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Winter Food Habits, Responses to Snow Cover and

Movements of Fisher (Martes pennanti) and

Marten (Martes americana) in Southeastern Manitoba

by

R. MICHAEL RAINE

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WINTER FOOD HABITS, RESPONSES TO SNOW COVER AND

MOVEMENTS OF FISHER (MARTES PENNANTI) AND

MARTEN (MARTES AMERICANA) IN SOUTHEASTERN MANITOBA

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R. MICHAEL RAINE

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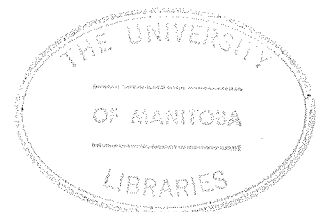of the degree of

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ABSTRACT

A trailing and radiotelemetry study of fisher
and marten was conducted from August, 1978 to August, 1980
in the boreal forest of southeastern Manitoba.

Snowshoe hares composed 81% of the winter diet
of fisher and 53% of the diet of marten. Marten displayed
more subnivean and arboreal activity, and ate more microtines
and squirrels than did fisher. Fisher ate marten twice.
Both fisher and marten were found to pursue hares actively
for distances of up to 1 km.

Fisher were found to be restricted by the soft,
thick snow cover that was present during midwinter. Fewer
tracks were observed at this time, and fisher travelled upon
snowshoe hare trails and their own trails to a greater
extent than in either the early winter period of thin snow
cover or the late winter period of crust conditions. Fisher
were also found to walk through the snow cover and leave a body
drag in midwinter.

Marten did not appear to be hindered by soft snow
cover to the degree that fisher were. Marten tracks were
encountered with equal frequency throughout the winter and
they never left a body drag in the snow cover. They did
travel upon hare trails and their own trails to a greater
extent in the midwinter, but never as much as did fisher.

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Two juvenile, female fisher had winter home ranges of from 15.0-20.5 km^2, while other juvenile females and males dispersed from the study area after their release.

One juvenile, male marten had a home range of 9.6 km^2 in early winter, while another wandered at random in late fall and early winter, but appeared to have a permanent home range of 8.1 km^2 by the following spring. A juvenile, female marten had seasonal home ranges of from 6.0 - 8.4 km^2.

A fire that swept through the study area in May 1980 caused one male marten to disperse 61 km, while a female marten did not alter her home range during the 2 months that radio contact was maintained.

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Manitoba

ABSTRACT

A trailing study of fisher and marten was conducted for two winters during the period of snow cover in the boreal forest of Manitoba. Snowshoe hares composed 81% of the winter diet of fisher and 53% of the diet of marten. Marten displayed more subnivean and arboreal activity, and ate more microtines and squirrels than did fisher. Fisher ate marten twice. Both fisher and marten were found to pursue hares actively for distances of up to 1 km.

INTRODUCTION

Fisher (<u>Martes</u> <u>pennanti</u>) and marten (<u>M</u>. <u>americana</u>) are opportunistic feeders. The main winter prey of fisher is snowshoe hares, porcupines, microtines and birds. They also use carrion when it is available. The winter food habits of fisher have been studied in Ontario (de Vos, 1952; Clem, 1977), New York State (Hamilton and Cook, 1955; Brown and Will, 1979), Maine (Coulter, 1966), New Hampshire (Stevens, 1968; Kelly, 1977), Michigan (Powell, 1977, 1978) and in Manitoba (Leonard, 1980).

Microtines are the main winter food of marten in Ontario (Clem, 1977), Maine (Soutiere, 1979; Steventon, 1979), Montana (Weckwerth and Hawley, 1962), British Columbia (Cowan and MacKay, 1950; Quick, 1955), Alaska (Lensink <u>et al</u>., 1955), the Yukon Territory (Boles, 1974), and the Northwest Territories (More, 1978). Studies in Washington State (Newby, 1951) and Montana (Marshall, 1946) indicate that squirrels are sometimes the most important food for marten there.

The European pine marten (<u>Martes</u> <u>martes</u>) and the sable (<u>Martes</u> <u>zibellina</u>) are closely related to the North American marten (Anderson, 1970). Microtines are the main food of the European marten in Scotland (Lockie, 1961), Finland (Pulliainen, 1980a) and in Poland (Goszczynski, 1976). Goszczynski (1976) tabulated the results of 17 studies from the Soviet Union that

show that the main prey of the European marten is small rodents. The sable also preys upon small rodents to a large extent (Bromley, 1956; Shaposhnikov, 1956; Danilov and Ivanter, 1967). These species also prey on hares, shrews and birds.

Winter trailing is the most common technique used to study the foraging behaviour of fisher and marten. Fisher (de Vos, 1952; Coulter, 1966; Powell, 1977; Leonard, 1980) have been found to have a capricious search path that involves the investigation of upturned roots of fallen trees, logs and brushpiles. Marten (Marshall, 1946, 1951a; Murie, 1961; Nyholm, 1970; Campbell, 1979; Steventon, 1979; Pulliainen, 1980a) have been found to hunt in a similar fashion.

I conducted a radiotelemetry and tracking study of fisher and marten at Taiga Biological Station (51° 05' N, 95° 20' W) from August, 1978 to August, 1980. A previous study (Leonard, 1980) of fisher provided background for this investigation. No marten were known to be present in the study area until 1978. A sudden influx of marten permitted their food habits and foraging behaviour to be compared with fisher. The increase in the local marten population appeared to be part of the widespread expansion of marten range in Ontario and northern Minnesota (Mech and Rogers, 1977).

Study Area

The 324 km^2 study area is part of the low boreal land region (Woo et al., 1977). The dominant features are bedrock knolls and ridges of up to 30m in height with bogs and fens in between. The mean January temperature varies from -22.8 to -19.8^{O}C and the mean July temperature varies from +18 to +19.5^{O}C. Annual precipitation varies from 410 to 535 mm, with 250 to 355 mm of this falling as rain between 1 May and 30 September (loc. cit.).

The study area is composed of 10 habitats. The most common habitat is jackpine (Pinus banksiana) ridge. The entire study area has been burnt at some time or other, although some parts not for 150+ years. Moderately open black spruce (Picea mariana)-tamarack (Larix laricina) bogs are the second most common habitat. Open bogs of the same species, thick alder (Alnus) bogs, black spruce bogs and beaver meadows are the other moist habitats. The remaining habitats are aspen (Populus tremuloides)-jackpine ridges, balsam fir (Abies balsamifera)-white spruce (Picea glauca) ridges, jackpine sandplains and rivers and lakes.

METHODS

Relative Prey Densities

Squirrel and Grouse - The relative densities of the most
common prey items were determined by track counts. All tracks
were recorded and then erased in the snow wherever I skied on
a system of flagged trails. The distance that these trails
traversed each of the 10 habitats had previously been measured.
Thus I could compare, using the Chi-square distribution, the
observed frequency of tracks per habitat and per winter with
the expected value calculated from the distance I had skied
in each habitat and in each winter.

Red squirrel (Tamiasciurus hudsonicus) tracks were not
recorded until January of 1979. As squirrel activity varies
with temperature (Pruitt and Lucier, 1958), between year
comparisons could only be made for the months of January through
March.

Ruffed (Bonasa umbellus) and spruce (Canachites
canadensis) grouse tracks could not be differentiated from each
other.

Snowshoe hare - Snowshoe hare track counts were made once per
month on 1 km transects in each of the five habitats in which
hares were most common. I initially ran transects in all 10
habitats, but dropped the five that hares rarely frequented

(moderately open bog, open bog, jackpine sandplain, beaver meadow, river and lake). The transects were run four days after a snowfall and all tracks that crossed the transects were recorded as being either single tracks or trails. I arbitrarily defined a "trail" to be wherever two or more hares had passed, and weighted trails to be the equivalent of three single tracks.

Small Mammals - Small mammal trapping was conducted in September of each year in all terrestrial habitats except open bogs. Permanent plots of 100 traps arranged 10 by 10 with 6.5 m between each trap were used. Fifty museum specials and 50 Schuylers were alternated on each grid and set for three nights.

Fisher and Marten Tracking - Both fisher and marten were trailed whenever their tracks were encountered. The distance moved by an animal was determined by counting its "paces", one pace being the distance covered by an animal through one complete cycle of motion.

The pace length varied with the animal's size, its speed, snow conditions and topography. However, it can be regarded as a unit of effort. Every time I trailed an animal I measured 10 of its paces, the depth it sunk in the snow cover and its track size. The number of paces that the animal took in each habitat was recorded, its activity was noted and any scats were collected.

I identified mammal remains in the scats by cuticular scale impression patterns (Adorjan and Kolenosky, 1969) and by comparing them with a reference collection of hair and skeletons.

Scat contents were classified in two ways, following the method of Knowlton (1964) and Hill (1979). The frequency occurrence of an item was calculated by dividing the total number of occurrences of a food item by the number of scats, while the frequency occurrence of a major item (M.I.) was calculated by dividing the number of times an item comprised 40% or more by volume of a scat by the number of scats. When two items in one scat occurred as a major item, each was tabulated as one-half of an occurrence to maintain the integrity of the sampling unit and to limit the sum of the percentage frequencies of occurrence as a major item to 100%.

RESULTS

Relative Prey Densities

Squirrel and Grouse - The total numbers of squirrel and grouse sign observed in each winter are compared with the expected numbers calculated from the distance skied in each winter in Table 1.

Both grouse and squirrel sign did not differ significantly from expected between years.

Flying squirrel (Glaucomys volans) were present in the study area, though not common.

Bird species that fisher and marten could eat in winter included gray jays (Perisoreus canadensis), black-capped chickadees (Parus atricapillus), boreal chickadees (Parus hudsonicus), pine grosbeaks (Pinicola enucleator), crossbills (Loxia curvirostra and L. leucoptera) and downy (Picoides pubescens), hairy (P. villosus) and pileated (Dryocopus pileatus) woodpeckers.

Snowshoe Hares - The results of the snowshoe hare transect counts are shown in Table 2. The changes between counts within years were not synchronous, however, the means of each habitat were lower in the winter of 1979/80 than that of 1978/79, and the aspen ridge, thick alder bog and balsam fir ridge habitats had the highest track counts in both winters.

Table 1. Comparison of grouse and squirrel track counts in
each winter.

		1978/1979 November–April	1979/1980 November–April	$X^2_{[1]}$	
Grouse	observed	458	513	2.178	⋝ 0.5 Not significant
	expected*	480.9	490.0		
		January–March	January–March		
Squirrel	observed	412	497	1.249	> 0.5 Not significant
	expected*	428.8	480.2		

*Based on the distance skied in each winter.

Table 2. Snowshoe hare transect track counts*

78/79 Count	Date	Aspen	Jackpine Ridge	Balsam Fir Ridge	Black Spruce Bog	Thick Alder Bog	Habitat Rank	79/80 Date	Aspen	Jackpine Ridge	Balsam Fir Ridge	Black Spruce Bog	Thick Alder Bog	Habitat Rank
1	9/XII/78	198	7	155	83	195	Aspen	6/XI/79	88	8	170	4	138	Balsam Fir
2	16/I/79	573	331	441	222	472	Thick Bog	1/XII/79	89	80	78	65	149	Aspen
3	22/II/79	483	178	211	102	259	Balsam Fir / Jackpine	18/I/80	271	104	253	66	120	Thick Bog / Jackpine Ridge
4	5/III/79	380	246	466	128	389	Black Spruce	19/II/80	192	129	229	153	70	Black Spruce Bog
Mean		408.5	190.5	318.3	133.8	328.8			160.0	80.3	182.5	72.0	119.3	
Mean of means		276							123					

*weighted track counts, where 1 "trail" = 3 single tracks

Small Mammals - Clethrionomys gapperi and Sorex cinereus
were the most abundant small mammals in both years, and their
densities did not change appreciably between years (Table 3).
In 2,400 trap nights in September 1978 a total of 52 C. gapperi
and 48 S. cinereus were caught. In the same number of trap
nights in September 1979 a total of 51 C. gapperi and 47
S. cinereus were trapped. The total number of all small
mammals in all habitats (115) did not change at all between
years, although the numbers within each habitat did change.
In the first fall the beaver meadow (32), thick alder
bog-jackpine ridge ecotone (22), thick alder bog (20) and
aspen ridge (20) plots had the most animals. In the second fall
the jackpine ridge (19), ecotone (24) and aspen ridge (21)
plots had the most.

Other Mammals - Porcupines were rare in the study area,
although one female fisher that was live-trapped had a quill
in her throat. Muskrats were common in the shallow bays of
lakes. Possible sources of carrion included beavers, moose
and woodland caribou (Rangifer tarandus caribou). There
were no white-tailed deer in the study area during the two
winters of the study.

Trailing Results

A total of 154,217 fisher paces and 142,023 marten paces
was followed, resulting in 159 fisher and 107 marten scats

Table 3. Small Mammal Snaptrap Results.

September, 1978

Habitat	Clethrionomys gapperi	Peromyscus maniculatus	Microtus pennsylvanicus	Synaptomys cooperi	Sorex arcticus	Sorex palustris	Sorex cinereus	Blarina brevicauda	Total
Jackpine ridge	5						6		11
Thick bog/jackpine ridge ecotone	8				2		12		22
Thick bog	11						9		20
Jackpine sandplain	2								2
Black spruce bog	1								1
Aspen ridge	16						4		20
Moderately open bog		3					4		7
Beaver meadow	9	7			2	1	13		32
Total	52	10			4	1	48		115

September, 1979

Habitat

Habitat	Clethrionomys gapperi	Peromyscus maniculatus	Microtus pennsylvanicus	Synaptomys cooperi	Sorex arcticus	Sorex palustris	Sorex cinereus	Blarina brevicauda	Total
Jackpine ridge	10						9		19
Thick bog/jackpine ridge ecotone	10		3	1			8	2	24
Thick bog	3	1	3	1	1		6	1	16
Jackpine sandplain	2			1			4		7
Black spruce bog	1						5		6
Aspen ridge	17						4		21
Moderately open bog	1	1	1				3		6
Beaver meadow	7	1					8		16
Total	51	3	7	3	1		47	3	115

being collected. The mean midwinter pace lengths of fisher and marten were 71.9 cm (n=510) and 57.1 cm (n=570), respectively. Thus a total of approximately 111 fisher and 81 marten km was trailed. The sexes could not be determined by track size in either species, despite the sexual dimorphism that both species exhibit (Moors, 1980). Track size varied enormously with snow cover thickness, vertical hardness, the age of the track, the animal's speed and the positioning of the animal's feet. Exceptionally large tracks, however, were most likely those of male fisher.

Fisher Scat Results

The scat analysis (Table 4) indicates that snowshoe hare was the most common prey of fisher in the two winters (84.3% occurrence; 81.1% M.I. occurrence). The next most common item was birds (8.2%; 6.8% M.I.). Fisher ate marten at least twice. On one occasion there was a large amount of marten fur in several scats, while on another occasion there was marten fur, bones and claws. Fisher hair occurred as a minor item twice and was probably the result of grooming. Marmot (Marmota monax) and snake (Thamnophis sirtalis) were eaten on occasion in winter, despite the fact that these species hibernate. Fisher dug through the snow cover numerous times to eat old eggs. Egg shell always occurred as a minor item in scats and I could not tell whether fisher were finding entire eggs or just empty shells. The occurrences of miscellaneous vegetation and graminoid-like

Table 4. Fisher and marten scat analysis.

	Fisher (n=159)		Marten (n=107)	
	Percent frequency occurrence	Percent frequency occurrence of major items	Percent frequency occurrence	Percent frequency occurrence of major items
Sorex cinereus			1.9	1.4
Martes americana	5.0	4.7		
M. pennanti	1.3			
Marmota monax	2.5	2.5		
Tamiasciurus hudsonicus	1.3	1.3	15.9	15.9
Clethrionomys gapperi	1.3	0.6	8.4	7.9
Microtus pennsylvanicus			3.7	3.7
Unidentified microtine	1.9	1.3	6.5	6.5
Ondatra zibethicus	0.6	0.6		
Lepus americanus	84.3	81.1	58.9	53.3
Grouse	6.9	4.7	4.7	3.7
Unidentified bird	1.3	1.3	13.1	7.5
Egg	7.5		0.9	
Vegetation	3.1		9.3	
Graminoid vegetation	8.2		12.1	
Seeds	1.9	1.9		
Thamnophis sirtalis	3.1			
Insects	1.9			
Total		100.0		100.0

vegetation were always in small quantities and they were probably taken inadvertantly.

Fisher kills and scavanges encountered during trailing are shown in Table 5. Excluding the egg and frog scavanges, fisher averaged one kill or scavange per 5.1 km of trail.

Marten Scat Results

The main prey of marten was also snowshoe hare (58.9%; 53.3% M.I.). Microtines were next in importance (18.6%; 18.1% M.I.) followed by squirrels (15.9%; 15.9% M.I.) and birds (17.8%; 11.2% M.I.). As with fisher, there were traces of vegetation in many scats (21.4%). Vegetation never occurred as a major item.

Marten kills and scavanges were similar to the prey items found in the scats. Marten averaged one kill or scavange per 5.8 km.

Comparison of Fisher and Marten Food Habits

Fisher ate more snowshoe hares (81.1% M.I.) than marten (53.3% M.I.), while marten ate more microtines (18.1% M.I. vs 1.9% M.I.), squirrels (15.9% M.I. vs 1.3% M.I.) and birds (11.2% M.I. vs 6.0% M.I.). These differences are significant at the 0.001% level (χ^2[5] = 378.02).

The diets of the two species appear more similar when compared within the same year (Table 6). The marten population was still low in the study area in the first winter (Section II)

Table 5. Fisher and marten kills and kill/scavanges found in two winters of trailing.

	Fisher		Marten	
	Kill	Kill/scavange	Kill	Kill/scavange
Snowshoe hare	5	10		6
Grouse	1	2	1	2
Eggs		6		
Red squirrel		1	1	
Gray jay		1		
Unidentified bird				1
Small mammal	2		3	
Ranid		1		
Total	8	21	5	9

Table 6. Percent occurrence of major food items of fisher
and marten.

	Fisher			Marten	
	1978/79	1979/80		1978/79	1979/80
	% Occurrence			% Occurrence	
	n = 107	52		18	89
Red squirrel		3.9		16.7	15.7
Marten, marmot and muskrat	6.1	11.5			
Microtines and Shrews		5.8		27.8	17.9
Snowshoe hare	93.0	56.6		55.5	52.9
Birds	0.9	16.4			13.5
Seed		5.8			
Total	100.0	100.0		100.0	100.0

and therefore only few scats were collected. Marten, however, still ate more squirrels and microtines, and fisher ate more marten, marmot and muskrat (χ^2[5] = 70.70; P < 0.001).

There is a marked difference in the fisher's diet between years (χ^2[5] = 59.67; P < 0.001). They caught fewer hares but more of everything else in the second winter.

Comparison of Fisher and Marten Foraging Behaviour

Both fisher and marten travelled long distances in relatively straight lines, and often stopped at the roots of fallen trees, logs and coverts of thick patches of young coniferous trees or the qali-laden lower branches of larger coniferous trees. At times they circled around such places.

Behaviours that were interpreted as foraging activities are listed in Table 7. Marten showed more subnivean and arboreal activity than did fisher. These differences are further accentuated by the fact that fisher were trailed farther than marten. Fisher dug holes in the snow more often than tunnels, whereas marten did the reverse. Marten also investigated more squirrel tracks. In the second winter, fisher encountered 91 squirrel tracks and stopped to sniff at or circled three of these, while marten encountered 128 and investigated 18. (χ^2[1] = 6.44; P < 0.05).

The mean length of 30 marten tunnels through the snow was 74.2 cm, and the mean diameter of 21 tunnels was 10.9 cm. Seven fisher tunnels had a mean length of 112.1 cm and a mean diameter of 12.9 cm.

Table 7. Frequency of foraging activities of fisher and marten.
        Two year total.

	Fisher	Marten
Investigate coverts	16	82
Investigate under fallen log	8	56
Investigate upended tree roots	11	40
Tunnel through snow	11	63
Dig hole in snow	28	16
Investigate base of tree	0	8
Climb up tree	0	10
Investigate holes in rocks	13	14
Investigate squirrel tracks	6	26
Investigate grouse tracks	3	1
Investigate microtine tracks	0	3
Snowshoe hare chase	5	2
Kilometers trailed	111	81

The number of observed subnivean foraging activities in each habitat is compared with the habitat use of each species in Table 8. Fisher showed significantly ($P < 0.005$) more subnivean activity than expected in aspen ridge habitat. Marten showed significantly ($P < 0.005$) more activity in thick alder bog and beaver meadow habitats.

Each winter was divided into three periods according to snow cover conditions. The first period was from the time of the first snowfall (13 November in 1978; 1 November in 1979) to when the snow thickness began to restrict the movements of fisher and marten. This thickness I arbitarily chose as 20 cm, and it happened to be reached on 26 November of both winters. The second period consisted of the midwinter months of soft, thick snow cover when the vertical hardness was less than 100 gm/cm^2 in all habitats except rivers and lakes, and was often less than 10 gm/cm^2. The third period began when a vertical hardness of greater than 100 gm/cm^2 was reached in all habitats. The change to crust conditions was quite abrupt in both winters and occurred in all habitats at about the same time (21 March in 1979; 23 March in 1980). A series of thaws and freezings occurred during the crust periods of both winters which caused the vertical hardness of the snow cover to increase to 1,000-5,000 gm/cm^2. Both fisher and marten had less subnivean activity than expected during the crust periods ($P < 0.005$; Table 9).

Table 8. Number of observed fisher and marten subnivean
          activities per habitat, excluding rivers and lakes.
          Two-year sum of tunnels in snow, holes in snow,
          coverts, logs and roots

Fisher	Aspen ridge	Jackpine ridge	Thick alder bog	Open and moderately open bog**	Black spruce bog	Balsam fir ridge	Jackpine sandplain	Beaver meadow	Total	$\chi^2_{[7]}$	P
Observed	21	36	5	2	5	3	0	2	74		
Expected*	7.7	39.6	6.3	5.4	9.4	3.4	1.6	0.7	74	32.1	<.005

Marten

	Aspen ridge	Jackpine ridge	Thick alder bog	Open and moderately open bog**	Black spruce bog	Balsam fir ridge	Jackpine sandplain	Beaver meadow	Total	$\chi^2_{[7]}$	P
Observed	34	110	63	19	18	6	1	6	257		
Expected*	27.8	139.5	34.0	19.2	19.0	8.2	8.0	1.3	257	57.0	<.005

*Based on the distance each species was trailed in each habitat.
**Pooled as similar habitats.

Table 9. Number of observed fisher and marten subnivean
          activities per winter period. Sum of both winters.

		Thin snow cover	Midwinter soft snowcover	Crust	Total	$\chi^2[2]$	P
Fisher	Observed	21	42	11	74		
	Expected	19.0	25.9	29.1	74	21.4	< 0.005
Marten	Observed	46	205	6	257		
	Expected	59.5	178.3	19.1	257	16.1	< 0.005

*Based on distance each species was trailed in each winter period.

