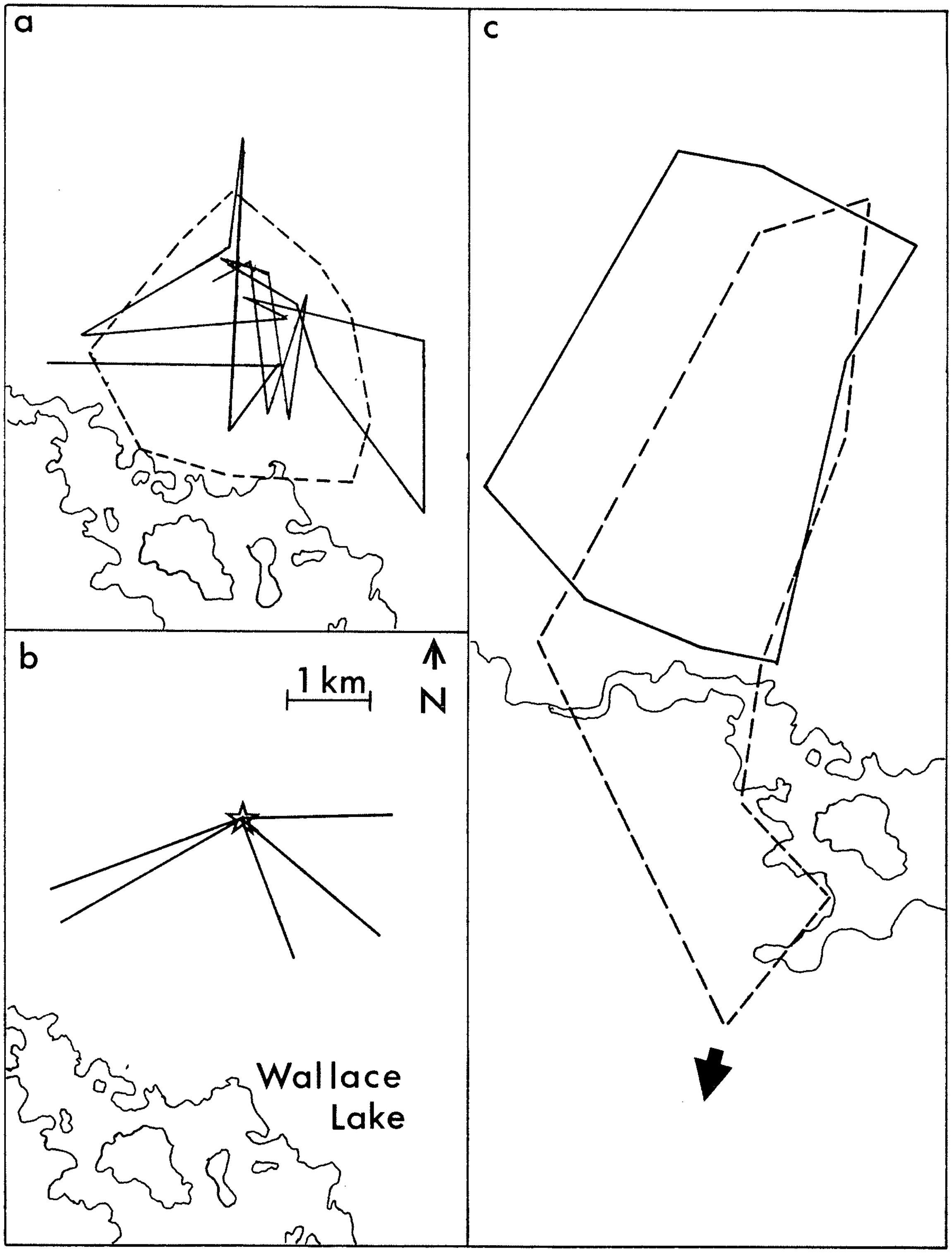
Although tracks of different males were observed less than 1 km apart, no male-male interactions were recorded. Skulls of males frequently exhibited fractured zygomas, an injury that was never observed in females. This type of injury was significantly more common in males that had experienced at least one breeding season (adults) than in males too young to have passed a breeding season (juveniles) $[\chi^2 = 13.5$, d.f. = 1, $p < .005]$. One of five juvenile males collected in March, during the onset of breeding, had a recently-fractured zygoma.

Radio-telemetry yielded data on movements of a juvenile and an adult female during the breeding period. Figure 15a and 15b show the movements of the adult female during two successive periods of estrus in April 1976 and April 1977. Figure 15c shows that the juvenile female extended her movements and travelled out of radio-reception during an estimated estrous period.

Figure 15. Movements of female fishers determined from radio-telemetry during the breeding period. a) Extensive movements of barren adult female in estrus in April 1976 (n = 71; solid line) in comparison to a polygon containing 95% of her activity during a subsequent four month period (n = 247; dashed line).

b) Movements of the same adult female during an estimated period of estrus the following year (n = 81). She attended recently-born kits in the den denoted by a star. Movements are typical linear type; see text for definition and explanation.

c) Change in movements of a juvenile female during the onset of the breeding period. Solid line is area used by the female from 22 February 1977 to 14 March 1977 (n = 31). Dashed line is area used by female from 15 March to 29 March 1977 (n = 68). Arrow shows direction of travel of the female when radio-reception was lost.


a
b
1 km
N
Wallace Lake
c

Movements during active pregnancy

Figure 16 shows the movements of the adult female during active pregnancy. Although hard snow present during this period was favorable for fisher locomotion and apparently effected an increase in fisher activity in the intensive study area (see Section I; Winter Activity and Movements), this female moved relatively short distances.

Fertility and productivity

Thirteen of 16 (81.3%) adult females were pregnant during winter. Mean and mode corpora lutea (CL) counts for pregnant females were 3.5 and 3.0, respectively. The mean number of CL per female was reduced to 2.8 when barren females were included in the sample. Figure 17 shows the regression of mean CL/female (including barren females) on age. Three adults in active pregnancy each had three embryos. For these females a total of 10 CL was recorded, indicating an *in utero* loss of 10 percent. A three-year history of reproduction was known from the adult female (Table 1): she whelped four kits in March 1976, whelped at least two (observation in field) and

Figure 16. Movements of adult female during active pregnancy from 13 March 1977 to 1 April 1977 (n = 88).

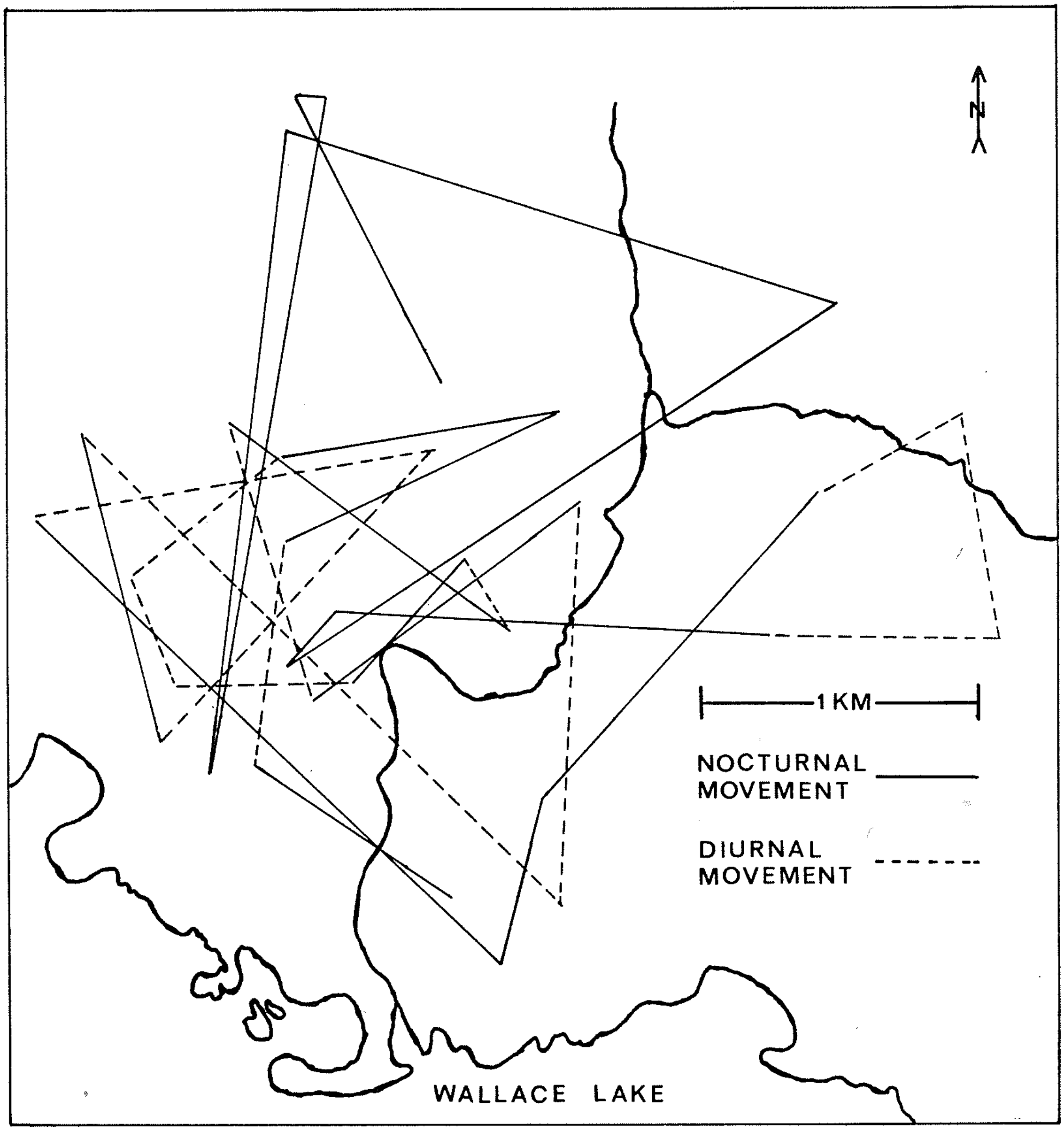
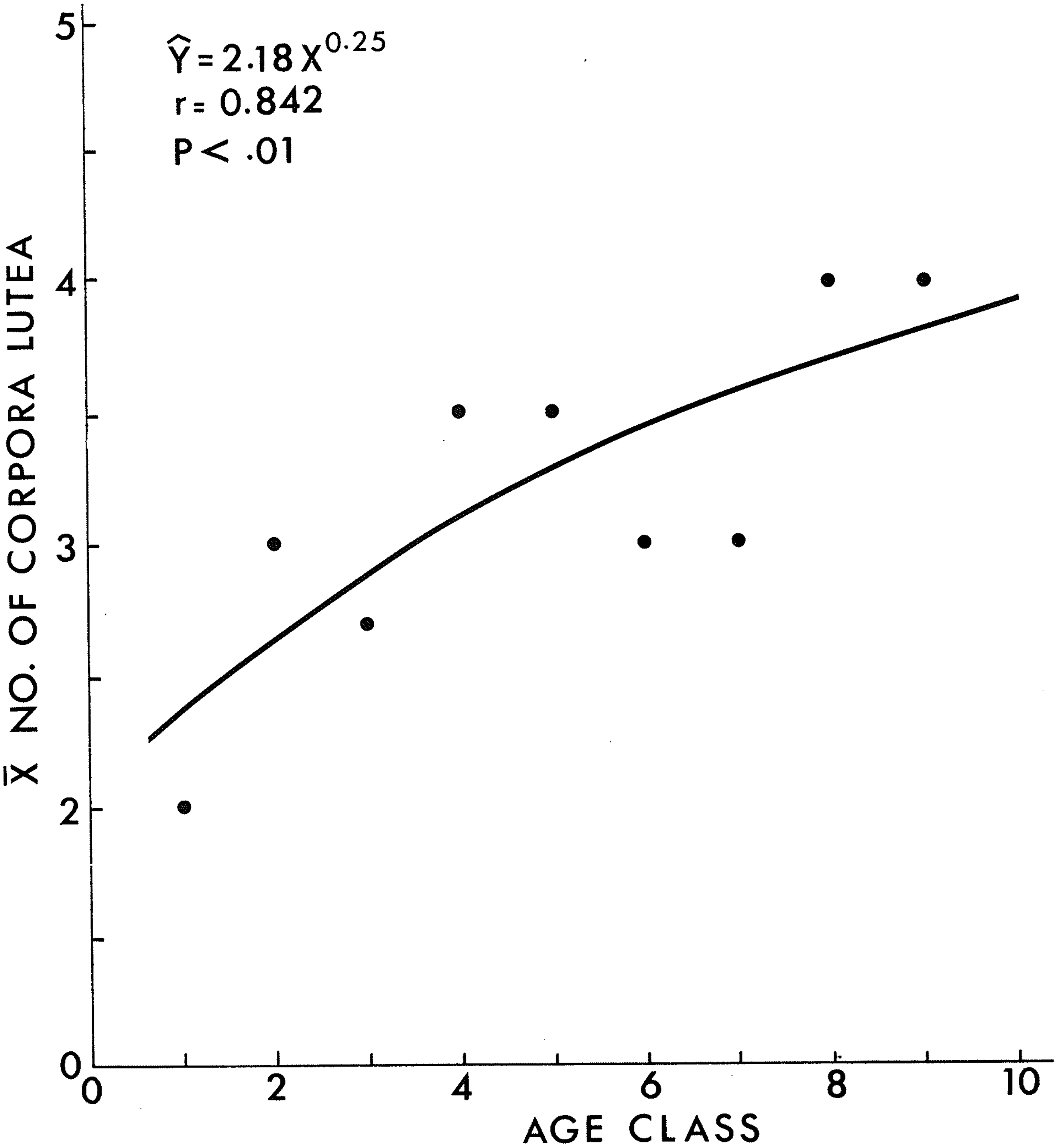

N
1 KM
NOCTURNAL MOVEMENT
DIURNAL MOVEMENT
WALLACE LAKE

Figure 17. Regression of mean number of corpora lutea per female on age class.


