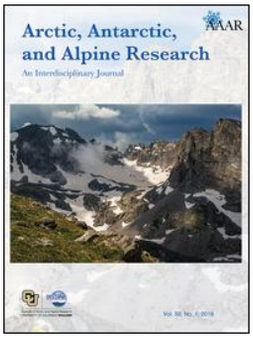

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THE EFFECT OF ABIOTIC FACTORS ON THE OVERWINTERING SUCCESS IN THE MEADOW VOLE, *MICROTUS PENNSYLVANICUS:* WINTER REDEFINED*

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ABSTRACT

Meadow vole mortality, nest construction, nest temperature, and environmental conditions were studied prior to and during the season of permanent snow at Sudbury, Ontario. Prior to snow the animals burrowed into the soil, and mortality was high owing to heavy rains followed by subfreezing temperatures. Grass nests were built beneath the snow with vole mortality being high under conditions of shallow or icy snow and saturation of nests during the thaw period.

Nest temperatures prior to the thaw varied on a diel basis between 6 and 19°C with ambient subnivean temperature at 0°C. Barely detectable penetration of shortwave solar radiation was observed under a 60-cm thickness of winter snow, but increased rapidly during the thaw period owing to freeze-thaw metamorphism.

The results support the redefinition of winter into four distinct periods, each with its own characteristic environmental conditions, namely, Pre-Nival, Nival, Thaw, and Post-Nival.

INTRODUCTION

The calendar describes winter as a period of 90 d that falls between 21 December and 21 March. Organisms living in the natural environment have their winter circumscribed not by the calendar but by a winter that is defined far more by weather and climate than it is by the position of the sun with respect to the equator. The patterns of migrating high and low pressure systems superimpose short-term fluctuations in radiation, temperature, and precipitation upon the longer term seasonal climate. It is these fluctuations that, at any given latitude, extend and modify the period that we call Winter.

There is a period prior to the establishment of a permanent snowpack that varies in length, depending upon latitude, during which small mammals have to survive without benefit of the thermal insulation and protection from predators that snow provides. Again, after snowmelt a similar, but often shorter, period exists before the start of the relatively benign conditions associated with renewed food abundance and mild weather. It is within these constraints of a winter described by the environmental rather than by the calendar that winter-active organisms must forage, avoid predators, and in some cases also reproduce.

The meadow vole, *Microtus pennsylvanicus,* is an example of a winter-active small mammal of north-temperate latitudes. Its diet consists primarily of herbaceous vegetation and its preferred habitat is moist meadows and open grasslands (Forsyth, 1985; Getz, 1985). In Sudbury, Ontario (46°28.0′N, 80°58.5′W), voles were observed to build grass nests at the ground-snow interface following the establishment of an adequate snow cover. The combination of nest and snow cover both aid in offsetting the energy demands of homeostasis that must be maintained not only when foraging but also when at rest.

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Pruitt (1960) has suggested that the stable environment that is found beneath the snow is an essential factor in the maintenance of homeothermy because the cold of winter imposes energetic demands upon the animal that must be met over and above the energy needed for foraging.

Wunder (1985) states that the meadow vole must allocate enough energy toward thermoregulation to maintain a constant body temperature of 38.4°C and that energy allocated to one function generally cannot be used for another. The cold of winter adds an extra energy demand on the vole that is minimized by the building of an insulated nest that lies below the insulation provided by the snowpack.

It must be recognized, however, that the onset of cold conditions occurs prior to the establishment of a permanent snow cover and that this period of cold may well be punctuated by precipitation that falls as rain rather than snow. Furthermore, after snowmelt a similar climatic regime may occur.

This paper seeks primarily to address the perspective of a winter period that extends considerably beyond the bounds arbitrarily set by the calendar or by the establishment of a permanent snowpack. The data used have been collected over a number of winter seasons during ongoing studies of meadow voles. The data base takes the form of a number of pilot studies, the results of which are far from "pure" by virtue of the constraints that winter conditions place both upon the researcher and upon the use of electronic equipment to collect abiotic data.

The following questions are posed by the present research: How does one define winter in terms of winter-active organisms? What are the characteristics of the winter climate to which meadow voles are vulnerable? To what extent and in what ways do meadow voles modify their environment during the cold part of the year? What roles do radiation, temperature, and precipitation play in the survival of meadow voles?