Fisher actively chased hares five times, twice for over an estimated kilometre (Table 10). I was never able to trail a complete chase although I twice reached the endpoints of chases and found a warm hare carcass. Both kill sites indicated that the kills had been very swift as no signs of a struggle could be seen. I witnessed the second of these chases on a lake. The hare did not seem to be running at full speed, although the fisher (a female) was approximately 7 m behind it. The hare made a number of zigzags before disappearing around a point of land. It was killed shortly afterwards. The fisher and hare had made bounds of up to 192 and 184 cm, respectively. The chase had alternated several times between the balsam fir ridge on the shore and the ice. After killing the hare, the fisher dragged it 95 paces in from the shore and ate it under a fallen spruce.

Marten twice chased hares for at least one-half kilometre (Table 10). During one of these chases, in thick snow cover, the marten's tracks registered perfectly in the hare's tracks for a long distance.

A fisher once dragged a hare 687 paces (approximately 317 m) to its subnivean den, while a marten once dragged a spruce grouse 657 paces (approximately 330 m) to its den. Remains of grouse and hare were often found at both fisher and marten dens.

Table 10. Fisher and marten snowshoe hare chase data.

Fisher date	Number of paces	Mean of 10 paces (cm)	Estimated number of meters	Track depth (cm)	Habitat
16/XI/78	373+	84.5	315.2+	3.5	Lake
30/I/79	152+			5.0	Moderately open bog and thick bog and aspen
14/XI/79	899+	92.3	829.8+	6.0	Jackpine ridge
26/XI/79	900+	118.2	1,063.8+	2.5-9.0	Lake
4/XII/79	573+	176.7	1,012.5+	2.0-5.0	Lake and balsam fir ridge

Marten

10/XII/79	500+			2.5-6.0	Jackpine ridge and lake
16/XII/79	482+	113.6	547.5+	7.0	Aspen and jackpine ridge

Both species often travelled on the tracks of other species (Table 11). Fisher followed mink, marten, lynx and fox trails more than marten did, while marten followed ermine trails more than fisher did. One female fisher travelled on a fox trail for 1,600 paces (1,392 m) on a lake, and a fox once actively pursued a male fisher for 1,418 paces (2,218 m). The fisher had been travelling in a relatively straight line for 4 km on 31 March 1979, during the crust period of the winter. It passed through an area where there were many fox tracks and possibly a fox den. The fisher sped up and began to zigzag erratically when a fox began to chase it. At each sharp turn the fisher made, the fox would glissade on the crust for several feet before continuing the chase. No blood or fur was found on the snow. Despite its zigzags, the fisher still travelled in the direction it had been going prior to the chase, and it never climbed a tree although many were available.

Fisher crossed open bogs and lakes as they encountered them. Thus they did not avoid open areas, although they did not actively hunt in them. In crossing large lakes they often skirted islands they encountered instead of crossing them. Once a male travelled 380 paces (367 m) across a lake, skirted an island for 147 paces (142 m), and then took a further 860 paces (831 m) to complete the crossing of the lake.

Table 11. Number of paces fisher and marten trailed other species

	Fisher		Marten	
	Number of paces	Number of occasions	Number of paces	Number of occasions
Mustela erminea			155	3
Mustela vison	417	3	4	3
Martes americana	956	6	*	
Martes pennanti	*			
Lutra canadensis	16	2	84	2
Lynx canadensis	393	5		
Vulpes fulva	1837	6	95	3
Alces alces or Rangifer tarandus	450	10	442	5

* Fisher and marten followed their own species tracks to a considerable degree. This was interpreted as sexual behaviour (Section II).

Marten sometimes hunted in moderately open black spruce-tamarack bogs up to 200 m wide. On one such occasion a marten hunted for 1,025 paces (528 m) in a bog.

DISCUSSION

Fisher Food Habits

Fisher had a higher percentage occurrence of hare
in their diet in the winter of 1978/1979 (93.0% M.I.) than
in any previous study. This was perhaps due to the fact
that the hare population was high during the study and
to the rarity of porcupines and white-tailed deer. Other
authors have found that fisher often eat porcupines (de Vos,
1952; Powell, 1978) and ungulate carrion (de Vos, 1952; Hamilton
and Cook, 1955; Kelly, 1977). Moose and woodland caribou
occurred in the study area, but I found no evidence that
fisher used carrion of these species. De Vos (1952) found a
25% occurrence of hare in fisher guts from Ontario, Powell
(1977) found 31% in scats from Michigan and Leonard (1980)
found a 52% occurrence in guts from Manitoba in the winter
of 1976/1977.

Leonard showed that fisher exhibited a functional
response in their diet to changes in prey densities. Studies
of lynx (Brand et al., 1976) and great horned owls (Bubo
virginianus) (Adamcik et al., 1978) have shown that these
predators will switch to alternate, less preferred prey when
the density of hares decreases.

Yearly hare drives indicated that the hare population
increased between 1974 and 1977 (Leonard, 1980).

As the hare population rose the occurrence of this species in the diet increased while the occurrence of small and medium sized mammals decreased. My data, when compared with Leonard's (Table 12), confirm this trend. Leonard's data are from carcasses collected over most of southeastern Manitoba and one part of western Manitoba, while mine are from scats collected from one small area. However, the trend is still clear. Fisher ate hares almost exclusively in the winter of 1978/1979. When the hare population began to fall in 1979/1980, as determined by track counts, fisher switched to alternate prey. This switch occurred despite the fact that the grouse, squirrel and small mammal populations remained constant over the two years.

The other prey that was taken by fisher in this study have been found to be eaten by fisher in other studies. Microtines, squirrels and birds have been found in all studies (de Vos, 1952; Hamilton and Cook, 1955; Coulter, 1966; Clem, 1977; Kelly, 1977, Powell, 1977; Brown and Will, 1979; Leonard, 1980), muskrats in three studies (Hamilton and Cook, 1955; Brown and Will, 1979; Leonard, 1980) and marmots in one study (Leonard, 1980).

Fisher averaged one kill or scavange per 5.1 km in this study. Powell (1977) found one per 8.8 km and Leonard (1980) found one per 10.7 km.

Table 12. Percent occurrence of fisher prey items 1974/1975
           to 1979/1980.

	Guts from S.E. and western Manitoba (Leonard, 1980)			Scats from Taiga Biological Station		
n	1974/75 23	1975/76 35	1976/77 42	1977/78 −	1978/79 107	1979/80 52
Snowshoe hare	17.3	20.1	52.4	−	94.4	63.5
Squirrel	13.0	8.6	23.9	−	−	3.9
Small mammal	51.7	25.7	23.9	−	−	9.7
Other mammal	30.5	14.3	11.9	−	6.5	11.5
Bird	47.8	60.0	42.8	−	2.8	19.3
Carrion	13.0	17.1	7.2	−	−	−

$\bar{\bar{x}}$ Hare transect count

					276	123

Marten Food Habits

Marten also had a higher frequency of hare in their
diet (53.3% M.I.) than in most other studies. Many of these
studies were done in areas of low hare population (Lensink
et al., 1955; Murie, 1961). Quick (1955), however, in
northern British Columbia, found that one male marten
exploited a localized hare population and had an 86.5%
frequency of hare in its diet. Boles (1974) found a 31%
frequency of hare in the diet of marten in the Mackenzie River
Valley.

Microtines (18.1% M.I.) and squirrels (15.9% M.I.)
were the next most important foods for marten in this study.
Most studies have found microtines to be the main winter prey
of marten (e.g. Weckwerth and Hawley, 1962; Koehler and
Hornocker, 1977; Soutiere, 1979; Steventon, 1979).

Clethrionomys gapperi and Sorex cinereus were the most
common small mammals caught in snap traps but only Clethrionomys
were eaten by marten in any appreciable quantity. Other
authors have also found that marten do not eat shrews in
proportion to their abundance (Cowan and MacKay, 1950;
Lensink et al., 1955).

Contrary to popular opinion, (e.g. Haley, 1975; Whitacker,
1980) squirrels are not the main food of marten, although two
authors have found them to compose from 40-60% of the marten's
winter diet (Newby, 1951; Marshall, 1946).

Grouse (3.7% M.I.) and unidentified birds (7.5% M.I.) were also important to marten in this study. Other authors have found that marten prey on birds in winter (46% occurrence; Quick, 1955; 12% occurrence, Soutiere, 1979).

Only 18 scats were collected in the winter of 1978/1979, thus between-year comparisons are not possible. Pulliainen (1980a) found that the European marten exhibited a functional response to changing microtine populations. During winters of high vole numbers the diet of marten was composed of 90-100% mice. When the vole population declined the marten ate more reindeer carrion, eggs, squirrels, grouse, berries and mushrooms.

Marten averaged one kill or scavange per 5.8 km in this study. Marshall (1951a) found that marten made one kill per 12.3 km in Idaho.

Comparison of Fisher and Marten Food Habits

The differences found between the diets of fisher and marten indicate that dietary competition between the species was probably not extensive. Clem (1977) found that fisher in Ontario ate more porcupines and fewer small mammals and birds than marten did. De Vos (1952) stated that many traplines that had high fisher populations had low marten populations, and vice versa. However, he also found many exceptions to this rule.

Yurgenson (1956) noted that as the sable population fell in western Russia in the 19th century, the European marten population grew and extended its range.

De Vos (1952) related one incidence of a fisher killing a marten and Brown and Will (1979) had one occurrence of marten hair in 322 guts. There were no active trappers in the vicinity of my study and so there was no possibility that the two occurrences of marten remains in fisher scats were from robbed traps. This is still not unequivocal evidence, however, that the fisher actually killed the marten.

Fisher Foraging Behaviour

The alternation between travelling long, straight distances and intensively hunting small areas has been noted by other authors (Coulter, 1966; Powell, 1977; Leonard, 1980). Fisher in this study stopped to investigate coverts, fallen logs and upended tree roots, and tunnelled or dug holes in the snow an average of 0.67 times per kilometre of trail. They dug holes in the snow more often than tunnelling in it. Perhaps their relatively large body size makes digging more feasible than tunnelling.

Fisher exhibited more subnivean activity in aspen ridge habitat, but this is a biased result as one male fisher made 11 of 21 aspen ridge occurrences in one spot while digging for grouse eggs (Table 8). Fisher had significantly less subnivean activity when a crust was formed on the snow in spring. A crust with a vertical hardness of 5,000 gm/cm^2 is strong enough to support a person and is likely a physical barrier to fisher. It may also prevent fisher from detecting prey by smell.

Fisher never climbed a tree or investigated a tree base in 111 km of trail. Other authors have also found that fisher rarely climb trees (de Vos, 1952; Coulter, 1966; Leonard, 1980), although Powell (1980) gave several examples of fisher climbing trees in Michigan.

Contrary to this study, other authors have not found evidence of extended hare chases (Coulter, 1966; Powell, 1977; Leonard, 1980). Pittaway (1978), however, recorded two observations of fisher chasing hares, with one chase being over half a kilometre.

Fisher often travelled on the tracks of other species (Table 10). This behaviour may be foraging or energy-saving behaviour. My own data and Leonard (1980) agree that fisher are hindered in their movements by the soft, fluffy snow of midwinter. Tracks of moose, woodland caribou and otter are large enough that they support fisher. Fisher, however, rarely travelled on these for any distance. They followed them for short distances as long as the trails went in the direction the fisher had been going previously. Occasionally fisher would turn about upon approaching a man-made trail, or would cross it rapidly with long bounds. De Vos (1952) noted this as well.

Fisher trailed marten six times for a total of 956 paces. This was not necessarily hunting behaviour although once a fisher that had been travelling in one direction for over 3 km turned 270° to follow a marten track for 500m.

Some authors believe that fisher avoid areas without a tree canopy (Coulter, 1966; Kelly, 1977). I found no evidence of this in my study.

Marten Foraging Behaviour

Marten trail patterns were similar to fisher, except that they were more often subnivean or arboreal than fisher. Koehler and Hornocker (1977), Campbell (1979), and Steventon (1979) also found that marten used windfalls and brushpiles extensively. Marten investigated such places and went under the snow an average of 3.2 times per kilometre in this study. Pulliainen (1980a) found the frequency of subnivean activity for the European pine marten to be 1.3 times per kilometer in Finland, and Shaposhnikov (1956) found the frequency for the sable to be 3-4 times per kilometre.

Marten exhibited significantly more subnivean behaviour in thick alder bog and beaver meadow habitats (Table 8) than expected. These habitats also have high small mammal densities (Table 3). Access to subnivean spaces are important. Alders in thick bogs are often bent over by the weight of the qali on them, and their branches, together with sedges and labrador tea (Ledum groenlandicum), support snow such that subnivean spaces are created. Beaver meadows are formed by flooding and thus many trees die and eventually fall over.

Marten, like fisher, showed significantly less subnivean activity when a crust was formed on the snow in spring. Pulliainen (1980a) found that subnivean activity of M. martes decreased as the winter progressed. He felt that marten depend upon the flow of air from the warm soil to the cold air to detect subnivean food items. He also found that female marten went under the snow more often than males.

Marten followed the tracks of other species several times (Table 11). Marten were also hindered by soft snow in midwinter (Section II), although not to the extent that fisher were. Thus most of their trailing behaviour was probably to save energy. Marten did trail ermine on three occasions however. As ermine tracks are quite small and offer no support for marten, perhaps the marten were actively hunting ermine on these occasions.

Marten spent most of their time on the ground during my study. Marshall (1942) found a similar result when marten climbed trees eight times in 61.6 km of trail. Pulliainen (1980a) found that M. martes travelled only 0.02% of 5,398 km in trees, and Nyholm (1970) found that they travelled 0.11% of 1,880 km in trees.

Marten ate more squirrels than did fisher, but I found no evidence that they caught them in trees. Newby (1951) and Quick (1955) believe that squirrels are more susceptible

to predation in their subnivean middens. Murie (1961) found that marten often used middens for dens, but that squirrels were rarely eaten.

Miller et al., (1955) described a 2.1 km hare chase by a marten in British Columbia, while Pulliainen (1980a) noted one occasion where a European pine marten chased a Lepus timidus unsuccessfully for 3.8 km.

Many authors state that marten avoid open spaces in winter (Newby, 1951; Lensink et al., 1955; Hawley and Newby, 1957; Grakov, 1972; Herman and Fuller, 1974; Pulliainen, 1980a). Koehler and Hornocker (1977) found that marten crossed openings of up to 100 m in width but did not hunt in them. They rarely used openings greater than 100 m wide. Campbell (1979) found that marten crossed open areas but did not hunt in them. Soutiere (1979) stated that marten travelled between softwood islands in clearcuts and crossed openings up to 200 m in width. They travelled more directly in the open than in the forest, but they did investigate slashpiles that were above the surface of the snow. He also stated that males travelled in clearcuts more than females did. Steventon (1979) also found that males used openings more than females.

Wooley (1974) found that marten hunted in larch fens up to 1.6 km in width where there were lots of ptarmigan and mice. They crossed an airstrip, however, where there were few prey, in a relatively straight line.

Marshall (1951a) and Krasnovskii (1970) believe that small clearings are beneficial for marten as they increase the amount of ecotone available.

Many authors have found that marten will use open areas in summer when they have access to mice and when fruit such as raspberries are available (Marshall, 1951a; Streeter and Braun, 1968; Koehler and Hornocker, 1977; Soutiere, 1979; Major, 1979).

In this study I found that marten seldom travelled on lakes, although they did not avoid them if they encountered them. Marten hunted in beaver meadows and moderately open black spruce-tamarack bogs if there was access to subnivean spaces.

Dietary Competition Between Fisher and Marten

Two sympatric species may compete with each other if they share the same food supply. However, diet overlap measured by the percentage of prey items common to two diets is not necessarily proportional to the amount of exploitative competition (Moors, 1980). It is only an estimate of the maximum competition possible. The actual level is probably less due to partitioning by habitat, activity patterns and search paths. In this study marten displayed more subnivean and arboreal activity than did fisher.

Rosenzweig (1966) stated that two predators of different sizes, but with similar morphology and hunting techniques, can coexist if each predator specializes on different sizes

of prey. This appears to hold true for this study. Marten ate more small prey (microtines and squirrels) than did fisher, while fisher ate more medium sized prey (marmots and muskrats). The relatively high hare population resulted in both species preying heavily on hares.

Rosenzweig also postulated that two competitors can coexist if the smaller, more efficient predator is occasionally preyed upon by the larger, less efficient predator. Fisher ate marten on two occasions in this study.

SECTION II

Winter Habitat Use and Responses to Snow Cover

of Fisher (<u>Martes</u> <u>pennanti</u>) and Marten

(<u>Martes</u> <u>americana</u>) in Southeastern Manitoba

ABSTRACT

A trailing study of fisher (<u>Martes</u> <u>pennanti</u>) and
marten (<u>Martes</u> <u>americana</u>) in the boreal forest of Manitoba,
conducted over two winters, showed that both species
preferred coniferous ridges.

Fisher were found to be restricted by the soft, thick
snow cover that was present during midwinter. Fewer tracks
were observed at this time, and fisher travelled upon snowshoe
hare trails and their own trails to a greater extent than in
either the early winter period of thin snow cover or the late
winter period of crust conditions. Fisher were also found
to walk through the snow cover and leave a body drag in
midwinter.

Marten did not appear to be hindered by soft snow
cover to the degree that fisher were. Marten tracks were
encountered with equal frequency throughout the winter and
they never left a body drag in the snow cover. They did travel
upon hare trails and their own trails to a greater extent in
midwinter, but never as much as did fisher.

INTRODUCTION

Most studies have found that fisher (<u>Martes</u> <u>pennanti</u>)
occur more frequently in mature coniferous forests or
softwood-dominated mixed forests than in other habitats
(de Vos, 1952; Coulter, 1966; Kelly, 1977; Leonard, 1980).
Marten (<u>Martes</u> <u>americana</u>) have been found to use the same
type of habitat (Marshall, 1942, 1951a; Newby, 1951;
de Vos <u>et</u> <u>al</u>., 1959; Francis and Stephenson, 1972; Wooley,
1974; Koehler and Hornocker, 1977; More, 1978; Campbell, 1979;
Major, 1979; Soutiere, 1979; Steventon, 1979). The European
marten (<u>Martes</u> <u>martes</u>) is also most frequently found in mature
forests (Danilov and Ivanter, 1967; Grakov, 1972; Pulliainen,
1980b), as is the sable (<u>Martes</u> <u>zibellina</u>) (Shaposhnikov, 1956).

Coniferous forests generally have less snow on the ground
(api) than do more open habitats as snow accumulates on the
trees (qali) (Pruitt, 1978). The physical effect that snow
has on mustelids has been largely ignored in the North American
literature. Formosov (1946) stated that the mustelids in
general are well adapted to snow. They have relatively large
feet and therefore relatively low weight loads, and their
bounding gait is suited for travel in soft snow cover. Animals
that jump simultaneously with all four feet are best suited
for snow (e.g., hares, squirrels, <u>Clethrionomys</u>). The bounding
gait of mustelids is the second best strategy. Their fore

feet are placed in the snow together and provide simultaneous support, after which their hind feet are placed in the snow to take over the weight of their bodies (Dagg, 1973). The jog-trot of canids and ungulates is a less efficient means of progressing through snow as the body is entirely supported by one limb at a time.

Fisher are restricted in their movements by the soft, thick snow cover of midwinter (Leonard, 1980), but no evidence has been found in the literature that marten are similarly hindered. Marten, however, depend upon access to subnivean spaces to hunt (Koehler and Hornocker, 1977; Campbell, 1979; Steventon, 1979).

The yellow-necked marten (Martes flavigula) of the far-eastern U.S.S.R. is the only other member of the genus Martes besides the fisher that is restricted in its movements by soft snow cover (Bromley, 1956; Nasimovich, 1973; Matjushkin, 1974).

A radiotelemetry and tracking study of fisher and marten was conducted at Taiga Biological Station (51° 05' N., 95° 20'W.) from August, 1978 to August, 1980. Leonard's (1980) study of fisher provided background for my study. No marten were known to be present in the study area until 1978, when an influx of marten permitted their habits to be compared with fisher. The increase in the marten population appeared to be part of the widespread expansion of marten range in Ontario and northern Minnesota (Mech and Rogers, 1977).

This study will report on the habitat use of fisher and marten and their reactions to soft snow cover.

Study Area

The 324 km^2 study area is part of the low boreal land region (Woo et al., 1977). The dominant features are bedrock knolls and ridges of up to 30m in height with bogs and fens in between. The mean January temperature varies from -22.8 to -19.8°C and the mean July temperature varies from +18 to +19.5°C. Annual precipitation varies from 410 to 535 mm, with 250 to 355 mm of this falling as rain between 1 May and 30 September (loc. cit.).

The study area is composed of 10 habitats. The most common habitat is jackpine (Pinus banksiana) ridge. The entire study area has been burnt at some time or other, although some parts not for 150+ years. Moderately open black spruce (Picea mariana)-tamarack (Larix laricina) bogs are the second most common habitat. Open bogs of the same species, thick alder (Alnus) bogs, black spruce bogs and beaver meadows are the other moist habitats. The remaining habitats are aspen (Populus tremuloides)-jackpine ridges, balsam fir (Abies balsamifera)-white spruce (Picea glauca) ridges, jackpine sandplains and rivers and lakes.

The intensive tracking area of 36 km^2 is shown in Figure 1.