$\hat{Y} = 2.18X^{0.25}$
r = 0.842
P < .01
$\bar{X}$ NO. OF CORPORA LUTEA
5
4
3
2
0
0
2
4
6
8
10
AGE CLASS

possibly four (placental scar counts) in April 1977, and had four CL in December 1977. Little among-year variation in indices of fertility rates and productivity existed (Table 18).

Breeding den ecology

Figure 18 depicts the home range use-relationships of the adult female that was radio-tracked during 1976 and 1977. In early (1-3) April 1977 she whelped a litter in a tree-den centrally located in her home range. The den was situated about 10 m above the ground in a partially hollow, living aspen (Populus tremuloides) (Figure 19a, 19b). The female was unable to enter the small opening to the outside that was near the floor of the den. Two other openings large enough to allow entry of the female were higher on the trunk.

Figure 20 shows the diel pattern of denning activity for this female between 12 April, when the presence of the kits was first noted, and 27 May, when she and the kits abandoned the den. Figure 21 shows the highly significant relationship between daily amounts of the female's activity out of the den and time in the denning period ($F = 27.2$, d.f. = 2 and 20, $p < .01$). Much of the variance in amount of activity out of the den could be explained by regression on time ($r^2 = .731$). The female

Table 18. Productivity and fertility indices from fishers collected in Manitoba during winter. CL = corpora lutea.

	Productivity				Fertility	
Winter	No. of juveniles	No. of adult females	Minimum No. of post parturient adult females[1]	Juveniles: Post parturient adult female	No. of pregnant adults	Mean no. CL/pregnant adult
1972-73	8	2	1	8:1		
1973-74	10	1	1	10:1		
1974-75	28	7	6	5:1	3 of 4	3.7
1975-76	44	4	3	15:1	3 of 4	2.7
1976-77	48	6	6	8:1	6 of 6	3.5
1977-78	8	1	1	8:1	1 of 1	4.0

[1] Adult females possessing two cementum annuli (estimated to be 2.5 years old).

Figure 18. Home range use relationships of adult female fisher determined by radio-telemetry.

---------- range during snow free period from April 1976 to September 1976 (n = 318).

_ . _ . _ . _ . range during denning period while attending kits from April 1977 to May 1977 (n = 258). Star denotes location of maternal den.

______________ range during active pregnancy (n = 88).

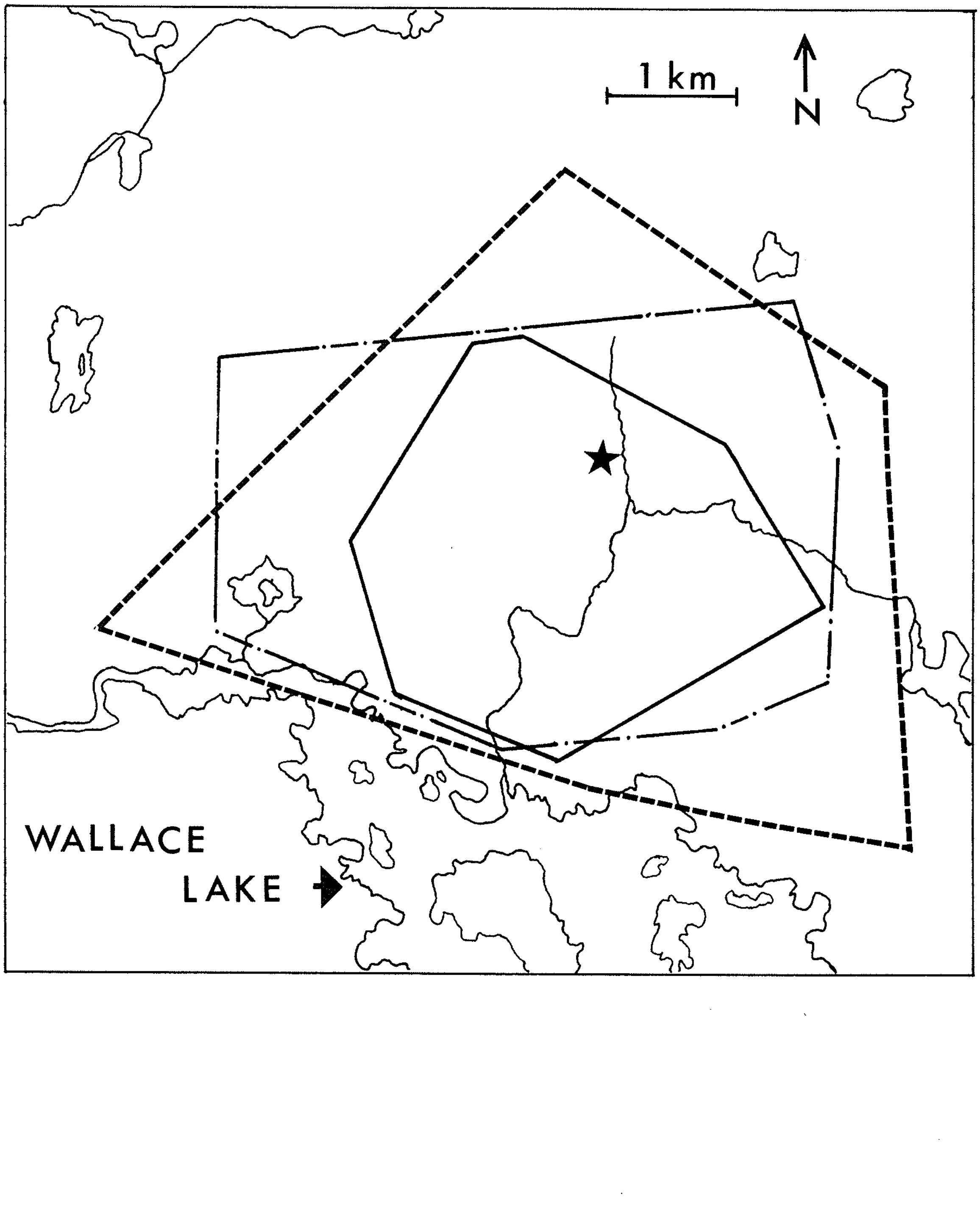

1 km
N
WALLACE
LAKE

Figure 19. a) Den in partially hollow trembling aspen (*Populus tremuloides*) tree.

b) Opening to the outside near the den floor.

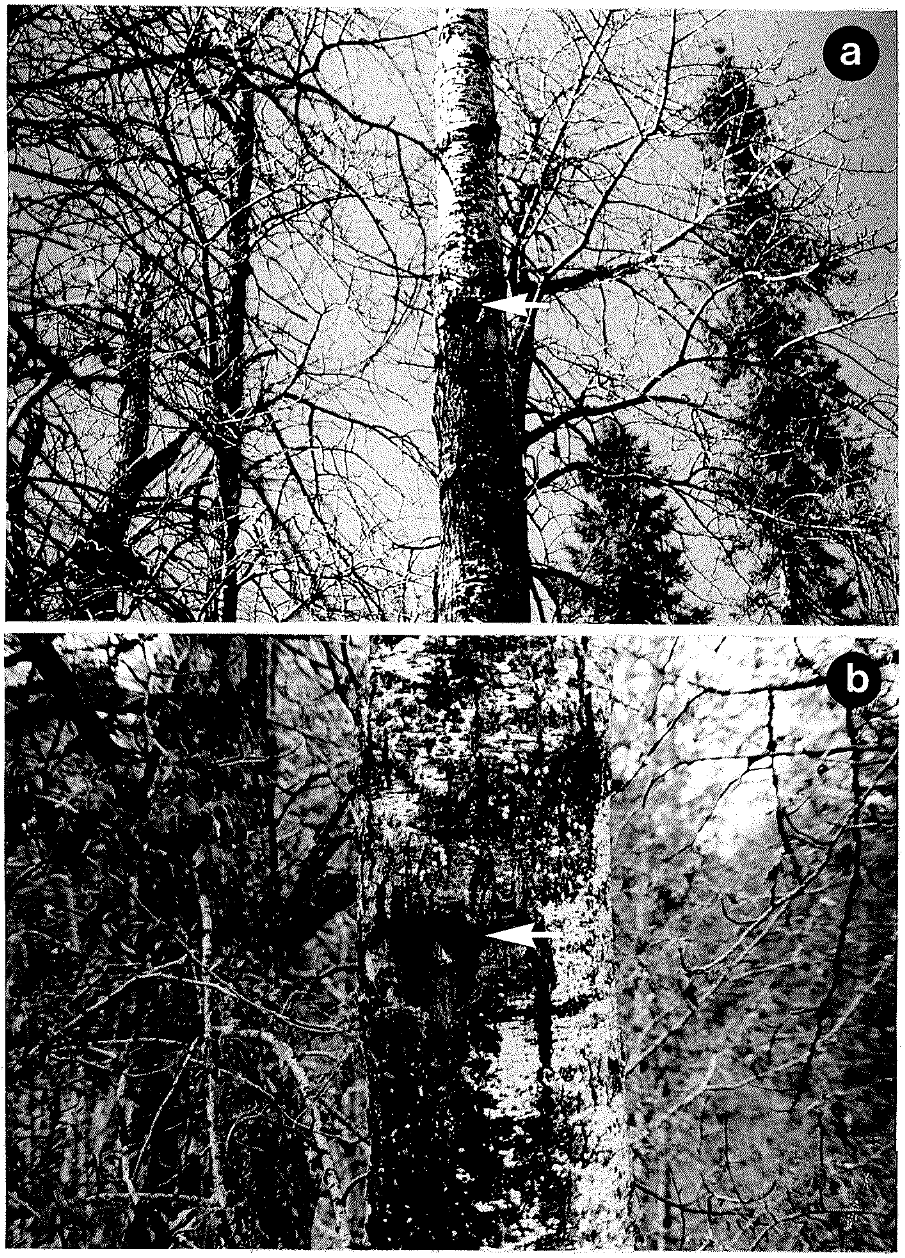

a
b

Figure 20. Diel pattern of den use by maternal female fisher from 13 April 1977 to 27 May 1977. Data from radio-telemetry (n = 233). Unsuccessful relocation attempts (n = 66) indicated that the female was out of the den.