METHODS

Methods may be most conveniently separated by season of year.

Autumn

A field study intended to study the formation and situation of grass nests prior to snowfall was initiated in October 1988. Meadow voles were caught in the wild and placed in three 1-m^2 enclosures ($n = 3$, 2, and 2) made of hardware cloth and fitted with a hardware cloth lid to prevent escape should voles climb the wire mesh sides. The bottom of the enclosure was sunk 20 cm into the ground to prevent escape by burrowing. Supplemental grass was added to ensure that grass was not a limiting factor to nest building. The enclosures were placed adjacent to the trapping area, an area of high meadow vole density. The area was low-lying farmland (46°27.5′N, 80°56.5′W) which was abandoned more than 25 yr ago and which is slowly being reinvaded by trees and shrubs.

Air temperatures and precipitation amount and type were taken from daily summaries issued by the Sudbury Airport, 23 km to the northeast of the research site. The enclosures were examined for nest building activity and mortality three times daily at the same time that the traps were checked. Supplemental food, in the form of oats, was provided every other day.

Winter

Abiotic parameters were studied as follows: temperature sensors were supported on a 1-m-high mast and positioned at 100, 50, 25, 10, 5, and 2 cm above the soil surface, at the soil surface, and at 5 cm below the soil surface. The temperature mast was marked off at 10-cm intervals and also served as a gauge to measure snow depth. Precipitation, both as rain and snow (liquid equivalent), was obtained from a standard precipitation gauge with a 10-cm diameter orifice.

Thermal index (Marchand, 1982) was calculated according to the equation:

$$I_T = \sum_{i=1}^{n} (z/G)i$$

where I_T = thermal index, z = snow layer thickness (cm), G = snow density (g cm^{-3}), i = any given snow layer for which z and G have been determined, and n = number of layers composing the snowpack. The use of symbols is in accord with the snow literature (Langham, 1981) and current scientific nomenclature.

Measurements of thermal index were made by exposing a vertical snow face and measuring the thickness and density of each discernible layer. Density was obtained by weighing a 500 cm^3 volume of snow that was collected in an aluminum scoop (12.5 cm long, 8.0 cm wide, and 5.0 cm high), fitted with a wire bail, that was inserted horizontally into the snowpack. Care was taken not to compact the snow. The scoop was suspended by its bail from a 250-g capacity spring balance to obtain the weight, and hence the density, of the snow.

Eight meadow voles (4 males and 4 females) were placed in an enclosure 3.5 m long by 2.5 m wide by 1.5 m high in a grassy area of known meadow vole activity in October 1982 and prior to the first occurrence of frost. In the expectation that grass nests would be built, these could be identified and marked for study of nest temperature following the establishment of the permanent snowpack. At no time during the period prior to snowfalls could any signs of nest activity be found. Subsequently, therefore, 1 pr (male, female) of meadow voles was confined in each of three hardware cloth cages (45 × 30 × 30 cm), having sides and a top but no bottom, were sunk into the ground to a depth of 15 cm. Such cages

allowed for percolation of rain and gave the meadow voles the freedom to burrow. Abundant grass was provided to give the voles the opportunity to build grass nests that could be located and into which temperature sensors could be placed.

Late Winter–Spring

Nest temperature of meadow voles during the late winter–spring period were measured as follows. Three pairs of meadow voles were acclimated in standard laboratory cages for 4 wk in a controlled environment at -5°C and a 12 h day/12 h night photoperiod. One week prior to being placed in the field, the cotton nesting material was removed and replaced with dry grass *ad libitum* to permit the voles to make grass nests. At the end of the fourth week (10 March 1988), a vertical trench was dug in a 60-cm-thick snowpack within the 3.5- × 2.5-m enclosure mentioned previously and the lower portion carefully excavated to make room for the three cages. The cages were placed in contact with the soil but separated one from the other by 15 cm. Two 20-gauge, Teflon-coated, copper/constantan thermocouples were placed in each nest and a third was placed at the soil surface outside the cage. Duplicate nest thermocouples were used in case of chewing by the voles. An abundant supply of oats was provided in each cage. A small Matrix, Inc., silicon radiometer was also placed at the soil surface to measure shortwave radiation penetrating the snowpack. The trench was then filled in as carefully as possible to minimize compaction of the snow. All sensors were connected to a Campbell 21X datalogger that was enclosed in a heavy gauge polyethylene bag with a generous quantity of desiccant prior to being buried beneath the snow. Sensors were scanned every 60 s and data stored in memory every 15 min. Data was downloaded to magnetic tape every 2 or 3 d and synthesized on a PC computer. Shortwave incoming radiation to the site was obtained from an Eppley Pyranometer situated 2 km distant.

