51ST EASTERN SNOW CONFERENCE
Dearborn, Michigan 1994

Winter Nesting Behaviour in Meadow Voles, *Microtus Pennsylvanicus*

R.L.M. ROBITAILLE[1] AND G.M. COURTIN[1]

ABSTRACT

A 100x50 m old field study site was established near Sudbury, Ontario. Winter and spring patterns of vole activity were located and mapped. Vegetation communities were described and mapped (% cover) in summer. All data were analyzed by means of GIS (IDRISI software). Air and snowpack temperatures, and short-wave radiation above and below the snowpack were monitored continuously. Snow depth and thermal index were measured from January through snow melt. Transmitters were implanted in live-trapped voles and their movements monitored in the field during the period of snow melt.

The number of nests found following snow melt increased from 16 in 1992 to 53 in 1993. Vole movement was greater during the day than at night and increased as more light penetrated through the snowpack. Vole activity is concentrated in areas of prefered food sources. Most air holes were not located in the same areas as those in which nests were found.

Key words: meadow vole, nest, GIS, behaviour.

INTRODUCTION

The meadow vole, *Microtus pennsylvanicus*, is a ubiquitous small mammal. The preferred habitat of the meadow vole is moist meadows and open grasslands (Forsyth 1985, and Getz 1985). When studying the herbaceous vegetation and its relation to vole habitat it must be stressed that the vegetation plays a dual role; both as a food source and as cover from predators.

Voles prefer graminoids but will feed on other food sources depending on environmental conditions. Zimmerman (1965) found that 93% of the volume of food consumed was vascular plants consisting mostly of stems and leaves. However, this preference may change from season to season and also depending on the habitat.

The density of the vegetation also plays an important role in meadow vole survival; the denser the vegetation cover, the greater the protection from predators. Vegetation cover also moderates the microclimate (humidity and temperature) of the site (Getz 1985). Heavy cover tends to prevent dense packing of the snow, thus making the subnivean environment more hospitable.

Exclusive use of grasses for nests has been reported for meadow voles (Maser and Storm 1970). Ambrose (1973) found that most meadow vole nests were located in slightly elevated, dense tussocks of living grass.

Webster and Brooks (1981) found that none of the winter communal mixed-groups of voles showed any significant differences between crepuscular activity and activity during the rest of the day. The frequency of movement, distance moved, or average length of travel were the same. During winter, neither sex showed any significant differences in short duration activities between day or night but for both sexes, time spent active and the amount of exploration tended to be greater during the day than at night. But Webster and Brooks fail to mention whether, during the spring thaw, activity is influenced by fluctuating daily temperatures, flooding, and increased light under the snowpack.

Every spring deserted grass nests built by meadow voles can be found scattered across throughout the summer or in early fall. It is not

---

[1] Department of Biology; Laurentian University; Sudbury, Ontario P3E 2C6 Canada

really understood when the nests are built and the role that they play. Whitaker (1980) stated that the meadow vole usually places its roughly spherical grass nest on the ground surface only in winter and so long as there was a snow cover. Robitaille and Courtin (1990) have shown a nest reduces heat loss from the vole to a colder environment when meadow voles are most vulnerable to death by hypothermia; namely when they are in a saturated nest with no access to drier areas or to drier nesting material. The condition of the nest also plays a role in the nest's capacity to retain heat. If the nest is not competely saturated it still provides an adequate barrier from the environment and this may be biologically significant to the meadow vole. The more voles huddle together, the warmer the nest, and the drier the inner wall. This behaviour should increase vole survival on cold rainy days when there is no snow cover. An established snowpack also reduces heat loss from the nest to the colder air. Within an undisturbed, non-melting snow cover, the subnivean environment maintains relatively warm and stable temperatures of approximately ±2°C and the air is relatively moist.

A redefinition of 'winter' was made by Courtin *et al.* (1991) to describe more completely the season of the year that has to be endured by winter-active animals such as the meadow vole. This was done by extending the period normally referred to as winter into four phases. The phases are the pre-nival, nival, thaw and post-nival periods. The prenival period is the time from the onset of freezing temperature until the establishment of the permanent snowpack. The nival period is from the establishment of a permanent snowpack until precipitation no longer falls as snow. The thaw is the period of snow melt and is characterized by freeze-thaw metamorphism. The post-nival period is from the end of snow melt until the danger of frost is passed.

The objective of this study was to obtain a better understanding of winter meadow vole behaviour with emphasis placed on the role of the nest. The following hypotheses were tested:

- Is there a relationship between vegetation and area of meadow vole activity during the prenival, nival and thaw periods?
- Is foraging and nesting behaviour of the meadow vole independent of the snow depth and the thermal index value?
- Is foraging time of meadow voles independent of subnivean short-wave radiation and air temperature?