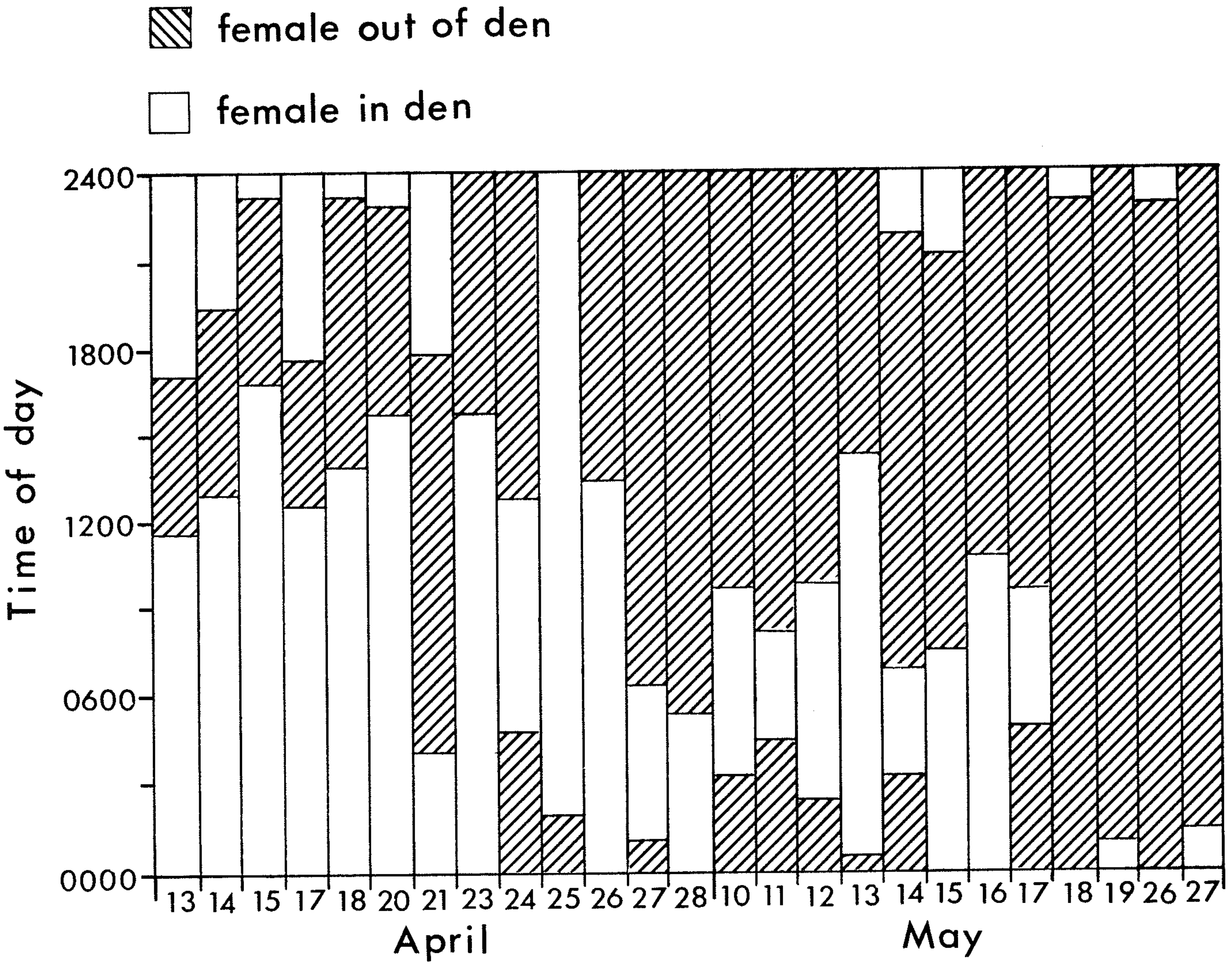
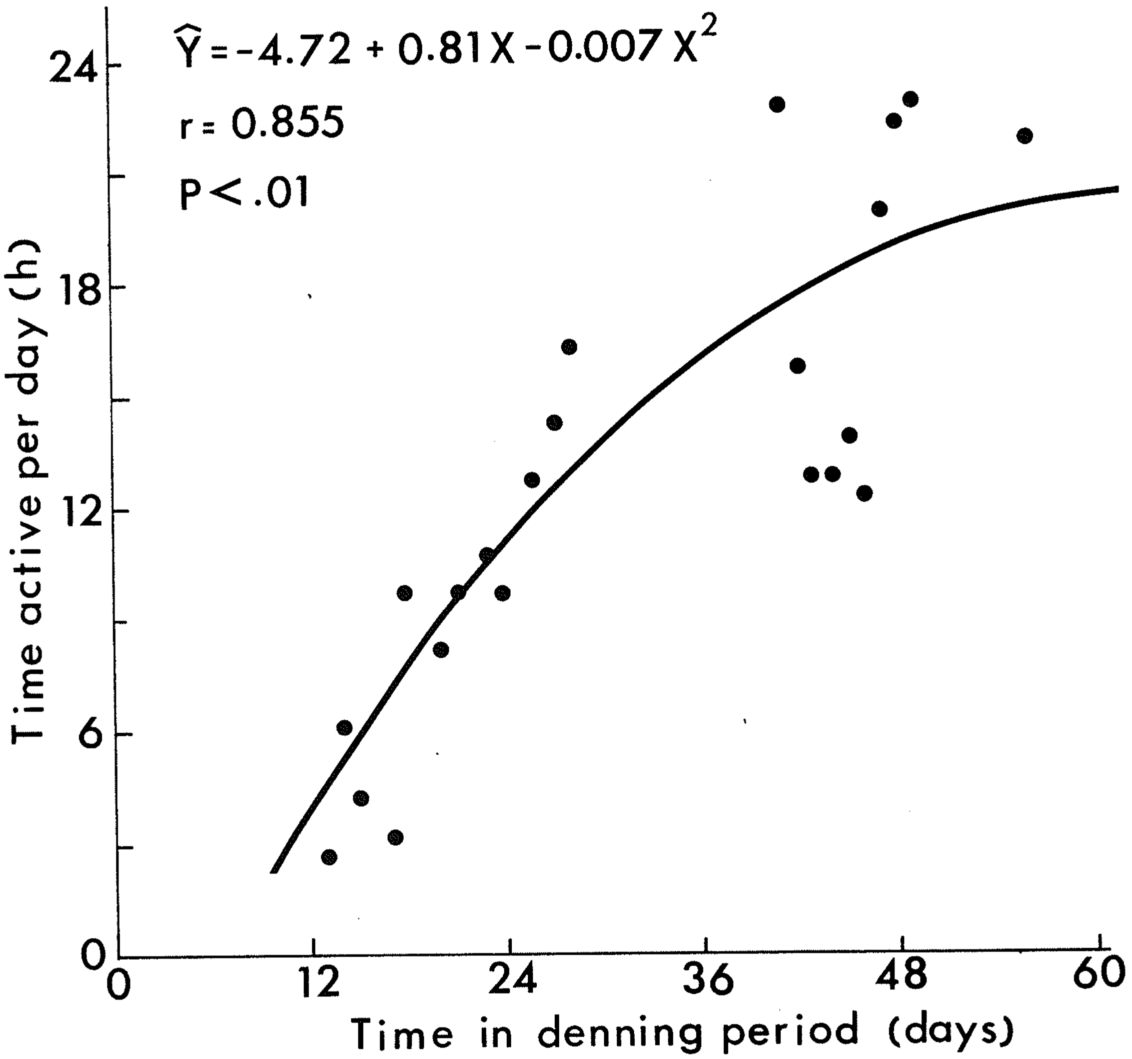

female out of den
female in den
2400
1800
1200
0600
0000
Time of day
13
14
15
17
18
20
21
23
24
25
26
27
28
10
11
12
13
14
15
16
17
18
19
26
27
April
May

Figure 21. Regression of estimated time spent out of the den by adult female on time in the denning period.

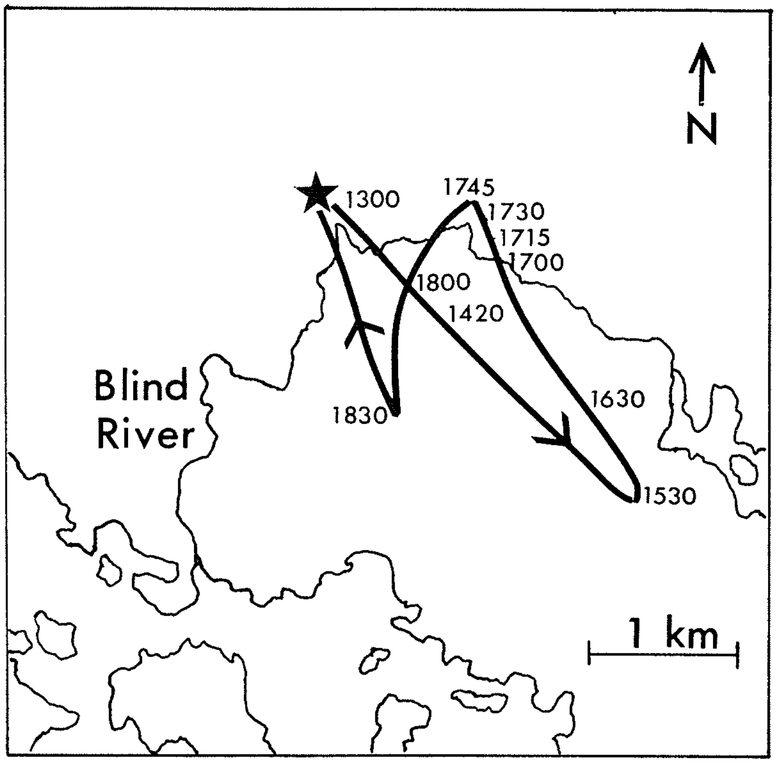

$\hat{Y} = -4.72 + 0.81X - 0.007X^2$
$r = 0.855$
$P < .01$
Time active per day (h)
24
18
12
6
0
0
12
24
36
48
60
Time in denning period (days)

left the kits during the warmest hours of the day when temperatures exceeded $0^{\circ}C$. She usually returned before the temperature dropped to $0^{\circ}C$, but on two occasions the temperature was $0^{\circ}C$ (at the Taiga Biological Station) when the female entered the den. Later in the denning period, when only 1 h per day was spent with the kits, the female selected early morning (0100) returns without obvious environmental stimuli.

Movements of the female were classed as linear or circuitous. Figure 22 depicts a typical linear movement in relation with time. Figure 23 shows the directions from the den and maximum distances of best-known linear movements. The female used the circuitous movements less frequently and later in the denning period (23, 26 April; 10, 13, 18 May). Figure 24 shows three circuitous routes estimated from radio-telemetry relocations.

There was a strong directional component in movements. Significantly more movements were followed on subsequent days by movements in a different general direction ($> 180^{\circ}$) than in the same general direction ($\leq 180^{\circ}$) ($X^2 = 5.4$, d.f. = 1, $p < .025$). Table 19 gives estimated distances that the female travelled each day in the denning period. There was no significant relationship between estimated distance travelled and time spent out of the den ($\hat{y} = 5.41 + .058x$; $F = 1.45$, d.f. = 1 and 18, $p > .05$). Little variance in estimated distance travelled could be explained by regression on time ($r^2 = .074$).

Figure 22. Typical linear movement in time exhibited by adult female when attending kits (n = 19). Star denotes location of den and kits.



N
1300
1745
1730
1715
1700
1800
1420
Blind
River
1830
1630
1530
1 km

Figure 23. Maximum distances and directions of best known linear movements of adult female when attending kits.

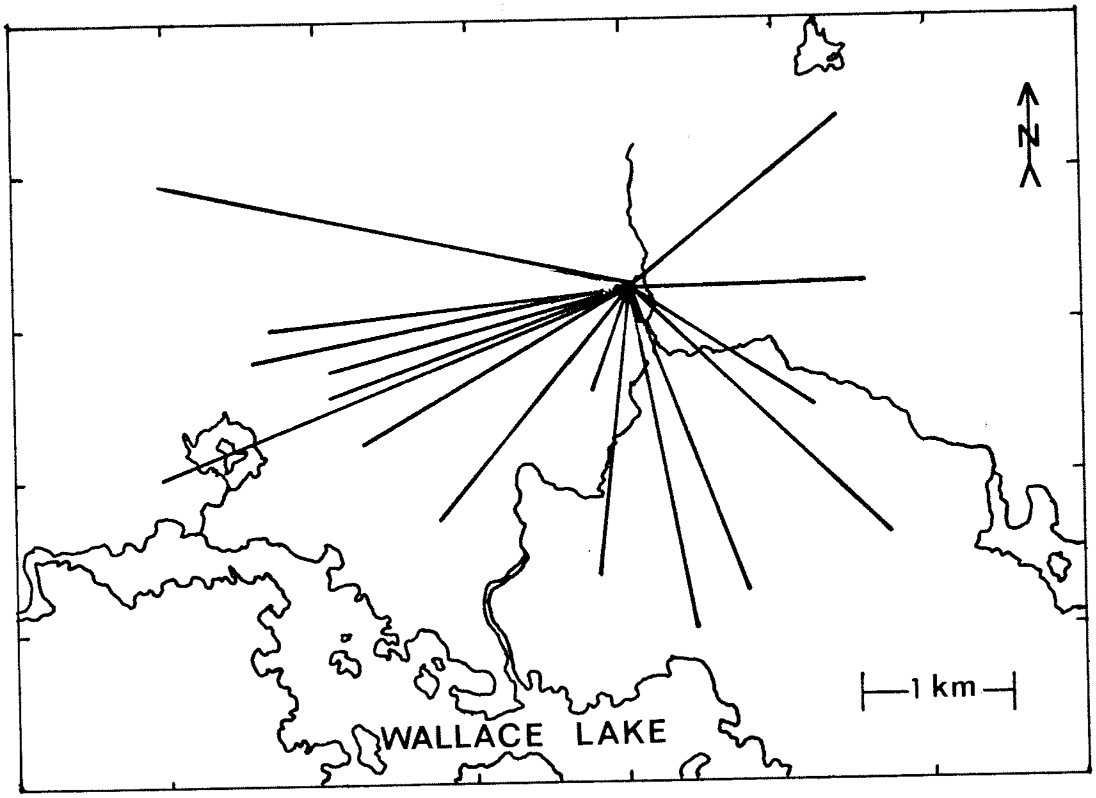

N
1 km
WALLACE LAKE

Figure 24. Three circuitous routes estimated from radiotelemetry relocations of adult female fisher when attending kits. Star denotes location of den and kits.