RESULTS

The conditions of temperature and rainfall at the end of October 1988 (Figure 1) are typical of mid to late autumn weather. The temperature and precipitation regimes during the latter part of the month are shown in Figure 1. Minimum daily air temperatures, however, did not drop below freezing until 25 October following over 14 mm of rain the previous day. Substantial rain fell again on 27 and 28 October after which minimum air temperatures dropped progressively to -6°C. Two of the seven voles died on 28 October and the remaining five died 2 d later following the onset of below freezing minimum air temperatures.

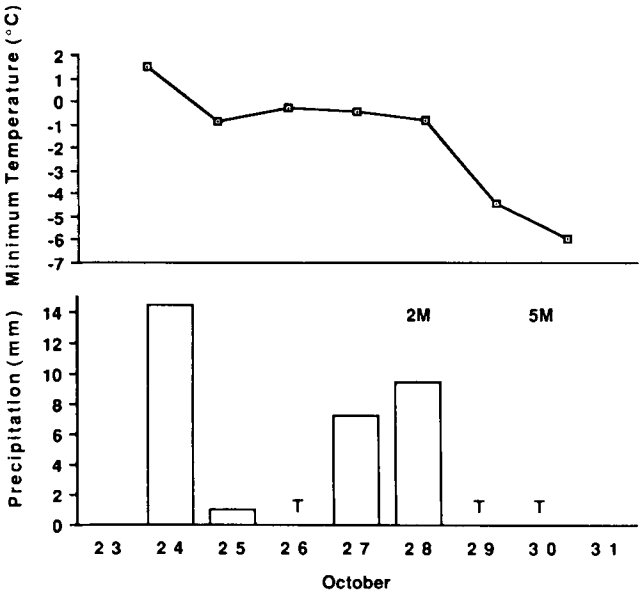

FIGURE 1. Minimum daily air temperature (°C), daily precipitation (mm), and meadow vole mortality during the period 23 to 31 October 1988. M = vole mortality and T = trace precipitation. Total precipitation for October was 119 mm.

In the region in which this study was carried out the permanent snowpack becomes established typically in early to mid-December. The thermal characteristics of the snowpack during a 9-wk period from mid-December to mid-February are shown in Figure 2. The mean depth of the pack was 51 cm but ranged from 42 to 71 cm. The mean temperature was almost isothermal above the snow but within the snowpack the well-documented increase in temperature to ca 0°C at the snow–soil interface is clearly seen. The mean soil temperature was above freezing during the entire period. Horizontal bars indicate the range in temperature during the measurement period. The range is greatest above the snow and in the vicinity of the air–snow interface but within the permanent pack (below 42 cm) a very rapid decrease in range is seen with a minimum of ca. 2°C, 2 cm above the soil.

The precipitation pattern experienced during two sequential winters, December 1982 to February 1983 and December 1983 to February 1984 (Figure 3), indicates the large variability that exists. Winter 1982/83 was exceedingly wet, especially in December and January, whereas during the following winter there was almost no rain. Furthermore, the periods between precipitation events in winter 1982/83 were very cold.

The effects of the wet and cold winter of 1982/83 on meadow vole mortality may be seen in Figure 4 where each "M" indicates the mortality of a single vole. The ground was bare of snow at the beginning of January and was restricted to less than 25 cm in thickness throughout the snow season with the exception of a 9-d period from 4 to 13 February. Values for Marchand's (1982) thermal index that take into account both thickness and density characteristics of the snowpack are also shown. By the time the thermal index had reached a value of 90, five voles that were caged beneath the snowpack had died. Two further mortalities were recorded in early March with a marked decrease in both snow depth and thermal index.