METHODS

The study site was located on a private property 21 km from Laurentian Unviversity, in Sudbury, Ontario, Canada and was an area of known meadow vole activity. A section of the meadow was divided into a 100 m by 50 m rectangle and then gridded into 10 m by 10 m quadrats (Fig, 1). Each quadrat was coded alphanumerically. The rectangle was mapped in April 1993 to obtain a description of the vegetation, and to record areas of meadow vole activity. During the month of July 1992, plant species located within the rectangle were identified and the plant communities mapped quantitatively by species and percent cover. In May 1992, in December 1992 before the establishment of the permanent snowpack, and in April 1993 the grid was searched for the location of nests. When doing the surveys the nests found were classified as being dome nests or flat nests. Nests that appeared to be in use were labelled as being dome nests. Nests that appeared to be abandoned (flattened to the ground) or water-saturated were labelled as being flat nests. In February 1993, the study grid was searched to obtain the location of 'air holes' dug through the snow by the voles. An air hole is the opening of a small circular

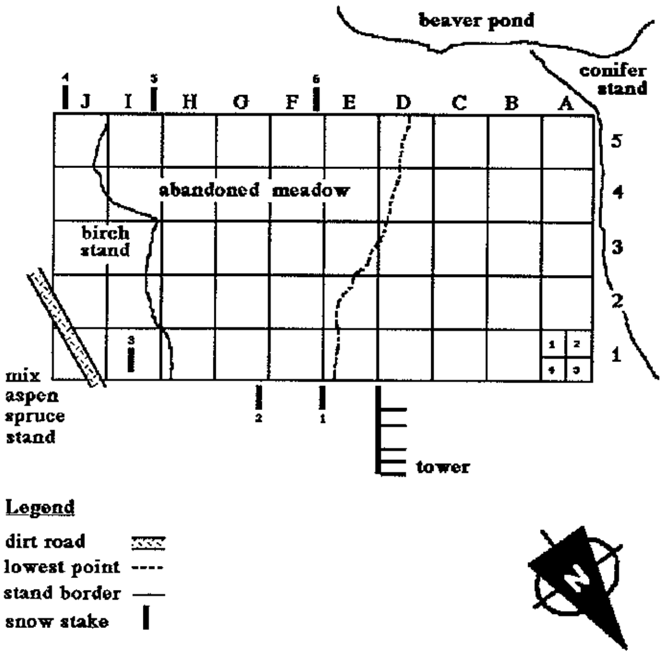

Fig. 1 Sketch of 100 m by 50 m grid suddivided into 10 m by 10 m quadrats used at the abandoned field research site.

tunnel communicating with the snow/air interface. The vegetation maps, the activity areas and the location of nests and air holes were digitized individually using PCI ARC/INFO software. The digitized images and points were analysed by using the GIS software IDRISI with emphasis put on overlaying maps and performing crosstabulations.

A 5m tower was erected at the site during the Fall of 1991 to monitor specific microclimate conditions such as temperature and short-wave radiation. All sensors associated with the microclimate tower were measured every 60 sec by a Campbell Scientific 21X datalogger that stored the data as hourly and daily means. The database was transfered to magnetic tape at two week intervals and was analyzed and synthesized on the computer by using Campbell Scientific PC201 software and Sigmaplot.

A Matrix IG pyrometer was installed near quadrat 1E (Fig. 1) at ground level to measure the short-wave radiation ($MJm^{-2}min^{-1}$) that penetrated the snowpack. The total amount of short-wave irradiance was recorded hourly and daily. A Kipp and Zonen pyrometer model GMJ-763139 was installed approximately 2 m from the microclimate tower to measure the hourly mean (KWm^{-2}) and total amount (MJm^{-2}) of incoming short-wave radiation above the snowpack. The daily means and daily totals were also calculated at midnight. Six copper-constantan thermocouples were installed, one at each of the following heights above ground: 1.5m, 0.4m, 0.25m, and 0.1m, one at the soil surface and one 0.05 m into the soil.

