

# Overwintering of Small Mammals near Great Slave Lake Northern Canada

W. A. FULLER, L. L. STEBBINS AND G. R. DYKE<sup>1</sup>

**ABSTRACT.** Temperature in the air and in the moss layer under the snow was recorded by means of thermistors, and snow depth and density were measured on a plot near the recording probes as well as on plots from about 3 to 60 miles away. *Clethrionomys gapperi*, *C. rutilus* and *Peromyscus maniculatus* were trapped at irregular intervals. Differences were observed between years and between plots in subnivean temperature, which is poorly correlated with air temperature, in snow thickness and in rate of accumulation of snow. The lowest subnivean temperatures were  $-14^{\circ}\text{C}$ . in January 1966 and  $-9^{\circ}\text{C}$ . in January 1967. Mortality rates varied by species and year. There was a marked decline in *C. rutilus* following a prolonged cold period in the subnivean environment in 1965-66. The winter weight of all three species is considerably less than their summer weight. Annual differences in mean body weight were small and not related to differences in population density.

**RÉSUMÉ.** *Surhibernation des petits mammifères près du Grand lac des Esclaves, Canada.* On a enregistré, au moyen de thermistors, la température de l'air et celle de la couche de mousse sous la neige; on a aussi mesuré l'épaisseur et la densité de la neige sur une parcelle voisine des sondes enregistrées, comme sur d'autres parcelles éloignées de 3 à 60 milles (5 à 100 km). On a recueilli, à intervalle irrégulier, des spécimens de *Clethrionomys gapperi*, *C. rutilus* et *Peromyscus maniculatus*. On a observé les différences dans les températures subnivales, d'une année à l'autre et d'une parcelle à l'autre, de même que dans l'épaisseur de la neige et dans son taux d'accumulation. Les plus basses températures subnivales enregistrées ont été de  $-14^{\circ}\text{C}$ . en janvier 1966 et  $-9^{\circ}\text{C}$ . en janvier 1967. Les taux de mortalité ont varié selon les espèces et les années. Il y a eu un déclin marqué de *C. rutilus* à la suite d'une longue période froide dans le milieu subnival en 1965-66. Pour les trois espèces, le poids hivernal était considérablement inférieur au poids estival. Les différences annuelles du poids moyen étaient faibles et sans rapport avec les différences de densité des populations.

**РЕЗЮМЕ.** *Зимовка мелких млекопитающих в районе Большого Невольничьего озера в Северной Канаде.* Температуры воздуха и слоя мха под снежным покровом измерялись при помощи термисторов, а также производились измерения глубины и плотности снежного покрова на экспериментальной площадке вблизи датчиков и на площадках, расположенных на расстоянии от 3 до 60 миль от последней. От времени до времени попадались в ловушки *Clethrionomys gapperi*, *C. rutilus* и *Peromyscus maniculatus*. В разные годы и на различных площадках отмечены различия в температуре под снежным покровом, связь которой с температурой воздуха выражена весьма слабо. Отмечены также различия в глубине и скорости накопления снега. Наиболее низкие температуры под снежным покровом наблюдались в январе 1966 г. ( $-14^{\circ}\text{C}$ ) и в январе 1967 г. ( $-9^{\circ}\text{C}$ ). Смертность изменялась по годам и видам. Число *C. rutilus* резко пало в результате продолжительного холодного периода в подснежной среде в 1965-1966 гг. Зимний вес представителей всех трех видов значительно ниже их летнего веса. Годовые колебания среднего веса животных были незначительны и не зависели от плотности их населения.

<sup>1</sup>Department of Zoology, University of Alberta, Edmonton.

## INTRODUCTION

This paper is the second in a projected series dealing with the ecology of *Peromyscus maniculatus*, *Clethrionomys gapperi* and *C. rutilus* in the region southwest of Great Slave Lake, Mackenzie District, Northwest Territories. The study began in 1964 (although some related work was done in 1961-63) and one phase was completed in 1967. Winter work was confined to the winters of 1965-66 and 1966-67 when the Heart Lake Laboratory of the University of Alberta was available as a base. Studies were made during the first winter by Stebbins and during the second by Dyke.

In this paper we consider winter to be roughly equivalent to the snowy period of the year, i.e. from early October until the end of April. This is an arbitrary division and raises some difficulties. We have had to include some May observations and refer to unpublished summer data. We have attempted to keep a continuous record of temperatures under the snow and in the air, to make routine measurements of certain characteristics of the snow cover and to operate small mammal trap lines. We present an analysis of temperature and snow records, body weights and changes in number of animals. The results are interpreted in terms of the hypothesis that winter mortality is directly related to conditions in the microhabitat of the animals and may be an important determinant of the size of the spring breeding population in snowy regions.

Changes in population density can be summarized as follows (Fuller 1969). *Peromyscus* and *C. gapperi* were scarce in 1964, increased in 1965, reached a peak in 1966 and declined (with some recovery during the summer) in 1967. *C. rutilus* differed only in that, instead of declining, they reached higher numbers in 1967 than in 1966.

The dearth of studies devoted to understanding the winter ecology of homiotherms, even in northern countries, is surprising. Russian biologists have pioneered this field and an important starting point is still Formozov's classic study (1946) in which he proposed an ecological classification of animals based on their reaction to snow and gave examples of the effects of excessive snow or too little snow in each category. Mass mortality of small mammals in winters with very little snow has been mentioned by Formozov (1946, 1961) and many other workers, of whom Kirikov (1946) and Semyenov *et al.* (1958) may serve as examples. But there have been few studies of the effects of normal as opposed to extraordinary winters. The only one known to us is the work of Il'enko and Zubchaninova (1963) who carried out a live-trapping program through the winter of 1960-61 in the vicinity of Moscow. In addition to changes in home range and sex ratio, they reported that the heaviest mortality of marked *Clethrionomys glareolus* and *Apodemus sylvaticus* occurred at the time of advent and disappearance of the permanent snow cover. The probable significance of late autumn and early spring conditions for small rodents has been discussed by other Soviet workers (see for example Dunaeva 1948, Koshkina 1957, 1966, Koshkina and Khalanskii 1962).

In Fennoscandia Siivonen (1962) has discussed the general importance of a snow cover in the lives of birds and mammals, and Coulianos and Johnels (1962)

have reported some subnivean temperatures and emphasized the importance of the subnivean air space. Bergstedt (1965) followed populations of *Clethrionomys glareolus* and two species of *Apodemus* through several complete years in southern Sweden; but since there was no prolonged period of snow cover, except in the winter of 1962-63, his results are not directly comparable with ours. Manniche (1912) observed a decline in *Dicrostonyx torquatus* during a winter of little snow in northeast Greenland. Kalela (1962) has shown that most microtine declines in northern Norway and Finland have occurred in late winter or early spring.