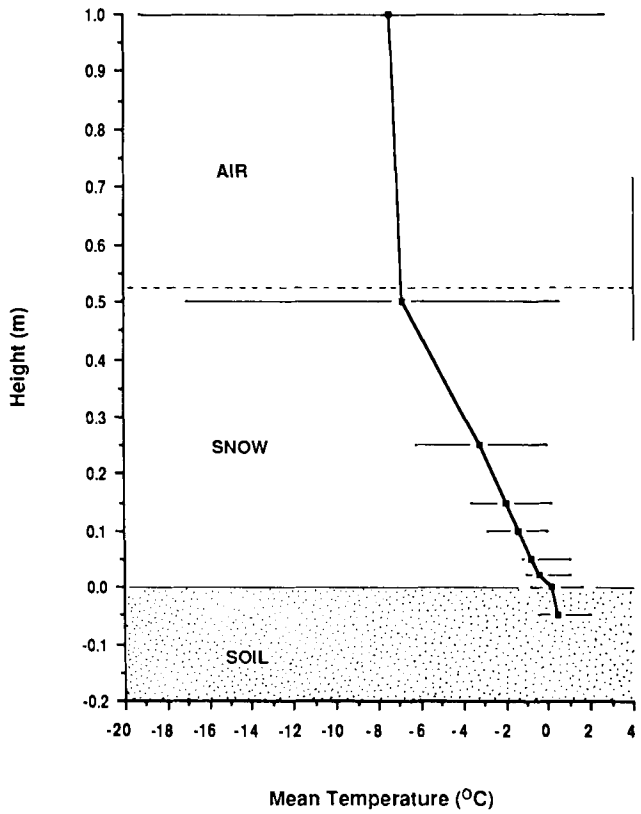

FIGURE 2. Mean temperature tautochrone (°C) from air to soil through a snowpack with a mean thickness of 0.52 m, from mid-December 1983 to mid-February 1984. Vertical bar indicates range of snow depth; horizontal bars indicate temperature range at each height.

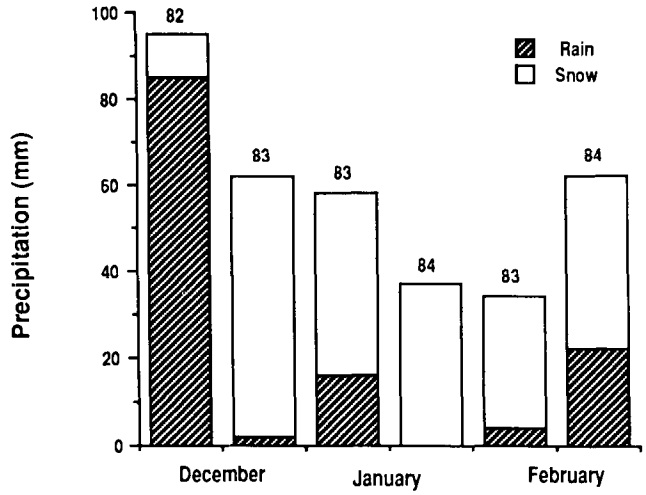

FIGURE 3. Precipitation (mm) in the form of snow (liquid equivalent) and rain from December to February for winter 1982/83 and 1983/84.

The period 11 to 29 March 1988 encompasses the transition from winter snow to thaw conditions (Figure 5). Snow depth increased from 60 to 75 cm owing to a snowfall on 12 March and declined thereafter to 40 cm on 29 March. Total daily incoming shortwave radiation fluctuated between 5 and 17 MJ m^{-2} d^{-1} with the lower values corresponding to days with either cloud or precipitation or both. The total daily subnivean radiation was measurable but very low (0.01–0.21 MJ m^{-2} d^{-1}) prior to 25 March following which there was an increase to 3.29 MJ m^{-2} d^{-1} in just 3 d.

During the same March period (1988), air, subnivean, and meadow vole nest temperatures were continuously measured. Temperature data for single days, at the beginning, middle, and end of the period are shown in Figure 6. The subnivean temperature never deviated from 0°C by more than a degree whereas air temperature varied between -3.3 and -15°C on 11 March and between -7 and -21.6°C on 20 March. On the final date, 27 March, the temperature decreased from just below freezing to -7.5°C during the day.