From the beginning of February 1992 to the end of snow melt, and from the beginning of January 1993 to the end of snowmelt, the thermal index of the snow pack was calculated according to Marchand's (1987) equation:

$$I_T = \sum_{i=1}^{n} \left(\frac{z}{G}\right)_i$$

where I is the thermal index, z is the thickness of any given layer i in cm, and G is the snow density of any given layer i. The thermal index is a measure of the capacity of the snow pack to maintain stable subnivean temperatures. These measurements were made by digging a snow pit to expose a vertical face of the snowpack from the surface of the snow to the snow-soil interface. By gently teasing away at the snow with a narrow spatula, the various layers of the snowpack were identified and described. The thickness of each layer within the snowpack and the depth of the snowpack was recorded. Using an aluminum snow density sampler with a volume of 500 cm^3, a sample of snow was taken from each distinct layer. This was done by inserting the sampler horizontally into the exposed snow face. The snow filled sampler was then weighed with a 250 g Ohaus spring balance. The weight of the sampler was subtracted from the overall weight of the snow. The density of each distinct layer was expressed in g cm^{-3}. The thermal index of the snowpack was calculated by using Marchand's (1987) formula. Three snow pits were dug outside the study grid approximately once a week until the end of snow melt. For each snow pit the depth of the pit, the density and the thickness of each distinct layer were recorded and the thermal index calculated. The thermal index was calculated twice a week during the thaw period.

Meadow voles were live trapped at the beginning of March 1993 from the study site. Chimneys were built into the established snowpack. The chimneys were constructed from plastic pails with the bottom sawed off. Two small half circles, 5 cm in diameter, were cut into the side of the pail at the bottom to allow access into the pail by the voles. The chimneys were placed in areas were meadow vole 'air holes' appeared around the grid boundaries. The pails were pushed into the snow until they made contact with the ground. The snow was then removed from the interior of the pail. Fourteen chimneys with lids were installed and baited with food. A few days later, baited Longworth live traps were put in each chimney and checked three times daily. The traps were locked open overnight. The trap line was in use for three nights.

Meadow vole movement was monitored in the field by means of AVM-SM-1 transmitters implanted intraperitonealy. The surgery was performed following the methods established by Merritt and Adamerovich (1991) with the exception that sodium pentobarbitol was injected into the voles as the anaesthetic.

Three voles were implanted with the transmitters. The voles were acclimated in a cold room after surgery for two weeks. The tagged voles were released within the grid in the vicinity of the area where they were captured, below the snow, from individual plastic cages that contained a nest and an escape hole in the side wall of the cage. One meadow vole 'G3' was released in quadrat G3, another 'E3' in quadrat E3 and a third 'B3' in quadrat B3. The meadow voles were monitored hourly on various days and during different time frames during the end of the nival period and through the thaw period to the middle of the post-nival period. The voles were radio tracked until the batteries in the transmitters expired or the vole was preyed upon. The area travelled by each vole during the various time frames was mapped. For the radiotracking part of the study three days were selected for in-depth study. These days correspond to Julian days 87 and 88 which represents the beginning of the thaw period, Julian days 94 and 95 which represents the thaw period and Julian day 97 which represents the end of the thaw period.

RESULTS

The maximum snow depth for the winter of 1992 was reached on Julian day 63 (Fig. 2). During the winter of 1992 the snow started to melt on Julian day 94 and most of the snow had melted by Julian day 104. During the same winter the highest thermal index value was 340.7 (Fig. 2) on Julian day 63 which corresponds with the maximum recorded snow depth. For the first winter of the study the hiemal threshold, as indicated by a thermal index >200 (Marchand, 1987), was exceeded for a span of 42 days (Fig. 2). A thermal index value greater then 200 signifies a stable subnivean environment.

The maximum snow depth for the second field season was measured on Julian day 50 (Fig. 2). Snowmelt started on Julian day 85 and by Julian day 90 most of the snow had melted. The highest thermal index was calculated on Julian day 28 and had a value of 240 (Fig. 2). But on the day of greatest snow depth the thermal index calculated varied greatly. For the second winter, a thermal index value exceeding 200 was measured for a span of 22 days.

During the Spring of 1992, sixteen nests were collected within the study grid (Fig. 3). Of the sixteen nests, nine were classified as being dome-shaped nests, four were classified as being tufts of loose, meshed grass and three were classified as being flat nests. In the Fall of 1992 twelve nests were located (Fig. 3). Eight were classified as being dome-shaped and four were classified as being flat. Fifty-three nests were found following snowmelt in 1993 (Fig. 3). Seventeen were classified as being dome-shaped and thirty-six were classified as being flat.

