

Fig. 1. Subarctic-spruce, air and soil temperatures, 1954-56.

## OBSERVATIONS ON THE BIOCLIMATE OF SOME TAIGA MAMMALS

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WHILE the study the ecology of small mammals of the tundra regions of North America appears to be progressing rapidly, the ecology of small mammals of the transcontinental subarctic forest or taiga seems by comparison woefully neglected. Indeed, there are a number of common misconceptions about the taiga environment in general. This state of affairs undoubtedly has been brought about by three factors: (1) the lack of biological stations with year-round research programs in the taiga; (2) the natural curiosity of temperate zone biologists regarding the completely foreign tundra environment; and (3) the acknowledged difficulty of winter field work in the taiga, particularly when one depends on mechanical or electrical devices. This paper will attempt to correct some of the common misconceptions about the bioclimate of some of the small mammals inhabiting the taiga and also to suggest avenues of needed research.

This study was initiated while I was employed as Biologist at the Arctic Aeromedical Laboratory, Fairbanks, Alaska. I am grateful to the Laboratory for supplies, equipment and support and to the University of Pennsylvania, School of Medicine for continuing support through contract with the United States Air Force, Office of Scientific Research of the Air Research and Development Command. I am grateful to Mrs. William D. Berry and Mr. Charles V. Lucier for their great assistance during 1954-5 and 1955-6, respectively. Without their constant devotion to accuracy and observation this study could not have been made. Especial thanks should go to Mrs. Ladessa Nordale of Fairbanks, Alaska for permission to use the land upon which the principal bioclimate study area was established.

In 1954 several one-acre quadrats for the study of population fluctuations of small mammals were established at widely scattered points in Alaska. Three of these quadrats, because of their relative accessibility, were selected for more detailed microclimatic study. Two of these, an area of subalpine spruce and an area of Arctic-Alpine tundra, are situated in the upper Gulkana River drainage and are being investigated by Dr. L. L. Huffman of Paxson Lake, Alaska. The analysis and discussion of the data from them will comprise separate reports by us. The third area, identified on charts and specimen labels as "SPR," forms the basis of the present report.

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This quadrat is situated in NE  $\frac{1}{4}$  Sec. 19, T 1 S, R 1 E of the Fairbanks Meridian, Alaska. It consists of a generally level moss-covered substrate with a mature forest of white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*). Also present are alders (*Alnus* spp.), a few willows (*Salix* spp.) and scattered tamaracks (*Larix laricina*). The entire stand comprises only some 80 acres of mature forest and is fast disappearing due to cutting for firewood. This stand was selected for study since it appears to be the only sizable remnant of virgin spruce forest within many miles of Fairbanks that is accessible by road all year. The acre under study lies in a stand of some 20 acres which is bounded on the north by Peede Road and on the south by Chena Slough, one of the tributaries of the Chena River (U. S. G. S. Fairbanks D-1 Quadrangle). From the air one can see that the entire region has been worked and reworked by the river, the present-day vegetation being a mosaic of mature forest, burned and cut-over brush land and interlacing sloughs, active, stagnant and filled-in. The study area resembles to a remarkable degree the taiga described by Keller (1927). A test hole sunk to a depth of 3 feet in summer showed no frozen ground.

This plot is equipped with 100 wire markers equally spaced over it so that traps may be placed every year in the same spot. On October 4, 1954, a series of 18 thermistor assemblies was installed on the plot. The sensitive elements of these assemblies were Negative Temperature Coefficient Resistance units, Type L2005-200-89, manufactured by Keystone Carbon Company, St. Marys, Pennsylvania. The units were connected to 24 ga. two-conductor 18-#36 copper strand wire with double-weight thermoplastic insulation and were protected by black "Microsol" plastic coatings. The assemblies were prepared by Mr. Kent Culver of Wood and Metal Products Company, Bloomfield Hills, Michigan. Thermistor resistances were read on a Simpson Model 260 volt-ohm-milliammeter. Air temperatures at 6 feet above the ground were taken with Arctic Maximum and Arctic Minimum thermometers, U. S. Army Signal Corps type. All temperatures are given in degrees Fahrenheit. The area has been visited almost daily since October 4, 1954, with the exception of Saturdays and Sundays. If especially interesting weather conditions developed visits were made on these days also.