In North America the role of winter weather in ending an irruption of *Microtus* spp. has been mentioned by Murray (1965). Beer (1961) studied the winter home ranges of *Clethrionomys* and *Peromyscus* and also concluded that a prolonged period of winter cold produced a population decline. Bee and Hall (1956) discussed *in extenso* the importance of winter for *Lemmus trimucronatus*, and Sutton and Hamilton (1932) described winter distribution of lemmings on Southampton Island. Howard (1951) made simple but significant observations on small rodents caged outside his office window in winter. Brown (1945) found breeding female *Peromyscus maniculatus noveboracensis* in every month of an abnormally mild Kansas winter. Dunmire (1960) found evidence of *P.m. sonoriensis* breeding under the snow at an elevation of 12,400 feet (3,780 m.) in California. Jameson (1953) found a difference in the onset of breeding in the spring in *P. maniculatus* and *P. boylei*. But of these studies only Beer's was primarily directed at an understanding of winter ecology.

The most serious attempts to understand the importance of winter, and especially of snow and the subnivean environment, have been those of Pruitt (1957, 1965, *in press*) and Johnson (1951). Pruitt introduced a terminology for various subdivisions of winter, and for different snow conditions. He also identified a potentially critical period for small mammals between the fall thermal overturn and the heimal threshold (Pruitt 1957).

The senior author has recently attempted to show how winter conditions could affect lemming (*Lemmus* and *Dicrostonyx*) populations, particularly on the lowland tundras of North America (Fuller 1967). He postulated that the snow cover of the tundra, particularly in early winter, is irregular and, because lemmings depend on a snow cover for winter survival, the tundra constitutes a mosaic of suitable and unsuitable microhabitats. He also showed, with reference to one particular tundra station (Baker Lake, Northwest Territories), that conditions in the early winter varied from year to year, so that the areal extent of the suitable part of the mosaic must also have varied. Longley (1960) showed that at another tundra station (Resolute, Northwest Territories) such differences in snow cover persisted throughout the winter, even at observation stations separated by only a few tens of metres. In this paper we report the extension of some of these ideas to the taiga which in general has a much more uniform snow cover than the tundra because of the relative absence of wind.

## STUDY AREA

The laboratory at which the temperatures were recorded is situated one-half mile (.8 km.) north of mile 81 on the Mackenzie Highway at latitude  $60^{\circ}51'N$ , longitude  $116^{\circ}37'W$ . (Fig. 1). Trapping and snow studies were carried out from mile 65 to 117 on the Mackenzie Highway and from mile 0 to mile 16 (south bank of the Mackenzie River) on the Great Slave Lake Highway. The Mackenzie Highway here follows, in general, the northern limit of the physiographic region

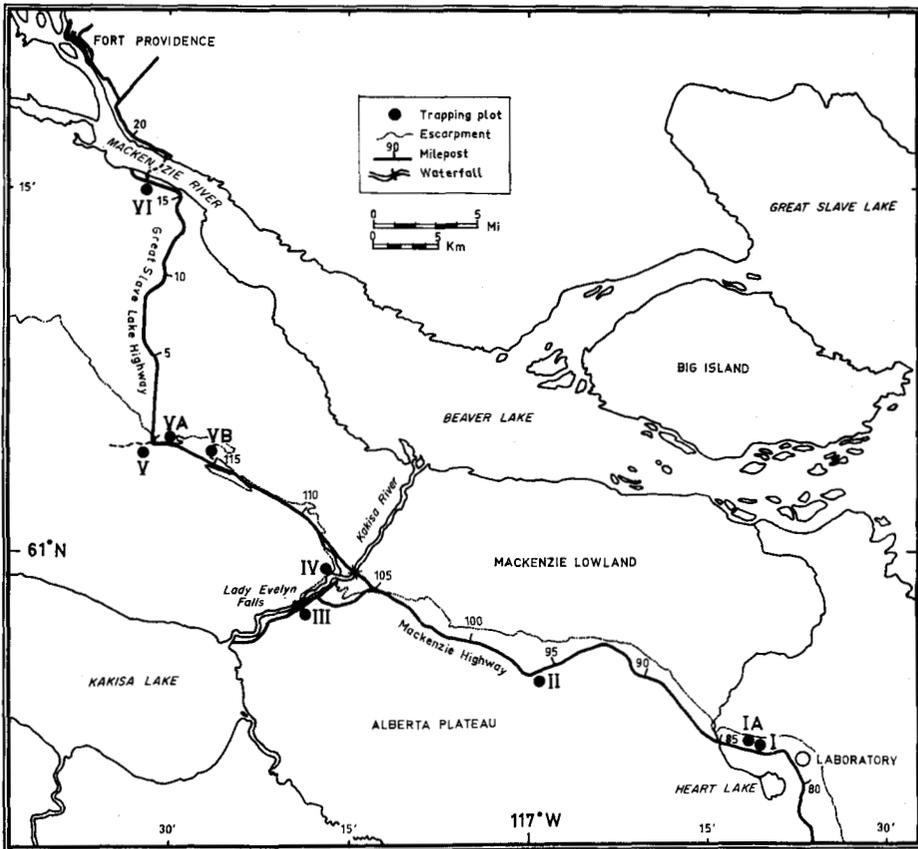


FIG. 1. Map of the study area showing major physical features, location of Heart Lake Laboratory and location of the live-trapping plots at which snow studies were made.

known as the Alberta Plateau, at an elevation of 700 to 800 feet (213 to 244 m.) a.s.l. The Great Slave Lake Highway descends from the Alberta Plateau to the Mackenzie Lowlands, and reaches an elevation of about 500 feet (152 m.) a.s.l. along the Mackenzie River. The boundary between these physiographic regions is marked by a more or less continuous escarpment 60 to 100 feet (18 to 30 m.) high. Most of the study was carried out on the Alberta Plateau, but one snow study plot and some trap lines were located in the Mackenzie Lowlands.

The escarpment also serves as the boundary between the Hay River Section

and the Upper Mackenzie Section of the boreal forest (Rowe 1959). In the former, which lies on the Alberta Plateau, jack pine (*Pinus banksiana*) is the most common tree. It grows on well-drained sites where the highly calciferous bedrock is close to the surface, and reaches a height of about 50 feet (15 m.) and a diameter of 10 to 12 inches (2.5 to 3 cm.). White spruce (*Picea glauca*) also occurs on well-drained sites. Areas from which white spruce were removed by fire are now mainly covered with aspen (*Populus tremuloides*) or jack pine. In poorly drained locations with peaty soil there are forests of black spruce (*P. mariana*) with small numbers of larch (*Larix laricina*). Along the first 15 miles (24 km.) of the Great Slave Lake Highway the forest is mainly stunted black spruce. On alluvial soil near the Mackenzie River there are some stands of white spruce, in one of which plot VI was located.