Figure 1. Habitat map of intensive trailing area.
⭐ = Taiga Biological Station; 1 = jackpine,
balsam fir, white spruce, black spruce;
2 = moderately open and open black spruce-
tamarack bogs; 3 = black spruce bogs;
4 = thick alder bog; 5 = aspen - jackpine
ridge; 6 = beaver meadow.
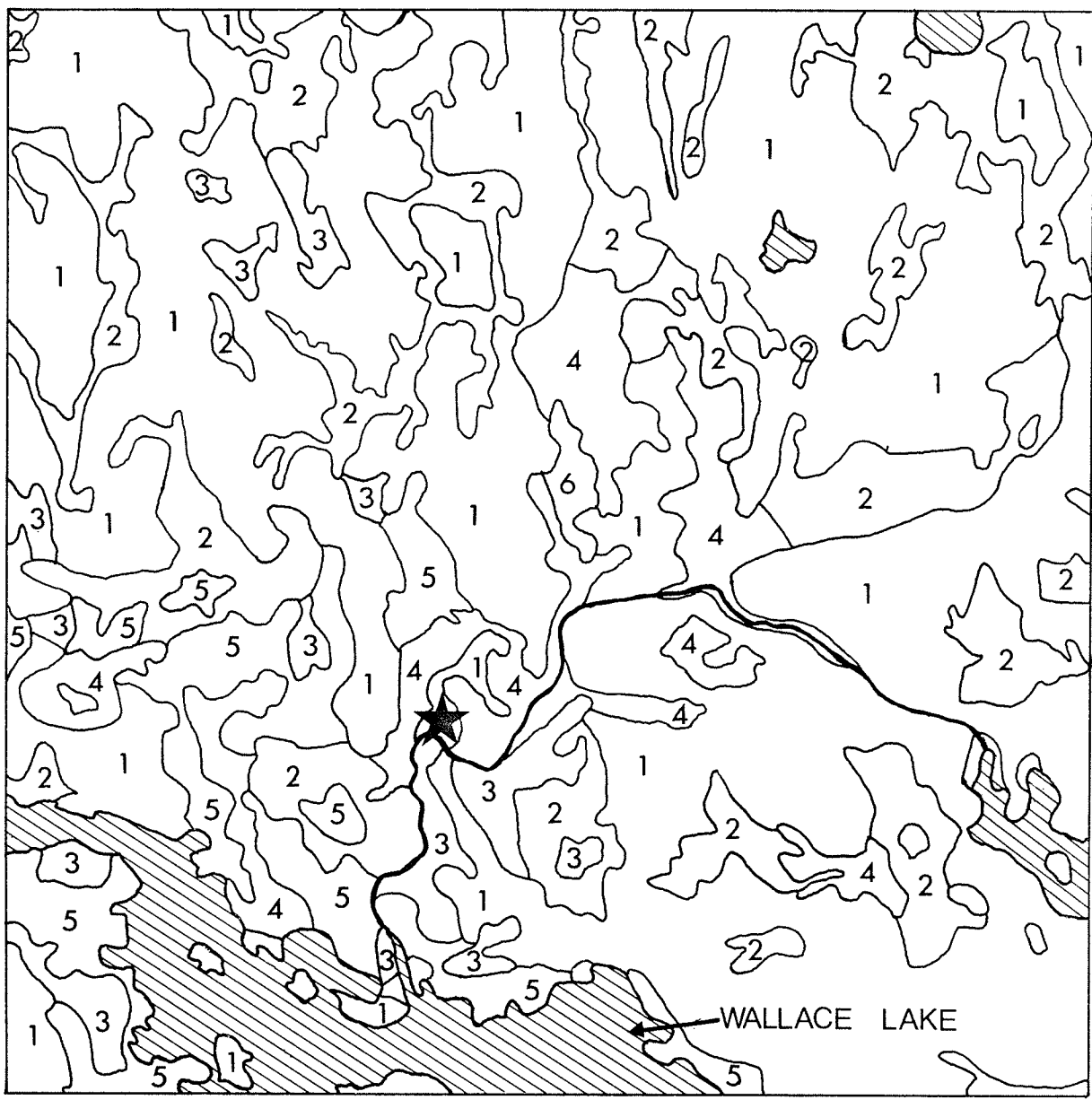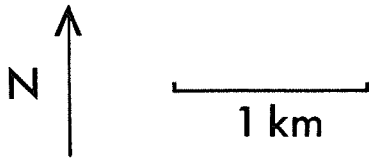
METHODS

The relative densities of fisher, marten, snowshoe
hares (Lepus americanus), red squirrels (Tamiasciurus
hudsonicus) and spruce (Bonasa umbellus) and ruffed
(Canachites canadensis) grouse were determined by track
counts made while skiing on a system of flagged trails that
had been measured previously. I attempted to ski most of
the trails on a regular basis. Observations of more than
one fisher or marten track per km were recorded as one track
per km of trail in each species because one animal often
crossed a trail many times within a short distance. Tracks
that crossed rivers less than 15m wide were recorded as
being in the surrounding habitat. I kept a record of the
distance I skied in each habitat in each day, and of the
number of days that had elapsed since the previous snowfall
or since I had previously skied the trail. Thus the distances
covered could be weighted to include time. For example, if
it had not snowed for three days, and I skied 4 km of jackpine
ridge, a distance of 12 "day-km" could be recorded. The
habitat use of fisher, marten and each of their prey species
was determined by comparing the number of tracks of each
species observed per habitat with the expected number calculated
from the number of day-km skied in each habitat. Chi-square
tests of goodness of fit were used.

Both fisher and marten were trailed whenever their tracks were encountered. The distance moved by an animal was determined by counting its "paces", one pace being the distance covered through one complete cycle of motion. The pace length varies with the animal's size, its speed, snow conditions and topography. However, it can be regarded as a unit of effort. Each time I trailed an animal I measured the length of 10 of its paces and recorded the depth it had sunk in the snow cover.

Single classification ANOVAS were used to analyze differences between means.

Biweekly api-profile snow stations (Pruitt, 1959 and 1979) were established in five habitats. At each observation profile, vertical hardness of the api surface and the horizontal hardness, thickness and density of each api layer were determined. The vertical and horizontal hardness of the top 10 cm of snow was often measured beside the trails of animals I was following. A snow index was derived for the top 10 cm of snow which was simply the sum of the products of the thickness and hardness of each snow layer.

$$\text{Snow Index} = 1,000 - \sum \text{thickness (cm)} \times \text{hardness (gm/cm}^2)$$

As both fisher and marten were usually supported by a hardness of 100 gm/cm^2, this value was taken as the maximum hardness of any layer, and therefore 1,000 was the maximum value of the sum of the products.

RESULTS

Prey Habitat Use

A total of 1,537km (2,869 day-km) of trail was skied in the winter of 1978/79 and 1,565 km (2,922 day-km) was skied in the winter of 1979/80.

More grouse kieppis and tracks than expected were observed on jackpine and balsam fir ridges and jackpine sandplains, while less sign was found on rivers, lakes and bogs in the winter of 1978/79 (P < 0.001) and in the winter of 1979/80 (P < 0.001, Table 1).

Red squirrel tracks were distributed in a similar manner to those of grouse (Table 1).

Snowshoe hare tracks were found to be more common in thick alder bogs, balsam fir ridges and aspen ridges than in jackpine ridges and black spruce bogs (Section I).

Clethrionomys gapperi and Sorex cinereus were the most common small mammals in the study area, and thick alder bogs, beaver meadows and aspen and jackpine ridges had the highest densities of these animals (Section I).

Fisher Track Counts

Each winter was divided into three periods according to snow cover conditions. The first period was from the time of the first snowfall (13 November in 1978; 1 November in 1979) to when the snow thickness began to restrict the movements of

Table 1. Observed and expected occurrence of grouse and squirrel sign per habitat in each winter

GROUSE		Aspen Ridge Thick Alder Bog Black Spruce Bog Beaver Meadow	Jackpine Ridge and Sandplain Balsam Fir Ridge	Open and Moderately Open Bog	Rivers and Lakes	Total	$X^2_{(3)}$	P
1978/79	observed	65	356	20	17	458	549.7	<0.001
	expected*	104.1	132.0	81.7	140.2	458.0		
1979/80	observed	119	321	58	15	513	581.4	<0.001
	expected*	115.7	108.8	142.1	146.3	513.0		
SQUIRREL								
1978/79 January– April	observed	64	451	21	2	538	796.7	<0.001
	expected*	121.7	156.9	104.3	155.1	538.0		
1979/80 November– March	observed	365	632	41	2	1040	1344.2	<0.001
	expected*	234.6	220.6	288.1	296.7	1040.0		

*Based on the number of day-km skied in each habitat.

fisher and marten. This thickness I arbitrarily chose as 20 cm, and it happened to be reached on 26 November of both winters. The second period consisted of the midwinter months of soft, thick snow cover when the vertical hardness was less than 100 gm/cm^2 in all habitats except on rivers and lakes, and was often less than 10 gm/cm^2. The third period began when a vertical hardness of greater than 100 gm/cm^2 was reached in all habitats. The change to crust conditions was quite abrupt in both winters and occurred in all habitats at about the same time (21 March in 1979; 23 March in 1980).

Sixty-five fisher tracks were observed in the first winter. The sex of the animals could be determined only for exceptionally large male fisher or radiocollared animals. Track size varied with snow cover thickness, its vertical hardness, the age of the track, the animal's speed and the positioning of the animal's feet.

More tracks than expected were observed on rivers and lakes in the first winter period of 1978/79 ($P < 0.025$, Table 2), while more tracks than expected were found on coniferous ridges in midwinter ($P < 0.01$). During the crust period fisher frequented habitats in proportion to their availability. In the first winter period of 1979/80 fisher showed no habitat preference, while in midwinter more tracks

Table 2. Observed and expected occurrence of fisher tracks per habitat in each winter period of each winter.

1978/79		Aspen Ridge Thick Alder Bog Black Spruce Bog Beaver Meadow	Jackpine and Balsam Fir Ridges	Open and Moderately Open bogs	Rivers and Lakes	Total	$X^2_{(3)}$	P
Thin snow cover	observed		5		6	11	9.76	<0.025
	expected*	2.8	4.0	1.7	2.5	11.0		
Midwinter	observed	7	15	4	3	29	11.67	<0.01
	expected*	6.8	7.8	4.5	10.0	29.0		
Crust	observed	5	10	7	3	25	1.68	NS
	expected*	4.9	8.1	6.4	5.6	25.0		
Total	observed	12	30	11	12	65	10.46	<0.025
	expected*	14.8	18.7	11.6	19.9	65.0		
1979/80								
Thin snow cover	observed	4	7	2	7	20	2.00	NS
	expected*	5.4	5.2	3.6	5.7	20.0		
Midwinter	observed	11	19	11	10	51	9.33	<0.05
	expected*	11.4	10.4	14.5	14.6	51.0		
Crust	observed		1	6		7	6.61	NS
	expected	0.9	1.5	2.8	1.9	7.0		
Total	observed	15	27	19	17	78	8.54	<0.05
	expected	17.6	16.5	21.6	22.3	78.0		

*Based on the number of day-km skied in each habitat.

Table 2, continued. Observed and expected occurrence of fisher
tracks per winter period in each winter.

1978/79 Winter period	observed	expected*	$X^2_{(2)}$	P
Thin snow cover	11	4.7		
Midwinter	29	44.7	19.61	< 0.005
Crust	25	15.6		
Total	65	65.0		
1979/80				
Thin snow cover	20	10.0		
Midwinter	51	64.2	15.43	< 0.005
Crust	7	3.8		
Total	78	78.0		

Observed and expected occurrence of fisher tracks per winter.

Winter	observed	expected*	$X^2_{(1)}$	P
1978/79	65	70.8		
1979/80	78	72.2	0.80	NS
Total	143	143.0		

*Based on the number of day-km skied in each winter period or winter.

than expected were observed on coniferous ridges (P < 0.05, Table 2). The crust period of the second winter was short and few tracks were recorded. Six out of seven tracks were found on open and moderately open bogs.

Fewer tracks than expected were found in the midwinter of 1978/79, while more tracks were found in early and late winter (P < 0.005, Table 2). Similar results were obtained in the winter of 1979/80.

The between winter totals did not differ significantly from the expected (Table 2).

Marten Track Counts

Thirty-one marten tracks were observed in the winter of 1978/79 (Table 3). More marten tracks than expected were found on coniferous ridges than in other habitats in the midwinter (P < 0.005) and crust periods (P < 0.05). The increase in the marten population by the 1979/80 winter was shown by the 251 tracks recorded that year. More tracks than expected were found on coniferous ridges in the thin snow (P < 0.005) and midwinter periods (P < 0.001). Marten also appeared to prefer coniferous habitats in the crust period, but the results were not significant (P < 0.1). Only three of 251 tracks were found on rivers and lakes greater than 15m in width.

Marten tracks were observed in proportion to the number of day-km skied in each winter period of each winter (Table 3).

Table 3. Observed and expected occurrence of marten tracks per habitat in each winter period of each winter.

1978/79		Aspen Ridge Thick Alder Bog Black Spruce Bog Beaver Meadow	Jackpine and Balsam Fir Ridges Sandplain	Open and Moderately Open Bogs	Rivers and Lakes	Total	X^2(3)	P
Thin snow cover	observed		1			1		
	expected*	0.2	0.4	0.2	0.2	1.0		
Midwinter	observed		19			19	51.77	<0.005
	expected*	4.5	5.1	2.9	6.5	19.0		
Crust	observed	1	8	2		11	8.80	<0.05
	expected*	2.2	3.6	2.8	2.4	11.0		
Total	observed	1	28	2		31	57.62	<0.005
	expected*	7.1	8.9	5.5	9.5	31.0		
1979/80								
Thin snow cover	observed	9	15	2		26	19.38	<0.005
	expected*	7.1	6.8	4.7	7.4	26.0		
Midwinter	observed	46	114	47	3	210	174.30	<0.001
	expected*	47.0	43.0	59.8	60.2	210.0		
Crust	observed	3	6	6		15	7.19	NS
	expected*	2.0	3.1	6.0	3.9	15.0		
Total	observed	58	135	55	3	251	194.30	<0.005
	expected*	56.6	53.3	69.5	71.6	251.0		

*Based on the number of day-km skied in each habitat.

Table 3, continued.   Observed and expected occurrence of marten

tracks per period in each winter.

Winter period	observed	expected	$\chi^2(2)$	P
Thin snow cover	1	2.2		
Midwinter ⎰ 1978/79	19	21.3	2.61	NS
Crust	11	7.5		
Total	31	31.0		
Thin snow cover	26	32.1		
Midwinter ⎰ 1979/80	210	206.6	1.79	NS
Crust	15	12.3		
Total	251	251.0		

*Based on the number of day-km skied in each winter period.

Fisher and Marten Habitat Use Determined from Trailing Data

A total of 154,217 fisher paces and 142,023 marten paces was followed in the two winters. As the mean fisher pace length was 71.9 cm (n = 510) and the mean marten pace length was 57.1 cm (n = 570), each species was trailed for approximately 111 and 81 km, respectively.

The percentage of paces that each species spent in each of the 10 habitats (Table 4) indicated that fisher and marten had remarkably similar habitat preferences. Fisher, however, utilized rivers and lakes (5.7 vs 0.2%) and black spruce bogs (12.0 vs 7.4%) more than did marten, and used thick alder bogs less (8.0 vs 13.2%).

Fisher Energy Saving Strategies

Fisher behaved in several ways that I interpreted to be means of saving energy. They travelled upon snowshoe hare trails, followed their own trails and walked in soft, thick snow cover, leaving a long furrow or vyvoloka (Formosov, 1946). They employed a higher percentage of each of these activities in the midwinter period of each winter (Table 5).

All fisher tracks that were superimposed on other fisher tracks were recorded as energy saving behaviour except for three cases where large, presumably male fisher followed smaller, presumably female fisher, for distances of up to 2,600m in March and April 1979 (Table 6). In all three

Table 4. Percentage of fisher and marten paces trailed per habitat.
Data for 78/79 and 79/80 combined.

	Aspen Ridge	Jackpine Ridge	Balsam Fir Ridge	Jackpine Sandplain	Black Spruce Bog	Thick Alder Bog	Moderately Open Bog	Open Bog	Beaver Meadow	Rivers and Lakes	Total
Fisher	9.8	50.5	4.3	2.0	12.0	8.0	6.3	0.5	0.9	5.7	100.0
Marten	10.8	54.2	3.2	3.1	7.4	13.2	7.4	0.0	0.5	0.2	100.0

Table 5. Percentage of fisher and marten paces on snowshoe hare trails, their own trails and walking due to thick, soft snow cover.

Fisher		Snowshoe hare trail	Fisher or marten trail	Walk with body drag	Regular gaits	Total number of paces trailed
1978/79	Thin snow cover	14.4	4.9		80.7	17,070
	Midwinter	35.0	6.5	7.4	51.1	14,522
	Crust	6.3	0.8		92.9	10,020
1979/80	Thin snow cover	9.7	3.2	0.8	86.3	22,463
	Midwinter	26.3	15.5	24.4	33.8	39,542
Marten						
1978/79	Midwinter	6.4	1.7		91.9	25,744
	Crust	0.3			99.7	10,569
1979/80	Thin snow cover	1.4	1.6		97.0	32,904
	Midwinter	10.2	9.0		80.8	72,806

Table 6. Examples of fisher and marten travelling upon their own trails or the trails of their own species.

	Date	*Number of paces (cm)	Mean of 10 paces (cm)	Estimated number of meters	Track depth (cm)	Habitat
Fisher travelling upon its own trail	9/IV/79	2326	100.6	2340.0	5.0	Aspen and jackpine ridge
	23/III/80	2695	61.4	1654.7	5.0-10.0	Aspen and jackpine ridge
Fisher following another fisher	28/III/79	3318[+]	79.3	2631.2	2.0	Jackpine ridge and black spruce bog
	31/III/79	839[+]	78.3	656.9	0.5-4.0	Moderately open bog and jackpine ridge
	3/IV/79	681[+]	73.1	497.8	4.0	Jackpine ridge
Marten travelling upon its own trail	4/III/80	389	56.1	218.2	5.0	Jackpine ridge
	8/III/80	2247	53.4	1199.9	4.0	Jackpine ridge
	18/III/80	1530	42.3	647.2	4.0	Jackpine ridge
Marten following another marten	29/III/79	812	95.3	773.8	2.5	Moderately open bog and jackpine ridge

instances the large tracks followed the smaller tracks and the animals appeared to be travelling together. These three occasions are not included in the data in Table 5.

Other cases were frequently observed in midwinter where a fisher would follow its own previously made tracks for up to 1,600 m and would often register perfectly in them (examples in Table 6). These instances were believed to be energy saving behaviour.

When fisher sank in the snow 9-11 cm while bounding they changed to a walking gait and left a long body drag in the snow up to 25 cm in width. They exhibited this behaviour almost exclusively in the midwinter periods (Table 5).

Marten Energy Saving Strategies

Marten also travelled upon hare trails and their own trails, but they never walked with a body drag (Table 5).

They used hare trails and their own trails to a greater extent in the midwinter periods, but not to the degree that fisher did. One case of intraspecific contact was not included in the data of Table 5. On 29 March 1979, two large, presumably male marten followed and chased each other for 812 paces (774 m) (Table 6). At four points scuffles took place and tufts of marten fur were left.

As with fisher, marten sometimes followed their own trails for long distances and often registered perfectly in the old tracks (examples in Table 6). One marten had a trail of approximately 1,400 paces (592 m) that it followed at least six times in a two month period in the second winter.

Fisher Gaits

Fisher had three gaits that they used according to snow cover conditions and terrain. They bounded in the typical mustelid fashion by moving their front legs and back legs together in pairs. This left a distinctive trail in the snow (Figure 2a). The mean depth that fisher sank in the snow while bounding was 8.1 cm (Figure 3) and the mean length of the bounds was 71.9 cm (Figure 4).

When the depth to which fisher sank while bounding decreased to a mean of 5.8 cm they changed their gait to a "gallop". In this gait fisher stretched their bodies out more than in bounding and each foot usually made a separate impression in the snow (Figure 2b). The mean depth to which fisher sank while galloping was 3.1 cm and the mean length of the gallop pace was 86.5 cm.

When fisher slowed down to investigate blowdowns or anything of "interest" they began to walk, leaving a trail of double impressions in the snow (Figure 2c). (Mean track depth: 6.1 cm; mean pace length: 51.3 cm). When fisher

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Figure 2

A - Tracks of a fisher changing from a walking gait in

the soft, thick snow cover of a balsam fir ridge

in the background to a bounding gait in the more

shallow snow cover of a lake in the foreground. Track

depth of bounds = 4 cm, track area = 30 x 13 cm

(11/XII/79).

B - Galloping gait of male F4 on a lake, next to a 15 cm

ruler. The three impressions were made by all four

feet during one cycle of motion. Track depth = 0.5 cm

(16/I/80).

C - Walking gait of the same fisher as in "A" on a jackpine

ridge. Each impression was made by two feet. The fisher

was on the verge of making a body drag in the snow cover.

Track depth = 11 cm, vertical hardness = 10 gm/cm^2,

track area = 14 x 9 cm (11/XII/79).

D - Tracks of a fisher changing from a galloping gait

(foreground) to a bounding gait (background) while going

up a hill. Track depth = 6 cm, pace length = 56-62 cm,

habitat = jackpine ridge (3/IV/79).