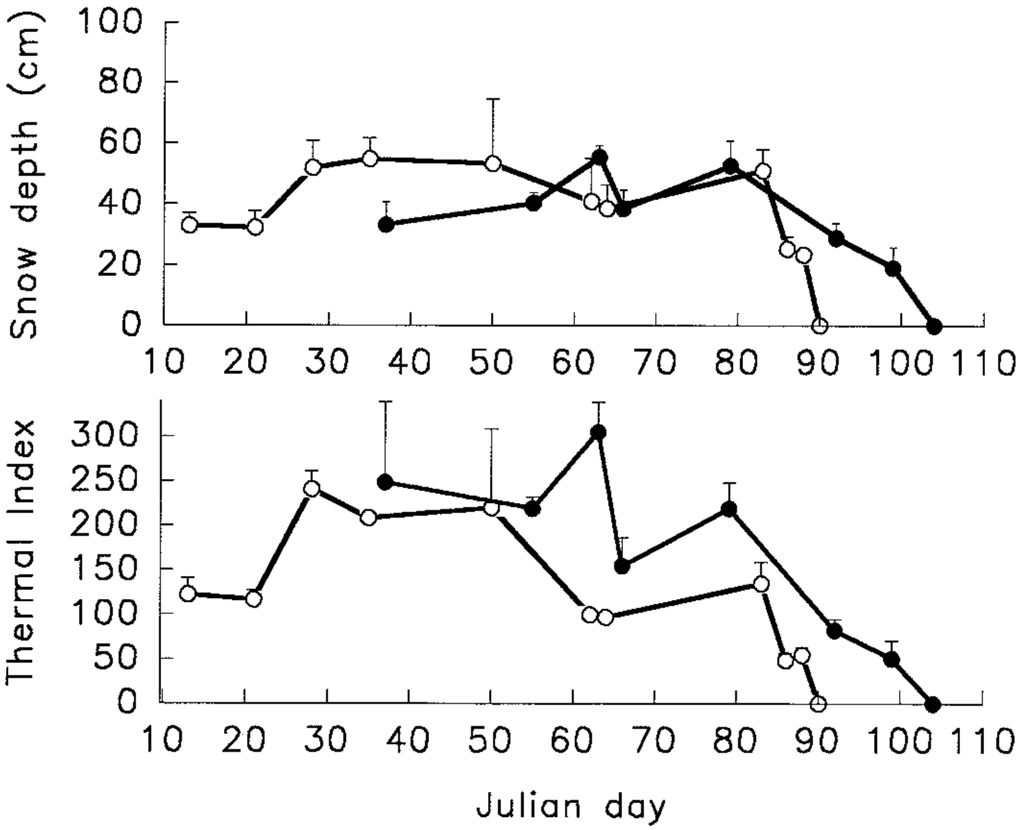

Fig. 2. Mean snow depth and mean thermal index (Marchand, 1987) for the nival and thaw periods of 1992 (•) and 1993 (o) for an abandoned meadow near Sudbury, Ontario.

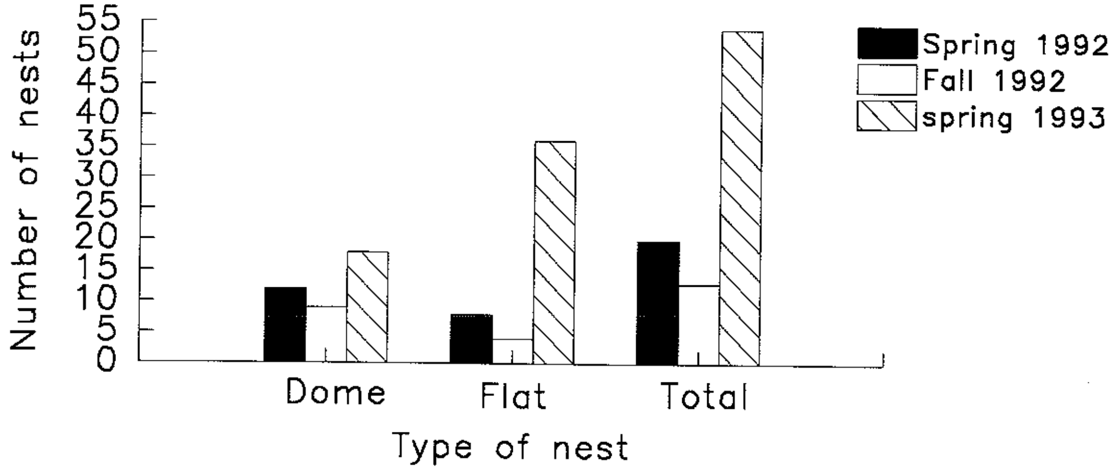

Fig. 3. number and type of nests collected in the spring of 1992, in the fall of 1992, and in the spring of 1993 from an abandoned meadow near Sudbury, Ontario.

