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SEASONAL AND GEOGRAPHIC VARIATIONS
IN THE THERMOREGULATORY
BEHAVIORS OF TWO SPECIES
OF PEROMYSCUS

by

JOHN WILSON EEDY, B. Sc., M. Sc.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

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The undersigned recommend to the Faculty
of Graduate Studies acceptance of the thesis
"Seasonal and Geographic Variations
in the Thermoregulatory Behaviors
of two Species of Peromyscus"
submitted by John Wilson Eedy, B.Sc., M.Sc.,
in partial fulfilment of the requirements for
the degree of Doctor of Philosophy.

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ABSTRACT

The thermoregulatory behaviors of white-footed mice (Peromyscus leucopus noveboracensis) and woodland deer mice (Peromyscus maniculatus gracilis) were investigated. Mice were live-trapped during summer and winter near the northern and southern limits of their respective ranges. Laboratory experiments were conducted within 1-7 days after trapping so that the mice would still be acclimatized to natural climatic conditions. Mice were also tested after acclimation for at least 2 months to a variety of constant laboratory environments. Three types of behavior were investigated: seasonal surface activity in the wild and in the laboratory, temperature selection in a gradient and nest-building behavior.

The winter catch of mice per 100 trap-nights increased from the most northern area trapped, in Quebec, to the most southern, in Virginia. P. m. gracilis appeared to be less surface-active in the winter than P. l. noveboracensis. The summer trapping results did not show these same patterns. Thus the northern mice appeared to reduce their surface activity levels from summer to winter to a greater extent than those from southern areas. Only in Virginia were more mice caught per 100 trap-nights in the winter. This was also the only area where winter breeding was evident. In Quebec, summer trapping success was relatively poor and no Peromyscus was

caught in winter in spite of considerable effort.

P. m. gracilis selected higher mean temperatures than P. l. noveboracensis after all categories of acclimation or acclimatization. Within each subspecies, the mice from the more northern locality selected higher temperatures than those from the south in otherwise similar experimental groups.

When tested after winter capture or after acclimation to 2°C, mice of both subspecies and from all study areas selected higher temperatures than they did after summer capture or acclimation to 22°C. Thus exposure to colder environments caused the elevation of mean selected temperatures. This elevation was always more pronounced in P. m. gracilis than in P. l. noveboracensis.

In the fall the mean temperatures selected by Ottawa P. l. noveboracensis rose prior to the drop in winter temperatures for which they tended to compensate. These mice also selected higher mean temperatures after exposure for 2 months to high (95%) relative humidity, short (8 1/2 hr. daily) photoperiod, isolation and lack of nesting materials in the 2°C room, or even sometimes after certain changes in handling or experimental techniques.

P. m. gracilis always built better nests than P. l. noveboracensis. Either acclimation at 2°C or conducting experiments in the 2°C room accentuated this

interspecific difference. In addition, pairs of P. m. gracilis of either the same or opposite sexes were more compatible and built better nests than P. l. noveboracensis.

All 3 types of behavior indicated that P. m. gracilis are better adapted than P. l. noveboracensis to live in a colder, more northern environment. Being less surface-active in the winter means that P. m. gracilis are exposed less often to the severity of the northern winter climate. Their selection of higher temperatures and building of better nests both indicate a greater drive to escape ambient cold. These behaviors are very important to the success of small mammals such as Peromyscus in a cold climate.

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INTRODUCTION

Small mammals can extend their geographic ranges into areas of inhospitable climate only by making maximal use of nests and other means to avoid exposure to environmental extremes that they cannot physiologically tolerate (Hart, 1971:12). Hayward (1965) stated that in a small mammal such as Peromyscus the selection and modification of a suitable microclimate are of major temperature-adaptive significance. King (1968b) remarked that Peromyscus frequently abandon intolerable conditions of temperature and humidity by moving until suitable conditions are encountered.

In spite of the fact that several reviews briefly discuss behavioral thermoregulation (Fraenkel and Gunn, 1940; Bodenheimer, 1941; Viand, 1955; Fry, 1947, 1967; Ivlev and Leizerovitch, 1960; Whittow, 1970, 1971), in most cases with mammalian studies it has been considered secondary to physiological processes. Bligh (1970) emphasized the fallacy of this approach by stating that behavior is the primary means by which animals survive in inhospitable places.

A study of comparative behavioral thermoregulation in two closely related species of mammals that overlap throughout part of their geographic range, but that experience quite different local climates throughout the

rest of their ranges, could provide valuable information as to how behavior helps small mammals survive despite a severe climate.

The present study involved 3 types of behavior related to thermoregulation: seasonal activity levels, temperature selection, and nesting. The investigation of seasonal changes and changes brought about by adaptation to controlled laboratory environments, as well as the interspecific and geographic nature of the study mean that behavioral thermoregulation has been looked at to a degree never before approached. Hopefully this will further elucidate an area of research that at present entails too much speculation and too little experimentation.

I. The Animals

Rodents of the American cricetine genus Peromyscus are perhaps the most ideal small mammals for studies of natural phenomena either in the laboratory or in the wild. They can be obtained with relative ease and in adequate numbers almost anywhere in North America, and are quite amenable to laboratory culture (Blair, 1968). Of the 57 species recognized by Hall and Kelson (1959), Peromyscus maniculatus and P. leucopus have the widest geographic ranges, the greatest number of subspecies and according to Blair (1956) we know more about the former than about any other species of wild mammal. The representatives of these two species found in southeastern

Ontario, southern Quebec and most of northeastern United States are P. m. gracilis (Le Conte) and P. l. noveboracensis (Fischer). These are the animals studied in the present thesis and will usually be referred to simply as "gracilis" and "noveboracensis" hereafter. Appendix I contains a discussion of the study made in an attempt to verify the identity of the Quebec form of Peromyscus used in this research. King (1968a) has edited a book that reviews extensively all the information known to date about Peromyscus.

Figure 1 shows that the ranges of gracilis and noveboracensis overlap extensively from Minnesota eastward through southeastern Ontario and parts of Quebec to New Hampshire and southern Maine (Hall and Kelson (1959) as modified by Waters (1962) and D.A. Smith (personal communication)). In this area of sympatry, the two forms resemble each other quite closely in size and other external features (Baker, 1968) as well as in breeding habits (Layne, 1968), feeding habits and food preferences (Cogshall, 1928; Klein, 1960). Both forms have been trapped in the same forest habitats within the area of overlap, often being caught in the same or adjacent traps (Trebella and Bradshaw, 1969; Smith and Speller, 1970). The apparent close ecological relationship between these two similar forms has given rise to much speculation as to whether the "competitive exclusion principle", which states that "complete competitors cannot co-exist" (Hardin, 1960), holds true. There do appear to be

Fig. 1. Ranges of Peromyscus maniculatus gracilis (broken line) and P. leucopus noveboracensis (solid line) in eastern North America. Hatched area indicates the area in which the ranges of the two subspecies overlap. Numbers represent the 4 trapping locations used in this study:
1) Westmoreland County, Virginia, 2) Ottawa, Ontario, 3) Algonquin Park, Ontario, and 4) Lac St. Jean-Saguenay River Area, Quebec. The map is reproduced from Didow (1972).

numerous small but significant behavioral, ecological, and physiological differences between the two forms (Miles, 1965; Smith and Speller, 1970; Didow, 1972).

In detailed studies of habitat selection in areas of mixed populations, Klein (1960) felt that the gracilis in New York had a more restricted habitat, generally being associated with a cooler, hemlock-birch-northern hardwood type of climate, while the noveboracensis, although not showing as clear a preference, tended to be found in the warmer oak-chestnut forests. Clark (1964) trapped both forms in southeastern Ontario in all the wooded habitats that he studied, with the exceptions that only noveboracensis were found in one particular warm, dry, deciduous woodlot, and noveboracensis were caught more often than gracilis along forest peripheries. Wrigley (1969) found that in southern Quebec, gracilis were caught in all types of wooded habitats but were most abundant in the cool, damp conifer and mixed forests while noveboracensis abounded in warm, dry, lowland forests and were absent in the boreal forest habitats. Smith and Speller (1970) agreed that one population of noveboracensis in southeastern Ontario avoided mixed and cedar forest associations while they found that gracilis inhabited the whole study area, co-existing with noveboracensis in the upland hardwood section.

The large zone of overlap between the two forms and the fact that each extends considerably either to the north or south of this area has led to several theories involving habitat selection or the physiological ability of the mice to adapt to the differences in the habitats involved. Klein (1960) felt that the selection of habitat depended largely on differences in soil temperature with the gracilis living in cooler areas. Ogilvie and Stinson (1966a) found that under laboratory conditions noveboracensis selected higher temperatures than gracilis. Other comparative studies have concluded that gracilis preferred cooler, damper coniferous forest macrohabitats, whereas noveboracensis prefer warm, dry deciduous areas (Osgood, 1909; Clark, 1964; Smith and Speller, 1970) in the areas where they overlap. It must be noted that none of these authors was investigating actual microhabitats. Dice and Sherman (1922) caught gracilis more often in dry hardwood than in damp coniferous areas when trapping north of the range of noveboracensis. This means that the habitat separation of the two forms in the zone of overlap is probably due to more than just habitat selection, with some other type of competitive behavior keeping the gracilis out of the hardwood areas.

The present study was designed to investigate behavioral thermoregulation in these two forms of mice taken from near their northern and southern limits and

from their zone of overlap. The mice were tested after either natural seasonal acclimatization or constant temperature acclimation in the laboratory. It was hoped to gain further insight into the ecological significance of thermoregulatory behavior to the actual microhabitat preferences, survival and distribution of these animals.

II. Seasonal Activity

A number of authors have compared the success of trapping small mammals in the summer to that in the winter (Beer, 1961; Beer and MacLeod, 1966; Fuller et al., 1969; Smith, 1971; Fordham, 1971). However, many of these studies have included only one species and almost all have been conducted in only one geographic area. Hart (1971: 21) concluded that behavioral mechanisms would tend to reduce the rate of energy expenditure of small mammals that could avoid environments of high cooling power. One way of avoiding such environments would be for the mice to remain for longer periods in their nest at times of the year when, or in geographic locations where, cold weather is prevalent. Comparing the results of trapping two species of Peromyscus during summer and winter and in several geographic areas would give an indication of the relative differences in the surface activity levels of these mice. This could relate to their relative success in surviving in a cold climate.

III. Temperature Gradient Experiments

A. Temperature Selection

When exposed to a gradient of temperature animals tend to move towards and spend more time within a particular temperature zone. Such movement is one of the simplest methods of evading unfavorable environmental conditions. Observation of these movements is one of the easiest methods to quantify behavioral thermoregulation. Viaud (1955) noted that the selection of the temperature zone within which animals spend the most time, hereafter referred to as the "selected temperature", is the psychological behavior corresponding to the physiological optimal temperature for the particular animal. It should be noted, however, that the "comfortable" environment chosen by an animal is quite often cooler than that which would be optimal for the animal's health (Lowry, 1969).

Temperature selection was first demonstrated by Mendelssohn (1895) who studied the temperature gradient response of protozoans. Since then this phenomenon has been studied in a wide variety of animals including mites (Madge, 1961), insects (Barlow and Kerr, 1969), fishes (Ogilvie and Anderson, 1965), amphibians (Lillywhite, 1971), reptiles (Herter, 1940), and birds (Ogilvie, 1970a).

Herter (1934, 1936, 1940) was the first to investigate mammalian temperature selection, experimenting with European bats and rodents. Since then it has been studied in a number of small mammals including Chiroptera (Herreid, 1967), Carnivora (Ponomarev, 1944), and Rodentia (Bodenheimer, 1941, 1949; Smith and Fisher, 1956; Sinichkina, 1962; Östbye, 1970; Eedy and Ogilvie, 1970). Several preliminary studies have also been done on Peromyscus maniculatus bairdii (Stinson and Fisher, 1953), P. leucopus noveboracensis (Scribner, 1956) and P. m. bairdii, P. m. gracilis and P. l. noveboracensis (Ogilvie and Stinson, 1966a).