The thermistors whose records are of greatest interest are installed near the center of the plot under a cover of spruce varying from 3 to 9 inches DBH and are inserted into the mossy forest floor at 9, 6 and 3 inches below the surface and at 0 inches among the tops of the moss plants. The 9-inch thermistor rests at the bottom of the moss just above the mineral soil. Thus we have an essentially continuous record of the thermal environment of the habitat of the small mammals which use the forest floor (Fig. 1).

The dominant small mammal on this plot is *Clethrionomys rutilus*, the boreal red-backed vole. Other mammals taken, observed or sign noted on the plot are shrews (*Sorex* spp.), red fox (*Vulpes fulva*), marten (*Martes americana*), weasels (*Mustela erminea* and *M. rixosa*), red squirrel (*Tamiasciurus hudsonicus*), flying squirrel (*Glaucomys sabrinus*), snowshoe hare (*Lepus americanus*) and moose (*Alces americana*). Marten tracks have

been seen only once, the other mammals have been noted many times. Observations on the behaviour and population fluctuations of some of these mammals will be covered in separate reports.

Let us now examine the environment of the forest floor. This becomes the year-round bioclimate of the red-backed vole and the shrews and during the period of snow cover that of the weasels, and for long periods, also that of the red squirrel (Pruitt and Lucier, in press).

### Snow-free period

In the spring of 1955 the snow cover had completed its disappearance by May 14 (Fig. 2). At this time the upper layers of moss warmed up rather suddenly and their daily temperature fluctuations began to agree with those of the ambient air. The 9-inch level continued its slow rise, however, and many times acted independently of the ambient air. The absolute maximum of the air temperature occurred on July 26 when this reached  $+97.5^{\circ}$ . On this day also occurred the absolute maxima at 3-inch and surface levels. The absolute maximum of  $+47^{\circ}$  at 9 inches did not occur until August 3. From these peaks the temperatures at all levels began an irregular descent until the time of the fall overturn. At this date, about October 1, the temperature of the air fell below that of the substrate and the moss surface temperatures started to fall below those of the deeper layers. This event may be called the *thermal overturn*.

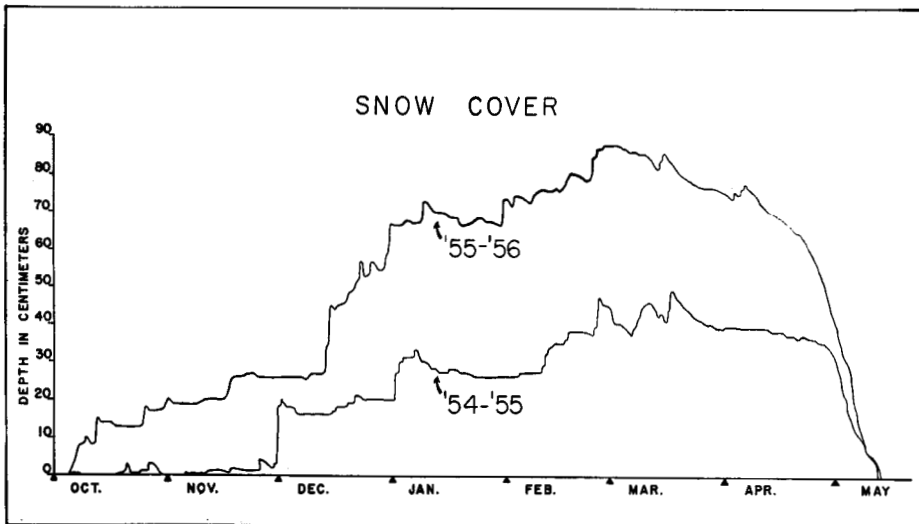


Fig. 2. Snow cover, subarctic-spruce area, winter 1954-5 and winter 1955-6.

It should be noted how the fluctuations at the 9-inch level follow those of the ambient air more closely during the snow-free period than during the periods of snow cover.