Figure 3. Mean track depths of fisher and marten for
each gait and change of gait. Means are
indicated by circles and the confidence
limits (95%) by vertical lines. A = gallop;
B = change from gallop to bound; C = bound;
D = change from bound to walk with body
drag; E = walk with body drag; E = "normal"
walk.
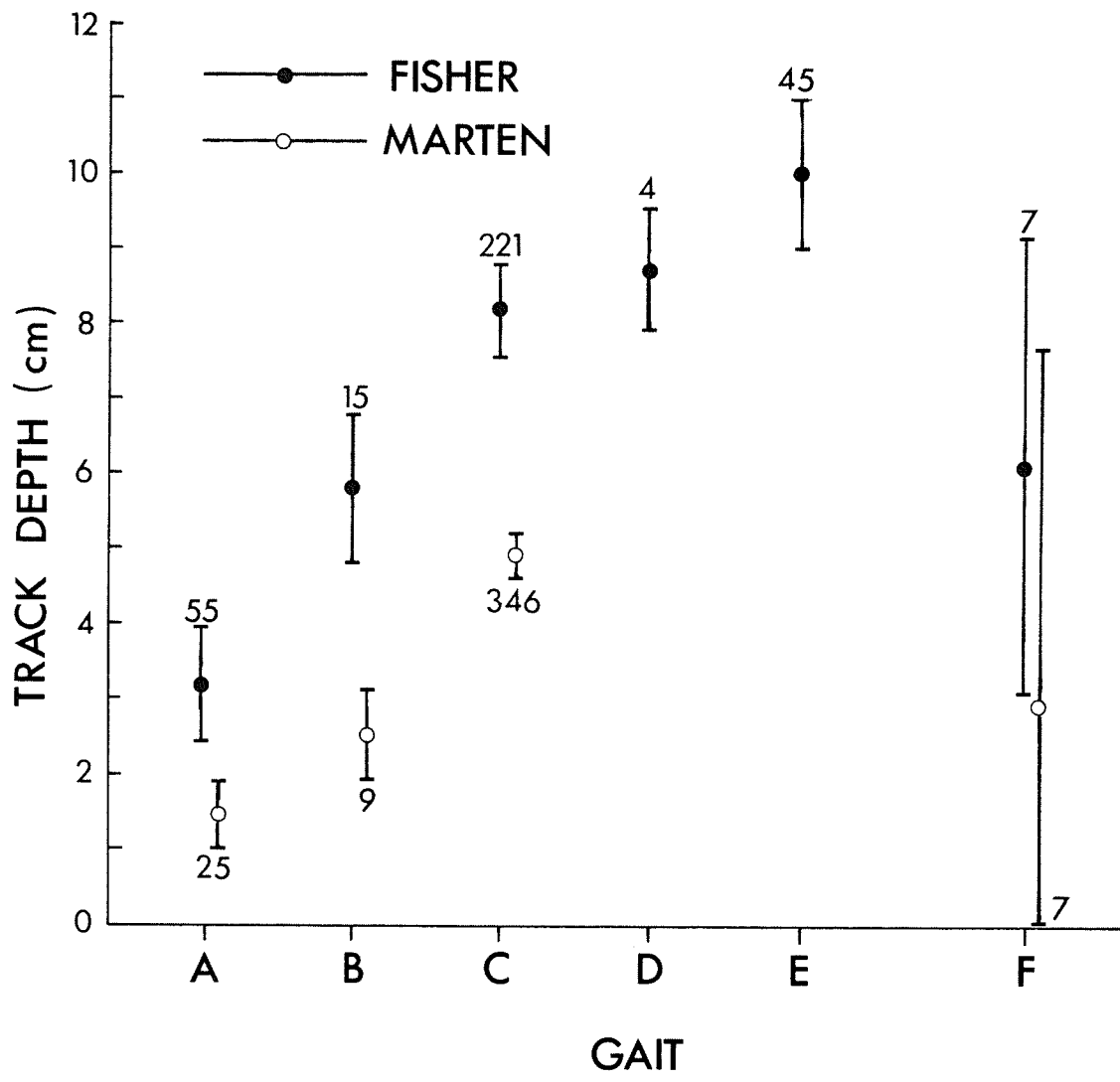
Figure 4. Mean pace lengths of fisher and marten for
           each gait and for both on and off hare
           trails. Means are indicated by circles,
           ranges by thin vertical lines and confidence
           limits (95%) by thick vertical bars.
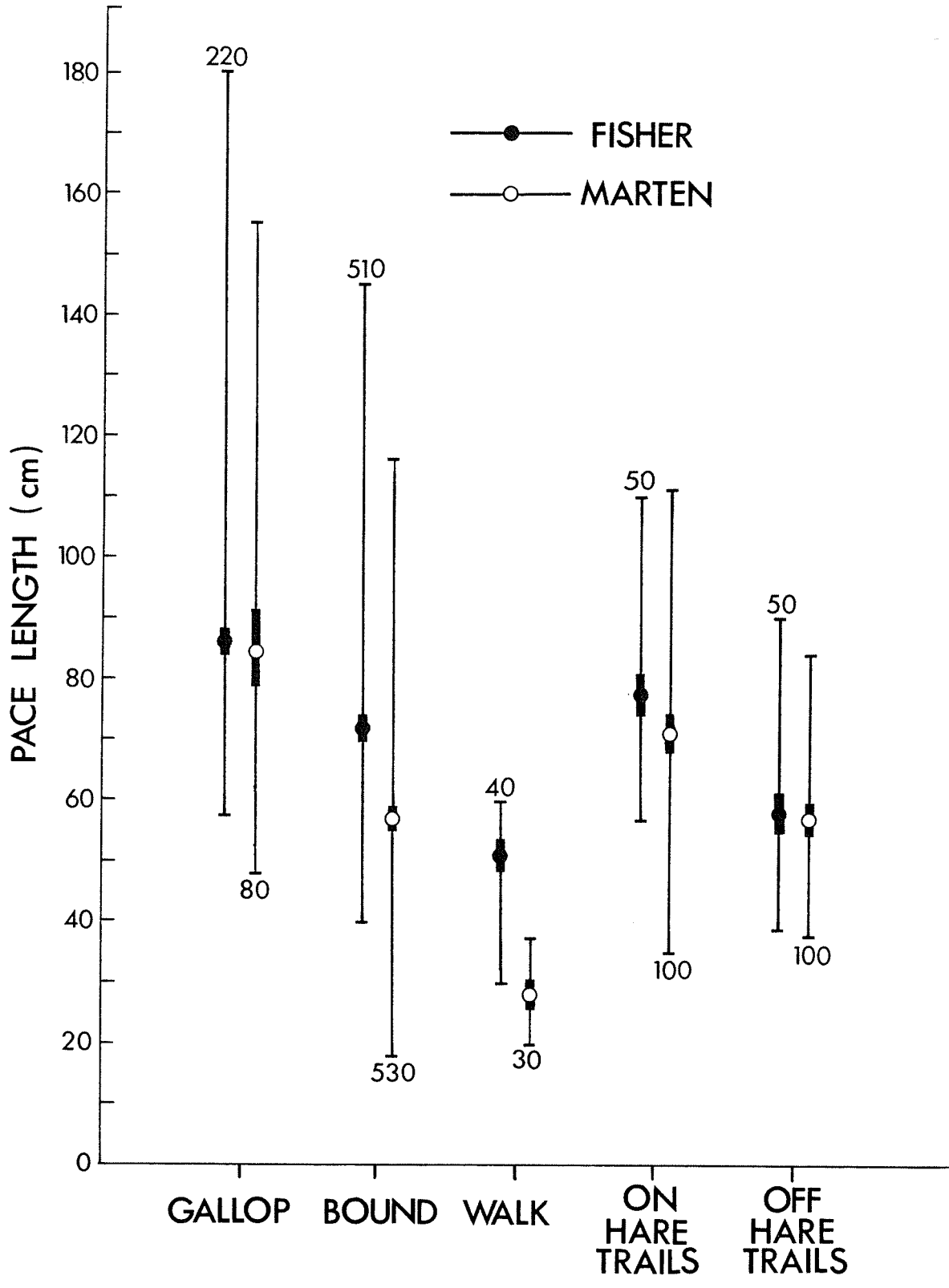
encountered very soft, thick snow cover and sank to a

mean of 8.7 cm they changed their gait to a walk and left

a long furrow in the snow. Fisher sank a mean of 10.0 cm

on these occasions and the mean pace length was 56.0 cm.

A one-way ANOVA performed on the depths to which

fisher sank in the snow cover for each gait except "normal"

walking gave significant results (F (2,318) = 51.57, P < 0.001).

Fisher galloped more in the thin snow cover and crust

periods than in the midwinter periods (Table 7), and they

spent the most time galloping during the crust conditions of

the first winter (80.9%). Undoubtably they also galloped

during the crust period of the second winter, but no trails

could be followed because no fresh snow fell on top of the

crust.

Fisher paces were longer on hare trails than off them

(F (1,98) = 69.41, P < 0.001; Figure 4).

Marten Gaits

Marten had the same gaits as fisher except that they

sank into the snow cover less and had shorter pace lengths

for all gaits except galloping (Figures 3 & 4). As previously

noted marten never walked with a body drag. The mean depth

to which marten sank while galloping was less than when they

bounded (F (1,69) = 50.08, P < 0.001).

Table 7. Gaits of fisher and marten. Percentage of gallops,
bounds and walking paces employed in each winter
period of each winter.

	Winter period	Gallop	Bound	Walk
Fisher				
1978/79	Thin snow cover	5.4	93.1	1.5
	Midwinter		91.4	8.6
	Crust	80.9	18.0	1.1
1979/80	Thin snow cover	9.7	86.6	3.7
	Midwinter	1.1	74.3	24.6
Marten				
1978/79	Midwinter		99.2	0.8
	Crust	46.5	52.4	1.1
1979/80	Thin snow cover	0.2	99.2	0.6
	Midwinter		99.1	0.9

Marten almost always bounded, except during the crust period of the first winter when they galloped for 46.5% of their paces (Table 7).

Marten paces were longer on hare trails than off them (F (1,198) = 55.92, P < 0.001, Figure 4).

Fisher Track Depth in Relation to Habitat and Winter Period.

Fisher made deeper tracks in the midwinter period than in the thin snow cover and crust periods of 1979/80 (Figure 5). Although the depth fisher sank was not that much lower on coniferous ridges in the first compared to the second winter period (7.0 vs 9.5 cm), these measurements are not a true indication of the energetic cost of travelling in each period. During the thin snow cover period fisher usually sank to ground level and therefore had a firm substrate from which to push off. This is less energetically taxing than to push off from a substrate of soft snow, as fisher did in midwinter.

Fisher sank less in the snow cover on rivers and lakes than on coniferous habitats in the early winter period (F (1,23) = 18.19; P < 0.001), while they sank less on rivers, lakes, moderately open bogs and open bogs than on other habitats during midwinter (F (3,172) = 11.9; P < 0.001). During the crust period they also sank less on bogs than on ridges (1.9 vs 5.0 cm), though this difference is not significant due to small sample sizes.

Figure   5. Mean track depths of fisher and marten per
            habitat for each winter period of 1979/80
            Means are indicated by circles and
            confidence limits (95%) by vertical lines.
            J = jackpine ridge; BF = balsam fir ridge;
            SP = jackpine sandplain; R = river; L =
            Lake; A = aspen ridge; BS = black spruce bog;
            TB = thick alder bog; MOB = moderately open
            black spruce-tamarack bog; OB = open bog.
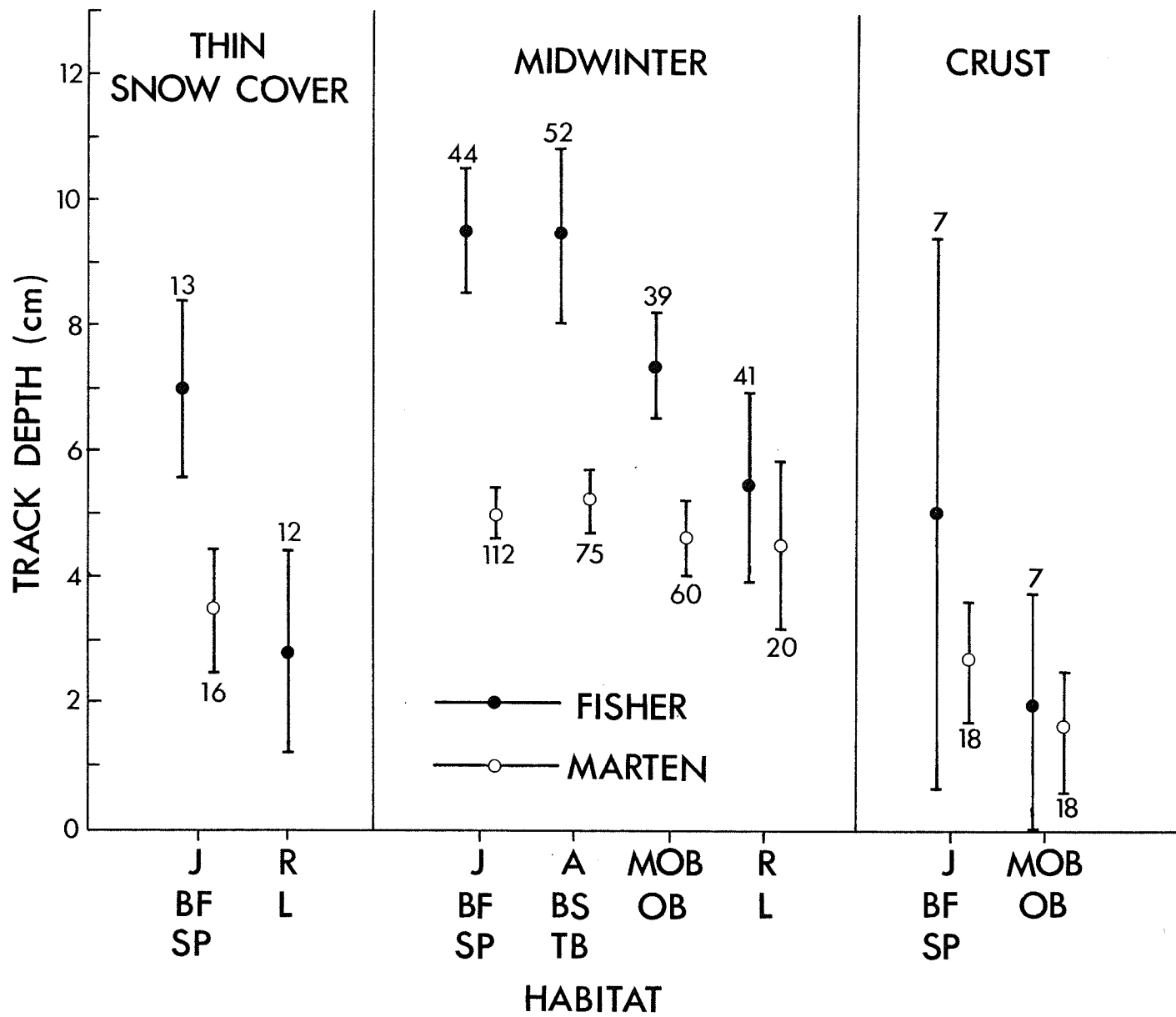
The mean track depth of fisher on all habitats except
rivers and lakes are graphed biweekly in Figure 6 and are
compared to the mean of the snow indices of the same habitats.

Fisher were most likely affected by more than the top
10 cm of snow cover as they sometimes sank up to 20 cm.
When I compared snow indices of the top 15 and 20 cm, however,
no large differences were found. As I had made more
observations of the hardness of the top 10 cm of snow cover,
the snow index of this thickness probably gives the most
accurate description.

A snowfall of 28 cm fell in the study area during
the first two days of November 1979. This resulted in a
mean snow index of 874 and caused fisher to sink to depths of
8.4 cm. This must have hindered the movements of fisher
to some extent. Much of this snow melted during November,
however, and the mean snow index fell to 299. As the weather
became colder and more snow accumulated, the mean snow index
rose to over 900, and fisher tracks were from 8 to 13 cm
deep. These conditions persisted until a thaw occurred
between 20 and 30 December. The mean snow index then increased
to 800 and fisher tracks decreased to 6.4 cm in depth. The
temperature then remained below freezing until a series of
thaws and freezings occurred from the sixteenth of March
onwards. A crust that would support fisher was developed

Figure 6. Biweekly mean track depths of fisher and marten
on all habitats, excluding rivers and lakes,
for the winter of 1979/80 compared with the
biweekly mean snow indices. Means are
indicated by circles and triangles, and
confidence limits (95%) by vertical lines.
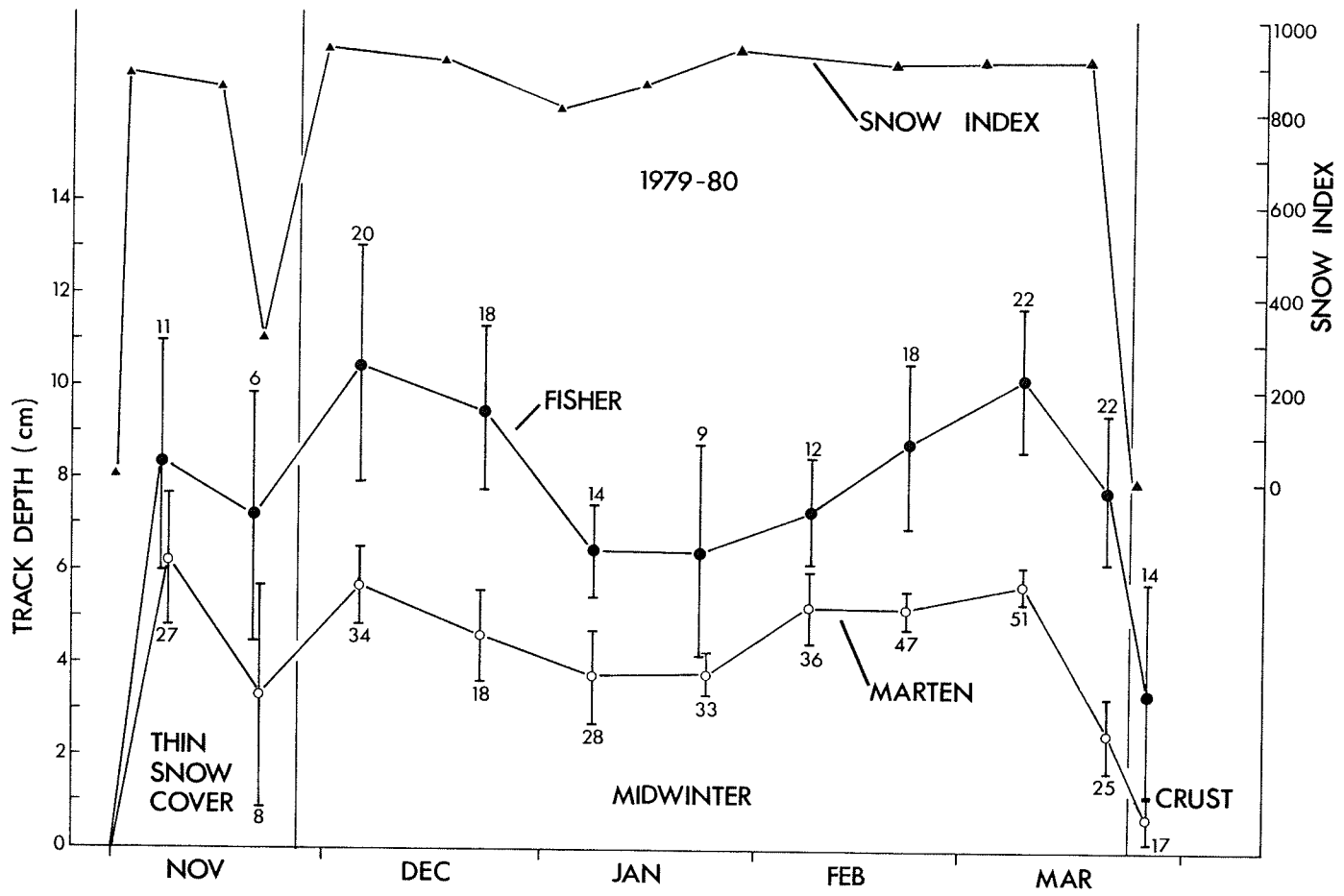
by 23 March when the snow index fell to zero. A one-way
ANOVA on the biweekly means of the depths to which fisher
sank in the midwinter period gave significant results
$(F (7,127) = 0.12; P < 0.005)$.

Marten Track Depth in Relation to Habitat and Winter Period.

Marten also sank less in the thin snow cover and
crust periods than in the midwinter period of 1979/80
(Figure 5). Unlike fisher, however, they sank to about
the same depth in all habitats during midwinter (1-way ANOVA:
$F (3,263) = 1.1, P > 0.5)$.

Marten sank less than fisher in all habitats except
rivers and lakes in the midwinter period.

The biweekly analysis of marten track depth (Figure 6)
shows that marten responded to changes in the snow cover
thickness and hardness in the same manner as did fisher.
A one-way ANOVA on the biweekly means within the midwinter
period gave significant results $(F (6,240) = 5.46, P < 0.001)$.

DISCUSSION

Fisher Habitat Use

Fisher appeared to prefer rivers, lakes and coniferous ridges during the periods of thin snow cover in early winter. During the midwinter periods of soft, thick snow cover they frequented coniferous ridges and generally avoided rivers and lakes, while in the crust periods fisher appeared to have no habitat preference. As the midwinter periods were by far the longest of the winter periods, coniferous ridges were the most important winter habitat for fisher.

Other authors have also found that fisher prefer mature coniferous forest (de Vos, 1952; Coulter, 1966; Kelly, 1977; Leonard, 1980). Coniferous ridges were the preferred habitat of some of the main prey species of fisher. Grouse and squirrels (Table 1) and Clethrionomys gapperi (Section I) all had high densities on coniferous ridges. Snowshoe hares were abundant on balsam fir ridges and both Clethrionomys and hares were common on aspen ridges and in alder bogs. Fisher used these last two habitats roughly in proportion to their abundance (Table 2 & 4). Hares may be more vulnerable to predation when they are resting in coverts. Coverts, composed of thick stands of young conifers and windfalls, are common on coniferous ridges and are often investigated by fisher. Access to rodents in

subnivean spaces is also important for fisher. Thirty-nine
of 74 occurrences of subnivean activity by fisher were
on coniferous ridges (Section I).

Leonard (1980) also found that fisher frequented
lakes in early winter. He attributed this to muskrat
hunting activity and to the ease of travel on the newly
formed ice. In addition, hares are common on the low,
balsam fir ridges that often border lakes. Three of the five
hare chases by fisher that I recorded occurred on lakes
in early winter (Section I).

Fisher sank in the snow cover less on moderately open
and open bogs than on coniferous ridges during midwinter
(7.3 vs 9.5 cm), although they did not travel on bogs any
more than expected at this time (Table 2). Prey species
were scarce in these bogs and thus fisher appeared to prefer
coniferous ridges with higher prey densities despite the
more difficult travelling conditions. Leonard (1980) also
found that fisher avoided open bogs in midwinter, but when
a crust formed on open bogs and not on other habitats, in
the spring of 1977, he found that fisher utilized such bogs
extensively. In the first spring of my study the crust formed
in all habitats simultaneously, and fisher appeared to have
no habitat preference (Table 2).

Marten Habitat Use

The marten track encounter data indicated that marten frequented coniferous ridges and avoided rivers and lakes in all winter periods (Table 3). Other authors have found that marten prefer coniferous habitats (Marshall, 1942; Francis and Stephenson, 1972; Campbell, 1979; Soutiere, 1979). As with fisher, the main prey items of marten are common in coniferous habitats (e.g., this study; Koehler and Hornocker, 1977; More, 1978). I found that access to microtines in subnivean spaces was more important for marten than for fisher, and that 117 of 257 occurrences of subnivean activity by marten were on coniferous ridges (Section I). Marten used subnivean spaces to a greater degree than expected in thick alder bogs, whereas fisher did not. The trailing data (Table 4) indicated that marten spent more time in thick bogs than did fisher, and thick alder bogs were also found to have high small mammal populations (Section I).

Access to subnivean spaces in coniferous habitats has been found to be important for marten in Idaho (Koehler and Hornocker, 1977), Maine (Steventon, 1979) and Wyoming (Campbell, 1979). Other authors believe that coniferous forests provide marten with the most suitable den sites (See: More, 1978).

Many authors state that in winter marten avoid areas without overhead cover (Newby, 1951; Hawley and Newby, 1957; Herman and Fuller, 1974; Koehler and Hornocker, 1977). Marten are occasionally killed by aerial predators (Nyholm, 1970) and access to subnivean spaces in open areas is usually limited.

Marten rarely crossed lakes in my study although they did not avoid lakes if they encountered them. A possible reason for this is that marten were not restricted in their movements by soft snow cover to the extent that fisher were. Thus they would not save as much energy as fisher would by travelling on lakes.

The mean depth to which marten sank on moderately open and open bogs was not different from the mean depths in other habitats in the midwinter period of 1979/80 (Figure 5). Thus marten would not have saved energy by travelling in these bogs in midwinter, and in fact they did occur less often than expected in these bogs in midwinter (Table 3).

The Influence of Snow Cover on Fisher

Fisher Track Encounters

Significantly fewer tracks than expected were observed in the midwinter periods of both years (Table 2). The biweekly distributions of track observations in the study

area for the winters of 1975/76 through 1979/80 are
presented in Figure 7. These bar graphs do not take
into account the distance skied by the observer in each
biweekly period, but each winter has the same trend of
fewer tracks observed in midwinter. Thus it would appear
that fisher are restricted in their movements by some factor
at this time. Possible factors include snow cover and
temperature. Leonard (1980) concluded that the soft,
thick snow cover of midwinter was the main restriction on
the movements of fisher. Coulter (1966) attributed an
increase in tracks in March to mating behaviour. Leonard
(1980), however, observed increases in tracks in February
of both 1976 and 1977 that were coincident with the
formation of crusts. February is too early for mating
behaviour in Manitoba (ibid.).

Fisher Energy Saving Strategies

The fact that fisher travelled upon hare trails,
their own trails and walked to a greater extent in the
midwinter periods of both years than in the early or late
winter periods is additional evidence that they are
restricted in their movements by soft snow cover.

Following hare trails could also be hunting behaviour.
Scat analysis, however, showed that fisher still used hares
to a large degree in the crust period of the first winter

Figure 7. Biweekly distribution of winter fisher and
marten tracks. Data of 1975/76 and 1976/77:
Leonard (1980); 1977/78: Kansas (TBS files);
1978/79 and 1979/80: this study.