A variety of methods of studying temperature selection has been employed. These include counting the number of bar-pressing responses that a rodent will produce to obtain a hot or cold reinforcement while being kept in an uncomfortable environment (Weiss and Laties, 1961; Panuska and Popovic, 1963; Epstein and Mileston, 1968; Carlisle, 1970). The problem with this method is that although comparisons can be made with the results of other experiments in the same apparatus, no absolute values or ranges for selected temperature can be determined. Also one has to train the animals to respond in these tests; this takes time, causes changes in the behavior of the animals, and makes it impossible to test animals soon after capture in their natural environment. Many authors have inferred temperature selection by simply observing the behavior of

the animals in their natural habitat. Licht and Leitner (1967), Daan and Wichers (1968) and Gaisler (1970) have used this technique with bats. One can catch or shoot reptiles, take their body temperatures immediately, and assume these to be the same as those of the preferred microenvironment (Myhre and Hammel, 1969; Brattstrom, 1971).

Perhaps the best and most frequently used method of determining the selected temperature of small mammals involves the use of a thermal gradient apparatus in which the animal is given the choice of a continuous range of many temperatures and observed to see in which range it settles most frequently. This is the method used by all the authors mentioned prior to the immediately preceding paragraph. Various types of gradient apparatuses have come into use. Gumma and South (1970) have used a multiple T-maze device that gave their hamsters a choice of 5 predetermined temperatures. This, however, does not give a continuous range of temperature and places too much emphasis on the subjective selection of the experimenter who decides which temperature choices to give the animals. Some authors (e.g. Kreiner, 1954) have given the animals a choice of air temperatures in a continuous gradient, but most authors feel that the temperature of the substrate is most important.

The greatest number of authors have used a linear floor-temperature gradient apparatus, modified after the design of Herter (1924). Their apparatuses have included the flat metal-floored gradients used by Eedy and Ogilvie (1970) and the tubular metal apparatus used by Stinson and Fisher (1953) and by Smith and Fisher (1956). These are heated at one end and cooled at the other by a variety of methods. Some parallel multi-gradient devices have come into existence and in one case such a system has been incorporated with digital output for direct computer analysis (Morrison and Warman, 1967).

Perhaps the latest modification to the Herter type of gradient is the circular gradient device first constructed by Kruger (1952). This apparatus solves the problem inherent in all the linear gradients that the ends of the runways form perfect retreats for positively thigmotactic animals such as small rodents, which tend to spend a large amount of time there. These so-called "end-effects" have been noted by almost all authors using linear gradients (Scribner, 1956; Ogilvie, 1965; Eedy, 1969). The type of apparatus utilized in this study will be described in more detail later.

B. Changes in Temperature Selection

Several authors have investigated factors causing changes in the mean selected temperatures of animals. It has been found in a variety of young mammals that the selected

temperature is quite high at birth and slowly lowers to adult levels as the animal matures (Baccino, 1935; Herter, 1936; Ogilvie and Stinson, 1966b; Eedy and Ogilvie, 1970). Eedy (1969) reported that treating shaven house mice with a local skin anesthetic caused a significant reduction in the precision of temperature selection with the mice being relatively insensitive to all but extreme temperatures. Smith and Fisher (1956) reported a similar lack of response from lemmings whose feet were protected by a thick layer of insulating fur from the temperatures of the gradient floor. Intraspecific genetic differences in house mice have been shown to cause a wide variation in mean selected temperatures, and breeding experiments have been run to determine how temperature selection behavior is inherited (Herter, 1936; Eedy, 1969). Ogilvie and Stinson (1966a) found that each of 2 different species of Peromyscus and each of 2 different subspecies of P. maniculatus selected a different temperature and with a different degree of precision. It is thus not surprising to find significant variation among the results of different experimenters, who determined selected temperatures for the same species, using a variety of apparatuses and techniques. In fact Hart (1971: 17) emphasized that although thermoregulatory behavior is very important as an ecological and behavioral characteristic of a species, owing to the variation caused by environmental as well as experimental conditions, temperature

selection has limited use as a tool in precise taxonomic studies.

The changes that seasonal acclimatization to natural conditions and laboratory acclimation to controlled conditions (as defined by Folk, 1966) cause in the thermoregulatory behavior of small mammals have been investigated. Herter and Sgonina (1938) found that the selected temperature of house mice decreased after they had been kept for several weeks at warm temperatures. A similar inverse relationship between selected temperature and acclimation to cold temperatures has been reported for house mice (Falls, 1956; Eedy, 1969), Mongolian gerbils (Eedy, 1969), and deermice (Stinson and Fisher, 1953; Ogilvie, 1965). It should be noted, however, that this inverse relationship may not be applicable to all small mammals since the opposite results have been obtained with voles (Wolburg, 1952) and lemmings (Falls, 1956). Eedy (1969) found that warm-acclimation caused a somewhat fluctuating rise in the selected temperature of house mice, but this was under conditions of abnormally high humidity, leading one to think that more than just temperature was involved.

In addition to these rather conflicting results concerning the effects of laboratory acclimation on temperature selection, a few reports are also available on variations of

selected temperature caused by acclimatization to seasonally changing outdoor conditions. For example Sinichkina (1962) reported that wild Norway rats selected higher temperatures when trapped in the summer than in the winter. Eedy (1969) reported that both wild-caught house mice, and white mice kept outside over a period of 1 1/2 years selected temperatures that varied inversely with the environmental temperatures at the times of experimentation. Ogilvie (1965) found that P. l. noveboracensis trapped in June selected higher temperatures than those trapped in November.

Thus, in view of the conflicting data regarding the effects of prior thermal experience of mammals on their temperature selection, it was felt that this area of research could bear further investigation. This is especially true when looking from a comparative point of view at mammals taken from their natural habitats. All previous acclimatization studies have been either very preliminary, using small numbers of animals, or else the animals have been semi-domestic or kept under semi-natural conditions.

In almost all studies of temperature selection the only environmental parameter investigated in connection with acclimation or acclimatization has been the ambient temperature. Many other variables can be equally important. A report of the National Research Council (1971) listed the most important climatic factors influencing animal behavior and physiology as temperature, humidity, wind velocity, solar radiation, precipitation and barometric pressure. Lowry (1969)

reported that in insects the behavioral reaction to a temperature gradient is inseparable from the reaction to the associated humidity gradient. Weihe (1971) stated that changes in the cooling power of air caused by wind velocity variation can be just as important to the behavior of a mouse as changes in ambient temperature. Photoperiod changes have long been known to influence mouse behavior (Falls, 1968). Also, solar radiation can have a profound effect on the energy budget of an animal (Gates, 1968). Precipitation has been found to cause increases in the activity levels of Peromyscus (Gentry et al., 1966). Studier and Baca (1968) stated that precipitation could cause changes in the relative concentrations of the atmospheric gases within a rodent burrow. I found no references indicating behavioral changes that were exclusively related to changes in barometric pressure.

C. Behavior Associated with Temperature Selection

Besides the fact that mice select a certain zone while in a temperature gradient apparatus, their other behavior in a gradient of temperature is important. The relative amount of activity has been noted to change not only the metabolic rate, and thus the heat production of mice, but also the conductance and thus heat loss (Hart, 1971: 41). The activity level could thus be expected to affect temperatures selected. Falls (1956) reported that

more active mice selected lower temperatures to compensate for the increase in metabolic heat production.

Posture is also an important thermoregulatory behavior. Didow (1972) remarked that variation in posturing behavior was one of the differences that caused laboratory, warm-acclimated noveboracensis to be less efficient at heat conservation than either noveboracensis acclimatized outside to summer or winter conditions, or than either acclimated or acclimatized gracilis. Mice lying fully stretched out on the floor of the gradient apparatus would greatly increase their body-surface area affected by the temperatures of that floor when compared to those curled up or sitting. Since the air above the floor has a much lower conductance than the metal floor, mice could be expected to be less affected by the thermal gradient while running, sitting, or grooming than when lying in close contact with the floor. Smith and Fisher (1956) reported that the frequency and location of a number of non-locomotory activities (voiding, grooming, attacking and resting) in normal lemmings were different in the temperature gradient than at room temperature.

IV. Nest-building Behavior

Nest-building and huddling are important heat conservation behavior patterns in Peromyscus (Thomsen, 1945;

Thorne, 1958; King et al., 1964; Hayward, 1965). Nest temperatures measured with thermocouples have been found to be as much as 20 to 24°C higher than ambient in the winter (Johnson, 1926; Eedy, 1969). Nicholson (1941) found that P. l. noveboracensis frequently nested together throughout the winter. He felt that the extra warmth provided by the group must be important to the survival of these mice during severe winter weather. Sealander (1952) noted that nest-building in P. leucopus was poorer in summer-caught mice than in winter-caught animals. Thorne (1958) found P. maniculatus built much better nests when kept at 8°C than when kept at 33°C. Kinder (1927) reported similar results with white rats. Gebczynska and Gebczynski (1971) found that at low temperatures the presence of a nest was more important in permitting a decrease in the energy consumption of voles (Clethrionomys glareolus) than was the number of animals grouped, although both huddling and nesting produced complementary reduction in the food consumption per vole.

From a comparative point of view, King et al. (1964) stated that the highly significant difference between species of Peromyscus in their utilization of nesting material provided correlates well with the north-south distribution of the animals, and the mean January temperatures of their habitats, with the animals from cooler areas using more nesting material. They found no significant differences

between sexes within each species. Layne (1969) and Wolfe (1970) also found no sex differences in nest-building behavior, each having studied three species of Peromyscus. However, both of these authors found distinct interspecific differences. They both said that microclimatic differences among their respective habitats were most important in causing these variations in nesting behavior. Wolfe thought that burrowers need not build as good a nest as tree- or surface-dwellers owing to the better insulation protection the soil gives to an underground nest. Layne stated that better nest-builders can survive in a more fluctuating climate.

V. The Present Study

Although there have been several studies of thermoregulatory behavior in small mammals, these have usually been rather superficial. The changes in this behavior occurring with seasonal, specific or geographic variation in animals have not been adequately covered. Most authors have treated seasonal acclimatization as equivalent to laboratory temperature acclimation. This study attempts to investigate changes in thermoregulatory behavior and most possible causes under both natural and artificially controlled conditions.

As nest-building may be the most important natural method of behavioral thermoregulation, it is important to compare changes in this behavior to those in temperature

selection in the same two species of mice adapted to similar environments.

By studying three different types of thermoregulatory behavior: seasonal activity levels, temperature selection, and nesting behavior, one might gain insight into the importance of these behaviors to the survival of small mammals. By using two similar forms of Peromyscus whose ranges overlap in one geographical region, but that otherwise inhabit areas differing both latitudinally and climatically, the ecological significance of these variations in behavior can also be investigated. Further, by trapping mice at each end of their respective geographic ranges in both summer and winter seasons, and also by acclimating them to various constant indoor environments prior to experimentation, one can hope to elucidate the importance of geographic, seasonal, and genetic differences in the thermoregulatory behavior of small mammals. No previous study has approached this problem with the thoroughness warranted by the importance of thermoregulatory behavior to the survival and distribution of small mammals.

METHODS

I. Field Studies

A. Live-trapping

A modified version of the Sherman live-trap (7.7 x 7.7 x 30.5 cm.) was baited with peanut butter. In the winter traps were supplied with terylene batting and Purina mouse chow to help the captured animals survive until collected. These supplements were omitted in the summer trapping as they became too easily fouled in wet weather. Traps were set at intervals of approximately 20 meters and were usually placed under logs, brush piles or beside trees in positions found by experience to be most successful. If the traps remained in a forest for several days without success, they were cleaned, rebaited and reset elsewhere. Captured Peromyscus were tagged with numbered monel fingerling tags in the ear for identification purposes. These mice were returned to the laboratory for experiments and breeding. Skulls and skins of all the Peromyscus that died were preserved in the Carleton University Museum of Zoology.