Nest temperature data were obtained for only two of the three cages containing paired voles because in one cage the voles moved their nest away from the temperature sensors. Nest temperature data for only one of the two remaining cages are shown for clarity (Figure 6). Nest temperature was elevated furing the entire period but highest on 11 March with values that fluctuated between 8.9 and 18.9°C. On 20 March both the fluctuation and temperature showed a marked decrease to between 2 and 5°C. On 27 March temperatures were higher and more variable than on the previous day, 9.8 to 1.6°C. Both temperature and variation decreased during the course of the day. In the second cage for which data were obtained nest temperatures varied between 2.8 and 5.6°C on 11 March, between 2.3 and 9.7°C on 20 March, and between 2.2 and 4.6°C on 27 March.

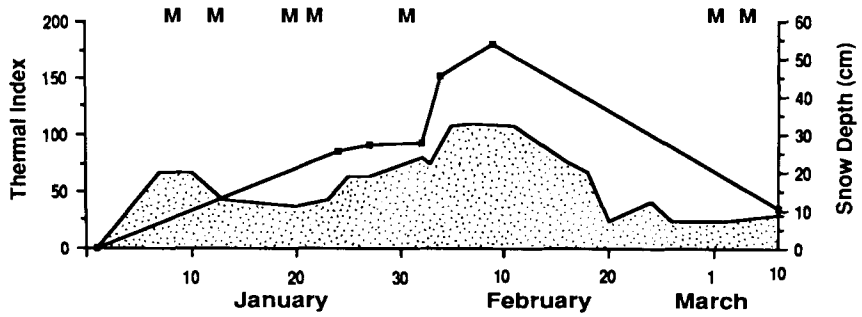

FIGURE 4. Snow depth (cm), thermal index, and single vole mortality (M) from 1 January to 10 March 1983.

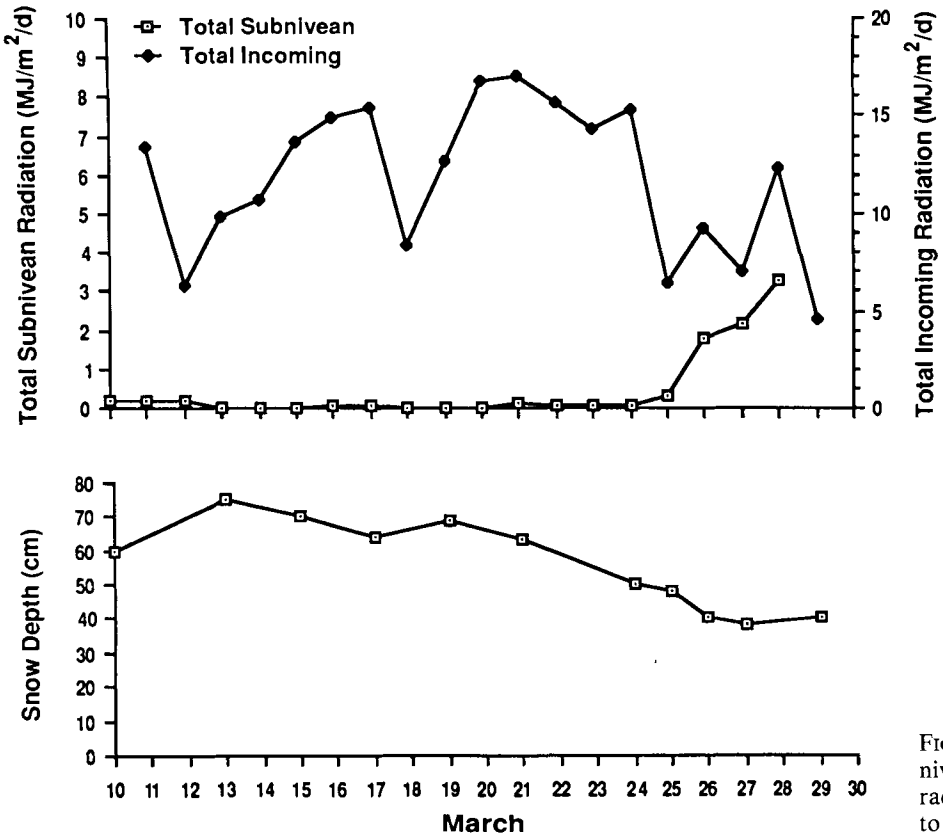

FIGURE 5. Snow depth (cm) and subnivean and total incoming shortwave radiation (MJ m^{-2} d^{-1}) for the period 10 to 30 March 1988.