Figure showing TRACK OBSERVATIONS / WINTER (%) versus MONTH for FISHER and MARTEN across winters 1975-76 (n=31), 1976-77 (n=86), 1977-78 (n=75), 1978-79 (n=65), 1978-79 (n=31), 1979-80 (n=78), and 1979-80 (n=251).
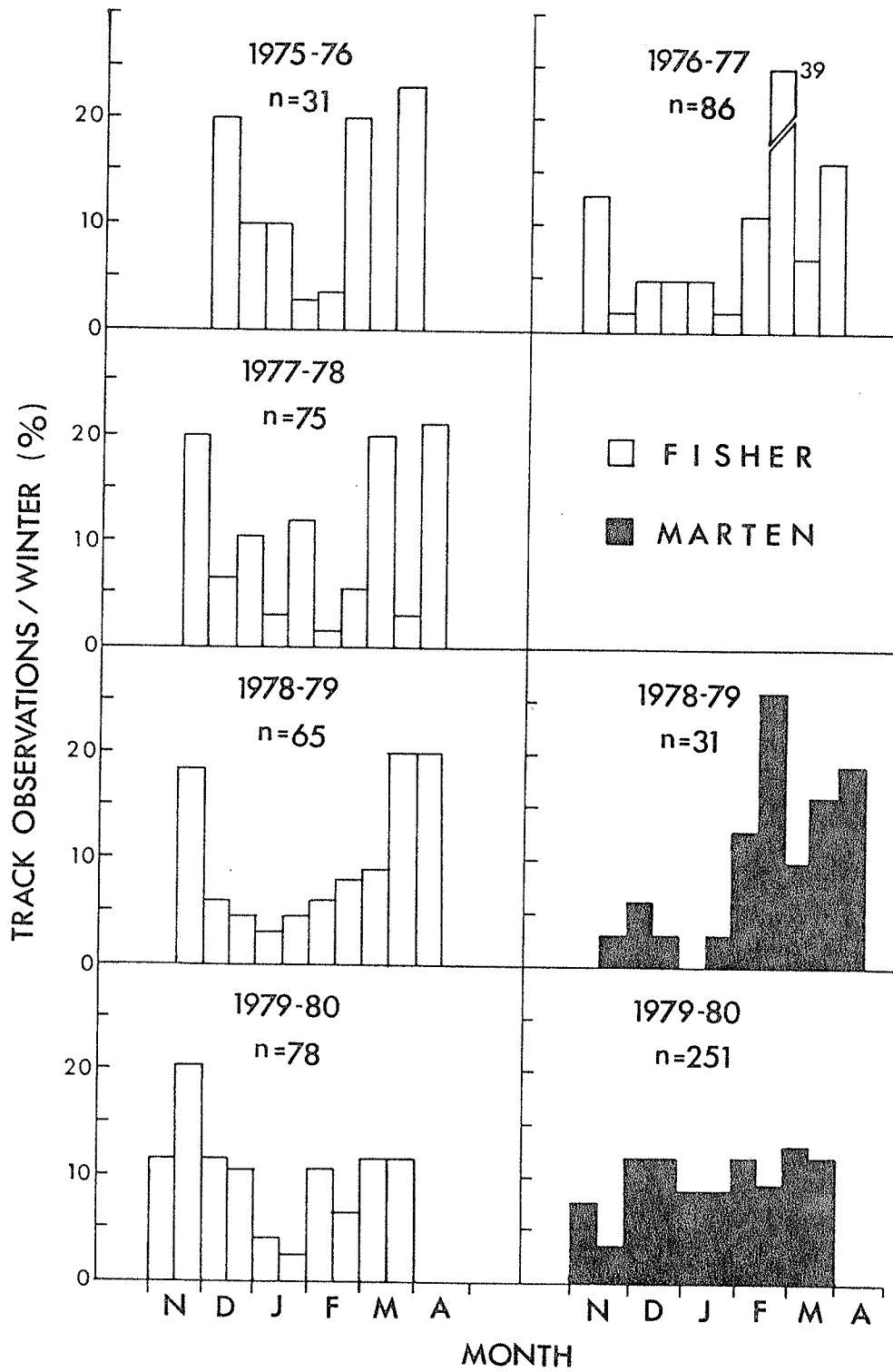
(85% M.I. of 50 scats, Section I) despite the fact that
they only followed hares 6.3% of the time. A well-used
hare trail often had a vertical hardness of 100 to 400
gm/cm^2, even when the surrounding snow had a vertical
hardness of less than 10 gm/cm^2. Hare trails such as these
gave fisher complete support and they took significantly
longer paces on these trails than off them (Figure 4).

Fisher do not always follow their own trails for
ease of travel. They may follow their own tracks to and
from kills or subnivean dens as a means of orientating
themselves, or they may follow the tracks of other fisher
out of curiosity, or territorial or sexual interest. The
three cases of large, presumably male fisher following
small, presumably female fisher in March and April of 1979
were obviously not examples of energy saving (Table 6).
All three cases occurred during the crust period of the
winter, and the fisher did not appear to be hindered in
their movements by the 0.5-4.0 cm of new snow on top of the
crust as they mostly used the galloping gait. De Vos (1952)
also recorded a case of one fisher following another for
over a mile in March in Ontario. However, other occasions
where fisher followed their own trails for long distances in
midwinter in my study appeared to be examples of energy
saving. De Vos (1952) and Quick (1953) both noted that
fisher followed their own trails occasionally. Fisher walked

and left a long, uninterrupted body drag in the snow to quite an extent in the midwinter periods of both years (Table 5). Walking in this fashion must be slow and energetically taxing. Formosov (1946) stated that species that left vyvolokas were not well adapted to fluffy snow. Leonard (1980) found that fisher left furrows in January when the snow thickness was 25 cm and the vertical hardness was less than 10 gm/cm^2.

The yellow-necked marten and the fisher are the two largest members of the genus Martes, and they appear to be the only ones that are restricted appreciably by snow cover. Bromley (1956) stated that the northern limit of the yellow-necked marten is determined by snow cover thickness. In the USSR they seek lower elevations during winter to avoid thick snow cover, but once a crust is formed they can run on the top of it and catch floundering musk deer (Moschus moschiferus) (Matjushkin, 1974).

The Influence of Snow Cover on Marten

Marten Track Encounters

Marten tracks were observed in each winter period in proportion to the distance skied in each period (Table 3), and the biweekly track distribution did not have a midwinter depression in the winter of 1979/80 (Figure 7). In 1978/79

marten were still in low numbers and patchily distributed in the study area. Therefore the biweekly trap distribution had no real meaning for this winter. Thus it appeared that marten were not restricted in their movements in midwinter to the extent that fisher were.

Bromley (1956) concluded that the main influence on the activity of sable was the availability of food and that snow and temperature were of lesser importance, while Pulliainen (1980b) found that European marten travelled less in midwinter and postulated that perhaps cold was the reason.

Marten Energy Saving Strategies

Marten employed energy saving strategies during midwinter, but not to the extent that fisher did (Table 6). Marten followed their own trails more in midwinter than in early or late winter, and sometimes did so for long distances (Table 7). Formosov (1946) stated that sable follow their own trails to save energy. Other authors have noted that marten trails sometimes occur together and they attributed this to evidence of social interaction (Marshall, 1951a; Pulliainen, 1980b). These instances, however, could have been examples of energy saving behaviour.

I recorded one occurrence of two large marten chasing one another for 744 m (Table 7). Pulliainen (1980b) noted one incidence of two European marten travelling together in March for 1,700 m and "playing" with one another, leaving scraps of fur and blood on the snow.

Marten never left a body drag in the snow in
this study, nor are there any recorded cases of this in
the literature.

Competition Between Fisher and Marten

Martes martes, M. zibellina, M. melampus (the
Japanese marten) and M. americana are closely related,
Holarctic, allopatric species that cannot coexist together
(Anderson, 1970). Fisher and marten, however, are sufficiently
different from each other that they are able to occur in
sympatry. Marten, by being smaller, are better adapted for
subnivean hunting than fisher. In this study I found that
marten went under the snow cover much more than did fisher,
ate more microtines and spent more time in thick bogs,
which had high small mammal densities (Section I). The
smaller size of marten also allowed them to be more arboreal
(Section I) and to be less restricted by snow cover than
fisher (Section II). Fisher, on the other hand, were found
to eat more medium sized prey (marmot, muskrat) (Section I).

Thus, fisher and marten can coexist, despite the
fact that they both have a similar morphology (Leach, 1977),
frequent mature, coniferous forests (Section II) and prey
heavily upon snowshoe hares when the hare population is
high (Section I).

SECTION III

Home Ranges and Movements of Fisher

(<u>Martes</u> <u>pennanti</u>) and Marten

(<u>Martes</u> <u>americana</u>) in Southeastern Manitoba

ABSTRACT

A radiotelemetry study of fisher and marten was
conducted from August, 1978 to August 1980, in the boreal
forest of southeastern Manitoba. Two juvenile, female
fisher had winter home ranges of from 15.0 - 20.5 km^2,
while other juvenile females and males dispersed from the
study area after their release.

One juvenile, male marten had a home range of
9.6 km^2 in early winter, while another wandered at random
in late fall and early winter, but appeared to have a
permanent home range of 8.1 km^2 by the following spring.
A juvenile, female marten had seasonal home ranges of
from 6.0 - 8.4 km^2.

A fire that swept through the study area in May 1980
caused one male marten to disperse 61 km, while a female
marten did not alter her home range during the 2 months that
radio contact was maintained.

INTRODUCTION

Trailing studies of fisher (<u>Martes</u> <u>pennanti</u>) have indicated that their home range can be very large (de Vos, 1952; Coulter, 1966). A radiotelemetry study by Kelly (1977) in New Hamsphire showed that fisher had a mean home range of 19.2 km^2, with the largest one found being 39.6 km^2. Leonard (1980) found ranges of similar size for radio-tagged fisher in Manitoba.

Live-trapping studies have indicated that marten (<u>Martes</u> <u>americana</u>) normally have home ranges of under 4 km^2 in British Columbia (Miller <u>et</u> <u>al</u>., 1955), Montana (Hawley and Newby, 1957), Ontario (Francis and Stephenson, 1972), and Maine (Soutiere, 1979). Marshall (1942, 1951a), however, trailed marten in Idaho and determined that their home ranges varied from 26 - 29 km^2. Recent radiotelemetry studies have established that marten often have home ranges from 5 - 20 km^2 in Minnesota (Mech and Rogers, 1977), Wisconsin (Davis, 1978), and Maine (Major, 1979; Steventon, 1979). Campbell (1979), however, found that the mean home range of two radio-collared male marten in Wyoming was only 2.2 km^2.

A radiotelemetry and tracking study of fisher and marten was conducted at Taiga Biological Station (51° 05' N, 95° 20' W) from August, 1978 to August, 1980.

Leonard's (1980) study of fisher provided background for my study. No marten were known to be present in the study area until 1978, when an influx of marten permitted their home ranges and movements to be compared with fisher. The increase in the marten population appeared to be part of the widespread expansion of marten range in Ontario and northeastern Minnesota (Mech and Rogers, 1977).

Study Area

The 324 km^2 study area is part of the low boreal land region (Woo et al., 1977). The dominant features are bedrock knolls and ridges of up to 30m in height with bogs and fens in between. The mean January temperature varies from -22.8 to -19.8°C and the mean July temperature varies from +18 to +19.5°C. Annual precipitation varies from 410 to 535 mm, with 250 to 355 mm of this falling as rain between 1 May and 30 September (loc. cit.).

The study area is composed of 10 habitats. The most common habitat is jackpine (Pinus banksiana) ridge. The entire study area has been burnt at some time or other, although some parts not for 150+ years. Moderately open black spruce (Picea mariana)-tamarack (Larix laricina) bogs are the second most common habitat. Open bogs of the same species, thick alder (Alnus) bogs, black spruce bogs and beaver meadows are the other moist habitats. The remaining habitats are aspen (Populus tremuloides)-jackpine ridges, balsam fir (Abies balsamifera)-white spruce (Picea glauca) ridges, jackpine sandplains and rivers and lakes.

METHODS

The movements of fisher and marten were determined by radiotelemetry. The animals were captured in wire box traps baited with duck, grouse, snowshoe hare and fish. A maximum of 44 traps were set at any one time (Figure 1). A sizeable piece of flesh was always left in each trap for food to prevent trap loss. The traps were covered with evergreen boughs and snow, and were checked every 24 hours. The animals captured were anesthetized with 15-20 mg of ketamine hydrochloride per kg body weight and with 2.5 mg of acepromazine maleate per animal. Similar dosages were used by Kelly (1977) to anesthetize fisher and by Hash and Hornocker (1980) to anesthetize wolverine.

Fisher and marten were fitted with radio-collars (AVM Instrument Company, Champaign, Illinois) that weighed 70-115 gm and 13-18 gm, respectively. The radios transmitted in the 150.8-151.1 mHz frequency range.

The first, lower, right premolar was extracted from some animals for aging purposes. The others were aged by the degree of development of their sagittal crests determined by skull palpation (Marshall, 1951b).

The animals were fed and kept in captivity 24 hours before release. They were then located by triangulation once a day when it was possible and occasionally twice a day. An AVM portable receiver and a four-element yagi antenna were used.

Figure 1. Trap distribution in the study area,
each square represents from 1 - 5 traps.
Trap locations were not permanent; the areas
trapped most continuously were those close
to the station (TBS).

N

■ TRAP
---- TRAIL

1 km

TBS

WALLACE LAKE
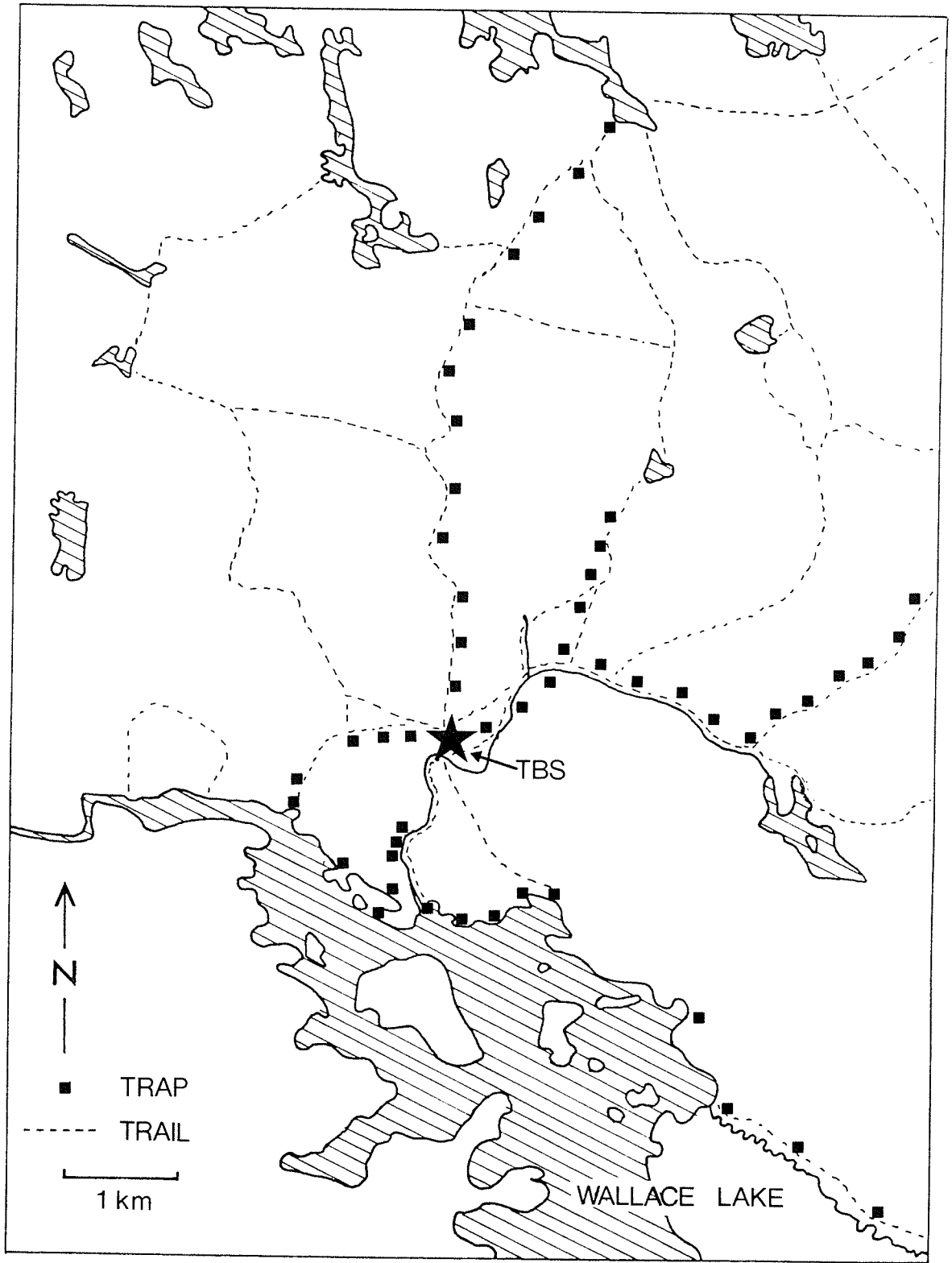
Home range estimates were based on the minimum area method (Mohr, 1947). The outermost locations of an animal were connected and the enclosed area measured. I feel that home range is a better term than territory for fisher and marten, as territory implies active defense.

Each winter was divided into three periods according to snow cover conditions. The first period was from the time of the first snowfall (13 November in 1978; 1 November in 1979) to when the snow thickness began to restrict the movements of fisher and marten. This thickness I arbitrarily chose as 20 cm, and it happened to be reached on 26 November of both winters. The second period encompassed the midwinter months of soft, thick snow cover when the vertical hardness was less than 100 gm/cm^2 in all habitats except rivers and lakes, and was often less than 10 gm/cm^2. The third period began when a vertical hardness of greater than 100 gm/cm^2 was reached in all habitats. The change to crust conditions was quite abrupt in both winters and occurred in all habitats at about the same time (21 March in 1979; 23 March in 1980).

RESULTS

Six fisher were captured a total of 13 times and 10 marten were captured 60 times in 13,510 trap nights. No fisher treed upon their release while marten did so three times. All of the captures were made between October and March despite the substantial trapping effort made during the summers (see Appendix 1).

Fisher Home Range

The two male (weights of 4.5, 3.4 kg) and four female ($\bar{x}$ weight = 2.4 kg) fisher live-trapped were all juveniles (Appendix 2). One male and two females moved out of radio reception range within 4 - 10 days of their release, and all three were later killed by trappers 9.5-18.0 km away (Table 1).

Two female fisher (F3, F5) were found to have midwinter home ranges of 20.5 (45 locations) and 15.0 km^2 (25 locations) (Figure 2).

F4, a male, exhibited unusual behaviour before he was captured. I followed his trail back from his capture site for 3.6 km. He had travelled on top of ski and other trails for 69% of this distance, and had followed every twist and turn of these trails. Other fisher trailed during the same midwinter period had spent only 2% of their time on such trails. Fisher generally only followed ski trails which were parallel

Table 1. Background information on radio-tagged fisher.

Catalogue number	Sex	Age	Weight (gms)	Date of release with radio collar	Winter period	Length of radio tracking period (days)	Number of locations	Minimum home range area (km²)	Maximum home range length (km)	Fate
F1	male	0½[1]	4,500	2/XI/78	thin snow cover	8	3			-travelled out of radio reception range -killed by trapper 16.0 km away, February 1977.
F2	female	0½[2]	2,500	4/XII/78	midwinter	9	10			-travelled out of radio reception range -killed by trapper 9.5 km away, January 1980
F3	female	0½[2]	2,300	4/XII/78	midwinter	64	45	20.5	6.8	-lost radio contact -recaptured 2/III/79; collar removed
F4	male	0½[1]	3,400	13/I/80	midwinter	16	31	12.0	5.7	-recaptured 6 times during radio-tracking period -found dead 29/I/80
F5	female	0½[2]	2,500	20/I/80	midwinter	24	25	15.0	5.9	-lost radio contact
F6	female	0½[1]	2,700	6/II/80	midwinter	4	4			-travelled out of radio reception range -killed by trapper 18.0 km away, 12/II/80

[1] Determined by tooth cross section

[2] Determined by skull palpation

Figure 2. Midwinter home ranges of female fisher
           F3 (○) and F5 (●) and of male fisher
           F4 (▲) as determined by radiotelemetry.

N

F5 ♀
1980

F3 ♀
1978-79

TBS

F4 ♂
1980

WALLACE LAKE

0   1   2   3

km
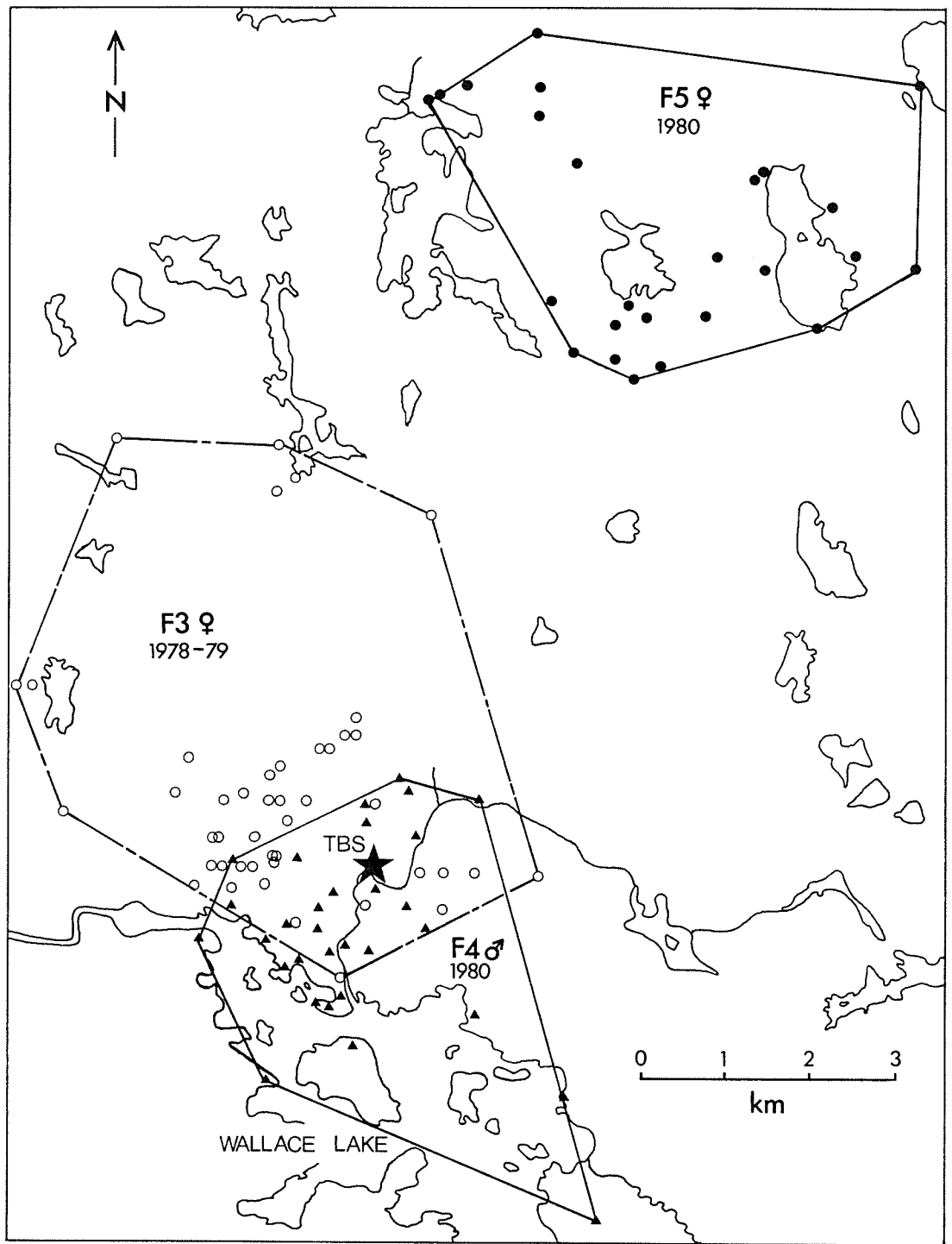
to the fisher's path (Section I). F4 was also unusually docile in the trap and was light in weight (3.4 kg).