B. Trapping Areas

The two forms of Peromyscus were trapped both in the summer and winter at the northern and southern limits of their respective ranges (see Fig.1). In the overlapping

area (Ottawa) both noveboracensis (near the northern limit of its range) and gracilis (near the southern limit of its range) were caught in the same localities in some cases and in different ones in others, but the localities had similar climates. Descriptions of the 4 trapping areas used in this study follow.

1. Virginia

Traps were set near Leedstown (about 14 km south of Colonial Beach) in an area of Westmoreland County bordered by Virginia Secondary Highways 637, 640 and 641 (38° 7' N, 76° 58' W). Trapping dates were February 17-21 and June 30-July 6, 1970. This primarily agricultural land on the northeast side of the Rappahannock River has an elevation of about 30 m and is similar to the western shore region of Maryland, about 30 km to the north, described by Paradiso (1969). Trapping was done in bushy hedgerows with pines (Pinus spp.), white oak (Quercus alba), tulip-tree (Liriodendron tulipifera), sweetgum (Liquidambar styraciflua), sassafras (Sassafras albidum), red maple (Acer rubrum), black walnut (Juglans nigra), laurel greenbriar (Smilax laurifolia), hazelnut (Corylus sp.), dogwood (Cornus sp.), dwarf juniper (Juniperus communis), staghorn sumac (Rhus typhina), grape (Vitis sp.), honeysuckles (Lonicera spp.), trumpet creeper (Campsis radicans) and raspberry (Rubus sp.). These lines of trees and shrubs bordered and served as

windbreaks between adjacent fields of corn, soybeans and wheat which provide abundant food supplies for small rodents that inhabit the bushy hedgerows and nearby woodlots.

The climate of this area is moderate because of its proximity to the ocean and many tidal creeks and rivers. Mean monthly temperatures range from 1°C in January to 25°C in July, and Fig. 2 shows that the mean monthly minimal temperature falls below 0°C only from December to February. Thus this has the mildest climate of the 4 study areas selected. The average annual snowfall is only about 0.3 m, but as snow seldom remains on the ground for more than a few days, it is of little importance as insulative cover for small mammal microhabitats or as a possible deterrent to foraging.

2. Ottawa, Ontario

The several localities trapped were within 48 km of Ottawa (45° 25' N, 75° 42' W) in Ottawa-Carleton, Ontario. This area is in the Upper St. Lawrence Section of the Great Lakes - St. Lawrence Forest Region (Rowe, 1959) and is either under cultivation or wooded. Trapping was done in two forest types: (a) Cedar area: This area was located along Ottawa-Carleton Road 3 about 43 km SSW of Ottawa, between Dwyer Hill Station and Burritts Rapids. Periods of trapping in this area were March 2-18, March 24-31, August 4-13, and September 1-5, 1971 and January 13-24, 1972. Traps were set in low-lying,

Fig. 2: The monthly mean minimal ambient temperatures in the four areas studied. These were taken from U.S. Department of Commerce (1969, 1970) and Canada Department of Transport (1969, 1970, 1971) meteorological records. The temperature data for the four areas are depicted as follows: Quebec (○), Algonquin Park (●), Ottawa (◐), and Virginia (▲), while the (●) points represent months when the values for the Quebec and Algonquin Park areas were identical.

generally wet forests of white cedar (Thuja occidentalis) which contained or converged with mixed stands of broad-leaved trees such as red maple, sugar maple (A. saccharum), yellow birch (Betula lutea), white birch (B. papyrifera), large-toothed aspen (Populus grandidentata) and black ash (Fraxinus nigra), and conifers such as balsam fir (Abies balsamea), white spruce (Picea glauca), black spruce (P. mariana) and tamarack (Larix laricina). (b) Hardwood area: The second forest type consisted of several upland hardwoods stands within a 20 km semicircle south of Ottawa. The dominant species is sugar maple, with beech (Fagus grandifolia), red maple, yellow birch, white elm (Ulmus americana) and large-toothed aspen also common. This area was trapped January 16-20, February 7-10, March 2-8, and September 14-15, 1970 as well as January 24-26, February 7-21, March 9-23, and November 2-8, 1971.

The elevation of the Ottawa area ranges from 90 to 120 m above sea level. The climate is temperate with mean monthly temperatures ranging from -11° to 21°C . Fig. 2 shows that the mean monthly minimal temperatures are considerably lower than those in Virginia. The mean annual snowfall is 2.2 m and snow cover persists for at least four months, providing insulation and protection against predators to small mammals that nest or tunnel beneath it (Formozov, 1963). Snow also affects foraging behavior by covering many types of foods.

3. Algonquin Park, Ontario

This provincial park consists of 7,540 sq km of forested land, lakes and rivers used primarily for recreation and lumbering. It lies in the Algonquin-Pontiac Section of the Great Lakes-St. Lawrence Forest Region (Rowe, 1959). The dates of trapping in this area were January 23-30 and March 13-19, 1970 as well as July 2-9, 1971. Traps were set in mature upland hardwood forests between park mileposts 10 and 33 along Highway 60 in Peck, Canisbay and Sproule Townships, Nipissing District (45° 35' N, 78° 30' W). The most abundant trees in the forest were sugar and red maples and yellow birch, with varying admixtures of eastern hemlock (Tsuga canadensis) and eastern white pine (Pinus strobus). Although the area trapped is not at a significantly higher latitude than Ottawa (it is approximately 220 km due W of the city), its elevation of 400 to 500 m has a great influence in making the climate cooler. The growing season is short and daily maximal and minimal temperatures often differ greatly in this area, more than in any of the areas studied, especially during the summer when night frosts may occur. Fig. 2 shows that the mean minimal daily temperatures are about 2°C lower than those in the Ottawa area; and the mean monthly temperatures range from -12° to 19°C. The average annual snowfall is about 2.4 m and snow cover is present for about five months.

4. Quebec

This study area was in the Saguenay River Basin from Lac St.-Jean eastward to the St. Lawrence River. It lies in the Saguenay Section of the Great Lakes - St. Lawrence Forest Region of Rowe (1959). The land is fairly flat; much is under cultivation, some is industrial land, while bogs and marshes are common. Much of the forest has been heavily logged or burned.

Most trapping was in selected small forest tracts in Chicoutimi County within a 48-km radius northwest, southwest and southeast of Chicoutimi (48° 25' N, 71° 4' W), especially around St. Leon-de-Chicoutimi near Lac Labrecque. The dates of trapping were December 29, 1969-January 9, 1970, August 7-18, 1970 and January 9-16, 1971. The forests trapped had various mixtures of balsam fir, white spruce, black spruce, trembling aspen and white birch, with small numbers of eastern white pine, jack pine (Pinus banksiana), eastern white cedar and grey birch (Betula populifolia). Smaller in size but fairly abundant were immature aspens, mountain maple (Acer spicatum) and bushy willows (Salix spp.). The dominant ground vegetation was bush honeysuckle (Diervilla lonicera) and sarsaparilla (Aralia nudicaulis). Some trapping was also done in similar habitats in Charlevoix-Est County near St. Siméon (47° 50' N, 69° 53' W).

The lower altitudes (65 to 230 m) and the numerous lakes and rivers in the Saguenay Basin moderate the temperatures from those of surrounding higher areas. The mean monthly temperatures range from -16° to 18°C . Fig. 2 shows that the mean minimal temperatures here are very similar to those of Algonquin Park during the summer but are more severe in winter. The mean annual snowfall of 2.5 to 3.3 m is greater and persists longer (almost six months) than that of any other area studied.

Climatic data were obtained from the Canada Department of Transport, Meteorological Branch (1969, 1970, 1971) and the U.S. Department of Commerce (1969, 1970).

II. Laboratory Studies

A. The Animals

Both sexes of mice were used in all laboratory studies. Whenever equal numbers of each sex were available, they were used in each experiment. Mice were kept in galvanized steel mesh cages 45 cm x 37 cm x 24 cm except in cases where special accommodation is mentioned. A stainless steel tray containing wood shavings was placed in the bottom of each cage. Mice were fed Purina Laboratory Chow ad libitum. All laboratory studies used mice at least 2 months of age and weighing over 15 g. Each mouse was

used only once in any one experimental group (i.e. in no case were the results of more than one experiment with each mouse used to calculate any mean temperature selection value). In the few cases which a mouse was retested, several months intervened between tests and the pre-test acclimation conditions were changed putting the animal in a different experimental grouping.

B. Temperature Selection

1. Apparatus

Figure 3 illustrates the temperature gradient apparatus which consisted of a 3 mm thick copper tube with a 6.5-cm. inside diameter. This was moulded into a circle with an internal circumference of 405 cm. The tubing was insulated with black-painted styrofoam covering it on all sides except at the inner surface. Here a clear plexiglass window was set at an angle about 45° from horizontal into a 4 cm. wide slit in the copper. This slit formed an observation window running completely around the inside of the apparatus except for the two points where the tube was entirely immersed in the heating and cooling baths at opposite ends of the apparatus. Sixty-two divisions, called "positions" below and each 6.3 cm. in length, were demarcated by black lines on the plexiglass window. A single position (1) 14 cm. long was the coldest compartment and a single position (33) also 14 cm. long the warmest. All other

Fig.3. The circular, continuous temperature gradient apparatus. a, cold bath; b, refrigeration unit; c, hot bath; d, control panel for the apparatus; e, temperature gauge; f, plexiglass-covered viewing slit; g, styrofoam insulation; h, observation blind; i, 4 60-watt lamps; k, seat for observer; m, timer and power switch; n, timer; and x, the 4 removable entrance sections.

positions (2 to 32) were double, one of each pair being on the left and the other on the right of the observer who faced the hot end (position 33). This gave essentially two identical gradients of temperature connected at the cold and hot ends.

The cold end was maintained at about 0°C by means of a portable refrigeration unit with an immersable cooling coil. The latter was placed in an antifreeze (polypropylene glycol) bath in which the cold end of the tube was located. At the hot end the tube was situated in a similar tank containing water and two immersion heaters. Temperatures along the floor of the apparatus were measured by means of disc-type thermistors placed at positions 1, 5-left & right, 9-left & right, 13-left and right, 17-left and right, 21-left and right, 25-left and right, 29-left and right, and 33. The thermistors were connected to a calibrated galvanometer on which the temperatures at these positions could be read directly. Temperatures at the intervening positions were determined by interpolation. Readings made at the beginning and end of each experiment seldom varied more than 1/2 C° at any position, and were averaged. The floor temperatures in a typical experiment ranged from about 0°C to 52°C in an approximately linear fashion (Fig. 4). The relative humidity of the air at various positions in the temperature gradient apparatus was measured using a Lovibond anhydrous

Fig. 4. The temperatures observed at different positions in the tube during a typical experiment. The closed circles (●) represent the right side, and the open ones (○) the left side of the apparatus.

cobalt thiocyanate humidity test kit. The relative humidity varied from 5% at the hot end to 95% at the cold end.

Herter and Sgonina (1938) suggested that in a gradient situation the animal responds primarily to the floor temperature. Stinson (1952) altered the air temperature gradient in a linear gradient apparatus by blowing air through it. As the animals continued to select the same floor temperatures, he concluded that they responded mainly to these. Smith and Fisher (1956) came to similar conclusions when they found that the fur on the feet of lemmings kept these animals from reacting to thermal gradients to which they reacted in a normal way after the fur was removed. In the present study, selected temperatures have been expressed in terms of floor temperature in keeping with the procedure followed in most previous temperature gradient work.

Figure 5 shows the apparatus and the associated structures erected so that the presence of the observer would not disturb the behavior of the mice. A black cardboard shield was erected in the centre of the circle. The observer sat within this and viewed the mice through red plastic-covered slits. Peromyscus supposedly cannot see well in red light and are thus not disturbed by light passing through red filters (Finley, 1959). However, Vestal and Hall (1972) felt that Peromyscus reacted to red

Fig. 5. Photograph of the gradient apparatus.