A unique faunal feature of the area is the sharp boundary between *C. gapperi* and *C. rutilus* along the Kakisa River. This is analogous to the boundary between the same two species near Summit Lake on the Alaska Highway (Rand 1944) and between *C. rutilus* and *C. glareolus* in Scandinavia (Steven 1955). This circumstance permits us to compare many aspects of the ecology of these two closely related species and to compare both with the ubiquitous *Peromyscus maniculatus*.

#### METHODS

Temperature at the laboratory was measured and registered by means of thermistors connected to a Yellow Spring's Instruments sequencing telethermometer (model 47) and laboratory recorder (model 80). On the snow study plots we used a mercury thermometer.

In both winters one or more probes were connected to the recorder in addition to one placed in the moss near the soil surface and one in the air at a height of about 2 metres. This paper deals mainly with the latter two. The probes were not protected from radiation except by the natural shielding of the trees. The magnitude of any error introduced by lack of shielding is not known, although it is recognized that snow is transparent to the infra-red portion of the spectrum (Geiger 1957). Each month the records were transcribed from the chart paper to a graph. The charts could be read to a precision of about 0.5°C.

The snow studies were carried out with a set of instruments on loan from the National Research Council of Canada. The instruments and their use have been described by Klein *et al.* (1950). We report here only snow thickness and the density of separate layers since these properties are thought to be the most important ones influencing the thermal conductivity of snow and thereby regulating the temperature near the soil surface (Williams and Gold 1958). Measurements of other physical properties of the snow are on file in the Department of Zoology, University of Alberta.

One set of measurements was taken near the recording probes. Other measurements were taken adjacent to some or all of a series of 8 one-acre (.4 hectares) plots that were used for a summer live-trapping study. In 1965-66 snow studies were undertaken only on 3 plots (I, II, III; Fig. 1) whereas in 1966-67 all 8 were studied. In all cases areas of undisturbed snow were used.

No regular routine of trapping was possible for a number of reasons, including storms, extreme temperatures and duties associated with other research and maintenance at the laboratory. Sampling the natural population was, however, a part of the program of each of the junior authors and trapping was done as often as possible. Traps were set mainly under small trees, shrubs, leaning logs and in other such snow-free spaces, and in biotopes dominated by each of the major tree species. Museum special traps, baited with peanut butter, were used. All dead animals were measured, weighed and autopsied.

## RESULTS

### *The Environment*

**ONSET OF WINTER.** It was not possible to record temperatures at the onset of winter in 1965 because of an unavoidable delay in obtaining our power source. We can only present a qualitative picture of conditions before recording began on 20 November. On 16 and 17 October about 10 cm. of snow fell each day. This gradually settled over the next 10 days and even melted in exposed places, showing that the weather remained mild. Snow was frequent in early November resulting in a 30 cm. accumulation by 9 November and 45 cm. by the end of the month.

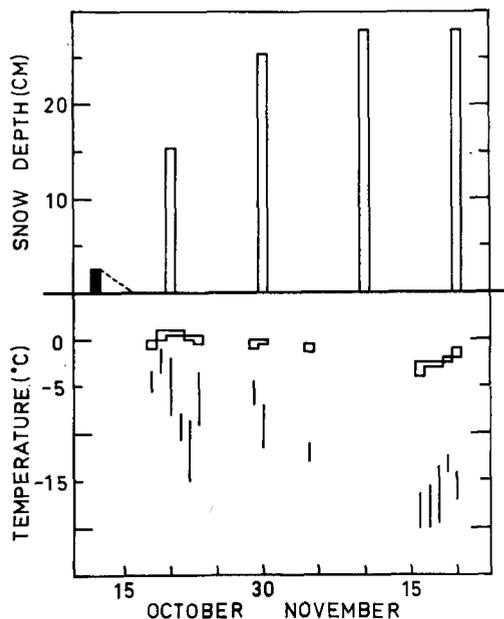


FIG. 2. The onset of winter in 1966. Snow depth is shown in the upper part of the figure, temperature in the lower. The solid bar represents an early snowfall that melted in the next few days. The vertical lines represent the daily variation in air temperature, the boxes, the variation in temperature under the snow.

In 1966 a mechanical failure in the power plant again prevented us from getting a complete record. The information that we have is presented in Fig. 2. It is clear that there was an early and rapid accumulation of snow and that sub-nivean temperatures probably stayed in the range 0°C. to -4°C. until mid-

November. Our data, though incomplete, suggest that early winter conditions were not difficult for small mammals in either year.

**AIR TEMPERATURES.** An analysis of air temperatures is given in Fig. 3. Maxima and minima read from the chart paper were averaged for the first to tenth, eleventh to twentieth and twenty-first to last day of each month. These will be referred to as 10-day periods although 3 of them cover 11 days and 1 covers only 8 days. No mean temperature was calculated because we consider that the extremes have greater biological significance than the mean.

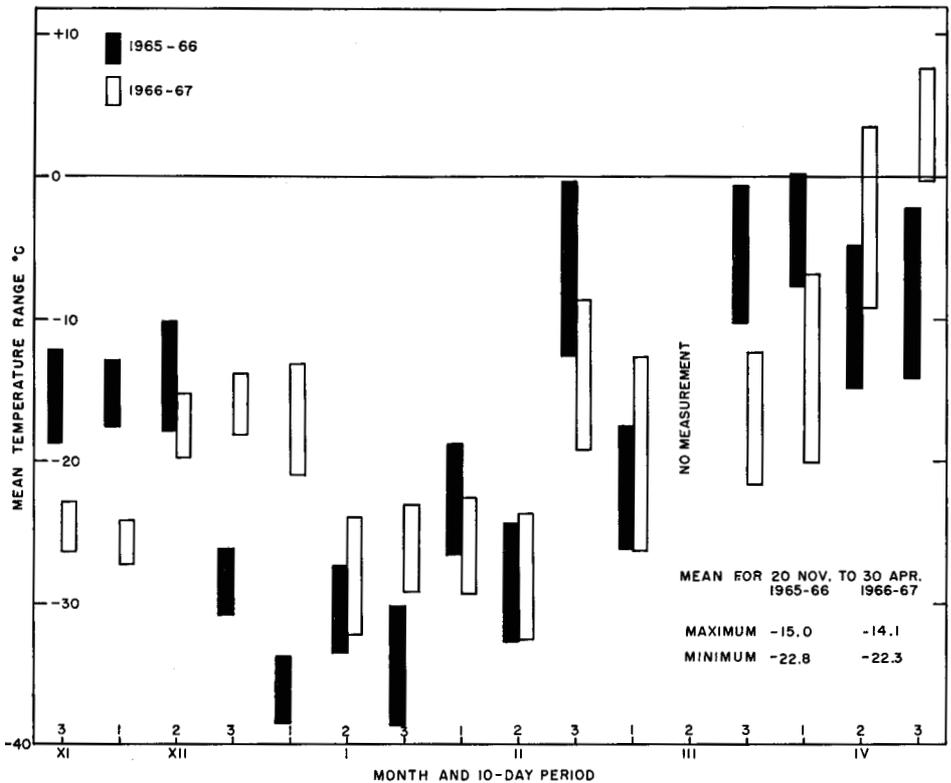


FIG. 3. Air temperatures recorded at the laboratory during the two winters of study. The range between the mean daily maximum and mean daily minimum is plotted for each 10-day period.