### Snow period

After the fall thermal overturn the temperatures of the upper moss layers fall more rapidly than do the deeper ones. From the time of the overturn until the snow cover reaches a depth of 15-20 centimetres the fluctuations in temperature are quite marked and agree well with the fluctuations in ambient air temperature. After the snow cover reaches this critical depth (Fig. 2) the fluctuations at the upper moss layers smooth out remarkably and the rate of fall at the lower moss layers lessens. It is noteworthy that the arrival of this critical snow thickness is usually accompanied by a change in behaviour of the forest floor mammals. Before this thickness is reached activity of shrews and red-backed voles is common on the snow surface; after this thickness is reached surface activity is markedly reduced. This phenomenon has also been noted in the Eurasian taiga by Formosov (1946). This critical snow thickness may well be called the *hiemal threshold*. In 1954 the hiemal threshold was not reached until December, while in 1955 it was reached in late October. The period between the thermal overturn and the hiemal threshold is undoubtedly the most critical interval in the annual cycle of the bioclimate of the forest floor mammals, because during this period occur the greatest fluctuations in bioclimate temperatures. The onset of the thermal overturn appears to be governed by the regular decrease in solar radiation, whereas the appearance of the hiemal threshold is governed by the more or less fortuitous date of arrival of the snow cover which varies greatly from year to year.

The absolute minimum at 6 inches occurred on December 25-26, 1954, when a temperature of  $+18.5^{\circ}$  was recorded. The absolute minima at moss surface, 3 inches and 9 inches did not occur until February 8, 9 and 10, 1955, when the temperatures there reached  $-9.5^{\circ}$ ,  $+0.5^{\circ}$ , and  $+20^{\circ}$ , respectively. This sequence nicely illustrates the insulating properties of taiga snow. The "cold snap" in late December, 1955, occurred with a cover of 19 centimetres of loose, uncompacted snow and the 9-inch level reached  $+21^{\circ}$ . During January a thaw occurred with several falls of wet, heavy snow and accompanying compaction of the cover. During the "cold snap" of early February, 1955, the 9-inch temperature reached its minimum for the winter, even though the snow cover was now 22 centimetres in thickness and the ambient air fell to only  $-47^{\circ}$ , a point 7 degrees above the absolute minimum.

The subnivean temperature regime of the winter 1955-6 was somewhat different from that of the preceding winter. The thermal overturn occurred about October 4, the first measurable snow cover on October 10, and the hiemal threshold during the last 10 days of October. The absolute minima at all depths occurred on December 12 when the moss surface reached  $+5^{\circ}$ , the 3-inch layer  $+6^{\circ}$ , the 6-inch layer  $+15^{\circ}$  and the 9-inch layer  $+23^{\circ}$ . For the rest of the snow period the moss surface, with the exception of one  $+6^{\circ}$  reading, did not drop below  $+11^{\circ}$ ; the 3-inch layer, not below  $+11^{\circ}$ ; the 6-inch layer, not below  $+19^{\circ}$ ; and the 9-inch layer, not below  $+26^{\circ}$ . The fluctuations were not so marked as those of the previous winter. For nine consecutive visits in early February, 1956, the 9-inch layer remained

constant at  $+29.5^{\circ}$ , even though the ambient air fluctuated between  $+24^{\circ}$  and  $-28^{\circ}$ .

The thermal regime of the 6-inch layer appears to have been different in the two winters, but because the thermistor was replaced during the intervening summer this difference may be an artifact due to slightly different positions. I have noted, however, in the thermal gradient of peat and coniferous needle litter in a bog in Cheboygan County, Michigan, a "thermocline" similar to that which occurred in the SPR area during the winter 1954-5. In the peat of the temperate zone the irregularity occurred between 1 and 3 inches below the surface.

