Influence of snow depth on prey availability and habitat use by red fox

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Received May 6, 1987

HALPIN, M. A., and BISSONETTE, J. A. 1988. Influence of snow depth on prey availability and habitat use by red fox. Can. J. Zool. **66**: 587–592.

Habitat use by red fox (*Vulpes vulpes*) was studied during the winters of 1982 and 1983. A total of 125 km of fox trails in eastern Maine were followed during periods of snow cover to examine the influence of snow conditions on fox habitat selection and prey availability. Red foxes used all available habitats but showed preferences for softwood stands and open areas. Hardwood forests were avoided. During both winters, snow depth was greatest in hardwood and mixed stands where soft, powdery conditions prevailed. Windblown, supportive crusts were found in open barrens. Foxes showed habitat preferences for traveling and hunting. Fox sinking depths were least in all habitats when crust conditions prevailed, and during these periods travel distances were more evenly distributed among habitats. Snow influenced relative prey availability. Hunting activities shifted among habitats for small mammals during most of the second winter, when snow was shallow. Proportions of small mammals in the fox diet decreased as snow accumulated and as crusts formed. When snow was deep, foxes hunted in habitats with softwood regeneration and other dense understories that supported snowshoe hare concentrations.

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L'utilisation de l'habitat par des renards roux (*Vulpes vulpes*) a fait l'objet d'une étude durant les hivers 1982 et 1983. Cent-vingt-cinq kilomètres de pistes de renards sur la neige, ont été examinés, dans l'est du Maine en vue de déterminer les effets de la condition de la neige sur la sélection d'habitat du renard et sur la disponibilité de ses proies. Le renard utilisait tous les habitats, mais a manifesté une nette préférence pour les forêts de bois mous et les endroits ouverts. Les forêts de bois durs n'étaient pas fréquentées. Les deux hivers de l'étude, l'épaisseur de la neige s'est avérée maximale dans les forêts de bois durs et les forêts mixtes où prévalaient des conditions de neige poudreuse; une neige croûtée balayée par le vent, mais assez solide pour soutenir les renards, s'est formée dans les endroits ouverts peu productifs. Les renards semblaient choisir des habitats particuliers pour leurs déplacements et leurs chasses. Lorsque des surfaces glacées recouvraient la neige, les renards s'enfoncaient peu et, dans ces conditions, leurs déplacements étaient répartis plus uniformément dans les divers habitats. La neige semblait influencer aussi la disponibilité des proies : durant presque tout le second hiver, la neige était peu abondante et la chasse aux petits mammifères se faisait dans tous les habitats. La proportion de petits mammifères dans le régime diminuait à mesure que la neige s'accumulait ou se recouvrait de croûtes. Lorsque la neige était épaisse, les renards chassaient dans les forêts de bois mous en regénération ou dans d'autres sous-bois denses où étaient concentrés les lièvres.

[Traduit par la revue]

Introduction

Harsh and seasonal climates, characterized by cold temperatures and frequently deep accumulations of snow during the winter, have long been known to significantly influence animal distribution and activities (Formozov 1946), at least in a general sense. With few exceptions (Wells and Beckoff 1982; Palm 1970, cited in Curio 1976), specific effects of winter conditions on carnivore behavior have generally been poorly documented. It was the purpose of this study to investigate how changing snow depth and structure influence use of winter habitat by red foxes and the availability of their prey.

Specifically, we sought to address four questions. (1) How do different habitat types influence snow depth and crust conditions? (2) Are there differences in habitat use due to traveling conditions caused by snow depth and structure? (3) What effect does the resulting snow depth and structure in a particular habitat type have on prey availability, as evidenced by their use by red fox? (4) How do prey availability and traveling conditions influence fox hunting behavior during winter?

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Printed in Canada / Imprimé au Canada

Study area

The study was conducted on a 625-km^2 area in a sparsely populated region in Washington County, Maine. Located in the spruce – fir – northern hardwood vegetation zone (Westveld et al. 1956), over 75% of the land was forested. Open barrens, managed for the commercial culture of lowland blueberries, and ericaceous – sphagnum peat bogs represented most of the nonwooded area. Lakes and ponds were numerous. Paved roads bordering the area, and an interior network of secondary logging and access roads, skidder trails, and footpaths provided access throughout the study area.