DISCUSSION

A series of pilot studies was conducted over a period of years and collectively span the period described by the calender as autumn, winter, and spring. The data presented indicate that there is a period prior to the beginning of the calendar winter and the establishment of permanent snow during which voles are extremely vulnerable to weather conditions. Similarly, adverse conditions may prevail during and after snowmelt. Although these conditions extend beyond the bounds set by the calendar winter they tend to be considered as a part of winter in terms of winter-active organisms. Whitney (1976) draws from the literature in reporting that there are three periods of hardship for voles; the fall critical period, the spring critical period, and full winter. Whereas such terms identify the general time of occurrence, they fail to stress the importance of microclimate. Moreover, the time and duration of these potentially lethal periods vary with latitude and from year to year and this point needs to be addressed.

Table 1 presents a redefinition of that period of the year, where cold is a dominant climatic factor, to describe more completely the season of the year that has to be endured by winter-active animals such as meadow voles if they are to survive until the beginning of a new period of plant growth and abundant food. The Pre-Nival period begins with the onset of below-freezing temperatures. The conditions frequently occur when mean temperatures are still well above freezing. Cyclonic storms, however, bring precipitation in the form of rain that is followed by clearing skies and ground frosts as a result of strong reradiation. The protection that would be provided by a grass nest under these conditions does not seem to be a strategy adopted by meadow voles, at least in our study area, because we observed that voles burrow into the soil at this time of year. This is a period, however, when autumnal rains raise the water table significantly so that burrows frequently may fail to provide the necessary protection from wet and cold conditions with resultant high mortality (Figure 1) or possibly emigration to drier but generally less favorable habitats. Stark (1963) reported that the California vole which builds grass nests remained within its usual range even when the range was subjected to extensive and prolonged flooding. The animals survived by building new grass nests in tussocks of grass above water level. In the present study, this stratagem was not an option because water levels were sufficiently high to inundate the tussocks.

By the end of October, frost penetration into the soil in exposed areas can reach a depth of 15 cm (Sahi, 1983), and presents a barrier to the formation of burrows. Unpublished trapping data by one of us (R.L.R.) show 89 voles/1000 trap nights during the period covered by