For the days that telemetry was monitored the mean air temperature ranged from -9 °C to 19 °C, the mean temperature at 0.10 m ranged from -10 °C to 17 °C, the surface temperature range from -6 °C to 8 °C. The hourly average amount of subnivean short-wave radiation was too low to measure on 28 March but on 29 March rose to 0.18 KW m^{-2} $hour^{-1}$. By 5 April the average amount of subnivean short-wave radiation rose to 0.55 KW m^{-2} $hour^{-1}$. On Julian days 87-88 light reached the sensor by 0800h but on the three other days light reached the sensor by 0700 h.

Vole G3 disappeared three days after being released in the study grid. It is assumed that vole G3 was preyed upon since, a great number of fox tracks and fox nose prints were found in the area where the vole was released. The same assumption applies to vole B3 but it occurred at the end of the study period and vole B3 stayed within the grid throughout the study. Vole E3 moved approximately 80 m in a northeastern direction and, during the study, was not within the study grid but in the adjacent mix spruce and aspen stand.

On Julian days 87-88, the voles where radio tracked from 1220 h until 1100 h the next morning. Vole B3 was active every hour and travelled within the lower half of quadrat B3 and the upper half of quadrat B2 (Fig. 1). Vole E3 was also active during every hour monitored. Both voles stopped moving from 1820 h until 0600 h. By 0700 h both had moved but stayed within approximately 5 m of where they had spent the night.

On Julian days 94-95, the voles where radio-tracked from 1050 h until 1540 h the next day. Vole B3 was active almost every hour and travelled in quadrats B4, B3, B2, C4, C3, and C2. During the day, vole B3 travelled an area 25 m by 15 m. Vole E3 travelled an area approximately 6 m by 20 m. Both stopped being very active around 1900 h and no movement was recorded from 2100 h until 0600 h the next morning. By 0630 h both were on the move again.

On Julian day 97, radio tracking started at 0745 h and ended at 1545 h of the same day. During this day voles E3 and B3 moved in lulls and spurts. When in a lull the voles only moved a few metres but during spurts moved *ca* 10 m. Vole B3, by the end of the day, had travelled an area 20 m by 15 m and had spent time in quadrats A4, B4, C4, C3, B3, and B2.

While studying the digitized maps created from the quadrat by quadrat surveys for vole activity, for plant species and structural morphology and for the location of nests and air holes certain trends were observed. When comparing the location of air holes and spring nests to the type of summer vegetation the following trend was observed (shown in Table 1 individually): Fifty-seven percent of 'winter air holes' were located where grasses such as *Phleum pratense*, *Poa pratensis*, and *Agropyron repens* were dominant whereas 15% where in patches of *Trifolium* spp. and *Vicia cracca*. Forty percent of spring nests were located in grasses especially were the density was not thick whereas another 25% were located in *Trifolium* spp and *Vicia cracca* patches and none were located in patches of vegetation where a dense mix of *Deschampsia flexuosa* and *Danthonia spicata* were dominant. When comparing the vole activity patterns to vegetation species the following trend was observed (shown in Table 1 individually): Forty-four percent of areas of 'visible surface runways' and 'chewed holes in the vegetation' where found in

Table 1: Represents the results of the crosstabulation of the map of the distribution of the dominant summer plant species and the map of meadow vole activity patterns. The results are tabulated by the number of pixels of each meadow vole activity class found within each dominant plant species class (calculated as a percent).

	*Meadow vole activity classes**										
Dominant plant species classes	*Mix 2 & 8*	*Run visible*	*Mix 2, 4 & 7*	*Holes in soil*	*Mix 2 & 4*	*No activity*	*Runs in soil*	*Holes in grass*	*Air holes*	*Spring nests*	*Fall nests*
Sparse grass mix①	31.3%	13.2%	13.4%	7.4%	71.6%	34.8%	27.2%	0	30.2%	24.5%	27.3%
Dense grass mix②	3.0%	2.4%	0.3%	68.6%	0	11.5%	0	4.6%	0	3.8%	0
Phleum pratense	4.7%	3.4%	31.9%	10.9%	0	19.4%	0	0	4.7%	17.0%	9.1%
Poa pratensis	3.9%	17.6%	13.4%	0	0	13.6%	0	12.1%	14.0%	5.7%	0
Agropyron repens	2.8%	0.9%	0	0	0	0.4%	0	0	7.0%	1.9%	0
Vicia cracca	10.3%	7.2%	7.7%	8.5%	0	5.5%	0	7.3%	7.0%	9.4%	9.1%
Lotus corniculatus	10.5%	0.8%	13.0%	0	0	2.2%	22.1%	0	4.7%	1.9%	9.1%
Solidago graminifolia	1.8%	2.9%	6.6%	0	22.2%	3.9%	0	0	2.3%	3.8%	27.3%
Trifolium hybridum	5.1%	0	2.0%	0	0	3.7%	41.8%	76.0%	7.0%	9.4%	9.1%
*Trifolium species*③	17.6%	1.5%	0	0	0	2.2%	8.8%	0	2.3%	11.3%	9.1%

*The activity classes denote areas where one type of activity dominated, or more then one type of activity was found, within the area: the classes with numbers represent mixtures; eg 2 is an area where runways through the vegetation where observed, 4 is an area where holes where dug into the ground, 7 is an area where runways dug into the ground where found, and 8 is an area where holes chewed through the flattened grass were observed.