Fig. 5. Photograph of the gradient apparatus.

light in much the same way as to dim white light. In my experiments though, the mice seemed less disturbed by movements of the observer with red plastic covering the viewing slits than without it. The apparatus was illuminated by fluorescent room lighting supplemented by four incandescent 60-watt bulbs positioned to give a relatively even illumination of 16 to 18 foot-candles, measured by a photographic light meter, at the window surface. This illumination exceeded 1 foot-candle, above which level Peromyscus show less activity (King, 1968b). It was hoped that because of this and the fact that experiments were run during the daytime, the mice would be more quiescent and select the temperature at which they would nest or sleep.

2. Procedure

In each experiment a single mouse was placed in the gradient tube by means of one of four removable entrance sections and left for one hour to adjust to the conditions of the apparatus. Then every minute for one hour, the location of the mouse in the gradient was recorded, giving a total of 60 observations for each experiment. After a mouse remained at the same position for five minutes, it was made to move by tapping on the window. This ensured that the mouse had to sample new temperatures. The mid-point of the animal's body was

used as the selection point. If this was on the line between two positions, the two were recorded alternately. A sample data form used to record an animal's behavior in the gradient is illustrated in Appendix II.

The inside of the apparatus was cleaned after each experiment with a 1% solution of R2L disinfectant (G.H. Woods Co. The original product was a 10% solution of alkyl dimethyl benzyl ammonium chloride.) This was to eliminate the orientation of animals towards the position occupied by a former test mouse, a behavior noticed by Scribner (1956) and Ogilvie (1965). An attempt was made to lessen the effects of variables such as time of day, or the position at which the mice entered the tube. The four removable entrance sections were used in rotation as entrances for the experimental animals. Experiments were also run at various times of the day between 1000 and 1800 E.S.T.

(a) Control Experiments: The basic type of control experiment was performed by placing a mouse in the tube with the heating and cooling apparatus shut off so that the entire apparatus was at the uniform temperature of 21°C. The apparatus was thus uniform in all aspects except at positions 1 and 33 where the absence of a window made these compartments darker. Experiments were run with 15 noveboracensis and 14 gracilis under such control conditions.

A second type of control experiment was run in which the temperature gradient was present. A group of CF #1 white laboratory mice (Mus musculus) was tested in the gradient apparatus after being acclimated for periods of 2 to 3 months in temperature controlled rooms. Twelve were acclimated at 22°C and 10 at 2°C. This same highly inbred type of mouse from Carworth Farms, New York, had been used previously in similar experiments (Ogilvie and Stinson, 1966a; Eedy, 1969) and thus provided a good test for the compatibility of the results of experiments by the aforementioned authors using a linear gradient apparatus, and the present experiments using a circular gradient.

Also with the gradient present, a third group of control experiments was run with 5 noveboracensis acclimated at 22°C and 5 at 2°C. Each of these experiments consisted of 3 separate 20-minute observation periods, one after the animal had been in the gradient for each of 2, 4, and 6 hours. This group of experiments was designed to determine if the animals were selectively acclimating themselves to the gradient temperatures in the time they were in the apparatus. It should also have indicated if the time that the animals were left to accustom themselves to conditions of the apparatus prior to observations was long enough.

(b) Gradient Experiments: In experiments with the heating and cooling apparatus in operation the gradient was turned on to run for at least one hour to stabilize the temperatures before a mouse was placed in the tube. The procedure was otherwise the same as in control experiments.

3. Estimation of Selected Temperatures

Previous workers have employed a variety of statistical methods to estimate selected temperatures. For example, Herter (1934, 1936, 1940) used the mean of the gradient temperatures at which the animals were seen to rest. Stinson (1952) used both mean and modal values, and Smith and Fisher (1956) expressed selected temperatures in terms of modes alone, while Falls (1956) used medians. Perhaps the most meaningful estimate of temperature selection is the range of all temperatures at which the animals stop taken in its entirety (Stinson and Fisher, 1953; Østbye, 1970), but this does not lend itself well to comparative or statistical analytic techniques. In the present study, in keeping with most of the recent work (Ogilvie and Stinson, 1966a, 1966b; Eedy and Ogilvie, 1970) and with the original work of Herter (1934, 1936), the selected temperature of each mouse was expressed as the mean of the 60 temperatures at which the animal was observed in a one-hour experiment. The selected temperature of all of the mice of one subspecies and in the same experimental

category is expressed as the mean of all observations plus or minus two times the standard error of the mean ($\bar{x} \pm 2S_{\bar{x}}$). This error factor is an estimation of the 95% confidence interval (Steel and Torrie, 1960) and allows a quick estimation of the significance of differences ($p < .05$). The distribution of the numbers of observations at the various floor temperature was close to a normal curve, so that conventional statistical methods could be used. Statistical methods and tables were taken from Steel and Torrie (1960), Kemeny and Kurtz (1968) and a computer program lent by the Statistical Research Service, Canada Department of Agriculture, Central Experimental Farm, Ottawa. A complete description of statistical techniques is given in Appendix III.

C. Exposure of Mice to Various Natural and Artificial Climatic Regimes

1. Natural Climatic Regimes

Peromyscus were caught in both summer and winter in Virginia, Ottawa and Algonquin Park and in the summer only in the Quebec region as described p.20-27. The upper half of Table 1 gives the values of a number of climatic parameters to which the mice were potentially exposed in the field prior to capture and subsequent experimentation.

Table 1. Environmental parameters for the field and laboratory regimes to which mice had been acclimatized or acclimated prior to experimentation.

Climatic Regime	Mean Relative Humidity %	Mean Temperature °C	Mean Minimal Temperature °C	Daily Light hr	Vapor Pressure mm Hg	Temperature Humidity Index *	Heat Accumulation **
a) Field:							
Virginia							
summer	70	23.4	17.3	15	15.0	29.15	—
winter	67	0	-6.4	11	3.6	10.55	—
Ottawa							
summer	72	18.0	15.6	14	11.1	24.08	2093
fall	81	10.2	5.4	10	7.6	15.23	1527
winter	70	-8.4	-15.9	11	1.7	2.50	399
Algonquin Park							
summer	71	17.1	9.7	15	10.4	22.05	1959
winter	77	-15.5	-20.3	9½	1.6	-6.24	260
Quebec							
Summer	76	16.8	11.3	14	10.9	22.28	1947
b) Laboratory							
2°C Room	95	2	2	12	5.0	3.51	1068
22°C Room	60	22	22	12	11.9	29.92	2148
Greenhouse	28	21	16.6	9½	5.2	35.65	—
25°C Room	90	25	25	12	21.4	26.67	2310

* see National Research Council (1971)

** see Baskerville and Emin (1969)

2. Laboratory Climatic Conditions

Differences in the temperatures selected by mice after seasonal acclimatization and after acclimation to various laboratory regimes have been reported in the literature. Thus manipulation of some of the environmental parameters while controlling others at constant levels might further elucidate the question of how seasonal or geographic environmental changes affect the behavioral thermoregulation of small mammals. Peromyscus were acclimated for periods of 2 to 3 months to various combinations of temperature, light and humidity and then tested in the temperature gradient apparatus. Many authors have stated that these aforementioned parameters are the most important environmental factors affecting the ecology and behavior of natural populations of small mammals (e.g. Hart, 1971:47; National Research Council, 1971).

Peromyscus were acclimated in 2 temperature controlled rooms for which parameters are indicated in Table 1. Mice of both subspecies and from all trapping areas were acclimated in a constant temperature room at $22^{\circ} \pm 1^{\circ}\text{C}$. The photoperiod was regulated so that 12 hours of light alternated with 12 hours of darkness, and while the relative humidity was not regulated, it was recorded continuously by means of a hair-hygrograph recorder (Table 1).

Mice were kept in groups of 3 to 5 in wire mesh cages with wood shavings for litter and nest-building. Both wild-caught and laboratory-born mice were tested in each experiment type depending upon availability. The mice were fed Purina Laboratory Chow, with supplements of sunflower seeds, and water supplied ad libitum.

Twenty noveboracensis were isolated in a well ventilated, light-tight box in this 22°C room. The inside light was controlled by means of two time switches and a series of three 7 1/2-watt light bulbs. The latter were controlled so that first one, then two and finally all three bulbs turned on each morning to imitate the gradual increase in morning light intensity. The reverse occurred each evening to simulate dusk. It was hoped to approximate outdoor ambient light conditions both in daylength and, to some extent, in intensity of light from summer, when the animals were put in, until December when gradient experiments were run. The box and the same mice were then maintained at this December photoperiod until the following June, when a second set of experiments was run in the gradient. The physical conditions in the box varied from those of the outside room because of the smaller plastic cages necessitated by the lack of space in the box, and the greater isolation from disturbance by persons entering the room. Temperature and humidity conditions were the same however.

Both subspecies were also acclimated at $2 \pm 1^{\circ}\text{C}$ in a temperature-controlled room with 12 hours of light per day. Owing to deaths, no Quebec gracilis were available by this time in the study, but all other groups were represented. The only variation in cage conditions from the previous acclimation at 22°C was that terylene batting was provided as nesting material. In a further test to determine what effect nesting and huddling had on acclimation, 29 Ottawa noveboracensis were kept at 2°C in separate cages with metal mesh floors to keep them away from any nesting materials. The extreme stress of these conditions can be deduced by the fact that 10 of the 29 mice exposed in this way died during the 3 months of the experiment. At least 2 months of adaptation time was allowed in all constant temperature acclimation experiments prior to gradient trials. This should be more than enough according to Andjus et al. (1971).

A third controlled temperature room was set up with a temperature of $25 \pm 1^{\circ}\text{C}$ and 12 hours of light per day. The relative humidity was controlled at 90%, slightly lower than that in the 2°C room but much higher than that in the 22°C room (Table 1). Thirteen Ottawa noveboracensis were acclimated to these conditions for periods longer than 2 months. Twelve noveboracensis were also exposed to conditions of winter ambient light, from December 10 to February 20, with the relative humidity less than 28% and

warm, fluctuating (from 18 to 25°C) temperatures (mean 21°C) in a greenhouse on top of the Tory Building. It was hoped that this variety of exposures might elucidate some of the seasonal environmental factors causing changes in the thermoregulatory behavior of mammals.

D. Behavior Associated with Temperature Selection

A number of behaviors were observed while the mice were in the temperature gradient apparatus. An attempt was made to relate variations in some of these parameters to the differences observed in temperature selection.

Postural and activity behaviors observed included attacking the sides of the apparatus, locomotion, sitting, curling up, lying and grooming. Estimations of the precision of temperature selection included the standard deviation about the mean of the observations during each experiment and the average size of the zone of the temperatures at which each mouse rested most frequently. Other data such as weights of mice and numbers of feces left after each experiment were also recorded.

E. Nesting Behavior

Both noveboracensis and gracilis from the Ottawa "overlap" area were tested in various ways to attempt to detect differences in nest-building behavior. Members of both subspecies were acclimated to either 2°C or 22°C for

periods over 3 months; some nesting experiments were then run in these same constant-temperature rooms. The cages were at times moved so that acclimation and experiment at times occurred in the same and at times in a different temperature room. In 104 experiments mice were put in cages singly to determine sexual or interspecific differences. Forty-seven tests were also run with 2 mice of the same sex and 21 tests with pairs of the opposite sexes in each cage. At times the same mice were used in several experiments, but care was taken that they were kept in the same experimental acclimation group. The 23 cm. x 23 cm. x 27 cm. cages used were made of heavy metal mesh, with a tray on the floor holding wood shavings and food. Adequate mouse chow and water were provided. Some of the mice were also provided with terylene batting that they could pull from a dispenser and strips of paper towelling that they could tear up for use in the nest. The mice were observed (with attendant disturbance kept to a minimum) twice daily for 4 days.

Several criteria were used to measure the nest-building behavior. These included the amount of terylene used, whether paper strips were torn up and used, whether wood chips were used, whether food was stored in or near the nest, and the quality of the nest built. These criteria are similar to those used by Thorne (1958), Layne (1969) and Wolfe (1970). The method of assessment

of quality of nest-building was modified from that of Thorne (1958). Nests were rated on a numerical scale referred to as the Nest Quality Index (NQI) and ranging from 1 to 6, with 1 representing a very good, completely rounded nest and 6 represented no nest at all (see Fig. 6). Twice daily evaluations meant that the time taken to construct a certain standard of nest could be used as an additional evaluation factor.