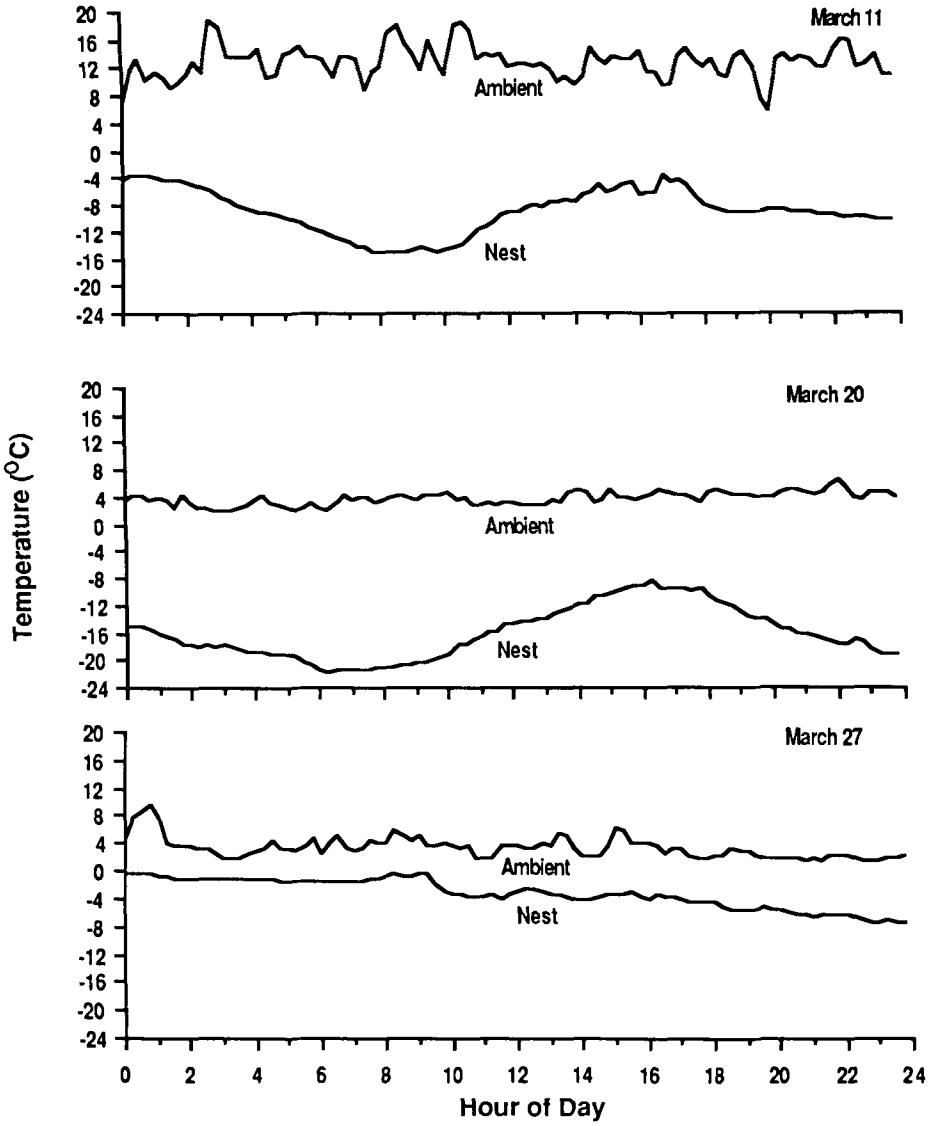

FIGURE 6. Diurnal air and meadow vole temperature (°C) for 11, 20, and 27 March 1988. Subnivean temperature was 0 ± 1 °C during the entire measurement period.

Figure 1, whereas during the entire month following not a single vole was caught using the same trap lines, probably because of emigration to a higher but normally less favorable habitat. Pruitt (1960) and Halfpenny and Ozanne (1989) acknowledge the Pre-Nival period as one that imposes severe environmental conditions on small mammals but stress the factor of cold rather than the combination of cold and wet. Formozov (1946), on the other hand, recognized the role that precipitation in the form of rain plays prior to permanent snow.

Although the winter snowpack provides the best protection of the entire cold season, the Nival Period (Table 1) can be hazardous if precipitation takes place under mild conditions. Surface thaw, or rain-saturated snow, refreeze into ice layers with a very low thermal index. At best, the effect of such conditions is simply to reduce the effective insulation of the pack and to lower subnivean temperature below freezing. At worst, total snowmelt can occur, or the remaining pack freezes into a solid mass, or enough rain and melted snow percolate through the pack to saturate nests and their occupants. When the snowpack is thick, the effect of thawing or rain is minimized because the proportion of the pack whose insulative capacity is reduced is much less than when the pack is shallow. Conditions during the Nival period 1982/83 illustrate the mortality that occurs when the snow is thin and a high proportion of the precipitation falls as rain (Figures 3 and 4).

During the following Nival period (1983/84), subnivean temperatures remained within a degree of 0°C with about 50 cm of snow (Figure 2). Although comparable data to that of the previous winter in terms of thermal index were not obtained, there was no mortality of experimental animals ($n = 3$ pr) until the onset of thaw. These findings are in conflict with those of Whitney (1976) who found good survival of voles even with conditions of shallow, crusted snow cover.

Formozov (1946) and Pruitt (1960, 1970) have stressed

Table 1. Definition and environmental conditions that describe the four phases of the cold period for organisms

PHASE	DEFINITION	CONDITIONS
Pre-Nival Period	From the onset of freezing temperatures until the establishment of the permanent snowpack	- Precipitation predominantly in the form of rain - Reradiation frosts associated with clear skies and calm winds - Sub-freezing temperatures associated with arctic airmasses
Nival Period	From the establishment of a permanent snowpack until precipitation no longer falls as snow	- Precipitation principally in the form of snow - Temperatures predominantly below freezing
Thaw Period	The period of snow melt	- Precipitation predominantly in the form of rain - Snowpack dynamics dominated by firnification - Rapidly changing light conditions beneath the snow - Lowermost portion of the snowpack often saturated
Post-Nival Period	From the end of snow melt until the danger of frost is passed	- Precipitation predominantly in the form of rain - Reradiation frost associated with clear night skies and calm winds - Soils wet to saturated

that the protection afforded by snow is critical to small mammal survival because of their inability to withstand severe cold owing to their small mass to surface area ratio. Pruitt (1957) proposes the concept of the hiemal threshold that is crossed only when the snow pack is deep enough (20–25 cm) to stabilize subnivean temperatures. Pruitt contends that the arrival of the hiemal threshold is the true beginning of winter for small mammals from which one may infer that the Nival period is one of relatively little thermal "stress" to subnivean creatures provided that the snow has a low water content and hence a low density.