Sixteen days after his release he was found dead in a cave. During this time his minimum home range was 13.0 km^2 (31 locations) (Table 1, Figure 2) and he travelled on ski and animal trails for 58% of the 3.7 km that I trailed him. I found no scats while trailing him, and when dead he weighed only 2.7 kg. F4 was the only fisher I caught that became trap prone and I recaptured him six times. Upon autopsy no abnormalities were noted although nine specimens of _Baylisascaris_ _devosi_ were found in the stomach.

Marten Home Range

Of the six male ($\bar{x}$ weight = 1.2 kg) and four female ($\bar{x}$ weight = 0.7 kg) marten that were live-trapped, all but two were juveniles. One male was 1½ years old and one female was 4 years old (Appendix 3).

Two juvenile males (M3, M4) and one juvenile female (M9) were radio-collared.

M3 was first caught in October 1979 (Table 2). During the 14 days before the first snow fall of the year he had a minimum home range of 6.7 km^2 (24 locations) (Figure 3,A) and during the 26 days of the thin snow cover period he had a home range of 5.5 km^2 (n = 18) (Figure 3,B). During 30 days of the midwinter period of soft snow cover before radio contact

Table 2. Background information on radio-tagged male marten.

Catalogue number	Age	Weight (gms)	Date of release with radio collar	Season or winter period	Length of season or period (days)	Number of radio locations	Minimum home range area (km²)	Maximum home range length (km)	Recaptures and fate
M3	0½[1]	1,350	18/X/79	fall-no snow	14	24	6.7	5.6	
			1/XI/79	thin snow cover	26	18	5.5	5.2	
			27/XI/79	midwinter	30	14	4.7	3.6	-lost radio contact 27/XII/79 -recaptured 7/II/80; collar removed
			8/IV/80	crust	10	9	2.1	3.6	-recaptured 8/IV/80; recollared and released
			19/IV/80	spring-no snow	31	26	8.1	4.7	-lost radio contact due to forest fire 20/V/80-3/VI/80
			3/VI/80	after burn	4	4			-travelled out of radio reception, killed by trapper 61 km away, 2/XI/80
				Total	223	95	42.4	10.6	
M4	0½[1]	1,100	20/X/79	fall-no snow	11	18	3.0	2.6	
			1/X1/79	thin snow cover	25	21	9.6	5.3	-lost radio contact 26/XI/79 -recaptured 17/XII/79; died during anesthesia
				Total	36	39	9.6	5.3	

[1]Determined by tooth cross section

Figure 3.   Seasonal home range of M3 as determined
            by radiotelemetry.   A = fall, no snow (△);
            B = thin snow cover (●); C = midwinter (▼);
            D = live-capture site (★); E = crust (○);
            F = spring, no snow, prior to fire (▲).
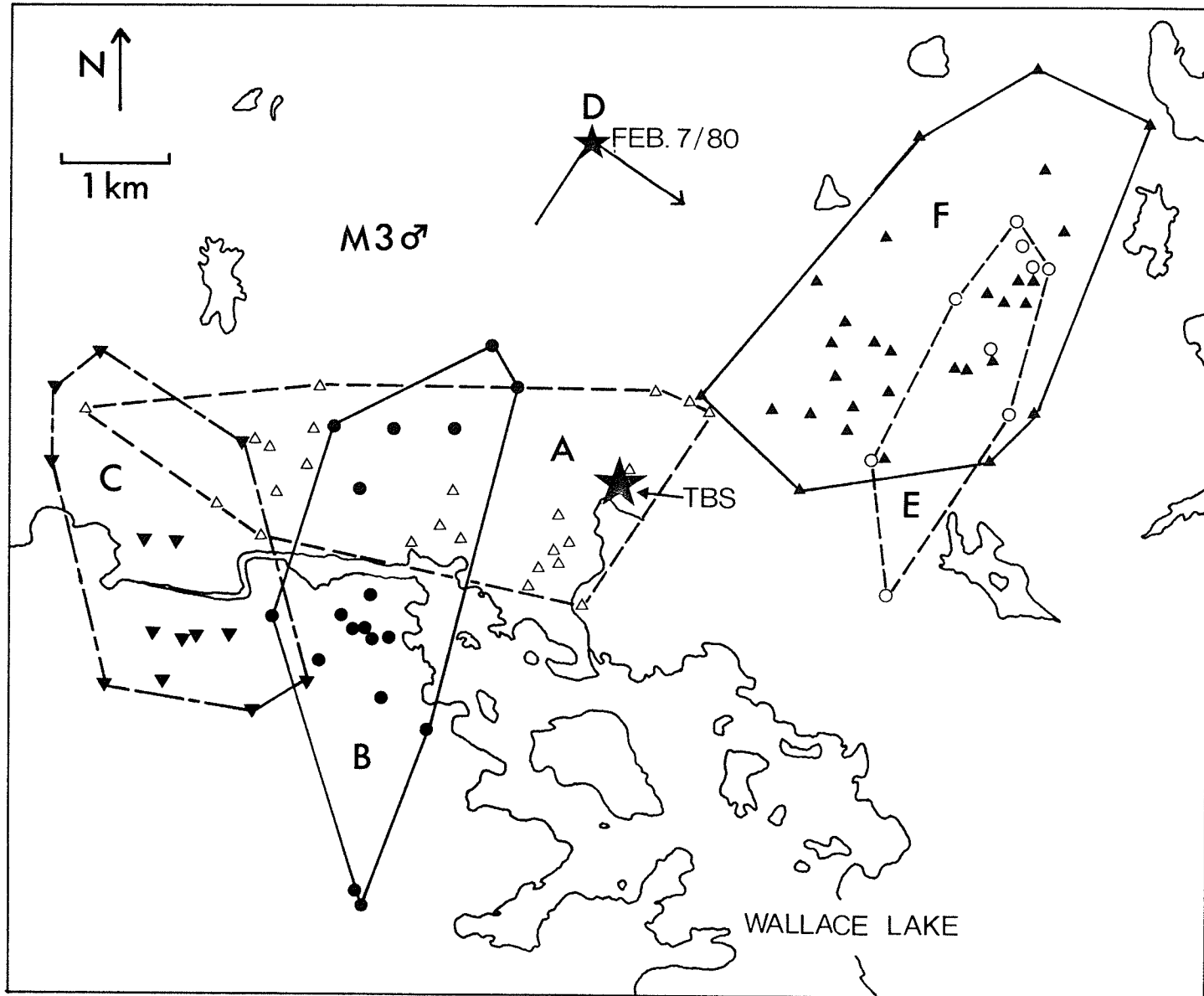
was lost he had a home range of 4.7 km^2 (n = 14) (Figure 3,C).
Forty-two days later (7/II/80) M3 was recaptured 5.3 km
northeast of his last radio location   (Figure 3,D). His
collar no longer functioned, but he was released without being
recollared as no collars were available at that time. He
was next recaptured 4.2 km to the southeast, recollared and
released on 8 April. During the next 10 days of crust
conditions M3 had a minimum home range of 2.1 km^2 (n = 9)
(Figure 3,E) and after the snow had melted his home range
was 8.1 km^2 (31 days, n = 26) (Figure 3,F). A chronological
linkage of the locations of M3 (Figure 4) shows that by
spring he had stopped his wanderings and perhaps had
established a permanent home range.

A forest fire that began on 20 May swept through the
study area and radio contact was lost from this date to 3 June.
Almost all of the study area north of Wallace Lake was burnt.
Most of the more moist habitats (moderately open, open and thick
alder bogs) were not burnt but the other habitats were burnt
severely. M3 survived the fire and I located him four times
in as many days before radio contact was lost. He was in
unburnt bogs for each of these locations. When I walked in on
him for one location and treed him he did not appear to have
any burns. On 2/XI/80 he was killed by a trapper 61 km to
the east. His total minimum home range, excluding the location
of his death, was 42.4 km^2 (n = 95, 223 days).

Figure 4. Chronological linked fixes of M3 showing
           exploratory behaviour in the fall and his
           final home range in the spring, prior to
           the fire.

N

1 km

FEB. 7/80

M3 ♂

APRIL 19 –
MAY 20

TBS

OCT. 18 – DEC. 27/79

WALLACE LAKE
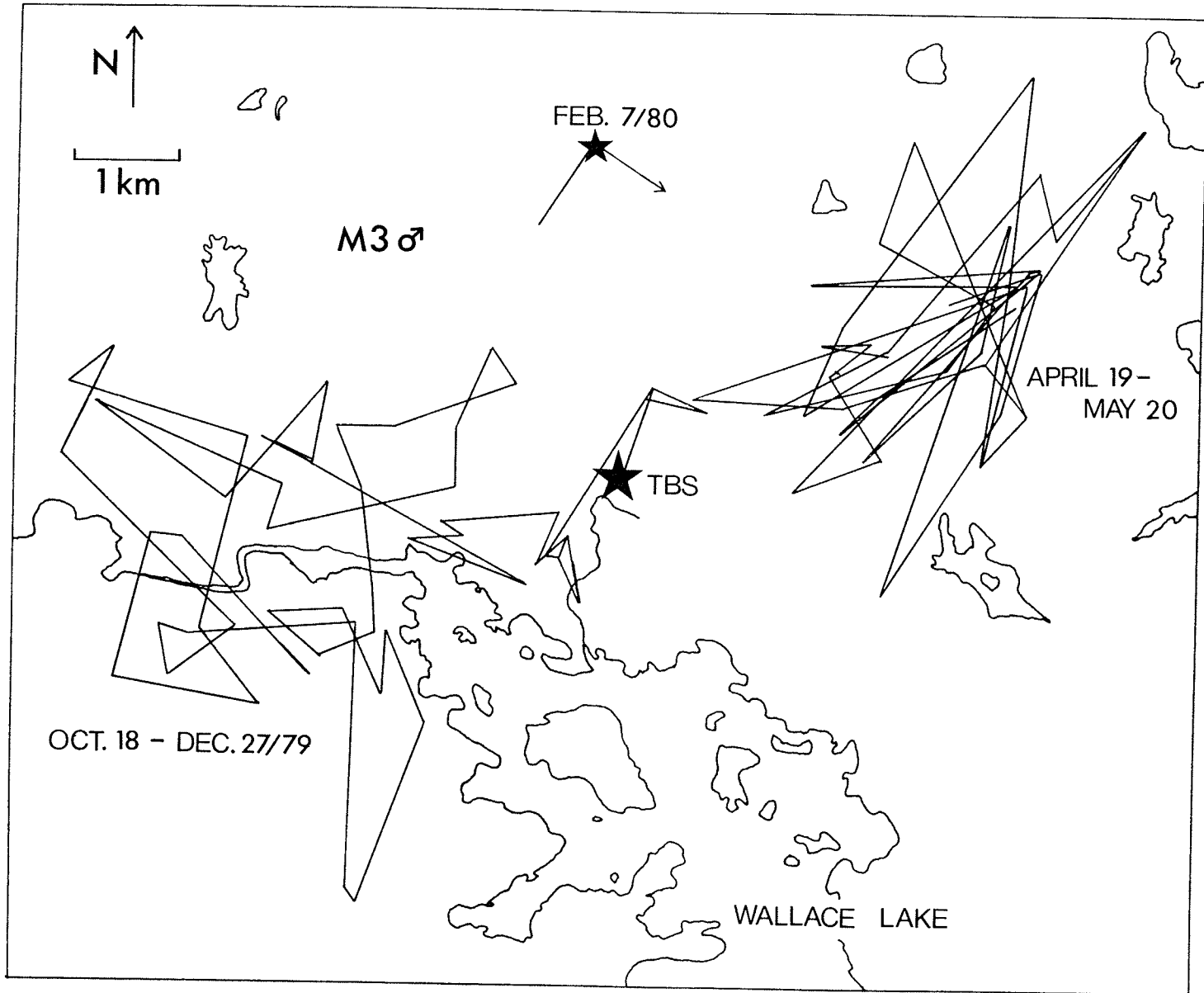
The second juvenile male, M4, was caught and released with a collar shortly after M3's first release (20/X/79) (Table 2). During the 11 days before the first snowfall he had a home range of 3.0 km^2 (n = 18) (Figure 5,A'). In the thin snow cover period he was located 21 times in 25 days and had a home range of 9.5 km^2 before radio contact was lost on 26 November (Figure 5,B'). M4 was recaptured within his previous home range 22 days later, but he died during anesthesia. M3 and M4 were radio-tracked concurrently during late fall and early winter. In Figure 5 it can be seen that there was little overlap in their home ranges during these periods.

A third juvenile male marten (M6) was live-trapped 19 times in a 103 day period during midwinter 1979/80 and had an estimated minimum home range of 5.3 km^2 (Figure 6). He was first captured on 6 December. By this time M4 was dead and M3 had a temporary home range several kilometers to the west of where he had been previously (Figure 6,C). As far as I could tell from live-capture data, the range of M6 remained relatively stationary through the winter while M3's range swung to the north and then to the east and south (Figure 6; D,E,F). Thus M3 appeared to circumnavigate M6's range.

A juvenile female (M2) captured 16 times in the fall of 1979 during 17 days of no snow cover and 12 days of thin snow cover had a minimum home range of 1.0 km^2. Shortly after her last live-capture she was killed by a trapper 9 km to the west.

Figure 5. Concurrent home ranges of M3 and M4,
           1979. A = M3, fall no snow (△);
           A' = M4, fall no snow (▲); B = M3, thin
           snow cover (●); B' = M4, thin snow
           cover (○); C = M3, midwinter (▼),
           D = M3, live-capture site, 7/II/80 (★).
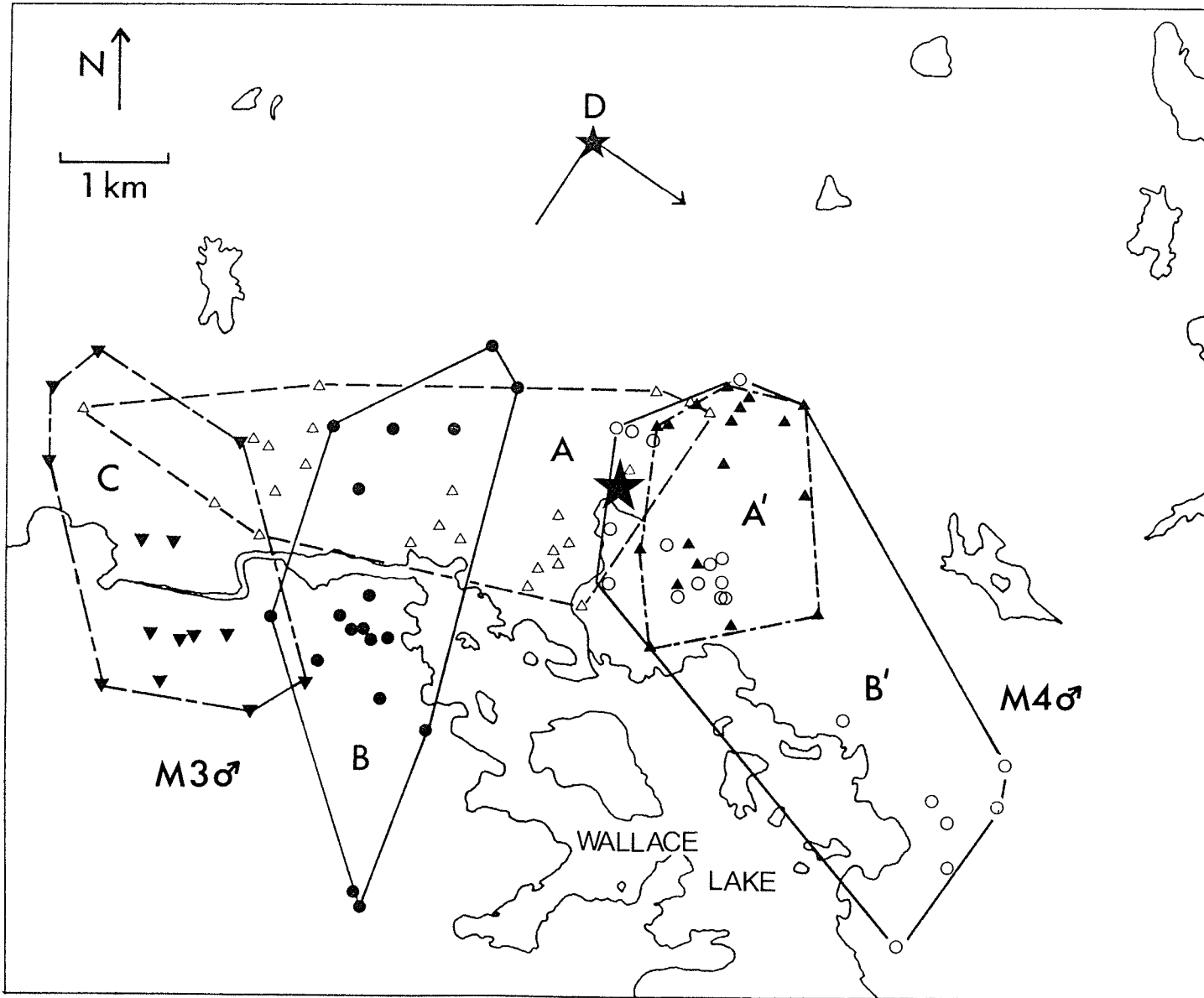
Figure 6. Concurrent home ranges of M3 and M6,
1979-80. C = M3, midwinter (▼);
D = M3, live-capture (★); E = M3,
crust (○); F = M3, spring, no snow (▲);
C' - E' = M6, midwinter and crust (●).

N

1 km

D

M3♂

F

M6♂
C'-E'

C

E

M3♂

WALLACE LAKE
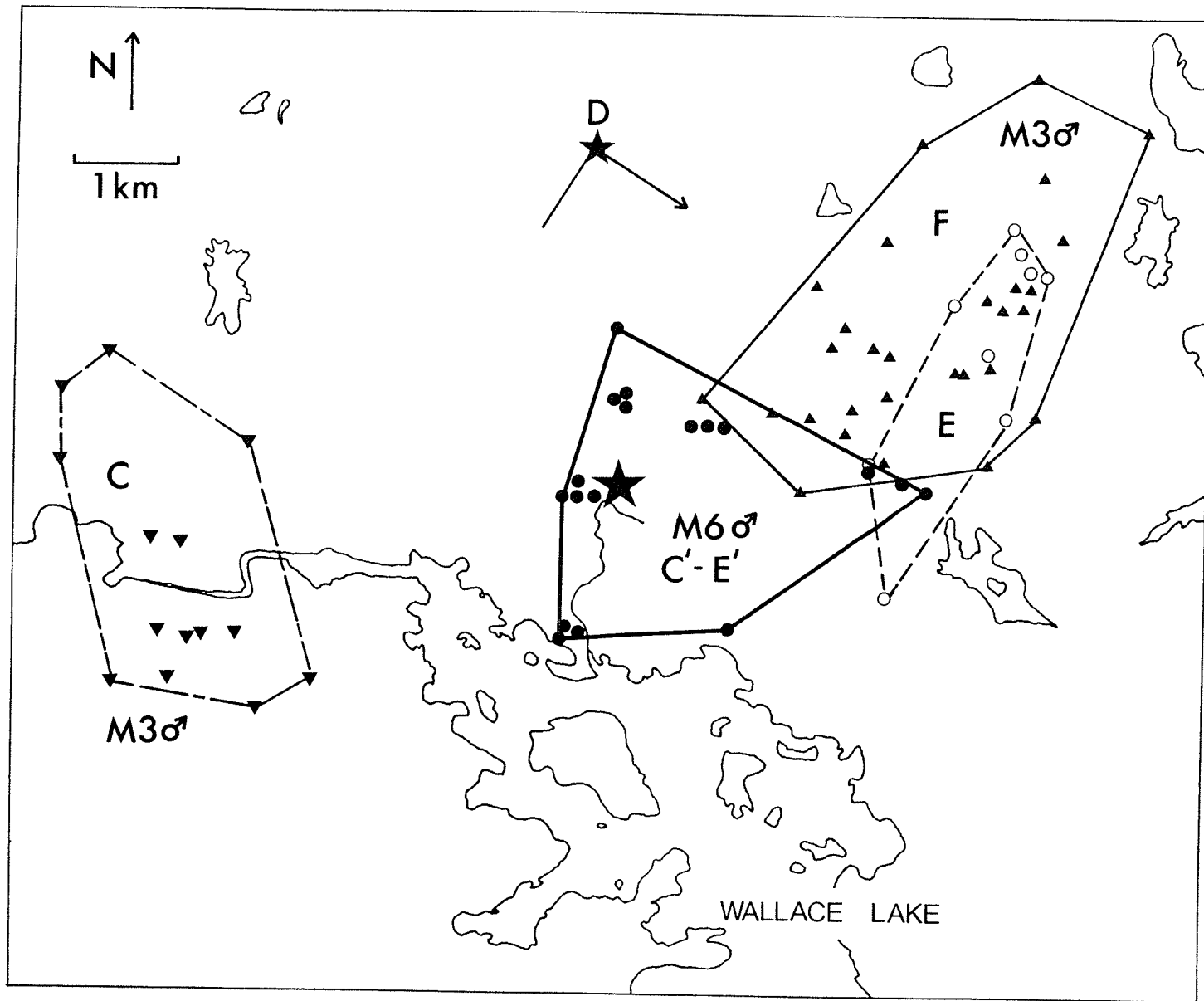
The third marten that was radio-tagged (M9, a juvenile female) was released on 7 April 1980. Her minimum home range during the remainder of the crust period (12 days, n = 15) was 8.4 km^2 (Table 3, Figure 7). After the snow had melted but before the fire her range was 6.6 km^2 (31 days, n = 34). She also survived the fire. Once it was safe to walk in the burn she was located nearly every day until radio contact was lost on 3/VIII/80 (minimum home range = 6.0 km^2; 64 days; n = 80). After the burn I approached her closely enough to be certain of what habitat she was in nine times. On every occasion she was in either thick or moderately open bogs, except for twice when I accidentally approached too closely and treed her. On these two occasions she climbed live spruce trees that bordered unburnt bogs. As determined by a habitat map of the study area, made from aerial photographs, bogs composed 32.9% of M9's home range during the snow free period prior to the burn, and 35.2% after the burn (Table 3). Her total home range was 12.5 km^2 (118 days, n = 129).