Fig. 6. Criteria for judging nest quality. Numerical values were given to the different types of nest as indicated, from 1 for a good, round, compact, complete nest to 6 for no nest at all. These values were designated as Nest Quality Indices (NQI).

RESULTS AND DISCUSSION

I. Field Studies: Trapping Results:
Seasonal Surface Activity

Table 2 shows the seasonal variation in numbers of the 2 forms of Peromyscus and other species of non-hibernating small mammals caught in each of the trapping areas. The number of animals of each species caught is indicative of the relative numbers of animals and their relative activity levels. The ratio of summer trapping success (catch per 100 trap-nights) to that of winter gradually becomes larger with increasing latitude. Only in Virginia was the winter success greater than that of summer. Gentry (1968) reported similar population peaks in February when trapping Microtus pinetorum in South Carolina. Juveniles and breeding female noveboracensis were caught in Virginia during winter trapping. Brown (1945) reported that noveboracensis bred throughout the winter in Kansas. Mice in Virginia experience milder winters than mice from any other area in this study. The abundance of food left in farmland after mechanical harvesting would also help make winter breeding possible. Both Smith (1971) and Fordham (1971) reported that supplementary food allows for higher densities and earlier breeding in populations of Peromyscus. The greatest difference in success among the four areas was during the winter, while the summer trapping

Table 2. Seasonal and geographic variations in the results of live-trapping studies. (non-hibernating mammals)

Species	Study Areas	Virginia				Ottawa Areas				Algonquin Park				Quebec	
		summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter
<u>Peromyscus leucopus noveboracensis</u>		127*	88*	1	6	22*	24*		3						
<u>P. maniculatus gracilis</u>				10*	14*			74*	14			25*			
<u>Oryzomys palustris</u>		1													
<u>Clethrionomys gapperi</u>					6		1		2					4*	
<u>Microtus pennsylvanicus</u>		3							2						
<u>Mus musculus</u>		43	21				1								
<u>Tamiasciurus hudsonicus</u> **					1	1	9	7				3		2	
<u>Sciurus carolinensis</u>						1	1								
<u>Glaucomys sabrinus</u> **				1	14										
<u>Blarina brevicauda</u>					7		1	2	25*			11		2	
<u>Sorex cinereus</u>					3		4		18			3		1	
<u>S. fumeus</u>					1		3		3						
<u>Mustela erminea</u>					2		4								
Trapping success (catch per 100 trap-nights)		14.5	17.3	8.5	3.6	6.4	2.2	11.6	2.4			3.1		0.3	
Number of <u>Peromyscus</u> as percent of catch summer/winter		75	78	92	37	85	55	89	25			59		0	
relative trapping success		0.84		2.36		2.91		4.84				10.30			

* predominant species caught in area per season

** Some of these 2 species were released and in a few cases may have been caught twice. All other species were removed as caught.

success in the three southern areas was approximately the same. Beer and MacLeod (1966) and Sadleir (1970) explained drops in the winter populations of mice as being due to high mortality rates at a time when there is no replacement breeding. Thus Virginia probably differs greatly from the other study areas on account of both its lower mortality, due to milder winters and abundant food, and its being the only one of the areas where winter replacement breeding took place.

Another factor accounting for the greater reduction in the number of animals caught in the winter from south to north may be the reduced activity levels of the mammals involved. Beer (1961) noted that although temperatures as low as -28°C did not stop the activity of P. l. noveboracensis and Clethrionomys gapperi outside the nest, their home ranges and movements were greatly restricted during the winter. The winter temperatures at night were often lower than this in Quebec, but seldom in Algonquin Park or Ottawa and never in Virginia during the present study. Howard (1951) also found Peromyscus to be less active when subjected to freezing temperatures. Falls (1953) reported that in winter P. m. bairdii were only one-third as active and spent only one-half the time out of the nest that they did in the summer. He also stated that during the winter, temperatures below -7°C caused a 20% reduction in the time spent out the nest as compared

with warmer winter nights. Fuller et al. (1969) found P. maniculatus to be almost impossible to trap in the winter near Great Slave Lake, N.W.T., Canada and attributed this to extensive periods of torpor in the mice.

The fact that Peromyscus are known to cache food for the winter (Abbot and Quick, 1970; and personal observations) means that less foraging is necessary in the winter. This again would not affect the Virginia results where the lack of snow cover and the ample food supplies result in an entirely different situation. The use of subnivean tunnels has been reported for Peromyscus as well as other small mammals (Smith and Smith, 1971; Formozov, 1963). However, Bovet (1968) and Smith and Smith (1971) have reported high degrees of Peromyscus surface activity even during extreme cold spells. This again would have no effect on the Virginian mice, where there is no substantial subnivean environment.

The percentage of Peromyscus among all non-hibernating mammals trapped declined greatly in the winter in all areas where gracilis was the predominant summer-caught subspecies. This did not occur, however, in either of the regions in which noveboracensis were caught in the greatest numbers. The relatively greater inactivity of gracilis during the winter may be due to behavioral adaptation to more severe northern winter

climate. The gracilis may spend more time at subnivean activity. Also they may have better food caches, and may be able to undergo longer periods in torpor than noveboracensis. All these factors would give advantages to a small mammal inhabiting a more northern habitat.

II. Laboratory Studies

A. Temperature Selection Experiments

1. Control Experiments

(a) Response to Uniform Temperature Conditions: Figures 7A and 7B show the irregular distributions of 15 noveboracensis and 14 gracilis respectively in the apparatus with the floor at a uniform 21°C along its entire length. A phenomenon similar to the so called "end effect" found by most authors using linear gradients (Stinson and Fisher, 1953; Ogilvie and Stinson, 1966a) was observed with the mice being recorded fairly frequently in positions 1 and 33, regions where the tube, inside the water baths, lacks a window slit. However, the percentage of observations involved in the "end effect" in these studies was considerably less than 30 to 80% of observations reported in linear gradient devices under similar uniform conditions.

Figure 7 shows that the noveboracensis were observed less frequently in the dark ends than were the gracilis. The single position at which the noveboracensis

Fig. 7. The distribution of mice in the gradient apparatus during control experiments at 21°C with no temperature gradient present.
A, results with 15 noveboracensis;
B, results with 14 gracilis.

*Note: The data for position 1 are shown on both sides of each histogram.

spent the highest percentage of time (8.1%) was position 2 (right) where a mouse could keep most of its body hidden and yet see through the window. The gracilis spent 25.4% of their time in the two end positions (1 and 33) while the noveboracensis spent only 8.0% of their time there.

(b) Control Experiments with Temperature Gradient

Present: The temperature selected by 12 white mice acclimated at 22°C was $30.3 \pm 0.38^\circ\text{C}$ while that selected by 10 white mice acclimated at 2°C was $31.4 \pm 0.50^\circ\text{C}$. The 1.1 C° difference between these mean selected temperatures was significant after analysis of variance ($p < .001$). Table 3 shows that both the mean selected temperatures were somewhat lower than those found for the same species by other authors. However, the degree of elevation of selected temperature after cold acclimation was approximately the same. The difference could be due in part to the authors who used linear gradient apparatuses overcompensating for "end-effects" by eliminating all observations at cooler than "normal" temperatures (see Eedy, 1969). In the present study, the mice stopped a number of times at various positions in the cooler regions of the gradient for reasons other than the thigmotactic "end-effect" response seen in a linear gradient. Since heat is more strongly avoided in a gradient apparatus than cold (see Herter's discussion in Kruger, 1952), the subjective elimination of cold observations

Table 3. Comparison of the mean temperatures selected by white mice (Mus musculus) in temperature gradient experiments.

Acclimation Temperature °C	Mean Selected Temperature °C	Range of Individual Means °C	Authors
22	32.3	29.8-35.5	Eedy (1969)
7	33.5	30.4-35.9	"
22	30.3	27.1-33.1	Present Study
2	31.4	28.4-34.5	"
22	31.8	26.2-34.7	Ogilvie and Stinson (1966a)
30	28.4	?	Falls (1956)
12	31.6	?	"
0	31.3	?	"
room	31.4	27 - 35	Bodenheimer (1941, 1949)
room	30.9	SD = 1.5	Maurus (1958)
room	25.1	SD = 0.12	Kreiner (1958)
room	34.6	?	Herter and Sgonina (1938)

by earlier authors could cause the mean selected temperature values to be biased towards the high end of the gradient. This was avoided here by use of an apparatus with reduced "end-effects" and the use of all resting observations in calculations. The range of about 6C° between the highest and lowest mean selected temperatures of individual mice was similar to that found by other authors.

The variation among the results of the authors listed in Table 3 agrees with the statement of Hart (1971) that temperature selection is too readily variable to be a species-specific character. Differences due to apparatus, experimenter, or other environmental variables mean that one cannot compare temperature selection results directly with those of other authors. Only when a comparative study is done using the same apparatus and techniques are the results and variations among results meaningful. Also it should be noted that the changes in the temperatures selected by mice acclimated to different temperatures appear to be largely unaffected by the variation of techniques and equipment; that is mice acclimated to cold temperatures by any of these authors appear to select temperatures consistently higher than mice acclimated by the same authors to warmer temperatures.

In the third series of control experiments in which 5 noveboracensis were observed during 3 twenty-minute periods, after being in the temperature

gradient for 2, 4, and 6 hours respectively, the variation in mean selected temperature due to differences among mice was greater than that due to the differences among the 3 tests given to each animal; however, the F-ratio of 1.95 between these two differences was less than the table value of 2.45 necessary to indicate significance ($p < .05$). This does indicate that the time in which the mice were in the gradient prior to experimentation did not cause significant variation in the results. The variation caused by acclimation in this case was not significantly greater than the variation among mice, or between treatments, but it was numerically greater in each case. The variation between mean selected temperatures after the mice had been in the gradient for 2 hours (25.2°C and 26.3°C), for 4 hours (26.1°C and 27.3°C), or for 6 hours (25.8°C and 28.7°C) for the warm- and cold-acclimated mice respectively, did not show any consistent pattern.

This indicates that the mice were not selectively acclimating themselves to the temperatures of the gradient during the short period of time in which they were in the apparatus. This is not surprising since Andjus et al. (1971) could find no significant acclimation or deacclimation changes in rats after periods of over 2 days. It must be noted that the cold-acclimated mice selected higher temperatures after each length of time (mean of 3 tests = 27.8°C) than the warm-acclimated mice (25.7°C). This will be discussed later.

2. Gradient Experiments with Peromyscus

(a) Interspecific and Geographic Variation: Figures 8A and 8B indicate the distribution of 30 noveboracensis and 20 gracilis during experiments with the temperature gradient present. These results can be compared to those in Fig. 7A and 7B where similar Ottawa mice, also acclimated to 22°C, were in the tube at a constant temperature. The presence of a temperature gradient eliminated the "end-effects" that had existed when the apparatus was at a uniform 21°C. The temperatures at the hot and cold ends of the apparatus must have been extreme enough to keep the mice from resting at these positions. Temperature selection was indicated by the mice in each individual experiment being observed in a normally distributed fashion about a central "mean" selected temperature when the thermal gradient was present. In contrast, in the uniform temperature experiments (Fig.7) the distributions were more random with no central tendency.

Table 4 shows the mean temperatures selected by gracilis and noveboracensis from each of the geographic areas studied. These were significantly higher for winter-caught animals or those acclimated to a constant 2°C environment than for summer-caught or warm-acclimated mice.

Fig. 8. The distribution of mice in the apparatus with the temperature gradient present. A, result with 30 noveboracensis; B, results with 20 gracilis. The mice were acclimated at 22°C and were all descendants of animals caught in the Ottawa area.

Table 4. Mean selected temperatures $\pm 2 S_{\bar{x}}$ (number of mice) for the various test groups.