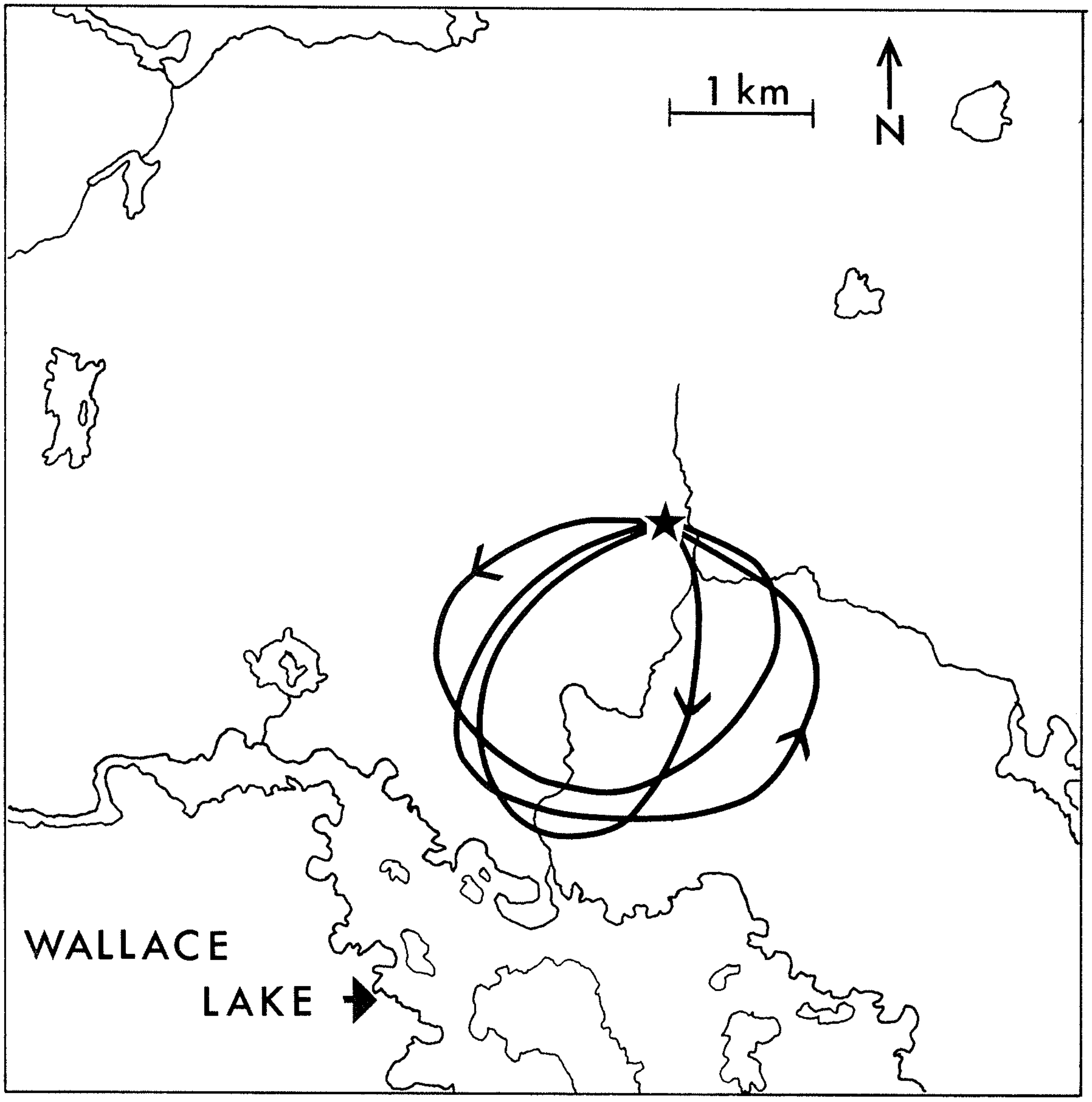

1 km
N
WALLACE
LAKE

Table 19. Estimated map-distance travelled by female fisher while attending kits, 13 April to 26 May 1977.

Date	Type of Movement[1]	Estimated distance travelled (km)[+]
13 April 1977	linear	4.2
14 April 1977	linear	7.1
15 April 1977	linear	6.2
17 April 1977	linear	5.2
18 April 1977	linear	7.8
20 April 1977	linear	7.1
21 April 1977	linear	5.4
23 April 1977	circuitous	5.9
24 April 1977	linear	4.9
25 April 1977	none	0.0
26 April 1977	circuitous	5.4
27 April 1977	linear	8.9
28 April 1977	linear	>4.9
9 May 1977	linear	6.4
10 May 1977	circuitous	6.0
11 May 1977	linear	9.0
12 May 1977	linear	6.3
13 May 1977	circuitous	5.4
14 May 1977	linear	6.2
15 May 1977	linear	5.4
16 May 1977	not known	
17 May 1977	not known	
18 May 1977	circuitous	5.4
19 May 1977	linear	6.2
26 May 1977	not known	

---

[1] See text for definition of linear and circuitous routes.

[+] See text for method of estimation.

Table 20 summarizes observations made on the kits and den from 12 April to 27 May. Table 21 lists the percent occurrence of food items found in scats collected during the first week after parturition. After this period no scats were found in the den area.

For a few days prior to 27 May, the opening near the den floor was covered with silk of forest tent caterpillar larvae (*Malachosoma dissgria*). After 27 May the kits were absent and the silk screen had been broken. Decomposed wood fragments from inside the den were hanging from the remaining silk, suggesting that the kits had exited through the opening. Radio-telemetry and ground investigations near the den failed to locate the female and kits. In December 1977 the female was killed 3 km from the den. She was no longer wearing the radio-collar, and absence of wear marks on her neck indicated that she lost the collar prior to re-growth of guard hair. There were two annuli in her cementum indicating that she was 3½ years of age.

Table 20. Summary of visual observations of den, adult female, and kits during maternal denning period, 13 April to 28 May 1977.

Date	Observations
16 April	observed adult female in den and heard vocalizations of kits
19 April	observed adult female rearrange position of kits in den; 2 kit tails dangled from den opening
22 April	observed adult female in den; one kit lifted head and vocalized; kits' eyes closed; possessed covering of short hair
15 May	piece of meat found smeared near den opening
27 May	kits left den sometime after 0135
28 May	climbed to den opening and verified observation of 27 May

Table 21. Frequency of occurrence of food items from scats collected from denning female fisher in early April 1977.

	Frequency of occurrence	
Food Item	Number	Percent
Lepus americanus	1	4.4
Tamiasciurus hudsonicus	5	22.0
unidentified cricetidae	3	13.0
Clethrionomys gapperi	12	52.0
cervidae	2	8.7
aves	2	8.7
egg shell (avian)	8	36.0

DISCUSSION

I Winter Activity and Movements

Physical factors affecting fishers during winter have not been analyzed in studies in Ontario (Clem 1977b), Maine (Coulter 1966), Michigan (Powell 1977), and New Hampshire (Kelly 1977). Only Powell (1977, 1979a) recognized the potential of snow in affecting daily energy expenditure of fishers. The pattern of winter track observations (Fig. 3), evidence from radio-telemetry on the adult female (Fig. 4), and temporal variations in cover type selection (Tables 3 and 4) suggest that fishers were influenced by environmental factor(s). Although it is difficult to separate completely the effects of factors deemed important, such as snow cover, temperature, moonlight, and interspecific and intraspecific relationships, changes in snow conditions appeared to be a dominant causality. This conclusion is supported by three facts: (1) the decline and resurgence of fisher activity were closely timed to major changes in the snow cover, (2) these fluctuations in activity were accompanied by changes in cover type selection and shifts in modes of locomotion, and (3) evidence from tracking, track observations, and radio-telemetry indicated that individual fishers possessed the potential to sense subtle changes in snow cover and could immediately react by changing gaits or cover types.

More specific evidence in connection with changes in use of cover types was particularly important. In November, December, and January fishers usually avoided open bogs in the same way that fishers in Maine (Coulter 1966) and New Hampshire (Kelly 1977) selected against clear-cuts, fields, and areas with less than 50% crown closure. In February 1977, when open bog was the only cover type with a supportive crust, fishers selected it frequently. This suggests that snow cover is a potent environmental component that is capable of modifying usual patterns of behavior.

According to Formozov (1946) snow is an integral factor in the evolution of mammals living in northern environments. Life histories of most boreal carnivores appear to have been influenced by selective pressures stemming from the winter period. Energy-demanding phases of the life cycle, such as lactation, breeding, and most growth, are usually relegated to the warmer, snow-free periods. During winter the most energy-demanding activities, other than maintenance, are probably the search for food and the sustaining of patterns of social organization. A logical corollary to this would be that any environmental factor that is capable of profoundly affecting winter activity would first have to modify the relationship between energy expenditure and energy intake.

The following discussion uses an energetics model to show that snow does have the potential to disrupt the energy cycle of fishers during winter.

Powell (1977, 1979a) used the following equation to estimate the daily energy expenditure of fishers during winter:

X = total energy expended = (energy expended when inactive) + (energy expended when running) + (energy expended during prey capture)

$$X = (k1\ t1\ W^{.75}) + (k2\ t2\ W^{.75} + k3d\ W^{.6}) + (k2\ t3\ W^{.75} + k3\ Sm\ t3\ W^{.6}) \qquad (1)$$

where:

k1 = a constant ($\mathrm{kJ/kg^{.75}h}$)
k2 = a constant ($\mathrm{kJ/kg^{.75}h}$)
k3 = a constant ($\mathrm{kJ/kg^{.60}km}$)
t1 = time spent inactive (h)
t2 = time spent running (h)
t3 = time spent capturing prey (h)
Sm = maximum running speed during prey capture (km/h)
d = distance run (km)
W = weight of fisher (kg)

This energetics model assumes that the main activities of fishers in a non-reproductive winter period are sleeping, running on the snow surface (hunting), and prey capture.

Powell (1977, 1978, 1979a) documented that these were major activities of fishers during winter in Michigan; he ignored increased energy expenditure for travelling on snow because the snow cover was hard and supported fishers (Powell, pers. comm.). In Manitoba, the winter activities of fishers were similar to those reported in Michigan, but fishers were exposed to softer snow conditions in mid-winter.

It is evident that travelling in deep, soft snow requires more energy than travelling on a level, hard surface, but no confirming energy measurements have yet been made. Work performed in negotiating a mechanical barrier, such as a snow cover, may be compared to work performed in travelling up an elevational gradient. Energy costs for vertical ascent are over ten-fold greater than expenditure for travelling the same distance on the level (Clapperton 1969; Blaxter 1967). Calculations from energetics formulae (Moen 1973:356) show that travelling up a 30 percent gradient requires about 2.7 fold more energy than travelling the same distance on a level surface. To account for energy expenditure in negotiating a snow barrier, a conservative factor of 2 could be entered into expression (1):

$$\begin{aligned} X \text{ soft snow} = {} & (k1\ t1\ W^{.75}) + 2(k2\ t2\ W^{.75} + k3d\ W^{.6}) + \\ & 2(k2\ t3\ W^{.75} + k3\ Sm\ t3\ W^{.6}) \end{aligned} \qquad (2)$$

Constants and activity patterns to implement this expression are taken from Powell's (1977, 1979a) work. No expenditure for hunting porcupines was included because of their almost complete absence from the intensive study area. Estimates of expenditure for two attempts of hare capture (Powell 1977, 1979a) are incorporated. The estimated daily energy expended by a 2.3 kg female and 5 kg male in their thermal neutral zones and under normal activity levels (Powell 1977, 1979a) are:

X♀ hard snow = 906 kJ
X♀ soft snow = 1396 kJ
X♂ hard snow = 1587 kJ
X♂ soft snow = 2432 kJ

Fishers active on soft snow may therefore use an estimated 54 percent more energy/day than fishers travelling the same distances on hard snow. The differential values of energy expenditure on a variety of soft and hard snows will no doubt vary greatly. In January 1976 fishers in the intensive study area could travel in most cover types only by using a walking gait that left a deep furrow in the snow cover. Under these conditions I believe that the two-fold adjustment to the original energy expenditure model (1) would greatly underestimate energy costs.

From the above calculations it is evident that snow cover has the potential to upset the balance between energy intake and energy expenditure. Fishers could use three different strategies to compensate for increased energy demand: (1) they could increase food intake and continue the same activity level, (2) they could maintain food intake and decrease activity accordingly, or (3) they could decrease both food intake and activity. Fishers faced with soft snow conditions could not easily increase food intake. In winter fishers make infrequent kill-scavenges (1/8.8 km in Michigan, Powell 1977, 1979a; 1/10.7 km in Manitoba; see Section II, Winter Diet) and soft snow would hinder the predator more than it would affect the principal prey. Making more kills to compensate for increased energy demand would also require additional energy. Field evidence indicated that if activity was maintained on a relatively high plane, it must have been concentrated a great distance from the winter trail system. Therefore, strategy (1) would be unlikely or impossible to implement. A logical conclusion, in light of the energetics calculations and field observations, is that the decline of activity on the trail system is symptomatic of a general reduction in total activity. Thus, strategies (2) and (3) are the most plausible, but since the techniques used in this study could not detect overwinter changes in food intake, rejecting either strategy is not possible. To reduce total activity fishers may have opted for discontinuing activities that required extensive movements, such as defense of home range against conspecifics or dispersal, and concentrated on prey capture in a restricted area. Lack of tracking and radio-telemetry data during mid-winter prevent testing this hypothesis.