I trailed a marten for 5.0 km in November 1980 and found that it spent 86.0% of its time on burnt coniferous ridges and only 6.7% of its time on unburnt bogs.

Fisher and Marten 24 Hour Movements

The two radio-collared female fisher (F3 and F5) moved a mean distance of 1.1 km (n = 32) and 2.5 km (n = 18),

Table 3. Background information on a radio-tagged, juvenile[1] female marten (M9).

Weight (gms)	Date of release with radio collar	Season or winter period	Length of season or period in days	Number of radio locations	Minimum home range area (km^2)	Maximum range length (km)	Percentage of Habitat				Fate
							Jackpine Ridge Black spruce bog	Moderately open and Open Bog	Thick Alder Bog	Lake	
660	7/IV/80	crust	12	15	8.4	4.3	69.7	22.4	7.2	0.7	
	19/IV/80	spring-no snow	31	34	6.6	3.8	66.3	18.9	14.0	0.8	-loss of radio contact due to forest fire 20/V/80-31/V/80
	31/V/80	burn	64	80	6.0	3.9	64.0	22.2	13.0	0.8	-loss of radio contact 3/VIII/80
		Total	118	129	12.5	4.6					

[1]Determined by skull palpation.

Figure 7.   Home range of M9 as determined by
            radiotelemetry, 1979.

BOG

RIDGE

LAKE

N

1 km

- - - - ▲ - - - CRUST

———○——— SPRING : NO SNOW   M9 ♀

—·—●—·— AFTER BURN
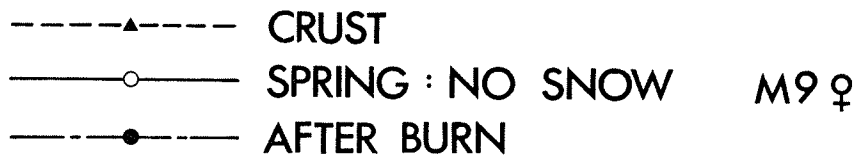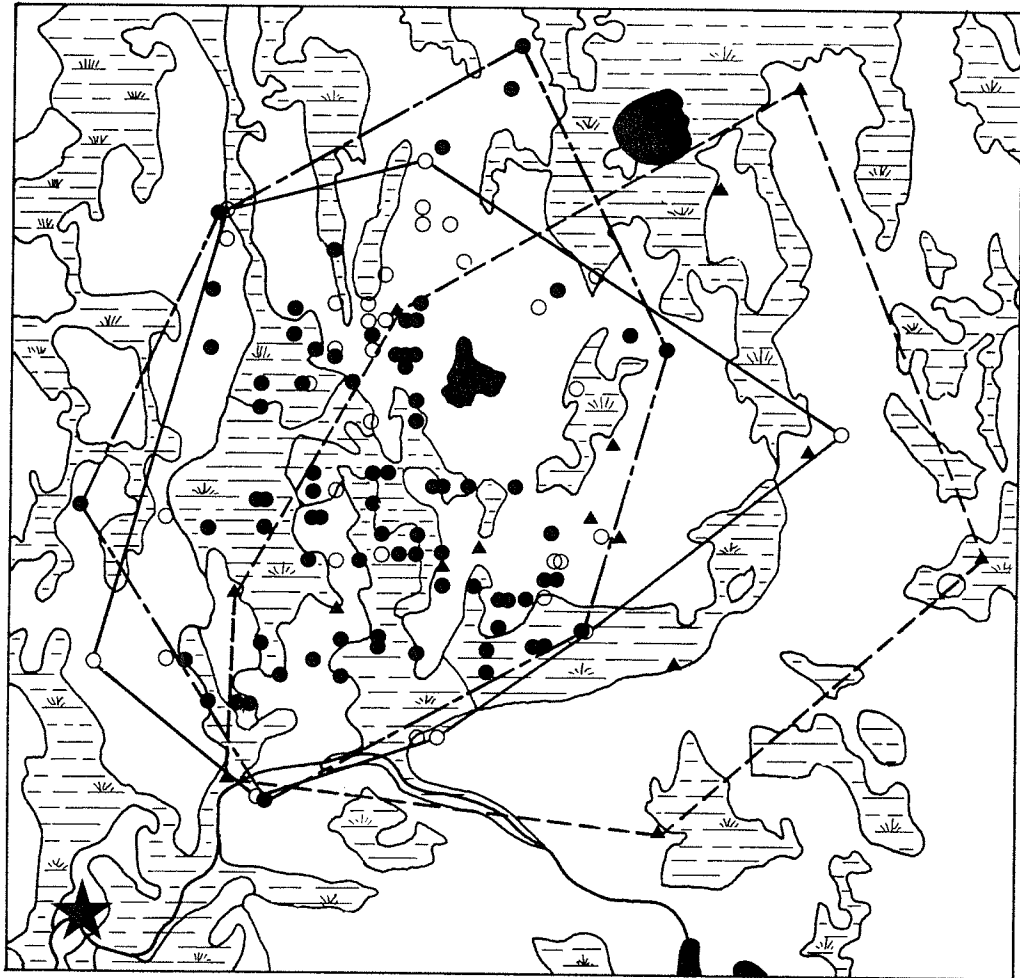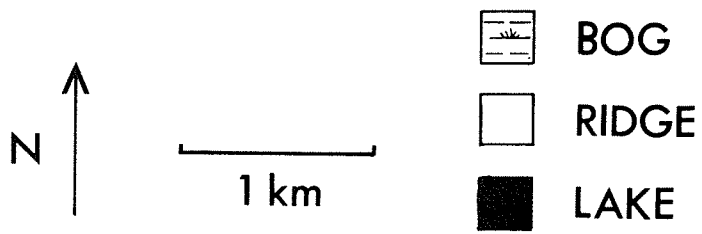
respectively, between successive daily locations (Figure 8).
These means are significantly different (1-way ANOVA:
$F_{(1,40)} = 14.61$, $P < 0.001$).

The means of the 24 hour movements of marten M3 did
not differ significantly between the winter periods and
the no snow periods ($F_{(4,48)} = 1.68$; $P < 0.25$) (Figure
8). There is a trend, however, as M3 moved less during the
thin snow cover and midwinter periods (1.0 km, n = 10, 1.1 km,
n = 6) than during the fall period of no snow (1.4 km, n = 12),
the crust period (1.5 km, n = 7) and the spring period of
no snow (1.8 km, n = 18).

M4 also appeared to decrease his activity from the fall
period of no snow (1.5 km, n = 8) to the thin snow cover
period (0.8 km, n = 14) ($F_{(1,20)} = 4.83$, $P < 0.05$). M9
decreased her daily activity from the crust period (2.1 km,
n = 9) to the snow free period of spring (1.5 km, n = 29)
and after the burn (1.3 km, n = 60) ($F_{(2,95)} = 4.63$,
$P < 0.025$).

Fisher Dens

Six subnivean dens were found by trailing fisher and
one den was located by radiotelemetry. Fisher went under the
snow cover 80 times in 111 km of trail (Section I), but most
of these occasions were interpreted to be foraging activity.
Only when a fisher dragged a prey item to a hole or when
numerous trails led to and from a hole was it considered
to be a den.

Figure 8. Mean distance moved by fisher and marten
between successive daily locations, 1979/80.
Confidence limits (95%) are indicated by
vertical lines with the sample sizes placed
on top. Data of F3 are from the winter of
1978/79.
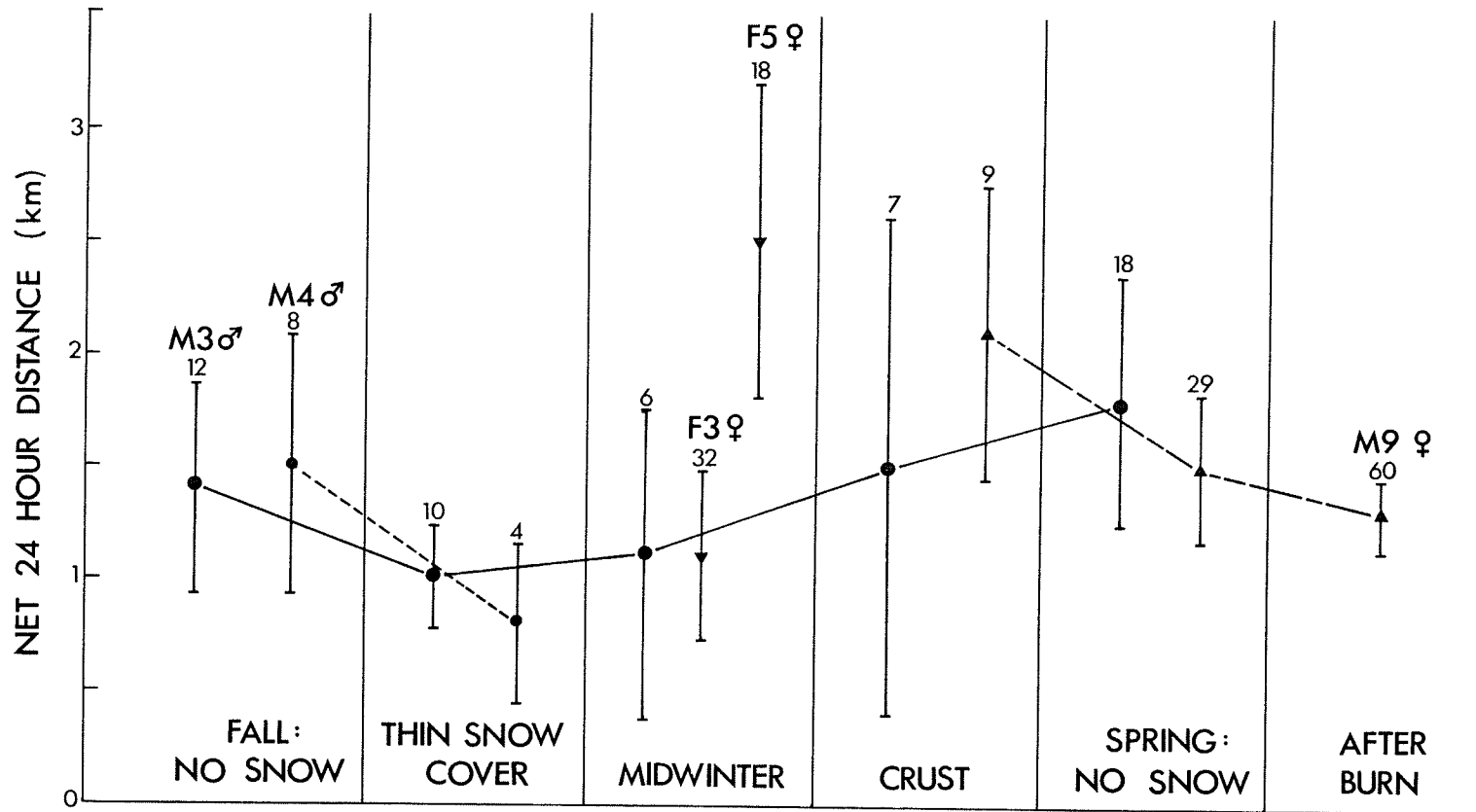
Of the seven dens, six were on jackpine ridge and one was in black spruce bog; three were under boulders, three were under upturned tree roots and one was in the subnivean spaces caused by the branches of a fallen birch. One was near a hare kill, two had hare remains nearby and one den was used off and on by a fisher for at least 30 days.

Marten Dens

Only three definite subnivean dens were found in 81 km of trail, although marten went subnivean to forage 257 times (Section I). All three dens were renovated red squirrel middens on jackpine ridges. One had spruce grouse remains and two had hare remains near their entrances. One was visited by a marten off and on for a minimum of 65 days.

Two summer dens of M9 were located by radiotelemetry. Both were on jackpine ridge and under the roots of fallen trees.

DISCUSSION

Both fisher and marten were easier to catch in winter than in summer. Food is less available in winter and thus they may be more trap prone. It is also possible that more juveniles in the population are dispersing in the fall and early winter (Francis and Stephenson, 1972) and therefore are more likely to encounter traps at this time. Other authors have also found that fisher (Leonard, 1980) and marten (Newby, 1951; Lensink et al., 1955; Miller et al., 1955; Jonkel, 1959) are more likely to be caught in winter.

Fisher and Marten Home Range

Three of the radio-collared, juvenile fisher moved out of reception range soon after their release. Kelly (1977) and Leonard (1980) both found that juveniles moved greater distances than adults. One juvenile fisher in Leonard's study was killed by a trapper 60 km from its release site.

The home range size of two female fisher in this study (20.5 and 15.0 km^2) compare favourably with the results of Kelly and Leonard. These two fisher, however, were only radio-tracked for short periods.

F4 lost 700 gm in weight before he died 16 days after he was collared and released. Thus he most likely died of starvation. He was underweight to begin with (3.4 kg as compared with the mean weight of 4.6 kg of the three other male

fisher that Leonard (1980) and I caught) and exhibited unusual behaviour in that he followed ski and other trails to a much greater degree than did other fisher. Thus he may have already been close to death before I caught him, although the trauma of being captured and collared could certainly have had an effect. I found that fisher were restricted in their movements in midwinter by thick, soft snow cover (Section II). When the depth to which they sank reached 9 cm they would walk and leave a long, uninterrupted furrow in the snow cover. This method of locomotion must be energetically taxing as both Leonard (1980) and I found that fisher decreased their activity in midwinter. Perhaps F4 was underweight for this reason.

Marten began to invade the study area in 1978. The population was still quite low during this study as the capture rate was only 0.4 marten per 100 trap nights. Other authors have caught 2.8 (Koehler and Hornocker, 1977), 3.8 (Soutiere, 1979), 6.8 (Campbell, 1979), 7.0 (Miller et al., 1955) and 13.1 (Hawley and Newby, 1957) marten per 100 trap nights.

My study was also unique in that I collared only juvenile marten. Other authors deliberately collared only adults (Campbell, 1979; Major, 1979; Steventon, 1979), while Davis (1978) did not age most of his animals.

M3 appeared to shift his range constantly during the fall and early winter of 1979 (Figures 3 & 4). Due to the paucity of track observations in this area, it was most likely that there were no other marten near M3 at this time. Marshall (1942, 1951a) also found that marten shifted their ranges. As his was a trailing study it was not determined whether the marten studied were juvenile or not. Marten reintroduced into northern Wisconsin made extensive movements, and only two females out of 21 radio-tagged marten exhibited sedentary movements that could be considered a home range (Davis, 1978).

M3 sometimes remained stationary, or nearly so, between successive daily locations. Other authors have found that marten will stay at the site of a kill or a carrion source for several days (Marshall, 1951a; Lensink et al., 1955; Steventon, 1979; Pulliainen, 1980b).

When M3 was collared in the spring it appeared that he had stopped his wanderings and perhaps had established a permanent home range of 8.1 km^2 (Figure 4). He was in the same area when the fire swept through and he remained for at least 17 days after it. Thick alder bogs have high small mammal populations (Section I), and although these bogs were not burnt severely, they perhaps were not extensive enough to support M3. He travelled 61 km to the east where he was killed by a trapper.

Many authors have stated that fires are detrimental to marten habitat (Yeager, 1950; Miller et al., 1955, Koehler and Hornocker, 1977).

M4 had a home range of 9.6 km^2 during the 36 days that he was radio-tracked. If he had been tracked for a longer period perhaps he would have exhibited the rambling behaviour that M3 did.

The behaviour of the collared female M9 was different from the behaviour of M3 because she appeared to have an established home range. She was not captured until April, however, thus she may have been roaming earlier in the winter. Her range was larger during the crust period than during the snow free period of spring (8.4 vs 6.6 km^2). This agrees with my observations that snow cover crusts are easy for marten to travel on (Section II) and that they hinder marten from hunting in subnivean spaces (Section I). Thus marten may have to travel farther to find food when there is a crust.

The home range size of M9 was comparable to that reported by Pulliainen (1980b) for female M. martes in Finland (9.5 km^2), by Mech and Rogers (1977) in Minnesota (4.3 km^2) and by Davis (1978) in Wisconsin (7.7 and 8.2 km^2). Steventon (1979) found that female marten in Maine had ranges of up to 2.5 km^2, while Campbell (1979) in Wyoming found one female to have a range of only 0.8 km^2.

M9's home range size was about the same before and after the fire, and the proportions of each habitat did not alter much (Table 3). M9 appeared to spend most of her time in bogs, which constituted 35.2% of her range. Thus approximately 2.1 km^2 of bog habitat was adequate to support her. The ridges were severely burned and few microtines or squirrels could have survived.

By fall, however, the small mammal population on the ridges had recovered, and Peromyscus maniculatus was especially abundant (Johnson, TBS files). This species prefers xeric conditions and is known to thrive on burns (Bendell, 1974; Krefting and Ahlgren, 1974).

Marten appeared to have reverted to their former preference of jackpine ridge (Section II) by November 1980. Not enough trailing data however were collected at this time for a proper assessment of marten habitat selection.

The ranges determined by live-trapping (M2 and M6) were much smaller than those determined by radiotelemetry. Radio-tracking studies of marten (Mech and Rogers, 1977; Davis, 1978; Major, 1979; Steventon, 1979) generally have found larger home ranges for marten than have live-trapping studies (e.g.: Hawley and Newby, 1957; Francis and Stephenson, 1972; Soutiere, 1979).

Harestad and Bunnel (1979) reviewed the literature on the home range sizes of North American mammals and concluded that it is directly proportional to body weight and trophic level, and is inversely proportional to habitat productivity.

I found that fisher had larger home ranges than marten in this study, which was to be expected, but the female marten M9 had seasonal home ranges comparable in size to those of the male marten M3 (Tables 2 & 3). However, the small number of locations, the fact that both of these marten were juveniles and the low density of marten in the study area are all confounding factors.

My impression from trailing fisher and marten is that both species are capable of covering large distances in a day. Because habitat productivity varies inversely with latitude one would expect mammals to have larger ranges in the north. That is perhaps why the marten in the boreal forest of Manitoba (my study) and northeastern Minnesota (Mech and Rogers, 1977) appear to have larger ranges than the marten in Maine (Major, 1979; Steventon, 1979) and Wyoming (Campbell, 1979).

The male marten in this study appeared to have a temporal-spatial separation of home range. Not enough female marten were caught or collared to determine whether they avoided each other's ranges. Many other studies have presented

evidence of marten intrasexual, but not intersexual separation of home range (de Vos and Guenther, 1952; Francis and Stephenson, 1972; Campbell, 1979; Major, 1979; Steventon, 1979), while other studies have shown that male ranges sometimes partly overlap (Hawley and Newby, 1957; Pulliainen, 1980b). Davis (1978) found that the ranges of two female marten overlapped approximately by one third.

Powell (1979a) reviewed the literature and found a strong correlation in mustelid species between body elongation, carnivory, sexual dimorphism and intrasexual spacing. Long, thin mustelids have been found to have an elevated metabolic rate compared to "normal" shaped mammals (Brown and Lasiewski, 1972; Iverson, 1972; Moors, 1977; Powell, 1979b) which may lead to increased intraspecific competition for food. Sexual dimorphism in body size and intrasexual territoriality may be one way of reducing this competition. Recently, however, several authors have postulated that it may be advantageous for the female to be small in order to reduce her overall energy needs during pregnancy and lactation (Erlinge, 1979; Powell, 1979b; Moors, 1980). Many mustelids have a polygynous breeding system and no paternal care, thus large males may be favoured through sexual selection.

The temporal spacing exhibited by the male marten in my study may have been due to the fact that most of the marten in the study area were juveniles. However, temporal spacing may

be more adaptive for solitary species with large home
ranges than strict, spatial territoriality as it is less
energetically taxing. If an animal can keep conspecifics
of the same sex away simply by scent marking while
foraging, it would not be adaptive for it to spend any
time and energy solely for marking a territorial boundary.

Twenty-four Hour Movements

The net distance an animal moves in 24 hours is
not a useful measurement if an animal crosses its home
range several times each day. The fisher and male marten
in this study did not appear to do this whereas the
female marten may have.

Why the net 24 hours movements of F3 in 1978/79 and
F5 in 1979/80 were so different (1.1 vs 2.5 km) is not clear.
Their home ranges did not appear to differ in habitat
composition and therefore productivity, and the snow
conditions between winters were comparable. Kelly (1977)
found that female fisher in New Hampshire moved a mean distance
of 1.5 km (n = 99) between successive daily locations.

Mech and Rogers (1977) found that male marten moved
an average of 1.8 km (n = 14) between days in winter
in Minnesota, while Davis (1978) found that dispersing marten
travelled up to 23 km in 30 hrs in Wisconsin.

Several authors have found evidence that marten movements are determined by the abundance and availability of food (Marshall, 1942, 1951a; Lensink et al., 1955). As the food supply decreases in winter one would expect fisher and marten to increase their movements. This tendency may be offset, however, by the restriction on movements by snow cover. My data are too limited to test these ideas, although the male marten M3 and M4 did have shorter 24 hour movements in the thin snow cover and midwinter periods than in the crust and snow free periods (Figure 8).

Fisher and Marten Dens

Subnivean dens offer fisher and marten protection from cold and predators. De Vos (1952) and Coulter (1966) found that fisher made winter dens in holes under boulders, hollow logs, upturned roots, brushpiles and in deserted beaver houses.

Francis and Stephenson (1972), Mech and Rogers (1977) and Pulliainen (1980b) found that marten usually denned in coniferous habitats. Newby (1951) and Murie (1961) stated that marten sometimes denned in squirrel middens whereas Marshall (1942, 1951a), Campbell (1979) and Steventon (1979) found they most often denned in decayed stumps and logs. Some authors have stated that marten rest in trees (Mech and Rogers, 1977; Masters, 1980). They based their statements on observations of radio-collared marten that observers walked

in upon. These, however, were most likely incidences of
escape behaviour. In my study marten climbed trees on
three occasions when I accidentally walked too close to
them.

Fisher and marten most likely prefer to den in
coniferous habitats due to the availability of windfalls,
decayed stumps and squirrel middens.

RECOMMENDATIONS

Mech and Rogers (1977) concluded that the increase in the marten population of northeastern Minnesota and adjacent Ontario was probably due to a lower incidence of fire and logging, and the coincident maturation of coniferous habitats. The complete protection in Minnesota of marten from trapping since 1933 must also have been a factor.

Marten were not known to be in the Taiga Biological Station study area until the winter of 1978-79, and at least 10 were present by the next winter. A viable population of marten, however, will not be able to establish itself unless fire, logging and trapping are controlled.

Fire - The Wallace Lake fire of 160,000 acres destroyed virtually all of the mature coniferous forest in its path. Research is needed to see if the surviving fisher and marten will be able to find sufficient food to live. The hare population may increase in a few years as a result of the new growth, and perhaps fisher and marten will be able to utilize them as a food source. Koehler and Hornocker (1977) concluded that the long term effect of fire on marten habitat in Idaho is beneficial as it helps to maintain forest diversity. The Wallace Lake fire, however, was quite severe and extensive, and had only negative effects for fisher and marten.