Climatic Regime	<u>gracilis</u>		<u>noveboracensis</u>	
	Algonquin Park	Ottawa	Ottawa	Virginia
Winter Outside	30.0 $\pm$.36 (12)	30.0 $\pm$.34 (12)	26.8 $\pm$.30 (31)	26.0 $\pm$.36 (21)
Summer Outside	27.9 $\pm$.30 (20)	25.7 $\pm$.22 (30)	26.1 $\pm$.30 (26)	25.7 $\pm$.22 (30)
2°C Room	30.3 $\pm$.42 (16)	29.3 $\pm$.24 (18)	27.3 $\pm$.28 (30)	26.0 $\pm$.36 (21)
22°C Room	26.3 $\pm$.32 (21)	26.8 $\pm$.26 (20)	25.8 $\pm$.32 (30)	23.5 $\pm$.38 (21)

The mean temperatures selected by the 22°C acclimated noveboracensis (23.5°C and 25.8°C) and gracilis (26.3°C and 26.8°C) varied considerably from the values reported by Ogilvie and Stinson (1966a); these were 32.4°C (S.D. = 4.7°C) and 29.1°C (S.D. = 1.3°C) respectively. One can explain the absolute differences in terms of techniques and apparatus, as was shown earlier. However, the fact that their noveboracensis selected higher temperatures than gracilis (the opposite of the finding in the present study) is hard to explain. A possible cause of this variation in results could be that Ogilvie and Stinson used noveboracensis from London, Ontario, which is a considerable distance from any of the regions trapped in the present study. They kept the mice in a completely different type of cage, and under less rigidly controlled laboratory conditions than those of the present study. The smaller number of mice used by these authors also resulted in higher standard deviations and consequently a greater relative difference in mean selected temperatures would be expected.

Table 5 gives the results of an analysis of variance by the method of fitting constants performed on the data of Table 4. This analysis indicated that the selected temperatures varied significantly between the two subspecies in all tests, that the selected temperatures

Table 5. The results of an analysis of variance by the method of fitting constants performed on the data of Table 4. (For explanation of the difference between adjusted and hierarchical methods see Appendix III (4).)

Cause of Variance	Adjusted Analysis		Hierarchical Analysis	
	F-Ratio	Significance	F-Ratio	Significance
Species	13.05	$p < .001$	4.91	$p < .001$
Sexes within Species	2.41	none	1.47	none
Acclimation vs. Acclimatization	2.56	none	1	none
Cold vs. Warm Temperatures	35.18	$p < .001$	32.29	$p < .001$
Area of Origin	5.58	$p < .005$	5.33	$p < .005$
Interactions:				
Species x Laboratory vs. Field Adaptation	1	none	1.05	none
Species x Cold vs. Warm	6.54	$p < .005$	6.18	$p < .005$
Sexes/Species x Adaptation	1	none	1	none

were affected by the geographic differences in origin of the groups of mice, and that they also depended on whether the pre-test adaptation regime was warm (summer and 22°C) or cold (winter and 2°C).

There was also an indication that the adaptation regime affected the two subspecies differently.

There appeared to be no sexual difference in temperature selection, nor any differences that could be attributed to whether the adaptation was under constant laboratory conditions or in a fluctuating field environment. However, there was a significant difference between acclimation and acclimatization results when the individual experimental group means were compared, as will be discussed shortly. Since there was no indication of an interaction of the sexes with the adaptation regimes, it can be concluded that the sexes do not react differently to the adaptation regimes and that sexual differences are relatively unimportant in the temperature selection behavior of these mice. These results supported those of other authors (Herter, 1936; Ogilvie, 1965; Eedy, 1969) who found no bases indicating sexual variation in temperature selection. Thus all mean selected temperatures expressed in the following study are pooled values for both sexes.

The individual mean selected temperatures of the various experimental groupings of mice were also compared

by analysis of variance. In all cases the differences between treatment groups were significantly greater ($p < .001$) than the differences between the 60 observations within each mouse experiment, and likewise the differences between animals within each treatment were greater ($p < .001$) than the differences between experiments with individual mice. Most important, however, the differences between treatments were significantly greater than the differences between individual animals in almost all cases tested. The only cases in which there were no significant differences were between winter and cold-adapted Algonquin Park gracilis, between Algonquin Park and Ottawa winter gracilis, and between winter and fall Ottawa noveboracensis.

These results agree with those of the earlier analysis of variance by the method of fitting constants in most ways. The major disagreement is that there appears to be a difference between acclimation of mice to indoor constant temperatures and acclimatization to outdoor fluctuating but similar temperatures. This only becomes apparent when one compares results using only one species from one area at a time. This disagreement occurs because the differences between areas and species must be great enough to overshadow differences between acclimation and acclimatization when analysis of variance is performed. Only when most of these former sources of variation are eliminated from the analysis by comparing only 2 test groups at a time do the latter ones become significant.

Although other experiments (Eedy, 1969) have not shown clear differences between the effects upon temperature selection of acclimation and acclimatization, several physiological and anatomical variables reported by Hart (1957), Heroux (1961), and Didow (1972) show that the effects of natural and artificial adaptation can be quite different. In fact Hroux (1970) felt that indoor cold acclimation results in unnatural pathological changes in mammals. He altered some of these changes artificially by varying the thyroxine content of the diet fed to rats in captivity. The lack of difference in mean selected temperature between the two populations of winter gracilis in the present study is not surprising since adaptation conditions are rather severe in each case (Table 1), the same subspecies is involved in both, and the two areas of origin are not far apart geographically. The microclimates in the two cases are likely more similar than the macroclimates since both have a large snow cover at the time of year in which trapping was done. Hayward (1965) found that the winter microhabitats of a number of P. maniculatus subspecies were very similar and uniform in spite of great differences in the gross climates of the areas investigated.

The similarity in temperature selection between fall- and winter-acclimatized noveboracensis from Ottawa could be caused by the lack of snow cover in the fall when the minimal night temperatures average 5.4C (Table 1).

A second reason is that there may be endogenous factors as well as exogenous ones involved in seasonal acclimatization (Hart, 1971:47). Also climatic factors other than temperature per se may be the clues for the onset of winter thermoregulatory behavior. This will be discussed further later. From a purely speculative point of view it would seem obvious that if differences in behavioral thermoregulation between summer and winter give mice survival advantages, these changes would help more if they occurred in the fall, before they were actually of vital importance to a mouse's survival. Eedy (1969) also found that white house mice kept outside selected temperatures as high in October as in the winter months, and significantly higher than those selected by summer-acclimatized mice. Hart (1971:50) reviewed data that suggest that the photoperiod and other environmental cues may cause acclimatization effects before the seasonal changes in temperature are actually perceptible.

The analysis of variance by the method of fitting constants was repeated while allowing for the incorporation of some environmental covariates (see Table 6). Of the four environmental covariates tested, (minimal temperature, relative humidity, hours of light, and mean temperature, all averaged for the three weeks prior to experimentation), only the mean temperature and relative humidity showed a significant effect on the mean selected temperature of the different groups of mice. Also mean temperatures appear as important

Table 6. Analysis of variance of the data from Tables 4 and 5 after allowance has been made for a number of environmental covariates. The following symbols are used: N, no significance ($p > 0.05$); *, significant ($0.01 < p < 0.05$); **, significant ($p < 0.01$); #, change has occurred from the results of the analyses shown in Table 5.

Cause of Variance	Covariates Allowed For				
	1) Minimal Temperature	2) Relative Humidity	3) Photoperiod	4) Mean Temperature	Both 1, 2, 3, 4
1) Minimal Temperature	N				*
2) Relative Humidity		**			**
3) Photoperiod			N		N
4) Mean Temperature				*	**
A) Species	**	**	**	**	N#
B) Sexes/Species	N	N	N	N	N#
C) Laboratory vs. Field	N	*#	N	N	N#
D) Warm vs. Cold	**	**	**	**	**
E) Geographic Area	**#	**#	**#	**#	**#
Interactions					
A x C	N	N	N	N	N
A x D	**#	N#	**#	**#	N#

as minimal air temperatures when changes in the selected temperature are being investigated. This is contrary to the opinions of some authors (Fuller et al., 1969) who stated that extreme temperatures are most important in affecting the biology of small mammals. The difference could be due to minimal temperatures being less important to mice that can avoid them during the coldest periods by staying in their nests. Hart (1971:10) emphasizes the importance of animals avoiding environmental extremes that could not be tolerated without protection.

The difference in selected temperature after outdoor or indoor exposure to warm or cold environments, which was not significant in the analysis of variance without covariates, becomes so when different combinations of environmental covariate regression effects are removed. This supports the conclusion stated earlier that there are probably differences between the effects of acclimation to indoor conditions and of acclimatization to outdoor seasons that, because of the unbalanced nature of the data, could not be detected in the analysis of variance.

Another interesting fact that emerges from this method of analysis is that when all four covariates are removed, the difference in selected temperature between the two species is not significant. This means that differences in selected temperature caused by species variation (genetic)

are largely a result of the influence of environmental factors on the two species. In other words the two species are different in their degree of adaptation to the environment as measured by the covariates analyzed, and that if allowance is made for these much of the specific temperature-selecting difference between them disappears. Thus if the noveboracensis were able to adapt to the same conditions as the gracilis, there would be little difference in temperature selection between the two species. Some other factor such as heat production capability (Riedel, 1967; Didow, 1972), foraging behavior, or food and microhabitat preferences (Smith and Speller, 1970) must be involved in the actual geographical separation of the two species. Miles (1965) speculated that gracilis and noveboracensis coexist in the Ottawa area because the whole biotic environment is dynamic, and favors a different species at different times. He stated that one could not explain the distribution in terms of a finite number of parameters, although he did emphasize differences in the reactions of these mice to the stresses of population density, predation and conflicts as being important. Differences between the two species in the ability to arouse from torpor have been noted by Morhardt (1970). He considered that the ability of P. maniculatus to arouse more quickly than P. leucopus may reflect a higher possible maximal metabolism (cf. Didow, 1972).

(b) Seasonal Acclimatization and Laboratory Acclimation Effects: In order to analyse further the effects of adaptation to different environmental parameters on thermoregulatory behavior, Ottawa noveboracensis were acclimated to various constant temperature regimes similar in all but one or two factors (Table 7).

(i) Effects of Varying Relative Humidity: During acclimation experiments the Ottawa noveboracensis were kept in a number of constant temperature rooms which exhibited a variety of relative humidities. Analysis of variance indicated that there were significant differences between the temperatures selected by warm-acclimated mice kept at 90% RH, 60% RH or in the greenhouse at 28% RH ($p < .005$) (see Table 7). The humidity was not the only factor involved as a cold-acclimated group of 3 to 5 mice per cage kept at 95% RH selected temperatures significantly lower than the warm-acclimated ones at 90% RH. Also there was little geographic variation in seasonal relative humidity among the areas in which mice were caught in the field although there were large differences in selected temperatures.

(ii) Effects of Varying Photoperiod: Varying the light alone caused inconsistent results. Mean temperatures selected by the 12 noveboracensis kept at 22°C for longer than 2 months with 9 1/2 hr. of light daily were $29.0 \pm 0.41^\circ\text{C}$ in the summer and $28.4 \pm 0.24^\circ\text{C}$ in the winter. Analysis of variance showed that these values are significantly higher

Table 7. The temperatures selected by Ottawa noveboracensis after acclimation or acclimatization to various conditions.