In comparing 1965-66 with 1966-67 the following points may be noted. First, 1965 was warmer than 1966 from 21 November until about 20 December when the situation was reversed. January 1966 was, for the most part, much colder than January 1967. On the whole, 1967 was colder in February, although in the middle period of that month the difference was slight. March began with similar minima in the 2 years, (although the maximum was a little higher in 1967) but ended with 1966 much the warmer. This continued into the first third of April, but the last two-thirds of April were warmer in 1967.

In summary, it may be said that in the macroenvironment the early part of

the winter was warmer, whereas midwinter and early spring were colder in 1965-66 as compared with 1966-67, with the exception of a period around 1 April when there was a pronounced thaw in the former year. Over the 151 days of record, the minimum air temperature averaged  $0.5^{\circ}\text{C./day}$  colder in the first winter. In addition the absolute minimum was considerably lower — a temperature of at least  $-44^{\circ}\text{C.}$ , the lower limit of the instrument, was recorded twice in that winter, whereas the coldest day the following year was  $-39.5^{\circ}\text{C.}$

**SNOW STUDIES.** Measurements of snow thickness and density on live-trapping plots for the 2 years of the study are shown in Figs. 4 and 5. It will be convenient to discuss data for 1966-67 first. Inspection of the raw data showed that thickness and density were nearly identical on all plots except VI in 1966-67. Thus, to construct Fig. 4 mean values were calculated for plots I to III, and for plots IV, VA and VB, whereas plot VI was entered separately.

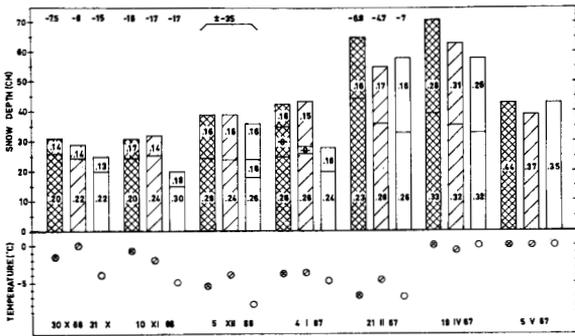


FIG. 4. Snow depth and density and subnivean temperatures on live-trapping plots in 1966-67. The length of the bar is proportional to the depth of snow in cm.; horizontal lines across the bars show the boundaries of recognizable layers; the figures on the bars are the density (g./cc.) in the given layer. Air temperature at the time of taking the snow measurement is shown above and subnivean temperature is plotted below each bar. Cross-hatching represents the mean of plots I-III; hatching — mean of plots IV, VA, VB; open — plot VI.

Fig. 4 shows first that there was a gradual buildup of the snow cover until mid-April, after which ablation began. Second, the accumulation on plot VI, the only plot in the Mackenzie Lowlands, lagged behind all the others in general. Third, there is a corresponding tendency for the temperature under the snow to be lower on plot VI, although the maximum difference is only  $2.5^{\circ}\text{C.}$  (10 November 1966). Fourth, there were usually only 2 recognizable layers in the snow and the boundary between them was usually indistinct. A third layer was recognized from late January to mid-February. Finally, the density of both upper and lower layers remained rather constant until mid-April when it increased by 50 to 100 per cent. There was a further slight increase in May, during active melting, when the snow became uniform from top to bottom. The major exception to this statement concerned plot VI on 10 November 1966, when the density of the upper layer was 0.18 and that of the lower layer 0.30. This fact along with the decrease in depth from 31 October suggests that plot VI had probably been subjected to a thaw which did not affect the other plots. It is well known (see for example Williams and Gold 1958) that the thermal conductivity of snow varies approximately as the square of its density. Thus, the decreased thickness and increased density

of the snow on plot VI could account for its lower observed temperature in comparison with the other plots.

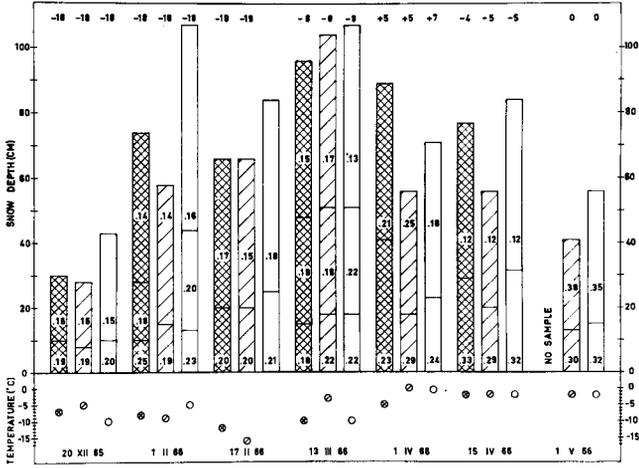


FIG. 5. Snow depth and density and subnivean temperatures on live-trapping plots in 1965-66. Symbols as in Fig. 4. Cross-hatching represents Plot I; hatching — Plot II; open — Plot III.

A striking feature of Fig. 5 is the variation in snow depth and subnivean temperature among plots I, II and III in 1965-66 which contrasts sharply with their similarity in 1966-67. The buildup of the cover was also erratic and seems to have been interrupted at least in mid-February and early April. There was, in fact, a strong thaw in late March-early April which will be examined in detail in a later section. Note, however, that the seasonal change in density followed a course similar to that followed in 1966-67.

Since densities were similar in the 2 years and the thickness (at least in mid- and late winter) was greater in 1965-66, it is surprising to find that the subnivean

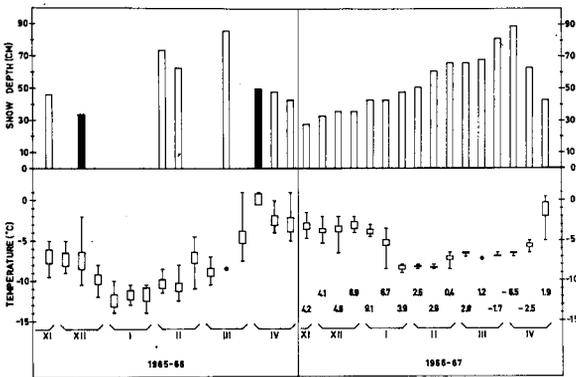


FIG. 6. Snow depth and subnivean temperatures at the laboratory 1965-66 and 1966-67. The solid bars are estimates based on the values for plots I and II. The temperatures are plotted for each third of the month (1-10; 11-20; 21 to end). The vertical line shows the range of temperature recorded during the period. The boxes enclose the range from the mean maximum to the mean minimum in each period. The value for mid-March is an estimate of the mean minimum for the period based on a partial record. The figures in the lower right give the difference in mean minimum temperature between corresponding periods in 1965-66 and 1966-67.

temperatures were lower in that year. This was not an artefact caused by differences in technique of the two observers because the same relationship was shown by the recorder at the laboratory.