Logging - Clear cutting of forests has been found to be incompatible with the maintenance of marten populations (Koehler et al., 1979; Steventon, 1979).

Koehler et al., (1975) recommended that logging should only be carried out on mesic sites and that at least a 30% canopy be left standing. They and Campbell (1979) found that the xeric conditions caused by fires and clear cuts decreased the populations of Clethrionomys and Microtus, favored marten prey, and increased the populations of Peromyscus, which marten appeared to avoid eating. Campbell (1979) also concluded that logging operations destroyed marten resting sites and their access to subnivean spaces to hunt. He recommended that slash piles should be left in order to facilitate marten in their resting and hunting.

Steventon (1979) in Maine found that male marten could incorporate small cut areas of forest in their range, but that females were entirely restricted to mature forests. If this is true, then uncut stands of up to 8.4 km^2, the size of M9's home range in my study, will be necessary for female marten to survive in southeastern Manitoba.

I found that marten and fisher could tolerate human presence as their tracks were often found close to the station, and on occasion one female marten would enter the porch to feed on bait that was stored there. Major (1979) found that marten would approach to within 100 m of active logging operations. Road closures, however, are necessary after logging or mining is terminated to prevent trappers from having easy access to

wilderness areas. Both fisher and marten are easily trapped and have low reproductive potentials.

Reintroductions - Introductions of marten into areas from which they have been extirpated have met with limited success (Shupbach, 1977; Davis, 1978). However, with better handling techniques, large numbers of marten, a 50:50 sex ratio and by using the "slow release" method, ongoing reintroductions of marten should have better success (M. F. Herman, personal communication, 1980).

Viable populations of fisher have been established in Michigan through reintroductions, and porcupines have decreased in abundance as a result (Earle, 1978; Powell and Brander, 1977).

Snow Measurements - The snow index that I derived for fisher and marten was only accurate on a large scale. More sensitive vertical hardness gauges are needed, particularly ones that can accurately measure hardness in the 1-50 gm/cm^2 range. If many hardness measurements were taken alongside the tracks of known animals (i.e. live-trapped or radio-collared individuals) perhaps a relationship between track depth, track area and snow cover hardness could be found. In the meantine, track depth alone seems to be a useful measurement to describe the degree to which fisher and marten are hindered in their movements (see Section III, Figure 6).

The vertical hardness of the snow cover must be taken into account when comparing the relative densities, determined by track count transects, of fisher in different areas. Research is also needed to see if soft snow cover affects the winter mortality rate of fisher.

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Appendix 1. Monthly trapping effort and capture success

		Trap Nights	FISHER		MARTEN	
			Initial Capture	Recapture	Initial Capture	Recapture
September	1978	211				
October		362	1			
November		506				
December		585	2			
January	1979	500				
February		1,120				
March		1,144		1	1	1
April		281				
May		—				
June		499				
July		1,209				
August		716				
September		1,131				
October		820			3	11
November		814			1	5
December		858			1	13
January	1980	977	2	6	1	7
February		196	1			
March		781			3	13
April		480				
May		320				
Total		13,510	6	7	10	50

Appendix 2. Measurements of fisher and marten captured.

	Sex	L	T	HF	EFN	Weight (gms)	Zygomatic breadth	Age	Date first caught	fore foot length	fore arm length	Neck circumference	Collar circumference	Ear tag of animal still at large	
														Right	Left
F1	♂	990	370	133	40	4,500	73	0½	27/X/78	85	180	180	200		
F2	♀	875	325	113	40	2,500	50	0½	26/XI/78	65	150	155	170		
F3	♀	860	330	100	42	2,300	55	0½	3/XII/78	70	140	160	170	1807	1808
F4	♂	1,005	370	130	50	3,400		0½	10/I/80	70	180	180	200		
F5	♀	830	320	107	42	2,500	66	0½	18/I/80	60	150	160	180	1897	1894
F6	♀	890	350	115	45	2,700	57	0½	3/II/80	60	160	160	180		
M1	♂	650	190	90	33	1,350	55		4/III/79	60	125	120	135	1809	1823
M2	♀	492	155	73	40	600	43	0½	14/X/79	52	97	100			
M3	♂	610	175	90	50	1,350	50	0½	16/X/79	48	128	130	140		
M4	♂	600	178	85	44	1,100	48	0½	6/X/79	36	114	120	135		
M5	♀	571	174	80	40	670	41	0½	14/XI/79	50	108	100		1882	1878
M6	♂	567	162	87	44	1,350	48	0½	6/XII/79	50	112	110	140	1849	1869
M7	♂	589	178	84	42	1,000	46	1½	18/I/80	51	115	120		1886	1839
M8	♂	627	180	89	48	1,250	50	adult	17/III/80	66	120	130		1884	1895
M9	♀	550	151	78	38	660	46	0½	22/III/80	58	105	108	115	1881	1876
M10	♀	553	171	78	40	680	43	4+	28/III/80	53	104	110			

Appendix 3. Background information on marten not radio-tagged.

Catalogue number	Sex	Age	Date of first capture	Season or winter period	Length of season or period	Number of captures	Minimum home range area (km^2)	Maximum range length (km)	Fate
M1	male	0½[2]	4/III/79	crust	19	2			-unknown
M2	female	0½[2]	14/X/79	no snow and thin snow cover	29	16	1.0	1.8	-killed by trapper 9 km away, November, 1979.
M5	female	0½[2]	13/XI/79	thin snow cover and midwinter	32	7			-unknown
M6	male	0½[1]	6/XII/79	midwinter	103	19	5.3	3.4	-unknown
M7	male	1½[1]	18/I/80	midwinter	1	1			-unknown
M8	male	0½[2]	17/III/80	midwinter	1	1			-unknown
M10	female	4[1]	28/III/80	crust	1	1			-died during anesthesia

[1] Determined by tooth cross section
[2] Determined by skull palpation

Appendix 4.   Observation of a Female Fisher

On 5 February 1979 at 1100 hr I was skiing in an open
black spruce-tamarack bog when I observed a female fisher
bounding along the base of a jackpine ridge, circling and
doubling back on occasion.   Every now and then she would
pause momentarily to poke her nose several centimeters
into the snow.   She travelled at right angles to me until
she was downwind, at which point she suddenly stopped and
sniffed the air.   She then proceeded to walk towards me,
sniffing the air, but not seeing me despite the fact that
the bog was very open at this particular spot.   After taking
10 walking paces, and coming to within 20 m of me, she
suddenly looked up, saw me and bounded off in the opposite
direction as fast as she could go.   At first she bounded
over unbroken snow cover, but when she approached a trail
that she had previously made she altered her course in order
to follow it.

Appendix 5. Fisher and Marten Den Information

A fisher den that I found on a jackpine ridge on
1 January 1979 is portrayed diagrammatically in Figure 1.
The fisher had made a tunnel into a hollow created by a
fallen jackpine. There were several centimeters of mouldy
leaves and jackpine scales lining this hollow. There were
three well developed fisher trails leading to the single
entrance and one snowshoe hare forepaw 3 m from the entrance.
The temperature at the snow cover surface was -26°C, while
the temperature of the pukak layer was -12°C and the den
itself was -11°C.

The second den diagrammed (Figure 2), a cave, was
found on a jackpine ridge bordering a black spruce bog.
A fisher had dragged a hare 687 paces (317 m) to this den
and the remains of a spruce grouse were found nearby.

A marten den on a jackpine ridge that had originally
been a red squirrel midden (Figure 3) was in use for at least
two months during the winter of 1979-80. I only went to the
den two times during this period as I did not want to disturb
the marten. Fresh tracks and scats were found each time I
visited the den.

A summer den utilized by M9 after the fire was on the
edge of an unburnt bog and was formed by the roots of a fallen
jackpine (Figure 4).

Photographs of some of these dens are presented in
Figure 5.

Figure 1. Fisher winter den on jackpine ridge with
measurements of the api profile. VH = vertical
hardness (gm/cm^2), H = horizontal hardness
(gm/cm^2), T = thickness of snow layer (cm),
D = density (gm/cm^3),
C = snow crystal diameter (mm). All other
measurements in cm.

9/1/79

VH < 10

H	T	D	C
4	2	0.17	< 1
	6		
	9	0.20	< 1
10			
	4		< 2
	20	0.21	< 3

-26°C

JACKPINE

API   41
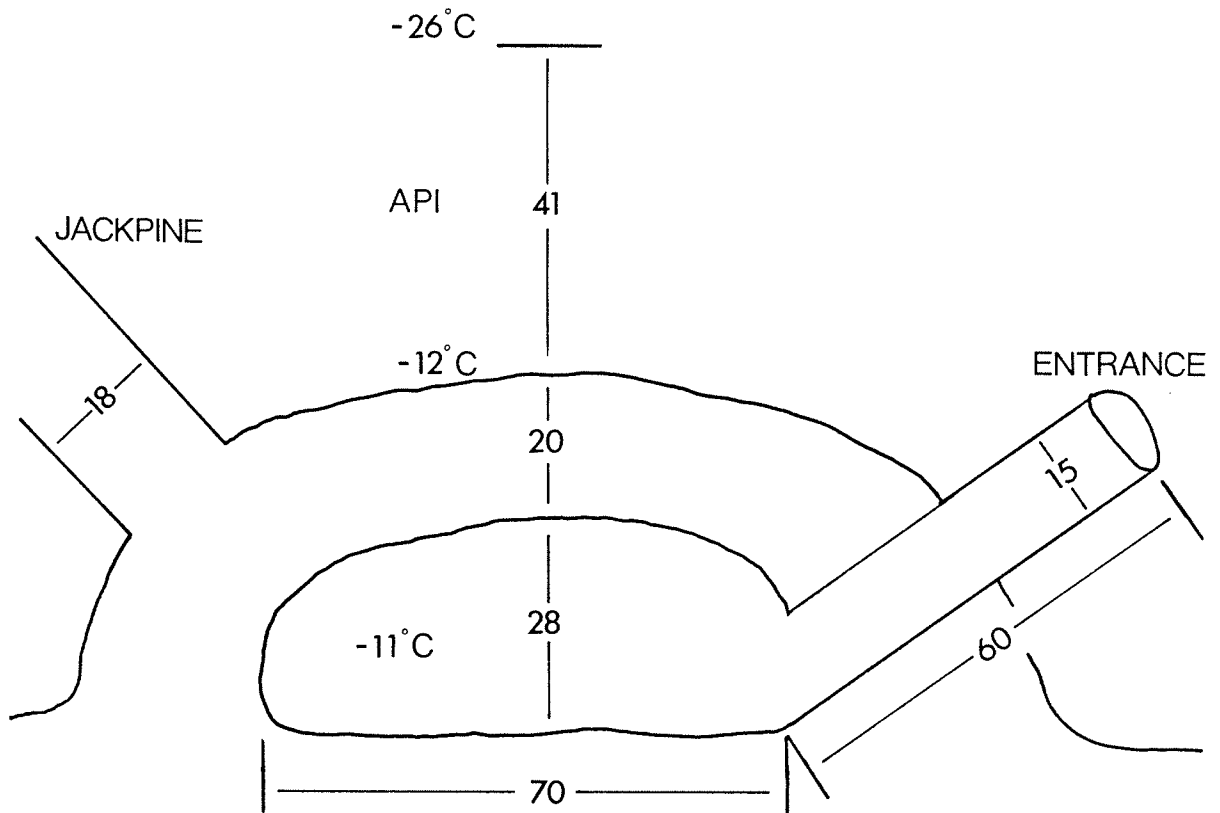
18

ENTRANCE

-12°C

20

15

-11°C   28

60

70

Figure 2.   Fisher winter den on jackpine ridge
            bordering black spruce bog. Fifty cm of
            api was on the ridge.

CLIFF

BOULDER

2m

ENTRANCE
30 x 30mm

BLACK SPRUCE
BOG

SPRUCE GROUSE
REMAINS

142
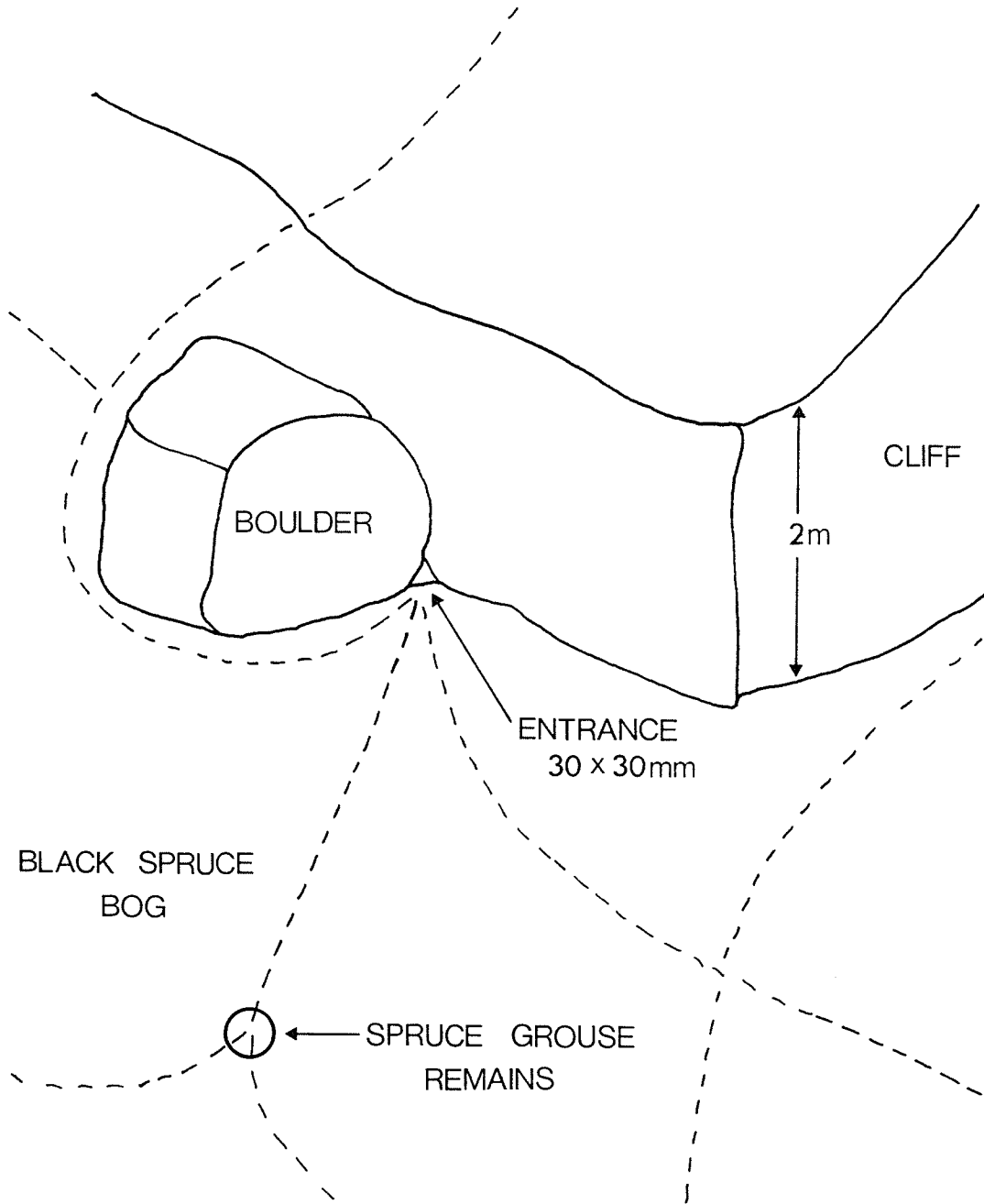
Figure 3.   Marten winter den on jackpine ridge.
            Measurements in cm.

IN USE
9/I/80 - 9/III/80

BLACK
SPRUCE

36 API

18

MOSS AND PEAT

22

11

25

9

11

35

35
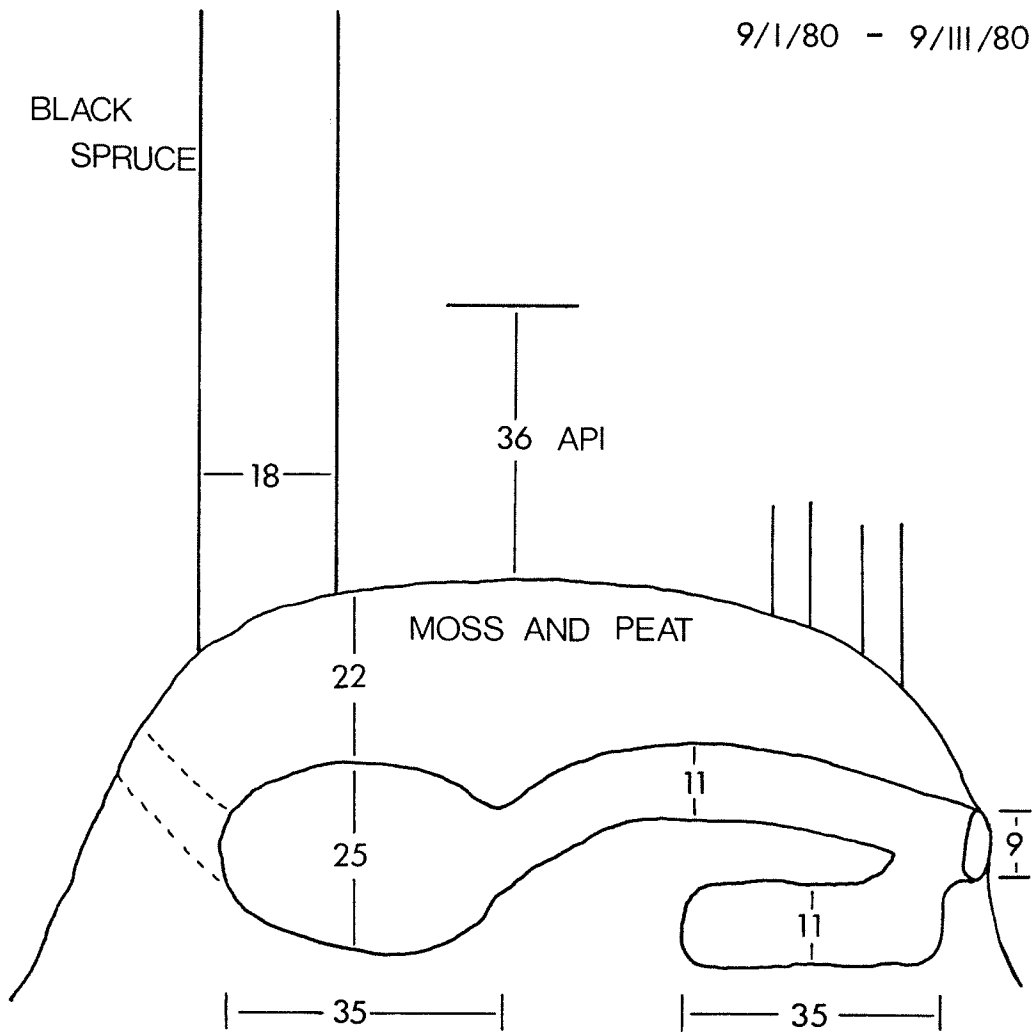
143

Figure 4.   Marten (M9) summer den on the edge of an
            unburnt bog.   Measurements in cm.

JACKPINE

20

30

35

180

2/VI/80
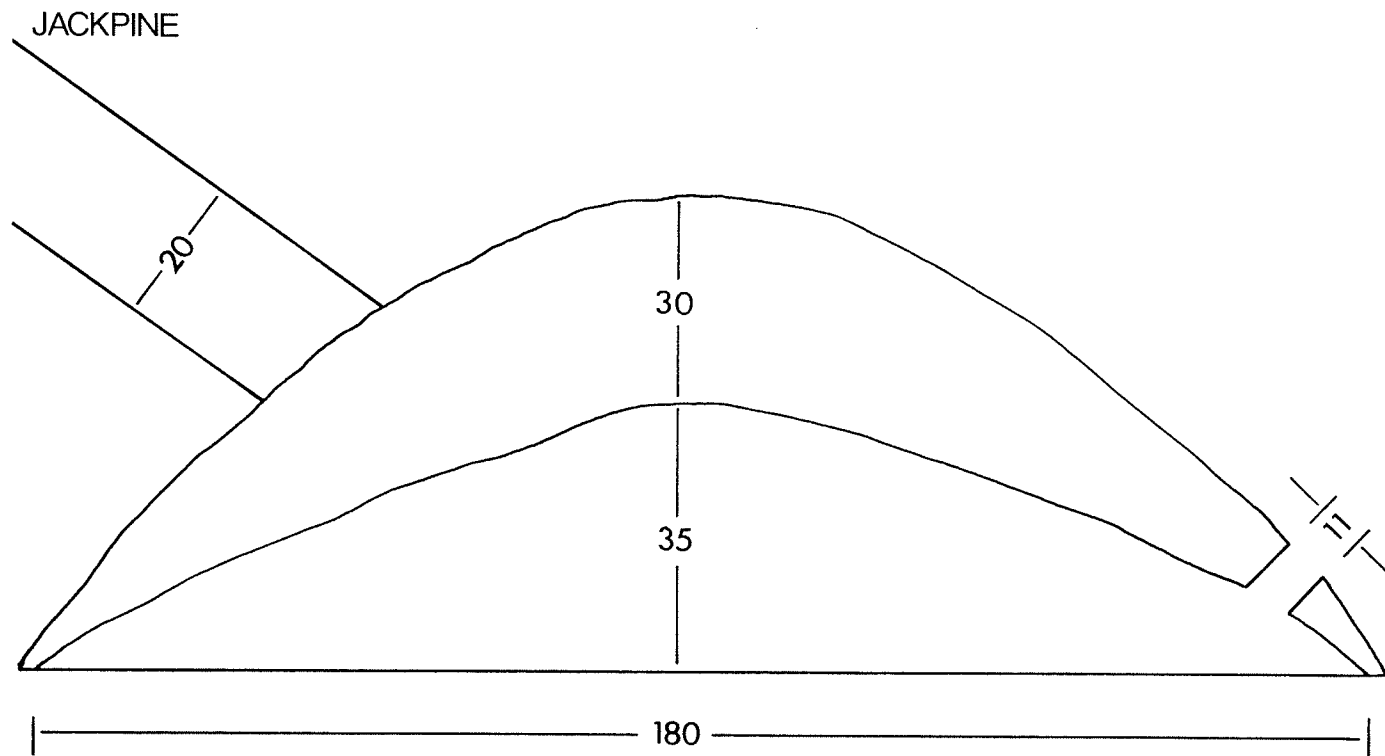
Figure 5.

A - Fisher subnivean den (diagrammed in Figure 1) on
    a jackpine ridge. Entrance is 15 cm in diameter
    (9/I/79).

B - Marten subnivean den (diagrammed in Figure 3) on
    a jackpine ridge. Entrance is 9 cm in diameter
    (20/II/80).

C - Summer den of M9 (diagrammed in Figure 4) Den
    cavity (◄—) was formed by the uplifting of the
    roots on a jackpine (20 cm dbh) (2/VI/80).