If snow conditions are as important as I have purported, then the literature should presumably show frequent accounts of how snow affects mustelids. In eastern North America, where most of the investigations of fisher ecology have been carried out (Coulter 1966; Kelly 1977; Powell 1977, 1978, 1979a), mid-winter snow cover is dense and hard compared with snow cover in forest regions of Manitoba. In eastern study areas snow cover is probably of only minor importance in affecting fisher locomotion and therefore has not been emphasized. Formozov's (1946) work is replete with examples of how soft, fluffy snow affects birds and mammals in Eurasia, but with the exception of arboreal activity of forest marten (Martes martes) being reduced by snow in trees, he cited few records of snow hindering mustelids. Low weight-loading per unit area of foot and a bounding gait were the adaptations that Formozov (1946) believed were most important in allowing mustelids a broad distribution in snowy regions. However, in boreal regions of Eurasia there is no ecological vicariant of the fisher. The largest *Martes* is the sable (*Martes zibellina*), which is only marginally larger than the forest marten. The fisher's larger body size and the fact that the surface area of its feet do not compensate for the increased body weight (Leonard, unpublished data) may be reasons why the fisher is apparently more susceptible to soft snow than are sable and forest marten.

Some support for the hypothesis that body size is a critical factor in determining the effects of snow on short-legged mustelids, such as *Martes*, may be found by examining the natural history of the yellow-necked marten (*Martes flavigula*). This predator is basically a member of Oriental faunas, approaches the body size of the fisher, and is sometimes found in snowy, mountainous areas of the far-eastern Soviet Union. Although the yellow-necked marten's response to the nival environment is not particularly well understood, available information suggests that body size dictates a similar reaction to snow as exhibited by the fisher. Nasimovich (1973) reported that yellow-necked marten avoided deep, snow-filled ravines by jumping from tree to tree. If thaws formed a crust on the upper levels of snow cover, yellow-necked marten that previously sank deeply were able to travel on the crust and effectively prey on musk deer (*Moschus moschiferus*) (Matjushkin 1974). It appears, at least superficially, that larger *Martes* such as fisher and yellow-necked marten are more sensitive to snow cover than are the smaller sable, forest marten, and American marten.

Environmental factors other than snow cover may also have been important, or perhaps acted in concert with snow in influencing winter activity of fishers. Tc values, particularly for females, were frequently attained in the study area and could explain some variance in activity. Although inadequate because of the lack of data on amount of time temperatures were below Tc, the data do indicate that temperatures were colder in Manitoba than in Michigan where winter expenditure estimates were initially carried out (Powell 1977, 1979a). Solar radiation is also at a low in mid-winter. Inactive fishers den in the subnivean environment (Leonard, unpublished data) which is warm, moist, and thermally stable (Pruitt 1957, 1970), and they may consequently avoid undue thermal stress simply by limiting supra-nivean activity during cold periods. High rates of heat transfer may be additive with soft snow in placing increased energy demands on active fishers, but reduction of total activity and use of subnivean dens could greatly reduce energy expenditure.

Breeding activity may have inflated late winter track counts. Males used the intensive study area more frequently than they did earlier in winter (see Section III; Breeding Biology). Since tracking in February did not reveal any reproductive-related behavior, counts were probably little affected by breeding activity until March, when reproductive organs revealed significant changes (see Section III; Breeding Biology). March track counts were relatively high, but certainly activity in February was higher. Therefore, breeding was probably not as important as environmental factors in affecting activity. Coulter (1966) found that fisher activity on his intensive study units greatly increased in March, presumably due to onset of the breeding period, but effects of environmental factors were not assessed.

Only on one occasion, when fishers hunted muskrats along shorelines, did prey appear to exert a control on fisher activity. Because snow cover on lakeshores thickened at the same time that muskrats became uncommon, it is not possible to determine absolutely which factor was responsible for decline of fisher activity. Probably both factors acted together; lower availability of muskrats made hunting energetically less productive in the thicker snow cover.

It is not clear if all age classes and both sexes exhibit the same changes in activity during winter. Considering the great degree of sexual dimorphism of fishers (Coulter 1966; Powell 1977; Kelly 1977), it is logical to conclude that environmental factors might differentially affect the sexes. However, the extremely low number of track observations in mid-winter suggests that no age or sex class was moving extensively.

Age and sex distribution from the trapper-catch (Table 7) may be interpreted on the premise that to be highly represented in the catch, an individual age or sex class must move greater distances in order to pass more traps and increase its probability of being trapped. Fishers demonstrate no learned response to avoid traps and if trapped they are either maimed or killed. Analysis of the trapper catch indicates that juveniles are captured far in excess of what would be expected by chance, suggesting that juveniles move more than adults during winter. This is also supported by the meager data from radio-telemetry. Data from New Hampshire (Kelly 1977) show that only one of 10 radio-tagged juvenile fishers positively remained in the intensive study area for more than three months. The winter movements of juveniles are best explained as dispersal, similar to that recorded by Francis (1958) and Hawley and Newby (1957) for American marten.

Snow cover, apparently the singularly most important factor responsible for decreased number of track observations in mid-winter, also has the potential to affect any important activity that requires extensive movement. Juvenile dispersal, defence of an area against conspecifics, and breeding are dynamic activities that are important in natural regulation of populations. Snow cover could limit dispersal and defence of an area for short periods during mid-winter, but breeding activity occurs in March (see Section III; Breeding Biology), when the presence of soft, movement-limiting snow would be highly irregular. This late winter timing of breeding may be a life history adaptation to avoid occurrence of an important, energetically demanding phase of the life cycle during a period when energy required for movement would be considerable.

II Winter Diet

According to the theory of Rosenzweig (1966) fishers should prey predominantly upon medium-sized species. The taxonomic composition of the winter diet of the fisher in Manitoba (Tables 8 and 9) confirms this supposition for the central portion of the species' geographic range. Prey varying in size from shrews to porcupines were eaten, but a preponderance of the diet was snowshoe hares and medium-sized birds. With the exception of a few variations, the winter diet in Manitoba does not differ substantially from the winter diet in the more frequently studied eastern areas such as Maine (Coulter 1966), New Hampshire (Stevens 1968; Kelly 1977), New York (Hamilton and Cook 1955; Brown and Will 1979), southern Ontario (deVos 1952; Clem 1977a, 1977b), and Michigan (Powell 1977, 1978). The fisher's ability to use a substantial variety of foods during winter appears to be an important dietary feature that enables this mustelid to exist in a relatively wide range of environmental conditions.

Ungulate carrion was a predominant food item in some areas (Kelly 1977; Hamilton and Cook 1955; Coulter 1966), but in Manitoba it was not frequently recorded (7.5%). Coulter (1966) felt that use of carrion was overestimated by analysis of alimentary tracts; fishers that visited sites where ungulates had died consumed mainly undigestable evidence such as hair and obtained little meat. The fact that ungulate carrion in the intensive study area in Manitoba was rejected by some fishers and did not create a local change in dispersion of fishers suggests that either use of carrion is a learned response, or most fishers had an alternate, more favorable source of food during winter.

The fisher and porcupine are believed to be members of a predator-prey system dating to the early Pleistocene (Powell and Brander 1977). Although Coulter (1966) believed that fishers were not able to control porcupine populations, other evidence (Hamilton and Cook 1955; Powell and Brander 1975; Powell 1977) suggests that fishers reduced porcupine populations to a low, stable level. The presence of porcupine quills in body musculature of fishers from the East Lake Winnipeg area, where porcupines were rare, parallels similar observations in New Hampshire (Kelly 1977). These data reinforce the hypothesis that fishers are effective predators of porcupines and lend credence to the theory that fishers can exert numerical control over porcupine populations.

The frequency of birds in the alimentary tracts of fishers in Manitoba is the highest yet recorded (48.3%). In Maine a wider variety of birds comprised 24% occurrence of the winter diet (Coulter 1966). Presumably fishers from Manitoba ate more birds as a substitute for the dietary absence of ungulates and porcupines which each comprised over 25% occurrence in Coulter's (1966) study.

Coulter (1966) found few geographic differences in the diet of fishers when he compared samples from northern and southern Maine that were collected from areas with known differences in prey availability. In Manitoba, a similar lack of geographic differences was recorded for all major food groups except porcupines. Fishers responded functionally to a wide range of porcupine densities, whereas in Maine fishers used porcupines to the same degree regardless of population levels. However, the great difference between forest types of northern and southern Maine (Coulter 1966) may have been more important than porcupine density in affecting the success of fishers in securing these rodents.

Despite considerable sexual dimorphism in body size, an almost complete absence of sex differences in diet was recorded from alimentary tracts collected in Maine (Coulter 1966) and Manitoba. Some confusion exists in sex-differential use of porcupines. Evidence from alimentary tracts from Maine show no significant differences in use of porcupine between the sexes (Coulter 1966). In British Columbia, Quick (1953b) found that five of seven fishers that had quills in alimentary tracts or body musculature were females. Contrarily, in New Hampshire (Kelly 1977) and Manitoba porcupine quills in body musculature were found significantly more frequently in males than in females. Males may be less agile than females when attacking porcupines and receive more quills, or males may attack more porcupines but have a lower success rate than females. Females in captivity have effectively dispatched porcupines (Coulter 1966; Powell 1977) but no data are available for males. More detailed study, probably by following radio-tagged individuals in the field, will be necessary to ascertain if available data on sex differences in use of porcupines is real or an artifact of sampling.

The foraging behavior of the fisher in Manitoba apparently differs little from that recorded in Maine (Coulter 1966) and Michigan (Powell 1977, 1978). In all regions fishers hunted opportunistically with no prolonged chases of prey. The use of fallen logs, a main travelling characteristic of fishers, was first reported by deVos (1952). Since the fisher forages by investigating areas likely to possess prey, such as brush piles and overturned tree roots, it follows that walking on logs may be the most successful way to capture prey, for example, snowshoe hares, that use logs for cover.

It is interesting, however, that fishers walked on nearly all logs encountered even when foraging was apparently not the main intent. The relatively long distance between successful capture of prey in Manitoba (10.7 km) was similar to the distance reported by Powell (1977, 1978) in Michigan (8.8 km).

Although opportunistic hunting can explain how fishers catch most of the recorded prey, certain types of foods are undoubtedly not acquired in the usual manner. The relatively high frequency of ducks (7.5%) at first appears anomalous until it is realized that fishers used shoreline ecotones extensively, particularly in early winter (see Section I; Winter Activity and Movements), and probably found dead or wounded ducks left behind from the large migratory flocks that frequented the region in the fall. Three hibernators, Zapus, Marmota, and Thamnophis, were found in alimentary tracts. Fishers probably encountered these taxa in some form of resting den presumably located below the frost-line. Coulter (1966) believed that some species of birds were attracted to carrion or remains of fisher kills and were consequently predisposed to predation by fishers. The corvids (5.8%) and the single hawk were probably captured in this manner.

Functional response to changing hare numbers

The cyclic fluctuation in numbers of snowshoe hares is an important characteristic of terrestrial ecosystems in forested regions of boreal North America. Population dynamics of many predators, such as lynx (*Lynx canadensis*) and great horned owls (*Bubo virginianus*), are influenced by the dramatic changes in hare densities (Rusch *et al*., 1972; Brand *et al*., 1976; Adamcik *et al*., 1978). The importance of hares in the winter diet of the fisher has been recognized (Coulter 1966; Powell 1977, 1978). Davison (1975) showed that among four food types used in feeding trials, hares contributed the highest proportion of nitrogen and were predictably important for growing fishers. Powell (1977, 1978) interpreted the irregular, zig-zag hunting pattern of fishers as an adaptation for opportunistic hunting of hares. In Manitoba, hares were the species that fishers ate most frequently (Tables 8 and 9) and during winter were the most conspicuous, supra-nivean mammal. This study is the first in which a functional response of fishers to changing hare numbers could be tested.

The indices of hare numbers were performed only in the intensive study area, but evidence indicated that they could be applied to all four of the extensive study areas in Manitoba. In a long-term study of hare population dynamics in Alberta, Keith and Windberg (1978) demonstrated that fluctuations in hare numbers were synchronous over most of the province. Leonard (1980) confirmed that some important characteristics of the hare cycle outlined by Keith and Windberg (1978) were present in a mixed-wood area in southwestern Manitoba. Studies from areas west of the intensive study area showed that hare populations were in a state of increase during years of the fisher dietary study (W. Koonz[1], pers. comm.; Rusch _et al_., 1978; Leonard 1980). Thus, although actual densities of hares were not known in any of the extensive study areas, the synchronous nature of hare fluctuations and the fact that hare population dynamics does not appear to differ substantially from Alberta suggest that the overall trend in hare densities agrees with the indices from the intensive study area.