**SUBNIVEAN TEMPERATURE.** An analysis of the temperature in the moss layer under the snow, and the thickness of snow near the thermistor probe, are shown in Fig. 6. These data show clearly that the temperature of the microenvironment of small mammals was higher and therefore presumably more favourable during most of the winter of 1966-67 than it was the previous year. In general, the differential increased to a maximum of  $9.1^{\circ}\text{C}$ . in early January, then decreased to essentially zero in late February. The trend reversed coincident with the thaw in late March and early April 1966, and reversed again in late April.

A second difference between the two winters concerns temperature stability. From late January to mid-April 1967 the temperature under the snow was extremely stable. The maximum fluctuation, about  $2^{\circ}\text{C}$ ., occurred during late February. Over the whole 89-day period there was a gradual warming trend within a temperature range of  $4^{\circ}\text{C}$ . The stability itself was probably due in large measure to the regular, gradual increase in snow depth that occurred at the same time. Such a regular increase implies frequent additions of new fluffy snow with low thermal conductivity so that the insulative value of the whole blanket of snow was maintained.

It is not easy to explain the comparative lack of stability in 1965-66 partly because of gaps in the snow data. In view of the depth of snow on plots I to III (Fig. 5) as well as the laboratory plot (Fig. 6), and considering that the density of the snow was about the same in 1965-66 as it was in 1966-67, so much temperature fluctuation is surprising. The explanation may be linked in part to fluctuations in the air temperature, which were more marked in 1965-66 than in 1966-67, and in part to lack of regular increments of new snow with a high capacity for insulation.

A third difference concerns the time of appearance of the absolute low temperature. This occurred during early January 1966 and late January 1967, that is, some 3 weeks later in the second winter. Whether or not this has any importance for small mammals is at present unknown.

A fourth difference concerns the nature and timing of the "spring thermal overturn" (Pruitt 1957). Ignoring the March-April thaw, the minimum subnivean temperature rose above  $0^{\circ}\text{C}$ . on 3 May 1966 and the temperature near the ground never fell below  $0^{\circ}\text{C}$ . again that spring. In 1967 the zero line was crossed on 21 April, but there were frequent returns to freezing conditions until mid-May or later. The possible significance of this difference is discussed in a paper dealing with the summer ecology of small rodents in the Great Slave Lake region (Fuller 1969).

**THE RELATION BETWEEN AIR TEMPERATURE AND SUBNIVEAN TEMPERATURE.** In summer, soil-surface temperature and air temperature fluctuate in unison, whereas in winter the soil-surface temperature is modified by the snow cover (Gold 1958b, 1963). But the temperature under the snow can never be entirely independent of air temperature, or more correctly, of the thermal gradient through the snow. Thus, we note the parallel rise and fall of the air and subnivean

temperatures at the time of the March-April thaw in 1966, and during the extreme cold of January in both years. But, that the relationship is not a simple one is shown by a comparison of air and subnivean temperatures for each 10-day period of the two winters under study (Figs. 3 and 6). The winter with the colder mean minimum air temperature also had the colder minimum subnivean temperature in only 8 of the 15 periods available for comparison. In the other 7 periods it was actually warmer under the snow in the winter with the lower air temperature. The non-conformities seem to be associated with times of instability of air temperature — early winter, a light thaw in late February 1966, the pronounced March-April thaw of 1966.

**EFFECT OF THE MOSS LAYER.** Fig. 7 has been prepared to demonstrate the importance of a moss layer as a temperature stabilizing factor. Readings of a probe placed 5 cm. above the moss are compared with those of a probe in the moss and with the air temperature probe at the time of the March-April thaw in 1966. The figure illustrates first of all a lag in the rise of the subnivean temperatures, with a slightly greater lag occurring in the moss. Of greater significance,

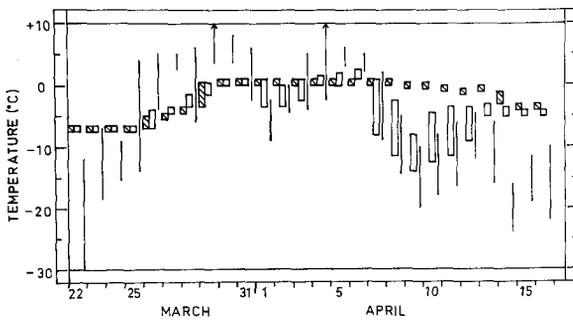


FIG. 7. The daily march of air temperature (vertical line), temperature in the moss layer (cross-hatched box), and temperature 5 cm. above the moss (open box) during the thaw of late March to early April 1966. The maximum air temperature on 29 March and 4 April probably exceeded  $+10^{\circ}\text{C}$ . which was the upper limit of the instrument in use. Note how the temperature above the moss begins to fluctuate with alteration of the physical structure of the snow as early as 1 April. The fluctuations are particularly marked with the return of colder weather on 7 April and succeeding days.

however, are the events of the first few days of the return to colder weather. The structure of the snow was obviously altered during the thaw (Fig. 5) allowing its thermal conductivity to increase sharply. As air temperature fell, the probe under the snow but above the moss recorded wide fluctuations in temperature which were considerably damped in the moss layer. In fact, the temperature just above the moss fell as low on 9 April as the lowest temperature recorded in the moss during the depth of winter ( $-14^{\circ}\text{C}$ .). Note that stability was reestablished about 12 to 14 April by a fall of new snow. Gold (1958a) has documented a change in thermal conductivity in melting snow at a station near Ottawa.

### *The Animals*

**WINTER WEIGHT.** Our data on winter weight are plotted in Figs. 8 to 10 which show the mean, 95 per cent confidence limits and observed range.

In spite of the small size of our samples of *C. rutilus* (Fig. 8) a tendency to lose weight in early winter and regain it in late winter can be seen. This agrees with a recently published weight curve for *C. rutilus* from Alaska (Sealander 1966).