The winter climate of the region is transitional between the coastal and southern interior zone of Maine (Lautzenheiser 1972). Snowfall occurred from November to April, with occasional but unpredictable storms in October and May. Snow cover often melted entirely in midwinter and was replaced with a new snow accumulation. Average annual snowfall is 150–200 cm. Mean January temperature is −6°C.

Methods

Field methods

Red fox habitat use and travel was monitored along fox trails during the periods of snow cover in 1982 and 1983. Fox tracks were located initially from roads and trails throughout the study area. The first distinguishable tracks intercepted on a given day were backtracked or followed whenever possible until tracking conditions became poor because of wind drift, snowmelt, or new snowfall, or until the trail could not be distinguished from older tracks. Distances traveled within habitats were paced and converted to kilometres. Care was taken to initiate track searches throughout the study area, so as to

TABLE 1. Distribution of habitats in 125 km of red fox trails in eastern Maine, 1982 and 1983

Habitat type	% of study area[a]	% of fox trails	α^b vector
Hardwood	43.2	20.1	0.076
Softwood[c]	10.0	25.9	0.422
Mixed	23.0	23.2	0.165
Open[c]	18.0	29.7	0.266
Bog	1.6	0.4	0.040
Waterway	4.2	0.7	0.027

NOTE: Expected vs. observed travel distances among habitats, $\chi^2 = 60.95$, df = 5, $p < 0.005$.
[a]Numbers rounded from original figures used to calculate totals.
[b]Expected value is $1/m$ or 0.167 (see Methods).
[c]Habitat preference by fox, indicated by significant α vector.

achieve near equal coverage of all habitat types.

Forest stands were classed as hardwood habitats when hardwood species represented more than 75% of the canopy vegetation. Similarly, canopies with more than 75% softwood vegetation were classified as softwood. Stands with a composition of less than 75% hardwood or softwood were considered mixed. Open habitats had little or no vegetation above 2 m in height. Lakes, ponds, rivers, streams, and beaver flowages were classified as waterways. Roads and trails traveled by foxes were included in the cover-type categories in which they occurred. Understory density was categorized as dense, moderate, sparse, or none. Snow depth and vertical profile were measured weekly at four monitoring stations in hardwood, softwood, and mixed cover types, and in an open area. Five measuring stakes were placed in the ground at random points at each of the four stations.

Fox activities, interpreted from signs in the snow, were classed as traveling, hunting, or resting and were recorded by habitat type. Pouncing and digging activities were counted to obtain an index of hunting effort toward ground-dwelling and subnivean prey, particularly small mammals. Rounded beds of melted and compacted snow along trails were recorded as resting sites. Surface snow characteristics and sinking depth of foxes were recorded by habitat at 100-m intervals along fox trails. Frequency of intersection of fox trails with tracks of other species was recorded. Prey remains and fox droppings found along trails and elsewhere on the study area were collected for diet analyses. Scat contents were identified (Moore et al. 1974; U.S. Forest Service 1974) and recorded by frequency of occurrence.

Analytical methods

Habitat selection was evaluated by comparing the distribution of fox travel distances among cover types with an expected distribution based on habitat availability in the study area. Goodness of fit tests were made and an α vector preference index (Chesson 1978; Lechowicz 1982) for habitat was calculated. Chesson's (1978) formula is:

$$\sum_{i=1}^{m} \alpha_i = r_i\, n_i^{-1} \left(\sum_{j=1}^{m} r_j\, n_j^{-1} \right)^{-1}$$

where (adapted for habitat selection) m is the number of available habitats, r_j is the proportional use of habitat i, and n_j is that habitat's proportional availability; α is a vector, the individual elements of which measure the deviation from the probability of selecting any habitat in proportion to its availability, i.e., its expected value. The expected value for random habitat use is $1/m$, or in this case, $1/6 = 0.167$. Chesson's index varies from 0 to 1 with values above $1/m$ indicating preference and values less than the expected value indicating avoidance. Determinations of availability of each habitat type were made using LANDSAT data (Ritter et al. 1983) (Table 1).