①Sparse grass mix class is composed of *Phleum pratense*, *Poa pratensis*, & *Agropyron repens* as the dominant plant species.

②Dense grass mix class is composed of *Deschampsia flexuosa* and *Danthonia spicata* as the dominant plant species.

③Includes the *Trifolium* species *T. dubium, T. pratense, T. procumbens.*

patches of *Trifolium* spp., *Vicia cracca*, and *Lotus corniculatus*. While 51% of areas of only 'visible surface runways' where found to be where *Phleum pratense*, *Poa pratensis* and *Agropyron repens* were dominant. Seventy-six percent of areas with only 'chewed holes in the vegetation' were located in *Trifolium hybridum*.

When looking at the crosstabulation of the map containing the summer vegetation patches and the map with the location of fall nests (Table 1), a slightly different trend was observed. Thirty percent of the nests were found on the edges of *Trifolium* spp., *Vicia cracca* or *Lotus corniculatus* patches whereas 23% were located in areas where *Solidago graminifolia* was dominant and another 23% were located in sparse areas were *Phleum pratense*, *Poa pratensis* and *Agropyron repens* were dominant.

When comparing the location of air holes and spring nests to vole activity patterns the following observation were noted: Sixty percent of winter air holes are found in areas where only 'runways in the vegetation' are visible and 20% of winter air holes are found in area where 'runways in the vegetation' are visible and where 'chewed holes' in the grass can also be seen. But 60% of nests are located in areas where 'runways in the vegetation' are visible and where 'chewed holes' in the grass can be observed, 20% of nests are located in areas where 'runways visible in the vegetation' and in the soil and where 'holes into the soil' are also seen. Nest and winter air holes are not commonly found within the same activity areas.

DISCUSSION

Discussion centres on the results that pertain to the location and use of nests, and the reasons for nest building.

During the pre-nival period of 1992, the grid site was surveyed on 28 October and 1 December to see if nests could be located before the establishment of a permanent snowpack. These nests varied from 10 cm to 13 cm in diameter and 7.5 cm in height. Ten nests were found during the October survey. These nests were located once frost was on the ground. By 1 December, two nests were abandoned and one had been destroyed by a predator. One new nest was found and one nest that was classified during the first survey as being flat had been rebuilt by the time of the second survey. Three nests remained classified as being dome nests.

The majority of nests in the pre-nival period were found in sections C and D of the grid. During the nival period air holes were rarely found within the two sections. Throughout the nival period the grid was again surveyed repeatedly. On 28 January only three air holes were located in the same quadrats that had fall nests but these air holes were slightly snow covered. Seven air holes were found in the section E-H of the grid (Fig. 1). It was discovered that the air holes did not lead straight to the ground but were slanted and winding. Cavities about midway through the snowpack with faecal matter and seeds were found. Section E-H of the grid was dominated by grasses such as *Agropyron repens*, *Phleum pratense*, *Poa pratensis*, *Carex* sp., *Solidago graminifolia*, and *Hieracium aurantiacum*. According to Bergeron *et al.* (1990) the preferred winter food selection of meadow voles consisted of *Festuca rubra*, *Poa pratensis*, and *Agropyron repens*; but, other plant species such as *Carex* spp., *Phleum pratense*, *Solidago* spp. and *Vicia cracca* where found in faecal material from winter trapped voles. All the plant species that were commonly found in the feacal material during the Bergeron *et al* (1990) study were found in the section were most of the 'air holes' were located. During a survey on 24 March a few air holes appeared in columns A and B of the grid but in quadrat A4 the 'air hole' was preyed upon by a fox. A nest was found wihin that same quadrat during the fall survey. Often when visiting the site, fox tracks were observed in areas where 'air holes' were located. This leads one to believe that voles who dig air holes that are close to their nest are vulnerable to predators.

The maximum number of air holes was observed on 27 February, again the majority of air holes where in section E-H. Air holes, however, where also found in quadrats A5, C4, and C2 where nests had been located in the fall but by 24 March the holes were snow covered and no longer distinguishable. In the spring three flat nests were found in these areas indicating either predation or abandonment.