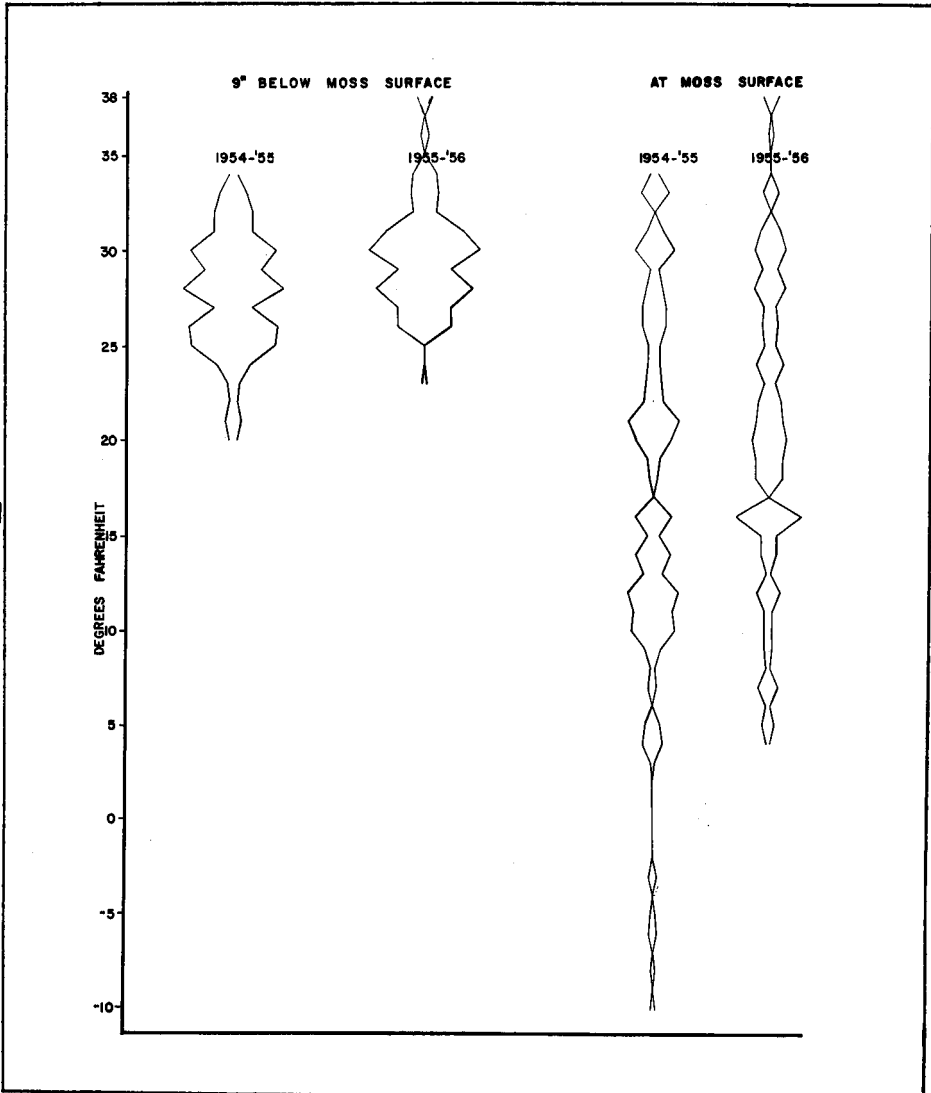


Fig. 3. Climograph of subnivean environment, winter 1954-5 and winter 1955-6.

One should note also the lag in temperature drop at the 9- and 6-inch layers when there is a marked drop in ambient air temperature during periods of snow cover, and how quickly these temperatures recover; and conversely how slowly they rise when the ambient air temperature rises during the summer and how quickly they recover. There is an apparent tendency to return toward  $+32^{\circ}$ .

### Discussion

From the foregoing resumé of the thermal environment of this sample of taiga one may make several generalizations. One feature of the forest floor environment is its stable temperature; comparatively warm in winter and cool in summer. During the two winters and one summer considered here the 9-inch temperature varied only 27 degrees while that of the air ranged through 152 degrees. Figure 3 graphically illustrates the stability of this environment during the periods of snow cover. It also illustrates the effectiveness of the moss cover itself as an insulator and, together with Figure 2, the effect of different thicknesses of snow cover on range and fluctuations of subnivean temperatures. A climograph such as this is constructed by plotting the frequency of observations of a given temperature on the abscissa and the temperatures on the ordinate. A line joining these points gives the resulting climograph figure. A completely stable environment would result in a horizontal line figure while an infinitely variable one would result in a vertical line figure. Scholander *et al.* (1950a, 1950b, 1950c) have shown that the physiological critical temperature of small mammals of taiga and tundra generally prevents them from using the supranivean environment for more than a few moments. Thus, the major adaptation to the taiga which these mammals exhibit is behaviour patterns that cause them to abandon surface activity almost entirely at the time of the hiemal threshold. A complete description of these behaviour patterns, the environmental stimuli and the releasing mechanisms, if any, would be a fruitful and revealing investigation. Those kinds of small mammals which are morphologically unable to take advantage of the subnivean environment or whose behaviour patterns are such that they cannot become subnivean are generally unable to ecise the taiga. Johnson (1951, 1954) has confirmed the suitability of this subnivean environment for small mammals. He puts great emphasis on the "meteorological event" or "cold snap." This is undoubtedly important in the lives of the animals living above the snow, but the "cold snap" is a distant and foreign event in the lives of the subnivean animals.