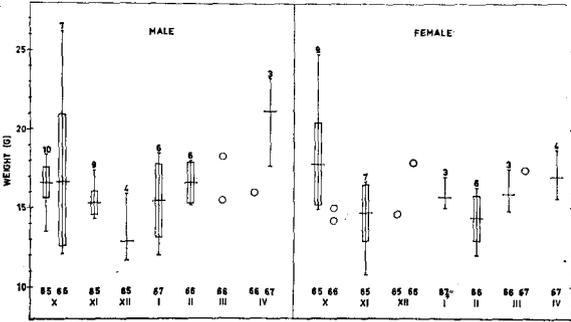


FIG. 8. Changes in the weight of *C. rutilus* during winter. The vertical line represents the range in weight and the horizontal line the mean. The 95 per cent confidence limits (box) are shown for all samples of five or more specimens. The number over each bar is the sample size. Circles represent individual weights.

We have no early May material and our April material is scanty, but it suggests that males increase in weight earlier than females do in the spring. There were a few large specimens of each sex in October but none later. These were probably animals that had been sexually mature during the summer and a few may even have been entering their second winter.

The curve for *C. gapperi* (Fig. 9) is based on larger samples than the curve for *C. rutilus* and does not suggest the midwinter weight loss. There appears to be stabilization at a mean weight of about 16 g. in both sexes. Here April specimens were scarce and early May (1 to 15) specimens are shown for comparison. Again males are heavier than females, suggesting an earlier onset of spring growth in that sex. The difference is almost significant at the 5 per cent probability level in 1967. There is a suggestion also, that males were heavier in May 1966 than in May 1967.

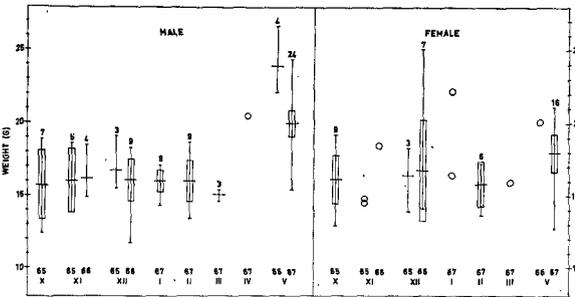


FIG. 9. Changes in the weight of *C. gapperi* during winter. Symbols as in Fig. 8.

*Peromyscus* are almost impossible to trap during winter. Our data, however, again suggest a midwinter loss followed by a spring gain (Fig. 10). Females seem to enter the winter lighter than males (the October 1965 weights are significantly different), allow their weight to drop lower during midwinter and have a slower recovery in spring. The difference between the weights of males and females in May 1966 is clearly significant and the trend is in the same direction in 1967. Males may have been larger in April 1967 than in April 1966. The single large

male plotted separately in 1967 was captured in the unheated porch of the laboratory where it had access to stored food.

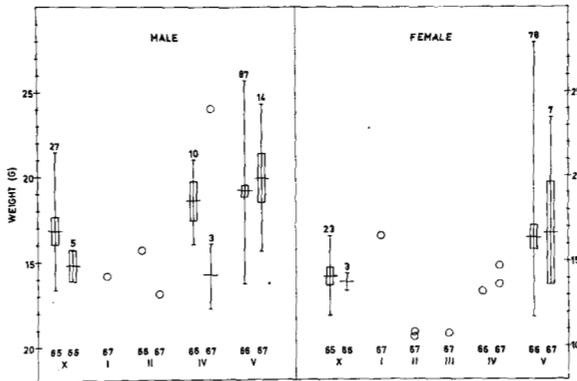


FIG. 10. Changes in weight of *Peromyscus maniculatus* during winter. Symbols as in Fig. 8.

**WINTER MORTALITY.** Snap trapping can only give a crude picture of population changes, especially when trapping sites are limited as they are in winter. However, indices expressed as catch per 100 trap-nights are shown in Tables 1 and 2. Traps were set in several biotopes during each trapping period but the data are too scanty to analyse by biotope and have been grouped. They are considered to be broadly representative for the area as a whole. The following observations seem to be justified.

*C. rutilus* underwent a serious decline in 1965-66 and it seems possible to establish approximately when it occurred. The rather sharp decrease between the February and March trapping periods (Table 1) suggests that the mortality was the direct result of exposure to the prolonged period of low temperature in the subnivean environment (Fig. 6). The high index for November is considered to result from a bias in that during much of that month the animals were fre-

TABLE 1. Results of snap-trapping in the winter of 1965-66.  
(TN = trap-nights, C = catch)

Date	<i>P. maniculatus</i>		<i>C. gapperi</i>		<i>C. rutilus</i>	
	TN	C/100 TN	TN	C/100 TN	TN	C/100 TN
1965						
1-31. X	761	6.57	386	4.66	375	5.07
1. XI-3. XII	410	0	290	7.93	120	13.33
1966						
23-26. II	205	0.49	—	—	205	5.85
15-17. III	225	0	—	—	225*	0.89
1-3. IV	381	2.89	—	—	381	0
3-8. V	480	20.21	—	—	480	0
11-16. V	501	5.59	120	6.67	861**	1.05
22-24. V	—	—	240	2.08	—	—

\*Traps left in place 15-31. III took 5 *C. rutilus* in 1300 TN. (0.38/100 TN). The first three days probably give a more meaningful comparison.

\*\*If only lines on which at least one *C. rutilus* was caught are considered there were 381 trap-nights which gives a maximum index of 2.36/100 TN for this period.

quently active on the snow surface. This allowed the trapper to select areas for trapping with a high probability of success. Although comparison of the February-March-April indices suggests virtual elimination, comparison of the October and May indices suggests that the overwinter mortality may only have been of the order of 80 per cent.

TABLE 2. Results of snap-trapping in the winter of 1966-67.  
(TN = trap-nights, C = catch).

Date	<i>P. maniculatus</i>		<i>C. gapperi</i>		<i>C. rutilus</i>	
	TN	C/100 TN	TN	C/100 TN	TN	C/100 TN
1966						
15-21. X	240	3.3	—	—	240	3.7
22. XI-2. XII	180	0	180	4.4	—	—
11-16. XII	440	0	200	2.0	240	1.7
1967						
5-12. I	440	0.5	200	4.0	240	3.7
13-18. IV	160	3.1	40	10.0	120	13.3
7-14. V	750	1.5	750	3.6	—	—

There is no evidence that a similar sharp decline in the numbers of *C. rutilus* occurred in 1966-67. The April index (Table 2) even suggests a population increase during the winter, but autopsies showed conclusively that winter breeding did not occur. The high spring index must have another explanation such as increased mobility of the animals or different response to traps. It seems reasonable to conclude that more *C. rutilus* survived the milder winter of 1966-67 than the preceding cold winter. Tables 1 and 2 suggest that *C. gapperi* survived about as well as *C. rutilus* — perhaps better in 1965-66.

The data for *Peromyscus* are difficult to interpret because of our inability to trap them during cold weather. Even the October indices are much too low judging by the results of live-trapping studies which showed *Peromyscus* to be at least 5 times as numerous as *Clethrionomys* in September 1965 and about 3 times as numerous in September 1966. Furthermore, the density of *Peromyscus* was about twice as great in 1966 as in 1965. The only clues to winter survival, therefore are given by the spring figures in Tables 1 and 2. These suggest rather strongly that more *Peromyscus* survived the winter of 1965-66 than survived the following winter, even though only half as many animals were alive at the start of winter in the former year. Thus, the mortality rate was almost certainly higher in 1966-67 than in 1965-66.