During the spring of 1993 only four nests from the fall surveys were found but only one was dome-shaped. In the area where the dome-shaped nest was found another dome-shaped nest was also present but the latter had recently been preyed upon since the top was flipped off.

During the spring fifty-four nests were located. The majority of the nests were classified as being flat. Throughout the whole study, a red fox (*Vulpes vulpes*) and a Harrier (*Circus cuaneus*) periodically hunted the abandoned meadow and occasionly coyote (*Canis latrans*) tracks also were observed. It is believed that the combination of a poor snowcover and predation is responsable for a majority of the spring nest being unoccupied.

One way of combating vulnerability to cold weather is to become a communal nester. Many researchers have found that meadow voles are communal nesters during the winter. Madison (1980) states that by December the communal groups basically do not overlap in territories but that members within a communal group may change during the midwinter as predation reduces the size of each communal group, or destroys groups altogether. He further explains that there seems to be an optimal group size and when a communal group is too small for adequate thermal benefit, individuals relocate to other non-kin groups. As the winter progresses the noncommunal groups become fewer and more dispersed. This could explain why so many flat, abandoned, nests were found.

A trend exists between the location of 'air holes' and of nests with regard to different types of meadow vole activity. Air holes and nests are not located within the same type of activity area which suggests that air holes are located in foraging areas and not in sleeping or huddling areas.

It is believed that voles use more than one nest and that they build multiple nests. While out foraging either the voles reshape an abandoned nest found in the area or build a new nest. For voles, building a nest is not time consuming but when environmental conditions are less favorable it may be quicker to reshape an abandoned nest. It was observed by the author that when caged voles were placed in a cold room at 0 °C with nesting material present, a rough nest was built within an hour and within two hours a finely-woven dome shaped nest had been completed.

While radiotracking, vole E3 and B3 did not return to the same area every night. Fourteen nests were found in the area vole B3 travelled in and eight out of the 14 nests were classified as flat nests. These observations continue to strengthen the idea that voles share nests and that not all nest are kept up but are repaired if need be. Vole B3 resident in an activity area classified as having visible runways, indentation into the ground, and runways dug into the ground. The runways dug into the ground resembled a drainage system. The vegetation found in this area consisted of mostly *Phleum pratense*, *Poa pratensis*, *Lotus corniculatus*, and *Agropyron repens.* The quadrats C4, C3, and B4 were very wet during the thaw and post-nival periods which could explain the runways found within that area having the appearance of drainage ditches.

The wettest area surveyed was within the activity class of no activity. Half of this area was flooded with 2 cm of water. Vole use was confirmed by the presence of six air holes within the area. Six nests were also located within the area but the nest where in non-flooded areas. Even though swimming has been observed in meadow voles, Evans *et al.* (1978) conclude that voles are one of the worst swimmers based on their reluctance to enter water and the amount of time spent swimming. Courtin *et al.* (1991) observed that when foraging for fresh shoots and roots becomes difficult because of flooding the voles turn to the nesting material for food. Such behaviour would decrease even further the little protection the voles would have against the cold. Within columns D and E of the grid fourteen out of fifteen nests were flat and the one dome shaped nest had a flat nest adjacent to it.

The 'winter' of 1993 had less snow covering the ground than the previous winter, which signifies a lower thermal index throughout the whole nival period, and the thaw period was very short. These environmental conditions suggest that huddling in a communal nest could promote vole survival. A shallow snowpack and a quick thaw period increase the exposure of the voles to predators. A short thaw period, moreover, means that the snow melts more quickly and that more water percolates to the ground, thus wetting nests. Robitaille and Courtin (1990) found that saturated nests cooled down more quickly while a vole is out foraging. While using a saturated nest a vole would have to forage during shorter periods of time and return to the nest more often. The radiotracking data shows that foraging does not decrease during the thaw period but increases. This signifies that voles probably abandoned saturated nests instead of maintaining them and offers an explanation as to why more nests where found during the second spring then in the first spring.

While the radiotracking part of the study was in progress the air temperature did not affect vole behaviour because the temperature stayed within the same range and the subnivean remained around 0°C. On the first days the voles did not move further than a few metres. The percent subnivean radiation was less than 1% and the snow depth was 21 cm. The voles stopped being active at approximately 1815 h and at 1800 h there was no measurable shortwave radiation that reached the ground. At 0615 h the voles were inactive but by 0710 h they were in an area close to where they had bedded down for the night. The first measurable shortwave radiation was recorded by 0800 h. It should be noted that the voles started moving only when the sun started to illuminate the site and not in the twilight that preceded sunrise. By Julian day 94 and 95 the snowpack was reduced to patches of hard snow 2 cm in depth and the radiation sensor was still snow covered and measuring subnivean radiation. Although sunset occured at 1900 h the voles remained active until 2145 h. There was measurable radiation by 0600 h the following morning and the voles resumed their activity between 0545 h and 0630 h. By 0700 h 2.5% of the total incoming short-wave radiation was reaching the sensor. Again it was observed that the voles were not active during twilight but became active by the time the sun's rays illuminated the snow surface of the study grid. When no snow covered the ground, the vegetation reduced the amount of incoming short-wave radiation also.