Acclimation Conditions				Selected Temperature °C ($\bar{x} \pm 2S_{\bar{x}}$ (n))
Temperature	Relative Humidity	Hours Light	Other	
2°C	95%	12	alone	30.0 $\pm$ 0.26 (19)
2°C	95%	12	group	27.3 $\pm$ 0.28 (30)
25°C	90%	12	group	28.2 $\pm$ 0.38 (13)
22°C	60%	9½	group	28.4 $\pm$ 0.24 (12)
22°C	60%	12	group	25.8 $\pm$ 0.32 (30)
22°C	60%	15	group	29.0 $\pm$ 0.41 (10)
21°C	28%	winter ambient	green-house	26.5 $\pm$ 0.40 (14)
Acclimatization				
summer				26.1 $\pm$ 0.30 (26)
fall				26.8 $\pm$ 0.38 (10)
winter				26.8 $\pm$ 0.30 (31)

than the temperatures selected by 30 Ottawa noveboracensis either kept in the same room with 12 hr. light daily, or kept in the greenhouse at fluctuating warm temperatures and winter ambient light which varied from about 9 1/2 to 11 hours daily; they are also significantly higher than the fall and winter values of Ottawa noveboracensis trapped outside. This inconsistency of results leads one to think that although winter light conditions may be one of the cues causing higher temperature selection, some other factors must have been involved, at least in the case of the 12 mice exposed at 22°C with 9 1/2 hr. daily light. Other factors involved could have been the isolation and lack of disturbance given these mice since they were kept in smaller plastic cages in a light-tight box and checked only once every two weeks. Later tests with 10 of the same mice in the same box kept over 2 months with the same 22°C temperature but with the light increased to 15 hr. per day also resulted in abnormally high selected temperatures. Mice kept in a similar warm environment with winter light conditions in the greenhouse selected temperatures statistically equal to those selected by fall- and winter-trapped wild mice immediately after capture. These results point out the importance of photoperiod to the seasonal changes in temperature selection. Although the photoperiod has not previously been shown to be correlated with mean temperature selection changes in mammals, such a correlation has been demonstrated in lizards (Ballinger et al., 1969)

and in snakes (Gehrmann, 1971). The photoperiod has been definitely associated with other acclimatization changes in rodents (Hart, 1971:50).

(iii) Effects of Varying Temperature: Acclimation to conditions of constant temperature was investigated in both species from each of their respective geographic areas as was indicated earlier. In addition to these studies, 29 Ottawa noveboracensis were acclimated to 2°C alone in cages and without nesting material. These conditions proved quite severe, as 10 of the 29 mice exposed in this way died within the two-month acclimation period. The mean temperature selected by the 19 surviving mice was $30.0 \pm 0.26^{\circ}\text{C}$, significantly higher than any of the other noveboracensis groups. This higher mean selected temperature could have been because those mice that survived to be tested did so as a result of exhibiting better thermoregulatory behavior when exposed to cold stress.

Gracilis from Quebec were also tested both in summer (mean temperature selected by 19 mice = $27.5 \pm 0.38^{\circ}\text{C}$) and after acclimation to 22°C (mean for 17 mice = $25.4 \pm 0.32^{\circ}\text{C}$). No winter tests were run since these mice could not be trapped in the winter and their poor survival and lack of breeding under laboratory conditions meant that few were left for cold acclimation. The summer temperature selection value was similar to that of the Algonquin Park gracilis but much higher

than that of Ottawa gracilis ($p < .001$). This could reflect the fact that temperatures in the Quebec and Algonquin Park areas were more similar in the summer than either one is to the Ottawa climate where summer temperatures are milder (Table 1). Didow (1972), who ran tests with many of the same mice used in this study, concluded that the physiological thermoregulatory ability of noveboracensis varied geographically mainly because of geographic differences in the climatic conditions to which they were exposed. He found that animals from the north maintained thermoregulation longer at low temperatures than those originating from the southern limits of the subspecies' geographic range. Hart (1971:17) quoted Kalabukhov and Ladygina as having found that Apodemus flavicollis from the Crimea selected temperatures 10°C higher than those from the more southern (warmer) Kharkov region. This finding is similar to the present ones since both species from the southern limits of their distribution selected lower temperatures than those from the northern limits.

(c) Correlation of Environmental Parameters with Temperatures Selected by Mice Exposed to Them: Coefficients of correlation between the various environmental parameters and the mean selected temperatures of Peromyscus exposed to them are presented in Table 8. The difference between this method of investigating the effects of single environmental factors upon behavior and the previously reported one of allowing for the

Table 8. Correlation of various environmental parameters with the selected temperatures of mice previously exposed to them.

Environmental Parameters	Significant When Considered as Covariate ? *	Correlation Coefficient	F-Ratio Value	Significance
mean monthly temperature	yes	-0.88	27.46	<0.05
minimal monthly temperature	not if mean temperature accounted for	-0.88	24.37	<0.05
heat ** accumulation	---	-0.49	4.03	0.05 < p < 0.10
hours of light	no	-0.62	5.10	0.05 < p < 0.10
relative humidity	yes	+0.65	5.81	<0.05
vapor pressure	---	-0.28	1.40	none
temperature-humidity index ***	---	-0.50	5.26	<0.05

* see Table 6, ** Baskerville and Emin (1969), *** National Research Council (1971)

regression effect can be seen in the high correlation shown in Table 8 between mean minimal exposure temperature and the mean selected temperature. Allowing for regression effects of minimal exposure temperature caused no significant changes in the results of the analysis of variance shown in Table 6. This emphasizes how minimal temperature or mean temperature are more or less inter-replaceable as parameters in regards to their effects on temperature selection in mice.

Heat accumulation, a method of estimating the ecological effects of temperature, according to Baskerville and Emin (1969), was slightly less than significant in its correlation with selected temperature. The reason for this is probably that only the macroclimate temperatures were available for all areas at all times to calculate this. As mentioned before, macroclimate parameters are important to the acclimatization of Peromyscus only in the degree to which they reflect the actual microhabitat of the mouse. Owing to snow and activity levels this degree is probably greater in the summer and the south than in the winter and the north.

Other environmental parameters were also tested this way. Hours of light did not show significant correlation to selected temperatures; this finding is much the same as was shown by the consideration of covariates during analysis of variance. Three methods of expressing humidity

were also tested. Relative humidity and the temperature-humidity index taken from the National Research Council (1971) showed almost the same degree of correlation with temperatures selected, but vapor pressure did not correlate significantly. This means that the conclusions of authors such as Lemaire and Benceny (1962a, 1962b) and the National Research Council (1971) who stated that relative humidity is a poor biological method of expressing humidity, are not corroborated by the temperature selection results.

It thus appears that the temperature, photoperiod and humidity of the environment to which they have been exposed all have some effect on the temperature selection of Peromyscus. These parameters are further discussed separately in the next 3 subsections.

(i) Relative Humidity: I found no literature reference on the effects of adapting mice to variations in relative humidity. Ivlev and Leizerovitch (1963) and Samosh (1969) reported that in house mice and hamsters, respectively, those living naturally in moist habitats select lower temperatures than those living in drier areas. This difference, however, is probably because the mice that have evolved to live in wet microclimates have also grown to select the coolness associated with them, rather than a short term seasonal acclimatization effect. Stinson (1952) found that within the temperature zone between 14 and 27°C, in which

P. maniculatus bairdii showed the greatest degree of wheel-running activity, high humidities caused decreases in this activity. He considered that this increased activity at lower humidities was related to higher evaporative heat loss. Lemaire and Benceny (1962a, 1962b) reported that high humidities are deleterious to the health of rats at both high and low temperatures. Orr (1959) and Gentry et al. (1966) found that rainy evenings caused higher activity levels in Peromyscus. Hart (1971:8) mentioned that the humidity is generally quite high in rodent burrows. Chenoweth (1917) felt that the reaction of noveboracensis to humidity was as important as, if not more important than, the reaction to temperature. Kreiner (1954) found that the temperature selected by white mice at 27% relative humidity was 0.6 to 1.0°C° higher than at 100% RH. His differences, however, were not significant. Lowry (1969) reported that temperature and humidity selection in insects are inseparable, and he felt that to investigate one without the other was meaningless. It is interesting also that the temperature gradient within any apparatus such as the one used in this study causes a humidity gradient from a high relative humidity at the cold end to a low one at the hot end. Measurements of relative humidity in the apparatus used indicated that it did not vary greatly in the areas where the mice spent the greatest amount of time. The relative humidity varied between 40-45% ($\pm$ 5%) in the area of the gradient with temperatures 20°C to 30°C. The humidity gradient throughout the apparatus was considerable,

running from 5% at the hot end to 90% at the cold. The very low humidity at the hot end would reinforce the aversion that mice show for high temperature.

The National Research Council (1971) stated that the temperature-humidity index correlated better with changes in animal behavior and physiology than any other environmental parameter. It is thus surprising that so little emphasis has been placed on relative humidity and its effect on adaptation physiology and behavior.

(ii) Photoperiod: The effects of different daily light regimes on adaptation were more difficult to analyze. The high temperatures selected by the Ottawa noveboracensis in the greenhouse during winter and those trapped in the fall lead one to speculate that light clues could be causing the mice to go through preadaptation changes in behavior to prepare for the coming winter cold. Gilbert and Page (1968) stated that both the photoperiod and light intensity may be involved along with temperature in the adequate stimulation to produce acclimatization changes. Sealander (1951) noted that both temperature and photoperiod were important in causing seasonal pelage changes in noveboracensis. King (1968b) asserted that the selection or construction of suitable nest sites or refuges prior to encountering intolerable conditions would be more advantageous than escaping from them after they occur. He remarked that while temperature and humidity

are probably the main cues, many others also exist. Among these photoperiod is probably very important. In the present study a short photoperiod in some cases caused the selected temperatures to approximate winter values, while in others the relationship was not so clear. The former finding could be explained by supposing that when all other factors (e.g. temperature, relative humidity) are at "neutral" levels, the selected temperature varies directly with the photoperiod. Changes in other environmental factors, however, override the effects of the light regime in most cases.

(iii) Temperature: Temperature is the only parameter that has received a great deal of attention in studies of adaptation. Reviews by Hart (1957, 1971), Hammel (1968), and Chaffee and Roberts (1971) amply cover the physiological changes associated with seasonal acclimatization or laboratory acclimation. In 3 previous studies that dealt with seasonal effects on temperature selection of house mice (Ladygina, 1952), Norway rats (Sinichkina, 1962) and P. l. noveboracensis (Ogilvie, 1965), a direct relationship between acclimatization temperature and selected temperature was observed. In other words, selected temperatures were generally highest during the summer and lowest during the late fall and winter, a relationship completely opposite to that obtained in the present study. The reason for this discrepancy is not immediately obvious, but it should be noted that at least one of these studies was strictly preliminary,

consisting of only a few experiments (Ogilvie, personal communication). The other 2 studies were reported in Russian papers from which little was learned of the experimental techniques or conditions.

On the other hand, Brown (1968) stated that woodrats selected warmer microhabitats in the winter and cooler burrows in the summer, in agreement with results of the present study. Kalabukhov (1953) and Mokrievich (1966) found that although the lowest temperatures selected by Apodemus and Cricetulus respectively were in the early fall, the spring-late winter selection was quite high, leaving one to speculate what the winter results would have been if experiments had been run during this season and the results compared to the summer peaks reported. In a previous personal study (Eedy, 1969) the results using both wild-caught house mice and white mice exposed outside in cages were similar to those of the mice tested in the present study in that in the former the mean selected temperatures of the 13 experimental trials over a period of 1 1/2 years varied inversely with the average seasonal temperatures at those times.

The effect of cold acclimation on mammalian selected temperature has been studied by a number of authors. The present findings that cold exposure caused a rise in the mean selected temperature agree with reports of authors

using white mice (Herter and Sgonina, 1938; Eedy, 1969), deer mice (Stinson and Fisher, 1953; Ogilvie, 1965) and Mongolian gerbils (Eedy, 1969). Two authors (Falls, 1956; Wolburg, 1952) have found the opposite results, both using microtines.

It is interesting to find that Ottawa noveboracensis acclimated to moderately warm temperatures (25°C) selected temperatures similar to those selected by mice that had undergone cold adaptation. Eedy (1969) found a similar result after keeping white mice in a chamber at 30°C. In both studies by the present author high acclimation temperatures were accompanied by high levels of humidity. Humidity can also be very stressful to animals, and it appears to cause changes in behavior. Perhaps one is getting a Selyé (1950) type of adaptation in which any stress condition results in behavioral changes, and a higher selected temperature. In fact the higher mean selected temperature could have been partially caused by a greater avoidance of areas outside the selected zone and thus fewer low temperatures involved in calculating the mean. Such a conclusion agrees with remarks by Herter in the discussion following a paper by Krüger (1952) and those of Ogilvie (1965) who stated that high temperatures are avoided much more than low temperatures when the animals are outside the selection zone.