The frequencies of intersections of fox trails and prey species' tracks were compared with fox travel distances among habitats to assess relative prey availability. In addition, the influence of snow conditions on fox diets was analyzed. Relationships among snow depth, prey sign, hunting sign, and the occurrence of small mammals and hare in the fox diet were evaluated with Pearson's product-moment correlation coefficients.

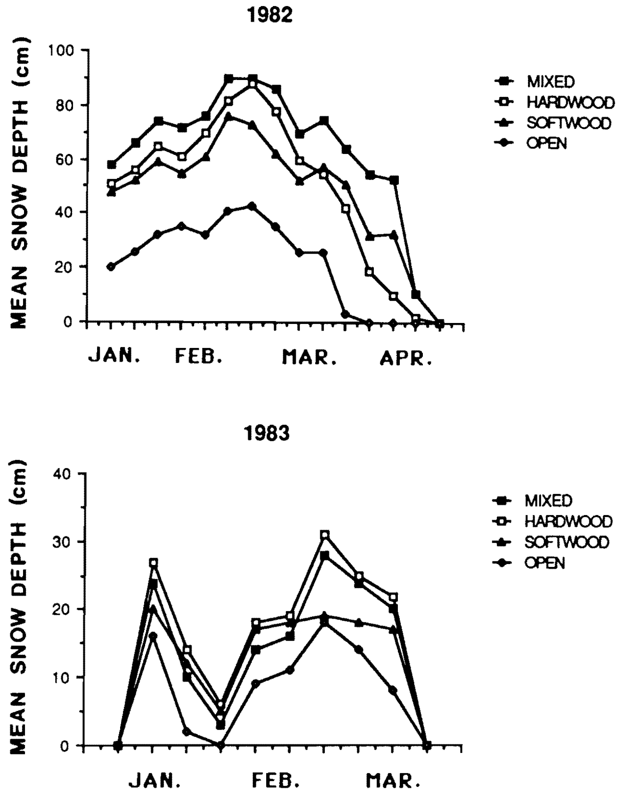

FIG. 1. Mean weekly snow depth in different cover types in eastern Maine, 1982 and 1983.

Means were computed from snow-depth data for each cover type. A two-way ANOVA and Duncan's multiple-range tests were made to identify differences in snow depth among weeks and habitats. Distribution of surface snow conditions along fox trails was examined for differences among habitats and time periods delineated by prevailing snow characteristics (FUNCAT procedures (SAS Institute Inc. 1982)). Differences in sinking depths of fox tracks among time periods within each winter, among snow conditions, and among habitats were evaluated by ANOVA. The influence of snow conditions on habitat use was analyzed. Changing proportions of total distances traveled among habitats were examined relative to snow structure and depth.

Results

Snow conditions in different habitats

Snow depth

In 1982, snow covered the ground from December to mid-April and was deepest (92 cm) during the first week of March (Fig. 1). In 1983, snow did not begin to accumulate until mid-January, thaw occurred in early February, and melt was complete by mid-March. Snow was deepest (31 cm) in late February. Snow accumulation was greatest and most rapid in hardwood and mixed stands. Patchy canopies in the mixed stands contributed to variable snow cover on the ground. Among the wooded habitats, snow accumulation was least in softwoods, but snowmelt was slowest in softwood stands. Snow depth was least in open areas throughout the season in both winters. Wind appeared to limit snow accumulation in openings, particularly in the large barrens.

TABLE 2. Predominant snow structures and mean sinking depths of red fox tracks during winter periods, 1982 and 1983

	Time period	Predominant snow structure	Mean sinking depth (cm)
1982			
Jan. 9–Feb. 5	Early	Crust	2.56
Feb. 6–Mar. 5	Mid	Powder (some crusts)	7.86
Mar. 6–Mar. 26	Late	Crust and wet	3.62
1983			
Jan. 16–Jan. 29	Early	Powder	10.52
Jan. 30–Feb. 12	Thaw	Crust	4.77
Feb. 13–Feb. 26	Mid	Powder	8.96
Feb. 27–Mar. 5	Late	Crust and wet	3.77

NOTE: Distribution of snow structures among time periods within the winter season: 1982, $\chi^2 = 127.31$, $p = 0.0001$; 1983, $\chi^2 = 90.31$, $p = 0.0001$. Differences in sinking depths among time periods: 1982, $F = 10.15$, $p = 0.0119$; 1983, $F = 7.71$, $p = 0.0074$.