#### DISCUSSION

We prepared Table 3 by converting the values in Thompson (1962) and Climatology Division (1965) from English to metric units so that our results (Fig. 3) could be compared with the climatic normal for the nearest official meteorological station at Hay River, Northwest Territories. We can assume that conditions in the study area are at least as severe as at Hay River which has its

TABLE 3. Temperature (°C.) and snow (cm.) normals for Hay River, N.W.T. based on the 30-year period 1931-1960. Original values in inches and degrees Fahrenheit, converted to metric units.

(Source: Meteorological Branch, Department of Transport).

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Winter**
<i>Normal daily Max. Temp.</i>	-7.7	-16.5	-19.6	-16.6	-9.8	+1.0	-11.54
<i>Extreme Max. Temp.</i>	+15.0	+12.2	+9.5	+13.3	+15.5	+23.3	
<i>Normal daily Min. Temp.</i>	-15.5	-25.9	-29.6	-27.7	-21.6	-10.4	-21.78
<i>Extreme Min. Temp.</i>	-40.5	-51.1	-52.2	-50.5	-47.2	-40.0	
<i>Normal Cumulative snowfall</i>	51.3	73.9	89.6	104.6	119.3	130.4	130.4
<i>Snow cover*</i>	22.9	33.0	48.3	61.0	40.6	0.0	73.7

\*Snow cover is reported as the depth of snow on the ground on the last day of the month.

\*\*Winter values are means for temperature, cumulative total for snowfall and the median value for snow cover.

fall weather ameliorated by the proximity of Great Slave Lake until the lake is covered by ice in December. Three periods may be singled out for attention on the basis of information in the literature and our own studies — the onset of winter (fall critical period of Pruitt, 1957); the end of winter (spring critical period of Fuller, 1967); full winter conditions (Pruitt 1957) when the period of deep cold occurs.

It is reasonably clear from Fig. 2 that the fall critical period in 1966 was very brief and probably of no significance for rodents because of the rapid accumulation of snow; it is also probable that the fall critical period was of little significance in 1965 though the snow cover was deficient, because the air temperature remained rather high. But it is also clear that the 1966 temperatures combined with the 1965 snow cover might have been lethal for small rodents without being in any way unusual. From Potter (1965, p. 60) and Hagglund and Thompson (1964, Fig. 6) it is possible to estimate the frequency of occurrence of given conditions of temperature and snow cover. November minima at least as low as in 1966, combined with a November snow cover at least as scanty as that of 1965 can be expected at Hay River about once every 4 to 5 years ( $0.25 > P > 0.20$ ). Thus, although we failed to detect any effect of the fall critical period on the population we think that a number of important questions remain to be answered. Are there special microhabitats protected from the extremes predicted for the subnivean environment generally? Do the animals adapt behaviourally by nest-building or huddling? What are the physiological tolerances of small mammals to acute stress of  $-20$  to  $-30^{\circ}\text{C}$ . and to less severe chronic stresses?

Full winter conditions were certainly not unduly severe in 1966-67, whereas they were, at least in part, in 1965-66. January 1966 was colder than normal, but it hardly warrants the label "extraordinary", especially since the low air temperature was partly offset for subnivean forms by the greater-than-normal snow cover. There is a distinct possibility therefore that midwinter subnivean conditions could be worse than those of 1965-66 if near normal temperature was combined with a less-than-normal snow cover. But we believe that the number of *Clethrionomys* was sharply reduced following the prolonged cold of late December 1965 and January and early February 1966. Would even sharper

reductions follow in a year with worse conditions than those observed in 1965-66?

The period of rapid environmental change in spring occurred in both years in May although Hay River is normally without snow on 30 April (Table 3). Spring conditions evidently departed farther from normal than either autumn or winter especially in 1967 when near-freezing temperatures persisted throughout May and the ground was completely snow-covered until after the twentieth. Our data suggest that *Peromyscus* continued to decline in this period. It seems clear that females, though not males, were unable to gain weight with snow on the ground, and because weight gain seems a necessary prerequisite to breeding, it is reasonable to suppose that reproduction was delayed in both years of our study in comparison with normal conditions. The serious delayed-effect of the particularly late spring of 1967 on the populations of *Peromyscus* and *C. gapperi* (but not *C. rutilus*) is discussed by Fuller (1969).

It is well known that the rate of accumulation and thickness of the taiga snow cover, which is seldom reworked by wind, vary from year to year (Potter 1965, Pruitt 1957). Pruitt (1957, 1959) has also shown that the taiga subnivean environment is not uniform but contains cold spots in the "shadows" of the trees (qamaniqs). We were not prepared to find marked variation from place to place in subnivean temperature in our study since we were careful to avoid sampling in qamaniqs. Both the year-to-year and place-to-place differences in subnivean temperature clearly have biological significance.

Much has been made of differences in body weight in different phases of a population "cycle" (Kalela 1957, Chitty and Chitty 1962, Krebs 1964) but nearly all the evidence relates to summer weight only. If cyclic changes in body weight are held to have a genetic basis they should be manifest in winter as well as in summer. If they have survival value, or are an expression of some other quality of the animals that has survival value, perhaps they should be more strongly expressed in winter when environmental stress is maximum. Stein (1956) has shown that *C. glareolus* were heavier in the winter following a peak than in the preceding winter.

Our data do not suggest that mean body weight in winter was influenced by population density at the beginning of winter (Figs. 8 to 10). There are only three possibly significant differences between years — male *Peromyscus* in October and April and male *C. gapperi* in early May. In the first instance it is probably only chance that no older male was included in the small sample of October 1966, and we hesitate to conclude that the animals were really smaller in autumn of the peak year than in the increase year. In the case of the spring samples, which are also small, we have shown that *Peromyscus* was probably more dense and *C. gapperi* less dense in April and early May 1966 than at the corresponding time in 1967. Thus, a relationship between population density and body weight does not seem to be demonstrable. On the other hand, growth may have been stimulated in both species by the March-April thaw of 1966. Thus, physical environment rather than population density seems to offer a better explanation for the larger weights observed in 1966.