The Thaw period (Table 1) is a period of very rapid change in environmental conditions beneath the snow. The strong diel (24-h) shift in air temperatures, an increasingly high irradiance, and a tendency for precipitation in the form of wet snow or rain initiate the process of freeze-thaw metamorphism or firnification. The onset of this process causes the coalescence of individual small grains of ice into firn grains that are frequently 5 mm or more in diameter. The effect is to reduce the amount of light refraction within the snow pack and the more efficient penetration of the light to the subnivean (Marchand, 1984, 1987). The total amount of solar energy penetrating the snowpack as a result of firnification increased in 4 d from 4 to 27% of the solar energy above the snow (Figure 5). It should be noted from the same figure that measurable light was detected through 60 cm of snow 14 d earlier at which time the subnivean radiation was 0.21 MJ m^{-2} d^{-1} or 3% of incident radiation. A review by Seabloom (1985) suggests that detectable levels of radiation beneath the snow may stimulate renewed breeding activity in anoestrous animals under the snow but there appears to be no agreement as to what that level might be.

At the same time, the formation of firn produces channels through the pack that reduces the resistance to percolating water with consequent wetting of both the soil and the grass nests of voles that were built beneath the snow. Conditions beneath the snow are severe. The danger of the fur of animals becoming wet is high and either movement or foraging is impeded because, although the wetted nests offer decreased thermal protection, they are still better than the environment outside the nest. Our observations are that when foraging for fresh grass shoots and roots becomes a liability the voles turn to the nesting material for food. This may be seen as an attempt at survival but serves only to decrease the already imperfect protection of the nest wetted by meltwater.

The Post-Nival period (Table 1) is one that seems to have received little if any attention. One can only postulate the environmental conditions faced by voles following the thaw. Although this period is similar to the Pre-Nival period, in that precipitation falls mostly as rain and below-freezing temperatures are still common, the major difference is that the radiant flux is markedly higher. As a result, days warm rapidly and surface litter, surface runways, and aboveground nests are likely to dry rapidly.

The soil, immediately after the thaw, is saturated in all but the best-drained sites which must mean that for a period of from several days to several weeks tunnelling is not an option to avoid freezing temperatures. Furthermore, temperatures are low enough to freeze the surface soil.

The redefinition of the cold season of the year into four periods, whose environmental characteristics are different and that differ in the degree to which they are hazardous to subnivean animals, is an attempt to avoid the ambiguous term "Winter." Winter is used variously to mean the period between the winter solstice and the vernal equinox, the period during which there is a permanent snow cover, and the period during which temperatures go below 0°C irrespective of whether or not there is snow on the ground. The period with permanent snow, however, serves as a focus of the cold season because it is easily recognizable and requires no specific measurement. At the same time, the beginning of permanent snow establishes the end point for the Pre-Nival period. The disappearance of the permanent snowpack establishes the start of the Post-Nival period with the wet and cold conditions that may prevail. The thaw is a period of transition, but one that is critical to the survival of subnivean organisms.

This proposed nomenclature has the advantage that it may be used to describe the cold season in its entirety without having to heed either the date or the latitude. At lower latitudes, the period of permanent snow contracts and the Pre-Nival period, Thaw period, and Post-Nival period contract with it. With increasing latitude the reverse is true. At the latitudinal extremes of the High Arctic the Pre-Nival period begins as soon as the 24-h day comes to an end with the sun touching the horizon (a month or more before the Autumnal equinox), the Thaw period occurs commonly after the summer solstice (Courtin and Labine, 1977), and the Post-Nival period is absent or very short. Across the entire latitudinal extent of the snowbelt, the terms have meaning and are descriptive of the conditions prevalent at the time.

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