Snow structure

Layers of powder snow were thickest in hardwood and mixed stands, but crusts were thickest and most common in softwoods and open areas. Greater weekly variability occurred in 1983, when temperatures varied throughout the season.

The structure of the top layer of snow along fox trails varied between weeks in both winters (1982, $\chi^2 = 165.14$; 1983, $\chi^2 = 113.41$). Each winter was divided into time periods according to prevailing snow characteristics (Henry 1979; Raine 1983). During the first winter, January was dominated by crust conditions, most of February by soft powders, and most of March by crusts and wet snows. In 1983, powder was the predominant snow cover during the early period in January. A thaw in early February and fluctuating daily temperatures produced crusts on existing snow. During a third distinctive period in mid-February, powder prevailed as snowfall and accumulation increased. Crusts again covered the snow surface by the end of February (Table 2).

Surface snow conditions sampled along fox trails also varied among habitats in 1982 ($\chi^2 = 16.87$, $p = 0.0098$). Crusts were encountered more often in open areas than in other habitats, and powder was found more often in hardwood and mixed stands than in other types. No habitat differences were detected in 1983 ($\chi^2 = 12.66$, $p = 0.1784$).

Traveling conditions

Fox sinking depths

Sinking depths of fox tracks differed among time periods in both years. Maximum sinking depths occurred during the second period (February 6 – March 5) in 1982 and during the first (January 16–29) and third (Feb. 13–26) periods in 1983 (Table 2). Sinking depths varied, ranging from 0.0 to 24.0 cm. Differences among habitats and snow structures were not significant, although greatest sinking depths were recorded in wooded habitats and on soft, wet, or powdery snows. At sinking depths greater than 20 cm, foxes change their gait to a wallowing walk or to an energy-expending loping gallop (Henry 1979). Few sinking depths greater than 15 cm ($N = 10$) were recorded along trails in eastern Maine, however, and only three of these exceeded 20 cm.

Habitat use

Not surprisingly, trends in habitat use were related to changing snow conditions and suggested that foxes selected travel routes offering the greatest relative support. Travel in hardwood stands increased during most periods of generally crusty snow. During periods of soft powder, travel in softwood and open areas was high. Mixed woods became important as snow depth increased and when crusts formed.