The decrease in mean body weight that occurs in winter in most, if not all, Holarctic microtines is brought about by 3 processes — death of the oldest

(largest) animals, cessation of growth in the youngest, and an actual decline in the weight of those older animals that survive. Nor is the phenomenon confined to microtines. It has previously been recorded in *Peromyscus maniculatus* (Sealander 1951) and in Palearctic shrews (Dehnel 1949, Mezhzherin 1964). We suggest that it will prove to be a universal feature of the biology of subnivean forms, if not all chionophiles. Since large body size would appear to confer an advantage from the point of view of thermoregulation, there must be some overriding advantage to being small. We agree with Kalela (1957) and Mezhzherin (1964) who think that the advantage must lie in a decrease in overall energy requirement. But this would only favour the individual and the population during a time of food shortage, which suggests that studies such as those of Grodzinski (1963) must be critically reevaluated. Subnivean forms probably pay two penalties for this advantage. First, they are necessarily more dependent on a snow cover for protection from temperature extremes, and second the weight deficit must be made good, at least in the case of females, before breeding can start. On this view it is easy to see how an insufficient snow cover in early or midwinter or a prolonged spring snow cover may have serious consequences for them. The importance of a snow cover for *Microtus arvalis* in northwestern Europe was demonstrated dramatically in 1962-63 (Frank 1964). Instead of losing weight, ceasing to reproduce and declining in number, *M. arvalis* gained weight, bred throughout the winter and increased in number. Besides being the third coldest winter in the last 70 years, 1962-63 was the snowiest winter in the past century in northwestern Europe.

The contrast in severity of the two winters studied enabled us to compare the relative merits of the strategies for winter survival adopted by local representatives of these two genera. One of us (Stebbins 1968) confirmed by means of a study of their activity under nearly natural conditions that both species of *Clethrionomys* remain active throughout the winter. In the same study *P. maniculatus* underwent frequent, prolonged bouts of torpor even when caged alone and supplied with laboratory chow in excess. This discovery explains why *P. maniculatus* is seldom trapped in cold weather. It also extends the observation of Howard (1951) that *P. maniculatus* allowed to huddle in groups entered torpor and the studies of Morhardt and Hudson (1966) on torpor in *P. maniculatus* deprived of food. It would be interesting to know whether *P. leucopus* enters torpor in view of Christian's (1967) prediction of a metabolic difference between *P. leucopus* and *P. maniculatus*.

*Clethrionomys*, which have efficient grinding molars, a long small intestine for absorption, and a large caecum for cellulose degradation (Górecki and Gebczyńska 1962) can satisfy their continuous need for energy, at least up to a point, by utilizing coarse but presumably low quality foods that are always available even under snow. But such foods are essentially unavailable to *Peromyscus* with their bunodont teeth and probably less efficient gut. Foods that *Peromyscus* can handle, such as seeds and berries, though rich in nutrients are presumably difficult to find under the snow. In these conditions torpor, probably combined with some food storage, is an obvious advantage.

Our results suggest that *Peromyscus* survived the cold winter of 1965-66

better than *Clethrionomys* did, which in turn suggests that torpor is superior to continuous activity under these conditions. We can also conclude that more *Clethrionomys* survived the milder winter of 1966-67 than the previous cold one. This result is in accordance with expectation since the energy required for thermoregulation alone must have been very much less during the 90 days from 20 November to late February when the minimum subnivean temperature was 4 to 9 degrees warmer than in the corresponding period of the preceding winter. In 1965-66 the energy requirement may have exceeded the capacity of *Clethrionomys* to metabolize the low quality food available. On the other hand, we can only speculate why *Peromyscus* apparently survived less well in the milder winter. Perhaps they spent less time in the torpid state in the milder winter and thus raised their energy demands above a critical level as is well known in the case of hibernators. If this is the explanation it suggests that torpor as an adaptation to cold has its greatest survival value under extreme conditions, which is analogous to the conclusion reached by French *et al.* (1967) with respect to torpor in *Perognathus* as an adaptation to heat.

From the point of view of population regulation we believe that our limited studies have shown that winter mortality may vary within and between species from year to year with differences in the temperature in the subnivean environment. This is not to deny the possible importance of other factors, but only to emphasize the desirability of additional winter studies. Because winter mortality is variable, and because it acts right up until the onset of breeding in the spring, it may well be a "key factor" (Morris 1957) in the population fluctuations of subnivean rodents.

#### CONCLUSIONS

Several obvious but important conclusions can be drawn from the foregoing analysis. First, conditions in the macroenvironment tell little about conditions in the microenvironment inhabited by small rodents; in fact they can be misleading. If only standard meteorological reports had been studied we would almost certainly have concluded that the early winter of 1965 was warmer and hence more favourable for small mammals than that of 1966, whereas the opposite was, in fact, true. At the very least, this suggests that weather cannot be eliminated as a factor in population studies of small mammals in snowy regions on the basis of standard meteorological data.

The last statement implies that conditions under the snow differ from year to year as Pruitt (1957) has already shown. We can now add that the mortality rate of *Clethrionomys* seems to be correlated with the severity of those conditions but we are not prepared to generalize about *Peromyscus* at this time. We emphasize, however, that conditions at least potentially damaging to small rodents may occur either during the fall critical period, in midwinter, in the spring critical period, or in any two or all three of these periods. A population can be drastically reduced in numbers by an unfavourable combination of factors during only *one* period, whereas a high survival rate requires that all three be favourable. We have studied two winters that did not differ appreciably from the climatic

normal, yet in one of them midwinter conditions under the snow were apparently severe enough to reduce drastically the population of one or both species of *Clethrionomys*, whereas in the second year, for reasons less clearly defined, *Peromyscus* was greatly reduced in number. The latter response was at least partly caused by the persistence of a snow cover beyond the normal time. We conclude that the probability of a series of winters in which all parts will be highly favourable for the survival of small rodents is vanishingly small, hence the likelihood of population increase continuing unaffected by winter conditions is also virtually zero.

Our third conclusion is that conditions may differ from place to place in the same winter even under the apparently uniform taiga snow. The differences may be negligible in some years and rather large in others. This finding carries two further implications. Because it is not possible to conclude without actual measurement that nearby populations have been exposed to the same "weather", this argument should not be used to reject weather as a factor in population control. Also, such differences provide a mechanism for a graduated, rather than an all-or-none decline of a population under severe conditions. (The fate of an individual member of a population is, of course, all-or-none — it lives or dies.)

Fourth, we have confirmed that populations of different genera and perhaps species may respond differently to the same (or closely similar) microenvironmental conditions. Thus, lack of synchrony in sympatric populations of different species is also a weak argument against the role of weather as a control factor.

Although there is a lively controversy between at least two schools of thought as to whether or not weather can operate in such a way as to "control" populations of animals over long stretches of time, it is widely conceded that extraordinary weather conditions may favour or destroy animal populations. There is also general agreement that one role of weather in population phenomena is to bring different populations into synchrony over moderately large areas. We argue that only weather so extraordinary that it causes catastrophic mortality will promote synchrony in populations of small subnivean mammals, whereas small deviations from normal may actually promote asynchrony. We argue further that the winter ecology of small mammals in snowy regions is deserving of more intensive study by those who hope to find an answer to the riddle of cyclic fluctuations.

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