The above evidence in trends indicates that for each extensive study area hare densities were probably greater than the previous year. Several lines of evidence show that fishers responded functionally to changing hare numbers.

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First, the percent frequency of snowshoe hares in alimentary tracts demonstrated a significant increase in proportion from 1974-75 to 1976-77 in East Lake Winnipeg and all areas combined (Table 11). In each area frequency of hares was, without exception, higher during each consecutive winter.

Second, as use of hares increased there was a concurrent decline in use of other food types. Frequency of small mammal and >1 small mammal decreased significantly in proportions (Table 11). By the third winter (1976-77) no fisher was examined with more than a single small mammal in its alimentary tract. The linear relationship between >1 small mammal and hares (Fig. 9) suggests that decreased multiple use of small mammals could be partially attributed to increased presence of hares in the alimentary tracts. Use of other mammals, such as porcupines, muskrats, and unidentified taxa also peaked in 1974-75 and declined 50% in 1976-77. Although percent frequency of carrion did not exhibit a decreasing trend, the energy value of carrion meals of East Lake Winnipeg fishers declined gradually from 1974-75 to 1976-77 (Table 15). These shifts of food types imply that fishers gradually selected hares as availability increased and concomitantly decreased use of presumably less favorable or less attainable foods.

Third, the number of alimentary tracts devoid of food decreased significantly as use of hares increased. This suggests that hares were a preferred food that the fisher was not able to replace fully with other foods when hare numbers were low.

Fourth, the number of food items per individual decreased from 1974-75 to 1976-77. This indicates that when hares were fewer in number, more types of prey were utilized as a response to absence of hares in the diet.

These four particulars strongly point to a functional response of fishers to changing hare numbers. However, examination of the above details gives no clue to actual differences in energy intake of fishers during three successive winters. The consumption rate model of Diana (1979) was adapted to estimate the daily rate of energy intake of fishers for separate winters so that the significance of a functional response to changing hare numbers could be assessed. Several sources of error are apparent in the data fed into the model and these must be identified.

The through-rate of 16 h cited by Davison (1975) stemmed from laboratory experiments on female fishers. Varying levels of activity of wild fishers would probably affect the rate. It is also quite conceivable that males could have a different through-rate. Also, the through-rate could differ in a field situation. Fishers were captured in steel traps and sometimes remained alive long enough to defecate. This would increase the frequency of empty tracts and reduce the estimated consumption rate. Since there was no evidence that fishers spent longer times in traps during any specific winter, this source of error would affect all winters equally. Meal sizes for foods too large to swallow without dismembering were estimated from the size of laboratory meals (Davison 1975). It is not known if wild fishers ate smaller or larger meals; therefore, consumption rate could have been biased either upward or downward. Errors in all estimates, such as energy values of carrion, prey sizes, and percent metabolizable energy of gross energy also undoubtedly produced sources of error in the consumption rate estimates.

Despite the trenchant errors in the model, the mean consumption rate of 1560 kJ metabolizable energy/day, for a 4 kg fisher ($\bar{X}$ weight of male and female) is only slightly less than the 2030 kJ required for a 4.0 kg fisher in laboratory feeding trials (Davison 1975). Powell (1979a) discussed reasons why laboratory studies would tend to overestimate energy requirements. The consumption rate results agreed closely with the approximately 1350 kJ expenditure Powell (1979a) estimated for a 4 kg fisher under a regime of high activity.

The partitioning of the estimated consumption rate (Table 16) indicates that hares were an important dietary component. The difference in consumption rate between 1975-76 and 1976-77 could be explained solely by increased intake of hares in 1976-77. As the estimated daily energy intake of hares increased during consecutive winters, the energy values of small mammals, muskrats, and carrion decreased in importance. Small mammals were energetically insignificant in the diet during all winters and the increase in use during 1974-75 could not supply sufficient energy to counteract decreased use of hares. Birds appeared to be a significant energy source, particularly in 1975-76. However, their value in the diet may have been overestimated since the amount of indigestable material in the body of birds is much higher than it is in mammals (Johnson and Hanson 1978). Birds would consequently be prone to over-representation in alimentary tracts.

The hypothesis of a functional response of fishers to changing hare numbers acquires acceptance both from analysis of proportions and calculations of the consumption rate model. The crux of the matter is, nevertheless, to identify whether fishers that ate fewer hares were subjected to nutritional stress. When the total consumption rates are examined for each winter (Table 17), it is evident that there was a progressive increase in energy intake from 1974-75 to 1976-77. Three reasons may be responsible for the change: (1) fishers ate progressively larger meals each winter, (2) each fisher fed more often during successive winters, or (3) some members of the population fed less often than others during 1974-75, but fed progressively more often in later winters. Alternative (1) may be eliminated because fishers that had recently fed had a metabolizable energy intake that varied less than 3.0% among winters (Table 17). The decreasing number of empty tracts in time indicates the occurrence of more frequent feeding and hence supports alternatives (2) and (3). Although mean conditions indices varied little among winters, the wider standard deviations of condition indices during earlier winters suggests that not all members of the population were equally capable of successful foraging. The regression of empty tracts on condition indices (Fig. 10) indicates that deviations of condition indices are closely related to less frequent feeding. Alternative (3) is the most logical hypothesis that can account for the progressive increase in energy intake.

The regressions of foods that showed a significant trend in proportions (Figs. 11 and 12) on condition indices strongly suggest that hares were important and small mammals unimportant in affecting the nutritional status of fishers. Thus, the reason that some fishers presumably fed less often than others may have been related to the lower availablity of hares during the winters of 1974-75 and 1975-76. The small sample sizes from each winter preclude analysis to test if any specific age or sex class was less capable of coping nutritionally during a period of relatively low hare numbers. Earlier I speculated that many of the juveniles were transient in status during winter (see Section I; Winter Activity and Movements). Because of their unfamiliarity with foraging areas, transients may have more difficulty than established individuals in locating scattered groups of hares during a low phase of the hare cycle.

The proposed functional response of fishers to changing hare numbers gains more support from the above discussion, but the degree that such a response could attain in a very high hare population is unknown. The three year period that this study spans includes neither drastically high or low phases of the hare cycle. It superficially appears that although the consumption rate of fishers is reduced when hares are relatively uncommon, this mustelid does not suffer the degree of nutritional stress reported for lynx (Brand *et al.*, 1976; Brand and Keith 1979). Indices of productivity (see Section III; Breeding Biology) did not vary appreciably during periods of low hare numbers, suggesting that fishers are not food regulated even in the presence of a cyclic, fluctuating food-base. The observed 10 year cycle in fisher fur returns that is reported to follow the hare cycle by about a five year lag (Keith 1963) may be due to sampling rather than a numerical response. Fishers that frequently have an empty alimentary tract during a period of low hare populations are probably more readily trapped. As hare populations increase, so does the consumption rate of fishers, thereby reducing the likelihood of responding to bait.

III Breeding Biology

Eadie and Hamilton (1958) inferred, from examination of skeletal reproductive characteristics of 39 female fishers from New York, that individuals displaying specific open skull sutures and absence of corpora lutea were members of a non-breeding, winter age-class. Wright and Coulter (1967) confirmed these observations in a study of development and reproduction of 99 females from Maine. They also presented, by finding tubal morulae in two fishers with juvenile skull characteristics, the first irrefutable evidence that wild female fishers breed at the age of one year. Studies of age-class structure and reproduction of fishers from Ontario (Strickland and Douglas 1974, 1979) also supported these earlier observations. In Manitoba, presence of pregnant females in the yearling age class, increased tract volume and follicular development of two pre-estrus juvenile females, and observation of a tract from a recently-bred juvenile indicate that first reproduction of females also occurs at the end of the first year of the juvenile age class.

Age of first reproduction of male fishers is poorly understood because a thorough study of a large series of testes has not been undertaken. To complicate matters, even if reproductive capability of juvenile males is demonstrated in the laboratory, there is no effective method of determining reproductive success of males in the wild. Wright and Coulter (1967) found sperm in epididymides of five adult males and two juvenile males collected during March in Maine. Although I use a method not strictly comparable, I found sperm in the epididymides of three juveniles and three adults from March, but I could not detect sperm from a larger series collected from November to February. The narrow range in monthly testes volumes of juveniles and adults implied that winter maturation of gonads followed a similar rate for both age-classes. These data are supported by the overlap in weights of bacula of adults and juveniles collected during late winter in Maine (Wright and Coulter 1967) and Manitoba (Fig. 14). Sexual maturation of males during winter appeared to differ in Ontario. In their southern Ontario study area Strickland and Douglas (1979) recorded no overlap in weights of bacula of juveniles and adults collected from November to March and reported a mean monthly testes weight of juveniles that was consistently lower than that of adults. It is noteworthy that when a shortage of adult males was apparent in this population, the juvenile males appeared incapable in a reproductive sense because numerous barren females were recorded the following year (Strickland and Douglas 1974). Management that favored protection of adults eliminated this phenomenon (Strickland and Douglas 1979). Age of sexual maturity of males is probably more variable than in females. Perhaps age of first reproduction in males varies geographically, or, as Crowe (1975) believed for bobcats (Lynx rufus), may be more closely related to physical development than age.

In Manitoba, all available information indicates that estrus and parturition occur in late March and April. The fact that early winter juveniles were very uniform in development suggests that a restricted whelping period and possibly a restricted mating period occur for all ages of reproducing females. The rigors of climate in Manitoba probably preclude successful whelping and raising of kits earlier than late March. Studies from areas with a less harsh climate, such as Maine (Wright and Coulter 1967) and southern Ontario (Strickland and Douglas 1974), have reported females in active pregnancy during nearly all winter months. Fishers from regions with less severe environmental conditions in late winter should not only show the wide spread of parturition dates, but the juvenile age-class should display more early winter developmental variation than Manitoba juveniles. However, variation in development of juveniles has not been examined in regions other than Manitoba.

No data are available on aspects of the reproductive cycle of male and female fishers between April and October in any portion of their geographic range. Danilov and Tumanov (1972) showed that some male mustelids, including forest marten, remain in breeding condition for two to four months regardless of the annual timing of breeding. If recrudescence of testes in the fisher requires about the same amount of time as development (Fig. 13), then it may be inferred that male fishers are sexually potent during March, April, and May in Manitoba. Few meaningful inferences may be made on reproduction of female fishers from April to October, but as Wright and Coulter (1967) implied, without availability of specimens the possibility of sterile matings and ovulation during implantation (Neal and Harrison 1958; Canivenc and Bonnin-Laffargue 1963) cannot be entirely dismissed.

There appears to be little geographic variation in mean corpora lutea counts for fertile females. The mean of 3.5 corpora lutea for Manitoba is similar to 3.3 (N=19) for Nova Scotia (van Nostrand 1979), 3.3 (N=47) for Ontario (Strickland and Douglas 1979), 3.28 (N=44) for Maine (Wright and Coulter 1967) and 3.67 (N=12) for New Hampshire (Kelly 1977), but is greater than the 2.72 (N=22) for New York (Eadie and Hamilton 1958) and the 2.6 (N=5) for Massachusetts (Cardoza 1979).

Counts of embryos probably more accurately reflect the true litter size, but data are rare due to limited availability of late-winter carcasses. Wright and Coulter (1967) recorded a one:one ratio between corpora lutea and embryos for each of eight females in active pregnancy. I recorded a 10% *in utero* loss that was similar to the 6% discrepancy between corpora lutea and blastocysts from 11 serially sectioned tracts from Maine (Wright and Coulter 1967). Although sample sizes are not comparable, the mean embryo count was lower in Manitoba ($\bar{X}$ = 3; N=3) than in Maine ($\bar{X}$ = 3.45; N=11; Wright and Coulter 1967), and Ontario ($\bar{X}$ = 3.16; N=16; Strickland and Douglas 1974).

Data on size of wild litters are non-existent, but records from captive litters indicate that a further decrease in fertility rate may occur after implantation. Hall (1942) reported that the mean number of young for 26 fur ranch fishers was 2.7. Other litters include two of three young each from Maine (Coulter 1966), one of two young from Michigan (Powell 1977), one of three young from Vermont (Fuller 1979), and the litter of four young I reported from Manitoba. Unfortunately, there are no data available concerning neonatal mortality in the wild. Coulter (1966) reported that a captive male kit died at the age of 44 days, but the cause of death was apparently unknown.

The regression of mean corpora lutea per female on age (Fig. 17) indicates that age-related fertility rates exist in Manitoba. Although similar data from other regions have not been analyzed, the information tabled by Strickland and Douglas (1979) appears to follow a similar age-specific trend. Data supporting age-related productivity are in contradiction with the evidence I presented for constancy in litter size in a single adult female. Kelly's (1977) report of a road-killed female that had three placental scars and three blastocysts also supports constancy of litter size for an individual. Change in fertility with age is probably more legitimate than constancy in fertility because of the larger sample size, but more detailed analysis is required.