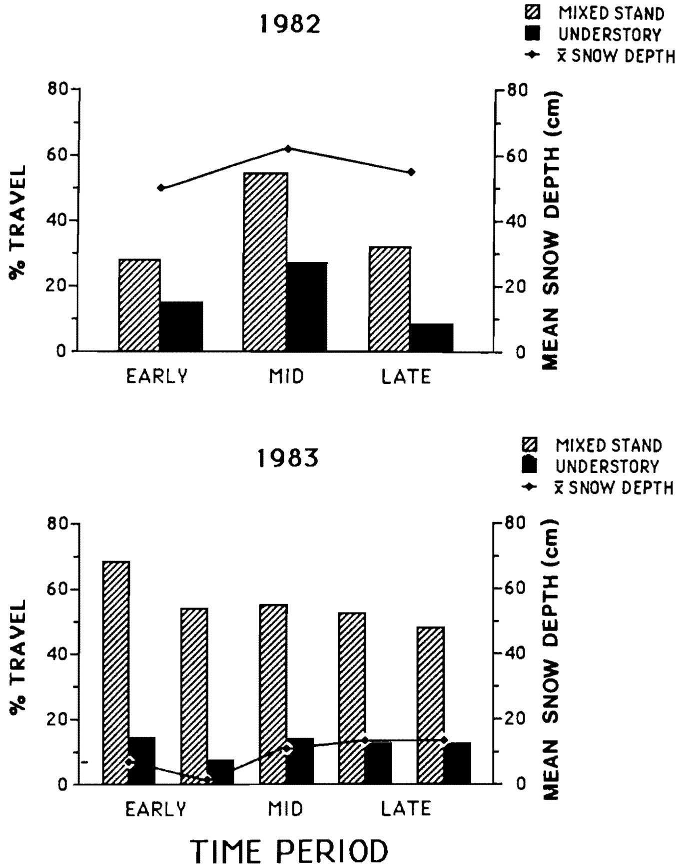

FIG. 2. Red fox travel distances (% of total trail traveled) in softwood and mixed cover types and in moderate to dense understories as snow accumulated in 1982 and 1983.

Habitats with dense understory vegetation were used most by foxes when snow depth increased. In mixed and softwood stands, trail distances in dense regeneration increased as snow accumulated (Fig. 2). Similarly, when snow was deep, most travel in hardwoods was also associated with dense understories or with alder growth.

Prey availability and use

Small mammal sign found along fox trails occurred disproportionally among habitats during both winters ($\chi^2 = 203.54$, df = 5). It was observed most frequently in hardwood vegetation (6.13 tracks/km fox trail) and exceeded the expected, based on distance traveled by foxes in these habitats. Less sign than expected was found in open barrens and softwood stands. Small mammal sign was found more frequently in 1983 (3.39/km) than in 1982 (0.63/km), and was more abundant in all habitats during the second winter. At the same time, snow accumulated much earlier in 1982 and was almost three times deeper at maximum accumulation than in 1983 (Halpin 1984). In contrast, hare trails were most abundant in mixed and softwood covers and understories (Table 3). Few hare tracks were encountered in open habitat or in areas of sparse understory. Litvaitis (1984) and O'Donoghue (1981) found strong associations between hare numbers and under-

TABLE 3. Total number of intersections per kilometre between red fox and snowshoe hare trails among cover types and understory habitats, 1982 and 1983

Habitat type	No. of intersections	Understory	No. of intersections	Understory density	No. of sections
Hardwood	8.36	Hardwood	8.76	None	2.43
Alder[a]	16.73	Softwood	15.18	Sparse	7.31
Softwood	13.98	Mixed	11.64	Moderate	21.17
Mixed	14.02	Open	0.50	Dense	35.69
Open	1.89				
Bog	1.78				

NOTE: Comparison of fox travel and distribution of intersections with snowshoe hare among habitats: cover type, $\chi^2 = 381.36$, df = 5, $p < 0.005$; understory, $\chi^2 = 330.71$, df = 3, $p < 0.005$; understory density, $\chi^2 = 649.58$, df = 3, $p < 0.005$.
[a]Alder segregated from hardwood category; waterways not included in analyses.

story structure in eastern Maine. In concurrence with their findings, greatest hare concentrations along fox trails were found in thick understory vegetation. Distribution patterns of hare tracks among habitats were similar for both winters.

Remains of snowshoe hare was the major food item occurring in fox droppings on the study area ($N = 128$) during both years. Small mammals (Cricetidae and Soricidae), deer, and birds were also prominent food items in the winter diets (Halpin 1984). Percent frequencies of prey and other foods varied between years. Hare and deer decreased from 1982 to 1983. Small mammals and plant material increased. The occurrence of bird remains, including grouse and songbirds, was similar between years. Other items identified in droppings were porcupine (*Erethizon dorsatum*), red squirrel (*Tamiasciurus hudsonicus*), and muskrat (*Ondatra zibethicus*). Prey remains, and carrion cached or left along trails, included hare, shrews, deer, porcupine, and birds.

Hunting behavior

The effects of prey availability

Areas of early spruce and fir regeneration as well as plantations of young pine commonly supported heavy concentrations of snowshoe hare (*Lepus americanus*). Prevalence of fox trails indicated that these habitats were hunted for hare (Table 3). Foxes wandered through dense understory vegetation, crossing and doubling back on their own routes, where mazes of hare trails were encountered. Intersections of fox and hare trails were greatest when understory density was highest (Table 3). The accompanying overstory was mostly alder thickets or mixed or softwood stands. Four locations of hare kills were identified; all were in mixed stands with dense softwood understories. Food items were frequently carried from point of capture and cached in shallow holes dug in the snow, although whole shrews were left at six pounce sites. Snowshoe hare remains were the most common prey items found along fox trails.