Sunrise seems to trigger vole activity and the amount of short-wave radiation reaching the voles seemed to regulate foraging distance. It was observed during the spring of 1992 in column H that activity sites were concentrated in areas that were not shaded by trees. It was especially noted in quadrat H4 with a mix of shaded and non-shaded sections, that activity was only found in the non-shaded portion.

CONCLUSION

There is a relationship between summer vegetation and areas of meadow vole activity during the nival and thaw periods. Vole activity was concentrated in areas of preferred food sources. Foraging and nesting behaviour of the meadow vole appears to be dependent on snow depth and thermal index. With a shallow snowpack voles are more vulnerable to the elements. During vulnerable times voles forage further and build more nests. Foraging time of meadow voles is independent of air temperature but dependent on subnivean short-wave radiation only in the mornings. With an increase in subnivean radiation there is an increase in distance travelled by the voles.

LITERATURE CITED

Ambrose, H. W. 1973. An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus.* J. Mamm., 54(1):70-100.

Bergeron, J.M., L. Jodoin, D.W. Thomas, J. de Traversay, Y. Jean and S. Lacasse. 1990. Variation in the quality of dietary components of summer- and winter-trapped meadow voles (*Microtus pennsylvanicus*). *In* F.G. Whoriskey, R.D. Titman and D.T. Brown (ed) *Behavioural stategies for coping with winter*. Proceedings of the SQEBC Symposium March 4-6, 1988. Special Publication 1. Macdonald College of McGill University, Montreal, Quebec, p. 82-94.

Courtin, G.M., N.M. Kalliomaki, T. Hillis, and R.L. Robitaille. 1991. The effect of abiotic factors on the overwintering success in the meadow vole, *Microtus pennsylvanicus:* Winter redefined. Arctic and Alpine Research, 23(1):45-52.

Evans, R.L., E.M. Katz, N.L. Olson, and D.A. Dewsbury. 1978. A comparative study of swimming behavior in eight species of muroid rodents. *In* Tamarin , R.H. (ed.) 1985, *Biology of New World Microtus.* Special Publication No. 8. The American Society of Mammalogists, Shippensburg University, Shippensburg, PA., 342.

Forsyth, A., 1985*Mammals of the Canadian Wild.* Camden East, Ontario: Camden House. 351 pp.

Getz, L.L. 1985. Habitats. *In* Tamarin, R.H. (ed.), *Biology of New World Microtus.* Special Publication No. 8. The American Society of Mammalogists, Shippensburg University, Shippensburg, PA., p. 286-305.

Madison, D.M. 1980. An integrated view of the social biology of *Microtus pennsylvanicus.* The Biologiste 62:20-33.

Marchand. P.J. 1987. *Life in the Cold.* Hanover, NH: University Press New England. 176 pp.

Maser, C., and R.M. Storm. 1970. A key to the *Microtinae* of the Pacific Northwest. *In* Tamarin, R.H. (ed.), *Biology of New World Microtus.* Special Publication No. 8. The American Society of Mammalogists, Shippensburg University, Shippensburg, PA., p. 342.

Merritt, J.F. and A. Adamerovich. 1991. Winter thermoregulatory mecanisms of *Blarina brevicauda* as revealed by radiotelemetry. p.47-64, In Findley and Yates, *The Biology of the Soricidae*. The Museum of Southwestern Biology, University of New Mexico, Albuquerque, 91pp.

Robitaille, R.L and G.M. Courtin. 1990. Morphological and thermal characteristics of winter nests of the meadow vole, *Microtus* *pennsylvanicus*. in Proceedings of the 47th Eastern Snow Conference, June 7-8 Bangor, MA. p. 231-236.

Webster, A.B. and R.J. Brooks. 1981. Daily movements and short activity periods of free-ranging meadow voles, *Microtus pennsylvanicus*. Oikos, 37:80-87.

Whitaker, J.O. 1980. The Audubon Society Field Guide to North American Mammals. A.A. Knof, Inc. New York. pp 495-496.

Zimmerman, E.G. 1965. A comparison of habitat and food of two species of *Microtus*. J. Mamm., 46:605-612.