The ratio between the number of juveniles in the sample and the number of females old enough to have produced these juveniles (Table 18) shows that there was no radical change in productivity from 1972 to 1978. Fertility rates of females from 1974-75 to 1977-78 (Table 18), although based on smaller samples, also support inferences from age ratio comparisons. It appears that despite the presence of a fluctuating prey base and a ten year cycle in fur returns of fishers in Manitoba (Manitoba Game Branch Records) there is no evidence to suggest that population dynamics of fishers is affected in the manner reported for lynx (Nellis *et al*., 1972; Brand *et al*., 1976; Brand and Keith 1979). However, in Ontario Strickland and Douglas (1979) did report a five-fold variation in the ratio of juveniles per adult female older than two years but they attributed the cause to a paucity of breeding males.

Breeding den ecology

Few data are available concerning the change in behavior of free-ranging female mammals at the time of parturition, mating, and raising young. The lack of information is particularly conspicuous among the small species of carnivores because of their secretive habits and ability to conceal litters. The data presented from a female fisher are valuable not only because the information elucidates previously unknown details of the fisher's life history, but because a great deal of the reproductive and ecological history of this female was known prior to denning.

The female's movements while in active pregnancy (Fig. 16) differed from her earlier movements (Fig. 14), from movements of another female radio-tracked simultaneously (Fig. 15C; unpublished data), and from general movements of other individuals that appeared to increase activity due to favorable snow conditions (see Section I; Winter Activity and Movements). Her generally reduced state of activity was probably a strategy to help conserve energy for growth of foetuses.

Scanty records from the literature suggest that tree-dens may be the most common, and possibly the only form of breeding-den used by fishers. Hamilton and Cook (1955) cited a record of a trapper who twice found kits in cavities high in trees. Seton (1909) referred to the capture of young fishers from a tree-den in Manitoba. In New Hampshire, Kelly (1977) radio-tracked a lactating female to a hollow tree and suggested that she was raising kits in the cavity. Although factors that influence a female's selection of a suitable den are unknown, all identified dens have been in hardwood species.

Use of a tree-den for raising young has several biological advantages. During early spring, when most female fishers whelp their kits, much of the diel cycle is below $0^{o}C$. Since kits are altricial (Coulter 1966; personal observation of two litters) they must have a source of heat, such as from the attending female's body, to survive freezing temperature. Heating and cooling curves indicate that during spring relatively high areas remain warm for a longer period than ground-level areas (Geiger 1965). Consequently, a fisher that whelped kits in a high tree-den would be able to forage away from the kits for a greater length of time than a fisher that whelped in a ground-level den. Cannibalism or infanticide are relatively common fitness strategies in mammals (Fox 1975; Hrdy 1977; Mallory and Brooks 1978). Since post-parturient female fishers are attractive to males for a period while attending kits, it would be adaptive for females to select a type of den that males would be unable to enter because of their larger size. Again, a hollow tree with openings to the outside would prove ideal because a female could potentially select an opening with minimal clearance for herself and thus eliminate possibility of entry by males. Finally, use of a high tree-den would prevent mortality of kits by ground-dwelling predators.

Several important details characterize the movements and activities of the female during the denning period. The diel pattern of use of the den (Fig. 20) and the regression of time out of the den on time in the denning period (Fig. 21) clearly indicate that the female spent more time away from the den as the kits became progressively older. Despite these observations, the female did not travel further during each successive day (Table 19) and the variance in estimated daily distance travelled could not be explained by the regression of distance on time ($r^2 = .074$). When these facts are examined in relation to the extensiveness and significant directional pattern of movements (Figs. 22, 23, 24), the known size of the formerly established home range (Fig. 18), and the central location of the den within this home range (Fig. 18), it is apparent that the female employed a consistent strategy throughout the denning period. She maximized use of a great deal of her former range, particularly areas that were near the boundary and a considerable distance from the den.

There may have been at least three reasons for this specific spatial and temporal use of the home range. First, lactation places significant energy demands on female fishers during this period (Powell and Leonard, in prep.). A female could use a familiar region, such as a home range, in as an effective fashion as possible to minimize the energy expenditure of foraging. Use of linear and circuitous routes and alternating daily directions would aid the female in covering much of her range in time and space. Second, since it is likely that fishers defend areas intrasexually against conspecifics (Powell 1979c), the type of movements the female demonstrated would also be effective in maintaining her social position.

The increase in time spent away from the den as the kits developed also supports the existence of a phenomenon related to social organization because the additional time was apparently not spent travelling greater distances for foraging (Table 19). It is curious that the female made extensive movements early in the denning period when she could leave the kits for only a few hours due to the colder temperatures and the necessity of her frequent stimulation of the kits' digestive and excretory functions (Ewer 1968). Therefore, the third reason for making extensive movements may have been to avoid males that would be attracted to her because of estrus. Because of the possibility of male cannibalism on the young, the female may have used far-ranging movements to divert male courtship activities from the vicinity of her litter.

The female used an area during denning that was only marginally smaller than the area she used when barren (Fig. 18). The use of a home range appears to be as important during denning as during other periods but it is not clear at what age fishers establish a range; for example, Kelly (1977) combined movement data from juvenile and yearling females because he rationalized that a female's behavior would not change appreciably until late in their second winter when blastocysts first implant. Cementum annuli counts indicated that the denning female was 3.5 years old at death. Since she whelped a litter in captivity in 1976, her litter of 1977 was the first she raised in the wild. I had no evidence that she left her home range between March 1976, when I first detected her in the study area, and December 1977, when she was killed by a trapper. It appears that she must have established her range during her juvenile or yearling period. Other evidence (see Section I; Winter Activity and Movements) suggests that during winter many juveniles are transients, but yearlings are as sedentary as older adults. Data from New Hampshire also support these observations; three of six radio-tagged adults remained in the study area for more than three months but only one of 10 juveniles was positively shown to remain for this amount of time (Kelly 1977). All available evidence suggests that female fishers establish home ranges between one and two years of age.

Home range size during the non-breeding period may be determined by the energetic capabilities of the female during the denning period. If adult females defend intrasexually against conspecifics (Powell 1979c), then a logical corollary would be that it is not adaptive for females to defend an area on a yearly basis that would be too large to defend when denning. An upper limit of range size determined by energetics would also explain why the home range of an adult female in New Hampshire (Kelly 1977) was nearly identical in size to the multi-seasonal range I presented for an adult female in Manitoba. Male fishers, free from energy-requiring activities of raising young, should presumably have larger home ranges than females. Preliminary studies have indicated that this is probable (Kelly 1977; Powell, pers. comm.[1]).

Young fishers demonstrate a rapid weight gain from birth to about 24 weeks of age (Coulter 1966; Fuller 1979; Powell, pers. comm.[1]). Access to a food source is important for the adult female because her milk and food she brings to the den is the sole source of nourishment for the kits. Kelly (1977:112-113) hypothesized that:

> "for a period of at least a month after parturition, the altricial young (fishers) must be extremely dependent upon the female for food and body heat. Her energy demands are high at this time and she cannot remain away from the den for extended periods. ... if a pregnant female fisher located the remains of an ungulate ... her food problem would be solved until maturation of the young allowed her to make more extensive forays."

Information from Manitoba shows that carrion was not the dominant food source of the denning female. The diet early in the denning period (Table 21) did not differ greatly from the winter diet (see Section II; Winter Diet).

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The fan-shaped pattern of linear routes differed in direction on a daily basis, suggesting that the female did not use the deer carcasses I had placed in the region earlier in the winter (see Section II; Winter Diet). From these observations it is not likely that presence of carrion is important in determining location of breeding dens. Presence of eggshell in eight scats is interesting because only a fraction of the birds in the region were probably incubating in early April. If this observation is an indicator of later use of birds' eggs and nestlings, then these foods may become as important for denning female fishers as they are for marten in summer (Francis 1958).

On 27 May two events occurred that are difficult to interpret: radio-contact with the female was lost and the kits left or were removed from the den. Since the female was killed 3 km from the den several months later, I presume that she did not abandon the area. Absence of the radio-collar and the fact that she had previously lost or removed a collar suggest that discontinuation of radio-contact may have been due to loss of the equipment. Kelly (1977) reported that kits severely chewed a radio-collar worn by a lactating female. Perhaps biting the neck region of the adult by young is a releaser for regurgitation of meat, and the particular design of collar I used interfered with this behavior.

The absence of the kits from the den is extremely puzzling because they could have been little older than eight weeks. At this age captive kits that had recently opened their eyes were capable of only awkward crawling (Coulter 1966), so it is unlikely that the wild kits could have climbed from the tree unaided. The subsequent development of muscular dexterity of the captive group was extremely rapid; kits crawled by the end of the eighth week and walked by the end of the ninth week (Coulter 1966). Therefore, if wild kits developed even a slight amount more quickly than Coulter's (1966) captive group, they would have possibly been capable of leaving the den through the den-floor opening as could be surmised from disturbance of the screen of tent caterpillar silk and den litter.

Circumstantial evidence from New Hampshire supports my observations. Kelly (1977) radio-tracked a lactating female during portions of two consecutive years. The first time she was captured her kits would have been about 10 weeks old and she did not use a tree-den. The next year she was captured when her kits were about 6-7 weeks old. She used a tree-den on a daily basis for about two weeks and then shifted her range and did not return to the den. Although Kelly (1977) did not observe the kits during either year, the age of kits when the female used a tree-den and the timing of the abandonment of the den agree markedly with my observations in Manitoba.

Although it is not known how the kits left, or were removed from the den, their increasing development may have made it necessary for a change in the type of den. The female of Coulter's (1966) captive group first carried food to her young when they were about 60 days old. At 80 days, about 20 days after the absence of the kits was noted in my study, the kits in Coulter's (1966) study actively fought each other for meat. Consequently, a ground-den may have been more suitable to allow kits more room to feed and to redistribute themselves as they became increasingly aggressive in time. At about 5.5 months of age the growth rate of female kits levels off and their body weight is close to the weight of the adult female (Fuller 1979). Coulter (1966) reported that the captive adult female killed one and injured another 5.5 month old kit. Again, a ground-den would facilitate dispersal of the kits as they became more self-sufficient, thereby reducing the possibility of this type of mishap in the wild.

The breeding system

Coulter (1966) provided the only source of information on changes of fisher activity during the breeding season.

In his intensive study units in Maine he found that fishers followed other fisher tracks, made trails, and used scent posts more frequently than earlier in winter. My observations from Manitoba basically support Coulter's (1966) work, but because of radio-telemetry data on animals of known sex and age I have a less limited basis for speculation about the breeding system of the fisher.

The adult female was relatively sedentary and remained within her established home range during two estrous periods which each differed, in a behavioral sense, due to her parental status. This suggests that adult females are closely tied to a core area and even if barren do not range widely during estrus in a fashion demonstrated by the radio-tagged juvenile female (Fig. 15C). Although there are no other data available on activities of females during estrus, an adult female in New Hampshire also used a small range in which she was captured twice during lactation (Kelly 1977).

Males must first locate females in order to copulate with them. Many of these females are adults which are presumed to occupy relatively restricted ranges. Because female fishers do not synchronously enter estrus and are not particularly dense due to the form of social organization usually attributed to a solitary carnivore (Powell 1979c), the resource for which males search, namely, a female in estrus, is no doubt limited both spatially and temporally.

If males defend a range against other males, as has been shown for other mustelids and suggested for fishers (Powell 1979c), then to maximize their fitness males must either: (1) continue to defend ranges against other males and mate with as many resident females as possible, or (2) they must allow dissolution of territorial defense and travel more widely in an effort to mate with additional females, but suffer the genetic expense of allowing other males to copulate with females within the original defended area. The following evidence points to the second strategy as being more plausible and perhaps ecologically more practical than the first.

The general increase in male track observations in the intensive study area, particularly in locations where numbers of males did not exist in early winter, suggests that during the onset of the mating season males moved more extensively than earlier in winter. The movement of males into the immediate vicinity of the adult female and the rapid long-range departure of the radio-tagged male support track observations and also imply that intrasexual spacing mechanisms of males had broken down. The increased track activity reported by Coulter (1966) may have been a close duplicate to the relationships I observed in Manitoba. He reported that much of the increased activity occurred in a three square mile area, a size that may typically represent the area occupied by a single adult female in or approaching estrus. If these observations are not a result of small samples or observer error, then it appears that fishers have a mating system in which males abandon non-breeding territoriality in favor of actively searching out females in estrus. The evidence presented is further strengthened by the fact that similar systems have been recorded for other solitary mustelids such as weasels (Mustela nivalis) (Erhlinge 1974; King 1975) and stoats (Mustela erminea) (Erhlinge 1977).