The effects of snow depth

The distribution of pounce and dig hunting activities ($N = 91$) did not differ among habitats in 1982 ($\chi^2 = 4.62$, df = 4). However, during the following winter, when snow was shallower, the distribution of pounce and digs ($N = 87$) indicated a preference for open areas, particularly those with grass and sedge vegetation ($\chi^2 = 19.76$, df = 5). Bogs were not used during the first winter. Pounce and dig sign was most abundant in open habitats during the second winter (Table 4).

Habitats with dense understory vegetation were used most by foxes when snow depth increased. In mixed and softwood

TABLE 4. Number of pounce and digs per kilometre of fox trail in each habitat type by month, 1982 and 1983

	1982			1983	
Habitat type	Jan.	Feb.	Mar.	Jan.	Feb.
Hardwood	2.57	2.05	1.16	3.69	0.77
Softwood	1.37	1.59	2.48	1.11	0.67
Mixed	0.82	1.79	0.73	3.26	0.74
Open	1.54	0.85	2.25	5.02	1.58

stands, trail distances in dense regeneration increased as snow accumulated (Fig. 2). Similarly, when snow was deep, most travel in hardwoods was associated with dense understories or with alder growth. Increased travel in dense understories reflected a greater dependence on snowshoe hare for food. Concentrations of hare were found in patches of softwood regeneration and other dense vegetation. As snow depth in all habitats increased, the occurrence of hare in the diet increased. At the same time, small mammal occurrence decreased (Table 5).

Hunting effort toward small mammals decreased as snow depth increased in 1983. The distribution of pounce and digs in 1983 indicated that foxes hunted open areas for small mammals, although as snow accumulated, foxes generally hunted less in open areas. In 1982, when snow was very deep, the distribution of hunting sign was random, suggesting that beyond some critical depth, snow equally restricted the availability of small mammals in all habitats. The occurrence of small mammals in the diet was limited during the winter, even during periods of snowmelt. Persistent crusts probably continued to restrict the availability of small mammals, and hare remained the dominant prey.

Discussion

Henry (1979) reported that red foxes in Saskatchewan used winter habitats on the basis of travel conditions. During midwinter periods of soft, powdery snow in boreal forests of Saskatchewan, foxes traveled extensively in conifer stands. Branches in closed-canopy softwood stands intercepted falling snow and limited ground accumulation. Foxes minimized travel in deep, soft snow to short distances between packed surfaces. Access to cover under individual softwood trees certainly may have been enhanced. During midwinter, fox movements were restricted to wind-crusted lakes, packed wildlife trails, and plowed roads. Although patterns of travel

TABLE 5. Correlation coefficients for snow depth, hunting and prey sign, and fox diet, 1982 and 1983 (total)

	Snow depth	Pounce and digs	Small mammal tracks	% frequency of small mammals in diet	% frequency of hare in diet
Snow depth	1.00				
Pounce and digs	−0.14	1.00			
Small mammal tracks	−0.28*	−0.24*	1.00		
% frequency of small mammals in diet	−0.58**	0.29*	0.18	1.00	
% frequency of hare in diet	0.72**	−0.13	−0.27*	−0.76	1.00

*Significant at $\alpha = 0.05$
**Significant at $\alpha = 0.01$.

among habitats in eastern Maine were not as distinctive, foxes did use roads and trails and the wind-blow snow surfaces of the open barrens. Coastal influences moderate the winter climate of eastern Maine, often limiting periods of deep, powdery snow. Snow conditions are probably less critical in affecting fox movements in these milder areas than in interior boreal forests. Even so, habitat selection was clearly related to snow conditions. The influence of snow on fox habitat use in eastern Maine was most important in affecting relative prey availability. Habitat use patterns reflected shifting availability of predominant prey species as snow depth and structure changed. The proportion of small mammals in the fox diet decreased as snow depth increased or as crusts formed within the snow profile. Small mammals are less accessible to predators as snow accumulates (Pruitt 1978). Wells and Beckoff (1982) noted that coyote detection of rodents decreased with snow depths of 10 cm or more and suggested that hunting success of foxes, which employ the auditory and olfactory senses in hunting small mammals, is similarly affected by snow. Reductions, caused by snow, in rates at which red foxes caught mice were observed by Palm (1970, cited in Curio 1976).