The temperature regime of the forest floor under the snow is very stable in time but not in space. Because of the protection afforded by the trees, the snow cover is not uniform in depth but is interrupted by bowl-shaped depressions about the base of each tree. In the language of the Kobuk Valley Eskimo these depressions are known as "qámaniq." Here the snow depth varies from scant at the tree base, slowly increasing towards the branch tips and suddenly increasing at the edge of the "snow shadow." The temperature regime varies from cold and fluctuating at the tree base to warm and stable beyond the edge of the qámaniq.

In the fall of 1954 a series of nine thermistors was buried 1 inch deep and at 6-inch horizontal intervals from the base of the south side of the trunk of a 12-inch DBH spruce out to 54 inches from the trunk. The last three thermistors were beyond the edge of the qámaniq. Sample readings are given in Table 1. Preliminary results from a study using subnivean live traps indicate that *Clethrionomys* tend to avoid the qámaniq in favour of those parts of their home range with a full snow cover.

Bader *et al.* (1954) observed that the air within a snow mass is practically always saturated with water vapour. This situation undoubtedly obtains in the atmosphere of a burrow or tunnel system through the moss under the snow. This saturated atmosphere offers ideal conditions for intraspecific communication by scent. As I have shown elsewhere (in press) for *Blarina*, a genus of temperate zone shrews, a saturated atmosphere in their tunnels is an essential feature of the habitats in which they occur. The genera of taiga shrews, *Sorex* and *Microsorex*, being smaller than *Blarina*, are probably even more susceptible to changes in atmospheric moisture.

Table I

Date	Air	Base of trunk		Beyond qámaniq	
	temperature	Temperature	Snow depth	Temperature	Snow depth
Nov. 22, 1954	+ 2° F.	+9.5° F.	trace	+14° F.	1 cm.
Dec. 22, 1954	-25° F.	-2.5° F.	8 cm.	+9.5° F.	17 cm.
Jan. 28, 1955	-11° F.	+2.5° F.	8 cm.	+13° F.	20 cm.
Feb. 21, 1955	-33° F.	-6.5° F.	13 cm.	+10.5° F.	35 cm.

The silence of the subnivean environment must be a potent factor in the evolution of the sensory systems of the mammals inhabiting it. This silence can be experienced by a human during a stay in a snowhouse. Disturbance of the snow cover by footsteps close by fairly explodes upon the ears against a background of silence. When the uncommon winds occur the roots and bases of trees creak and crackle.

Thus the subnivean environment of the taiga is characterized by temperatures with a narrow range of variation and rather gentle fluctuations, silence, darkness and a saturated atmosphere. The supranivean environment, in contrast, is characterized by air that varies from saturated to very dry and by air that can be still or in motion, by cyclic light and darkness, and by temperatures with a wide range of variation and markedly violent fluctuations. In addition the snow cover acts not as an insulating blanket above the animal but as a hindering mass through which the animal must wade. These factors and the morphological and behavioural adaptations to them have been considered in the classic work by Formosov (1946). Not only does the supranivean animal have to contend with the snow underfoot, but the snow which collects on the trees also exerts a powerful effect on arboreal activity. Formosov noted that this snow which collects on trees is known to the people of the Siberian taiga as "kukhta" or "navis." The Kobuk Valley Eskimo use the term "qali" to refer to the snow which collects



on trees, as distinct from "api," the snow which collects on the ground. The Athabaskans of the Fort Yukon region, Alaska, use the term "zá" for snow in a general sense and "dé-za" for snow that collects on trees. Biologists studying the taiga would do well to use these and other snow terms of northern peoples since English is notably deficient in them.

In summary, we see that those small mammals which have become adapted to utilize the subnivean portion of the subarctic taiga have available an environment that is climatically quite distinct from that which is 1 to 3 feet above them. No other ecotone, except the hydrosphere-atmosphere interface, affords such a sharp environmental gradient as does the snow cover in the subarctic taiga. Knowledge of the presence of this sharp ecotone between what are actually two quite distinct environments results in obvious implications for our understanding of such biological phenomena as geographic distribution patterns, ecological segregation, "Bergmann's Rule," "Allen's Rule," "Merriam's Life Zones," and seasonal changes in behaviour patterns.

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