Functioning of such a breeding system would demand that males will eventually confront one another and some form of behavioral interaction should result. The fact that I did not record male-male interaction in the field does not necessarily conflict with the proposed system because the adult female that was attracting the males was not yet in estrus, a condition that may be the most important, or perhaps the only factor, that could release a male fighting response. The circumstantial evidence of skull injuries present in breeding-age males certainly tempts one to propose a system rooted with a great deal of male interaction. The extreme sexual dimorphism of fishers (Coulter 1966; Powell 1977; Kelly 1977) is probably a result of pressures of sexual selection and is a very good indicator of the degree of male interaction in the breeding system.

A breeding system in which adult males actively search for mates and leave a well known, defendable range appears to be maladaptive. However, female fishers probably exhibit the same lack of mate selection that Poole (1967) showed for ferrets (*Mustela putorius*), and consequently mate with the first male encountered. Juvenile males are fertile and many are probably transients during their first winter (see Section I; Winter Activity and Movements). If adult males were to defend a fairly large area covering several adult female ranges, then they must expend considerable amounts of energy in an effort to prevent transient males from breeding with resident females. However, it may not be physically feasible for adult males to prevent juvenile males from stealing copulations because olfactory spacing mechanisms, such as scent posts, may be less effective during the breeding period. In addition, adult females are probably not closely spaced. Energy required by males for defense of an area may be more economically used for searching for receptive females in regions beyond the non-breeding defended area.

The degree of promiscuity of females is a feature of reproduction that is poorly known. It is generally believed that female mustelids are induced ovulators requiring stimulus of copulation (Ewer 1973). My record of corpora lutea and Graafian follicles in different ovaries of a single female may indicate that females sometimes require more than one copulation for release of the usual number of ova. Since little is known about any courtship bond between fishers, it is futile to speculate about the probability of individual litters being produced by more than one male, but if the phenomenon exists it would have an obvious effect on interpretation of the breeding system.

Regardless of the type of breeding system evolved, for solitary carnivores population density is perhaps one of the most important factors determining the ratio of fertilized to unfertilized females. Areas with dense fisher populations, such as New York (Eadie and Hamilton 1958) and Maine (Wright and Coulter 1967), have not reported barren females. Presence of barren females in a relatively dense population in southern Ontario was attributed to a shortage of adult males (Strickland and Douglas 1974). In Manitoba, indices of population density, such as sustainable trapper-catch, indicate the existence of a lower population density than many other areas. A total of about 19% of the adult females was barren, a figure that compares closely with the number of barren females in a low density population in Nova Scotia (van Nostrand 1979).

With the availability of only limited field data, caution is advised when hypothesizing about a mating system that is the result of a long evolutionary history. As Ralls (1977) correctly emphasized, contribution of genes in the successive generations is the most important parameter to be measured when addressing the related problems of sexual selection and mating systems. Sexual selection and male dominance may sometimes be poorly correlated with actual genetic contribution to future generations. For example, Duvall et al. (1976) showed, through a study of blood types, that a dominant male in a hierarchical primate social unit could have sired no more than 30% of the current young of the group. A considerable amount of field data will be required, preferably from marked individuals, to test adequately all speculations of breeding biology of fishers that I have proposed.

SUMMARY

1. From May 1975 to June 1977 I studied aspects of the ecology of the fisher at the Taiga Biological Station using radio-telemetry, tracking and track observations. Information on reproduction, food habits, age and sex distributions, and physical condition was available from 195 trapper-caught fisher carcasses collected from four areas during the winters of 1972-73 to 1977-78.

2. The temporal distribution of winter track observations was similar for the winters of 1975-76 and 1976-77. Fewest tracks were observed during periods in January and February. Indirect data from radio-telemetry also supported the occurrence of decreased mid-winter activity of fishers.

3. Cover type selection of fishers in the intensive tracking unit varied throughout winter and was significantly different from the expected values based on cover type availability.

4. Changes in the upper levels of the snow cover appeared to affect fisher activity and cover type selection. Major changes in fisher activity and locomotion were

qualitatively correlated with physical variations in snow cover. Effects of temperature, prey availability, and social behavior could not be separated absolutely from the effects of snow cover, but all available evidence suggested that snow was the predominant factor.

5. Application of snow factors into an ecological energetics model devised to estimate energy requirements of free-ranging fishers (Powell 1977, 1979a) strongly indicated that soft snow could increase fisher energy expenditure. A reduction of total activity was believed to be the most plausible response of fishers to adverse snow conditions. The noted response of fishers to snow conditions was considered to be unique for boreal _Martes_. The fisher's large body size was presumed to be an important factor that influenced the species' inability to negotiate soft snow.

6. Information from the age class structure of the trapper-catch and data from radio-telemetry indicated that juveniles were the age class that moved most extensively during winter.

7. Foraging behavior was recorded from following fisher trails 31.4 km in 1975-76 and 22.1 km in 1976-77. Fishers hunted opportunistically by investigating areas likely to harbor prey. The mean distance between kills and scavenges was 10.7 km. Experimentally introduced ungulate carrion elicited little response from local fishers. In general, hunting behavior of fishers in Manitoba differed little from that reported from other regions.

8. Twenty-two genera and 20 species of prey and carrion were identified from alimentary tracts of 120 fishers that contained food items. Mammals (particularly snowshoe hare: 35.8%) and birds (particularly grouse: 10%) were the dominant food sources during winter.

9. Data from scats collected in the intensive study area did not differ appreciably from information from alimentary tracts.

10. No significant differences in major food groups existed among fishers collected from four regions. Porcupine was the only food that showed marked geographic differences.

11. Porcupine was also the only food that showed significant sex differences in the diet, but these differences may have been attributed to males' increased probability of receiving quills when attacking porcupines.

12. Important variations in frequency of empty tracts, condition index, and food types were related to changes in the winter number of snowshoe hares.

13. Hares increased frequency in alimentary tracts as indices of hare numbers in the field increased. Use of small mammals and the number of food items recorded per individual fisher declined concurrently with increased use of hares. All available evidence supported a functional response of fishers to changing hare numbers.

14. A consumption rate model, adapted from a model developed for piscivores (Diana 1979), was used to estimate the daily metabolizable energy intake (in kJ) of East Lake Winnipeg fishers during the winters of 1974-75, 1975-76, and 1976-77.

15. The consumption rate estimates increased 42% from 1974-75 to 1975-76, and increased 16% from 1975-76 to 1976-77.

16. The consumption rate estimates showed a substantial degree of agreement with energy requirements of captive (Davison 1975) and free-ranging fishers (Powell 1977, 1979a).

17. Hares were an important component of diet as evidenced by their energy values in the model.

18. The consumption rate calculations support data from alimentary tracts and confirm a functional response of fishers to changing hare numbers.

19. Mean condition index for each winter did not vary appreciably, but when fewer hares were available a wider range in the index was evident. It was believed that some members of the population were less capable than others in coping nutritionally with relatively low hare numbers. Increases in consumption rate were probably due to increased feeding by the segment of the population that fed less frequently when hares were scarce.

20. The observed 10 year cycle in fisher fur returns that lagged 5 years behind the hare cycle (Keith 1963) could be explained by changes in trappability of fishers due to variations in the consumption rate during the hare cycle.

21. Presence of pregnant females in the yearling age class, increased tract volume and follicular development of two pre-estrus females, and observation of a tract from a recently-bred juvenile indicated that first reproduction of females occurred at the end of the first year of the juvenile age class.

22. Winter maturation of testes followed a similar pattern for juveniles and adults. All males were spermatic in March, and none were spermatic in other winter months.

23. Bacula from juveniles approached the weight of bacula from adults by March.

24. All available evidence indicated that estrus and parturition occur in late March and April. Uniform development of early winter juveniles suggested a restricted whelping period and possibly a restricted mating period occur for all ages of reproducing females. No evidence of parturition in earlier winter months was recorded in Manitoba; this differed from records from eastern areas of North America.

25. No data were available on the reproductive cycle of males and females from April to October. Inferences from the literature and the time span of maturation of testes suggested that males may remain in breeding condition for two to four months.

26. The mean (3.5) and mode (3) corpora lutea counts for fertile females differed little from reports from other areas.

27. Age-related fertility rates appear to exist in females from Manitoba, but the data contradict the known reproductive history of an intensively studied female.

28. Indices of fertility and productivity indicate that there was no radical changes from 1972 to 1978.

29. Movement of a radio-collared adult female during active pregnancy were not extensive; it was believed that reduced activity was a strategy to conserve energy for growth of foetuses.

30. A radio-collared adult female whelped a litter in a den in a hollow trembling aspen tree. The biological advantages attributed to use of hollow trees for maternal dens were: protection from cold temperatures, protection of kits from adult males that actively search for females in estrus, and protection of kits from ground dwelling predators.

31. The attending adult female spent more time away from her kits as time in the denning period progressed, but did not travel progressively further each day. Movements of the female were extensive and covered most of her formerly established home range. This

behavior was attributed to the necessity of using a well-known home range for more successful foraging, maintaining non-breeding period patterns of social organization, and diverting male courtship activities from the den area.

32. The use of a formerly established home range appeared to be an important characteristic of breeding den ecology. History of reproduction and home range use of the denning female coupled with information on movements of the juvenile age class suggested that most females establish a home range between one and two years of age.

33. The diet of the female during the early portion of the denning period differed little from the winter diet. Carrion was not a major food source for the denning female. Use of birds' eggs may assume importance later in the denning period.

34. Kits exited or were removed from the den when they were about eight weeks of age. This age corresponded to the period when captive kits in another study opened their eyes and showed rapid increases in muscular dexterity. It was hypothesized that the kits were moved to a ground den to reduce stressful interactions between kits and to facilitate dispersal of the kits as they became more self-sufficient.

35. Data from radio-collared fishers and track records during the breeding period led to speculation about the breeding system of the fisher. Adult females were believed to be sedentary during the breeding period due to the presence of a den and kits. Males appeared to abandon non-breeding territoriality to seek out females in estrus.

36. No male-male physical interactions were observed in the field, but presence of minor skull injuries in only breeding age males suggested that some form of behavioral interaction could occur. The extreme sexual dimorphism of fishers was believed to be a result of male interaction and sexual selection.

RECOMMENDATIONS

1. Age of first reproduction and fertility of fishers from Manitoba differs little from regions in the eastern portion of the species' geographic range, but populations in Manitoba produce a much lower sustained yield than many other regions. The frequency of barren females may indicate that populations are not dense enough to ensure insemination of all females. Powell (1979b) emphasized, through use of a population model, that it would take very little trapping pressure to extirpate fishers locally and reduce their status to the low-level populations present in the 1920's and 1930's. To ensure that fishers are responsibly managed, biologists in Manitoba must regulate trapping pressure to prevent overharvest. Various techniques may be incorporated with a carcass collection program to ensure that the biological statistics necessary for management are gathered.

2. Low density fisher populations in Manitoba that are showing a slow numerical increase should be protected from trapping until a dense population is attained. The resulting sustained yield from a dense population is a more favorable management practice than the current technique of harvesting whenever it appears that the resource is available.

3. Neonatal mortality due to adverse weather factors is more probable in Manitoba than in eastern areas. Biologists in Manitoba should monitor the ratio of juveniles to post-parturient adult females to ensure that production has not been affected by late winter and spring weather. If weather is shown to affect productivity, then a management scheme differing from other regions would have to be developed for Manitoba.

4. Little is known about social organization and natural mortality of fisher populations. This information is necessary to understand the biology of the species and make rational management recommendations. A study of social organization of a fairly restricted fisher population, by use of radio-telemetry and tracking, should provide these data. A great deal of ancillary information on neonatal mortality, maternal denning, natural mortality, and hunting behavior could also be gathered. The ultimate success of such a project would depend on selecting a study area that provides access to trapping areas, an adequate fisher population, an effective telemetry system, and freedom from commercial trapping.

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APPENDIX 1. Relevant details about the hare drive index.

The hare drive is performed as a teaching exercise each December in the intensive study area. The plot is permanently marked and is located in proximity to Wallace Lake.

Methods: Fresh hare tracks along the perimeter of the plot are obliterated from the snow cover. Observers are spaced evenly along the north boundary of the plot. At a given signal the observers walk slowly forward. Each observer looks to his right and counts hares that cross between individuals. When the opposite boundary is reached the number of hare tracks leaving the plot on the east, west, and south boundaries are counted. These numbers are added to the number of actual hares observed to give total number of observations.

Reliability: Although this technique is actually a total enumeration of hares in the plot, there are a number of reasons why it should only be used as an index. First, many observers have limited experience in forests and due to their inability in negotiating rough terrain, some hare observations are probably unrecorded. Second, the drive is performed only once per winter and cannot therefore be considered representative of the entire winter. Daily activity patterns of hares, predation, weather, and other factors undoubtedly influence the densities of hares found on the plot at a particular time. Since the variation in density of hares in boreal regions varies 40 fold between high and low portions of the cycle, it is probable that the hare drive could at least determine the direction of change of hare numbers over a span of several years. Conversely, the results of the drive should not be used for a single year estimate or index of hare numbers.