Habitat patterns in hunting efforts for small mammals were detected only in 1983 when snow was shallow. Most pounce and dig sign occurred in open areas although most small mammal sign along fox trails occurred in hardwoods. However, the numbers of pounce and digs were significantly correlated with percent frequency of small mammals in the diet (Table 5). During winter, small mammals are usually subnivean when snow covers the ground, but some species, such as *Peromyscus* spp., are more active above the snow than others (Scott 1943). The discrepancies in numbers of small mammal tracks among habitats may have reflected behavioral differences between the predominant species inhabiting the particular types. Small mammal census results for the study area (Rego 1984) indicated that deer mice (*Peromyscus* spp.), short-tailed shrews (*Blarina brevicauda*), and masked shrews (*Sorex cinereus*) were the most abundant species in hardwoods. Red-backed voles (*Clethrionomys gapperi*) were found in all habitats, but greatest numbers occurred in softwood and mixed cover. Meadow voles (*Microtus pennsylvanicus*) were found in open areas. In a summary of investigations of food habits, Ables (1975) concluded that red foxes preferred the microtine species over *Peromyscus*, probably because of the relative ease with which voles are caught. The distribution of winter hunting effort observed along fox trails in our study may reflect this preference for voles, which inhabited open areas. Shallower snow in open habitats also enhanced their relative availability. During periods of deep snow, foxes relied heavily on snowshoe hare. During midwinter 1982, hare was the only item found in fox droppings. Birds and carrion supplemented the winter diet, but the availability of most other foods diminished and foxes concentrated their activities in hare habitat. Indeed, our data show a strong negative correlation between percent hare frequency and percent small mammal frequency in the diet (Table 5). Similarly, if small mammal sign was evident, indicating increased availability, there was a small but significant decrease in the frequency of hare in the diet.

Other behavioral and environmental conditions not directly addressed in this study may also influence winter habitat use by foxes. Parker (1980), who tracked lynx, suggested that learned and traditional hunting patterns may partially explain habitat use. He further indicated that potential intraspecific and interspecific behavior patterns may preclude expected activities and habitat use. Red fox trails did intersect bobcat, coyote, and weasel tracks. Evidence suggests that foxes may avoid areas regularly used by coyotes even though suitable habitats may exist in those areas (Voigt and Earle 1983; Major 1983). In this study, intersections of fox and coyote trails ($N = 39$) were observed throughout both winters, but most ($N = 35$) occurred in February, coinciding with a peak period of juvenile coyote dispersal in Maine (Harrison 1983). Urine markings often occurred at intersections, and on several occasions coyotes rerouted their travel to follow the fox trails for short distances.

Red foxes are influenced by a complex of environmental and social conditions. The species is adaptable and is typically a generalist. The traveling and hunting trends observed in eastern Maine, however, suggest that residents of northern forests are forced by limiting winter conditions to narrow this role. Harsh climate plays a significant role in habitat selection by predators and, by inference, in their utilization of food resources.

Acknowledgments

The study was conducted as part of an extensive long-term investigation of furbearer ecology sponsored jointly by the

Maine Cooperative Wildlife Research Unit, the Maine Department of Inland Fisheries and Wildlife, and the University of Maine, and was completed as partial fulfillment of the requirements for an M.S. degree in wildlife management.

We appreciate the assistance provided by W. Halteman, P. Brown, J. Sherburne, J. Hunt, A. Clark, A. Ritter, M. O'Donoghue, D. Harrison, J. Harrison, J. Litvaitis, J. Major, F. DiBello, J. Barber, G. Costanzo, J. Cofske, J. Sherry, D. Livingstone, J. Howard, M. Horne, and G. Curless.

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