The importance of severity of adaptation regime could also explain further some of the results of the present study. It could explain why the exposure of mice to cold without nesting material or companions caused the selection of much higher temperatures than exposure to the same temperature of groups of mice with nesting material. Ogilvie (1970) remarked on the extreme severity of the former type of exposure on mice. Likewise many of the seasonal variations in temperature selection between the two species could be explained by the degree of stress previously encountered by the mice. The Virginia noveboracensis selected temperatures similar to those selected by noveboracensis caught in Ottawa in the winter. This could be partly explained by the lack of snow cover in the Virginia area resulting in the micro-environments of the mice being as severe as those in Ottawa. Here, although the weather is colder, the deep winter snow makes the microclimatic conditions beneath it much milder (Foromozov, 1963; see also the descriptions of the climate of the trapping areas on pages 20-27). Likewise the Ottawa gracilis selected lower temperatures in the summer than those from either Quebec or Algonquin Park. Similarly Ottawa gracilis selected lower temperatures in winter than those from Algonquin Park. These results may be due to the milder climatic conditions in Ottawa (Table 1).

It seems obvious that behavior leading to a mouse remaining in an area with a less stressful temperature (perhaps close to thermal neutrality) would be of great survival advantage, especially after the mouse had been exposed to some energy-consuming stress in its environment. A sick, injured, or physiologically stressed mouse would thus be more apt to remain in a warm, "comfortable" environment until it had recuperated from the previously encountered stressful conditions. This type of reaction is more apt to be caused by laboratory acclimation than seasonal acclimatization. Mice can usually escape severe stress of the environment in nature by behavioral reactions.

It might be noted at this point that the thermoneutral zones, or ranges of temperature in which the mice have the lowest metabolic rates, are considerably higher than the selected temperatures for both species in this study. The thermoneutral zones have been determined as approximately equal (24°C - 34°C) for both noveboracensis and gracilis (Riedel, Smith and Hart, in preparation). The temperatures cannot be directly compared, since those measured in metabolic studies are air temperatures, while selected temperatures are floor temperatures, and other conditions of experimentation are quite different. One could speculate that the stressed, or cold-adapted mice select temperatures closer to the thermoneutral zone and thus waste less energy in thermoregulatory processes than the summer or

less stressed animals. In the latter, exploratory or foraging drives could take precedence over those of energy conservation.

The similarity between the temperatures selected by Ottawa noveboracensis and gracilis in the summer may be due to the lack of severity of temperatures that the mice experienced during this season. The much greater rise in selected temperature shown by the gracilis in winter could be interpreted as indicating that during more extreme conditions, the gracilis show a greater capacity than noveboracensis for the adaptation of their behavior, as exemplified by temperature selection, to the climatic conditions involved. This could be an important factor in allowing this species to have a more northern distribution, and to be found in the more severe, damper conifer habitats in the region of overlap (see Introduction). Table 9, a comparison of temperatures selected by individual mice of each form after separate acclimations to both 2°C and 22°C, supports this argument. In gracilis there was only one case in which a mouse selected a significantly higher temperature after warm acclimation. Four of 9 noveboracensis selected higher temperatures after warm acclimation, and only 3 selected higher temperatures after cold acclimation. The other 2 showed no significant changes. Thus, although some mice of both forms selected higher mean temperatures after cold acclimation, this change was much more pronounced in gracilis.

Table 9. The temperatures selected by mice after acclimation to 2 different temperature regimes. A minimum time of 2 months in each acclimation chamber meant that the experiments with each mouse were widely separated in time.

Mouse Tag Numbers	Selected Temperature ($\bar{x} \pm 2 S_{\bar{x}}$ °C) after acclimation to 22°C	after acclimation to 2°C	Signif- cance
10 <u>Ottawa gracilis</u>			
1716	26.6 $\pm$ 0.8	25.3 $\pm$ 1.2	*
B630	27.0 $\pm$ 1.3	31.1 $\pm$ 0.6	+
B632	25.7 $\pm$ 1.8	28.0 $\pm$ 0.9	+
B634	29.9 $\pm$ 0.9	30.8 $\pm$ 1.1	+
B641	25.4 $\pm$ 0.8	30.5 $\pm$ 0.6	+
B645	26.7 $\pm$ 0.5	29.4 $\pm$ 0.7	+
B647	27.1 $\pm$ 1.0	30.0 $\pm$ 0.6	+
B741	26.6 $\pm$ 0.8	31.1 $\pm$ 0.8	+
B755	27.1 $\pm$ 0.8	30.0 $\pm$ 1.4	+
B884	28.1 $\pm$ 0.8	27.3 $\pm$ 1.2	N
9 <u>Ottawa noveboracensis</u>			
1557	27.6 $\pm$ 1.8	27.9 $\pm$ 1.2	N
1547	22.7 $\pm$ 1.7	31.7 $\pm$ 1.5	+
1556	27.7 $\pm$ 1.2	24.1 $\pm$ 1.3	*
1551	27.5 $\pm$ 1.5	25.5 $\pm$ 1.4	*
1559	24.8 $\pm$ 1.0	26.7 $\pm$ 0.6	+
1561	27.2 $\pm$ 1.1	25.2 $\pm$ 0.6	*
1554	25.1 $\pm$ 1.9	25.9 $\pm$ 0.8	N
1552	27.1 $\pm$ 0.8	25.9 $\pm$ 1.4	*
1560	25.5 $\pm$ 2.0	28.2 $\pm$ 0.7	+

* warm-acclimated mice selected significantly higher temperatures than cold-acclimated mice did.

+ cold-acclimated mice selected significantly higher temperatures.

N acclimation differences caused no significant change in temperature selection.

Temperature selection appears to be one of the behaviors involved in the choice of a suitable microclimate by small mammals. It must be an important ecological and behavioral characteristic of every species. Small mammals can survive the rigorous variations in their microclimates only by using the appropriate behavioral responses (Hart, 1971). Although increased pelage insulation often occurs during winter acclimatization, this is of relatively little significance to a small mammal in terms of increased ability to survive a cold stress (Hart, 1964). Again the key to small mammals' success has been their ability to seek out a non-stressful microenvironment (Hayward, 1965).

In view of the importance of behavior to the survival of small mammals in a changing environment, it is obvious that these mammals must adapt their behavior so as to avoid actively the extremes of climate associated with the region in which they live. There is usually an inverse relationship between the selected temperature and the degree of cold stress (or other secondary stresses in the absence of this). The mice select cooler temperatures during the warmer seasons when the environment is less stressful and thus temperature selection less imperative. During cold seasons or stressful acclimation they exhibit a higher drive towards seeking out and remaining in a non-stressful warmer microclimate. Indeed such a mechanism could mean that a mouse

can avoid the extreme temperatures associated with its environment. It would thus less often have to utilize energy-consuming emergency physiological mechanisms such as high heat production for the maintenance of body temperature (see Didow, 1972). This could be especially advantageous to survival in winter when food supplies are more difficult to find.

B. Behavior Associated with Temperature Selection

1. Posture and Activity

During temperature selection experiments the type of behavior engaged in by a mouse during each observation was also recorded. The noveboracensis from all test groups were observed resting an average of 40.1 out of 60 observations per trial. This was 4.6 times more than the average number of observations of resting by gracilis (mean 35.5). The noveboracensis spent an average of 14.2 times grooming and 5.7 times attacking the walls of the tube, while the gracilis spent 18.9 times grooming and 5.6 times attacking. As another indicator of activity, although the zone of mean temperatures selected (a range of over 14C°) was approximately equal in the 2 species, the gracilis showed a higher activity level by spending an average of 3.4 times more per experiment moving between the 2 sides of the gradient circle, and by having almost twice as large a standard deviation about the mean selected temperature (9.3 as compared

to 4.9). Miles (1965) also found gracilis to be much more active at exploring new situations than noveboracensis. However he reported that their levels of activity in running wheels to which they had previously become accustomed were not significantly different. Ogilvie and Stinson (1966a) reported that the standard deviation about the mean selected temperature of gracilis (4.7°C) was more than 3 times that for noveboracensis (1.3°C); this finding agrees with the data in the present study. Falls (1956) associated high activity levels of house mice with lower mean selected temperatures. She reasoned that high activity would lead to high metabolic rates, and the mice would thus select lower temperatures to compensate. However, both her work and the present study showed that the mice were most active at temperatures beyond the selected temperature zone. The gracilis selected the higher temperatures and were also the more active in this study. However, the finding that the less active winter mice selected higher temperatures than the summer ones is consistent with the conclusion of Falls.

There was no difference in activity levels in the gradient between the cold- and warm-acclimated groups. However, acclimated mice were found to be more active than the acclimatized ones. Laboratory-acclimated mice of both forms were observed resting an average of 34.5 times per experiment while mice tested soon after they were trapped were noted resting an average of 41.1 times per trial. This was especially obvious with

the noveboracensis, and agrees with the statement of Miles (1965) that the initial "freezing" behavior of noveboracensis is less prevalent when the mice are in known surroundings. Price (1970) found that P. maniculatus bairdii descended from several generations in the laboratory explored new situations more readily than wild ones. The acclimated mice in this study had been in laboratory conditions and had been handled for several months while the acclimatized mice had just been caught. This result emphasizes why one should do laboratory control experiments and be very careful about interpreting the causality of results when investigating behavioral phenomena in natural populations of wild animals.

2. Miscellaneous Observations

One interesting factor that could be associated with nervousness (which would slow down digestion) is the number of feces left in the apparatus by mice. The gracilis in all test groups left over twice the number (mean of 6.9 per experiment) on the floor that the noveboracensis (3.3/trial) did after an experiment. Miles (1965) made a similar observation comparing the behavior of the same two species in experiments in cages. Also the acclimated mice of both species in the current study left more feces ($\bar{x} = 5.7$ per experiment) than the acclimatized ($\bar{x} = 4.4$) showing that the mere habituation to laboratory handling can lessen the excitement and change physiological as well as behavioral reactions during experiments.

Student's t-tests indicated that there was no significant difference either between the weights of the two species (mean for both = 20.4 g.), nor were the northern representatives of either gracilis or novaboracensis (19.7 g. and 20.6 g. mean weight respectively) heavier than the southern ones (21.4 g. and 21.3 g. respectively). This is in contrast to what one might expect from Bergmann's Rule that "races of warm-blooded vertebrates from cooler climates tend to be larger than races of the same species from warmer climates". There is not actually any racial difference involved here, but each form is spread over a wide geographic north-south range. The winter gracilis ($\bar{x}$ = 17.7 g.) were significantly lighter than the summer ones ($\bar{x}$ = 26.8 g.). This relationship was not noted in the Ottawa noveboracensis and was reversed in the Virginia mice. Fuller et al. (1969) found the winter weights of a Northwest Territories population of P. maniculatus borealis to be lower than in summer. The disappearance and reversal of this relationship in mice from milder regions suggests that the weight variation is largely due to the more severe winter weather and poorer foraging conditions in the north in winter. It is also possible that gracilis spend longer periods in winter torpor than noveboracensis; this would mean less foraging. Fuller et al. (1969) felt that periods of torpor in the mice resulted in the poor trappability of P. maniculatus in studies of winter populations near Great Slave Lake.

The sizes and limits of the selection zones of various groups of mice were also investigated in the present study. Although the zone of temperature in which the mice spent most of their time may be more biologically meaningful than the mean selected temperature, the latter was used in the present study since it facilitates comparative and statistical analysis. Even though the $\bar{x} \pm 2S_{\bar{x}}$ gave a good estimation of the selected zone, the actual dimensions of the zone between the highest and lowest temperatures at which the mice rested were also examined.

The average lowest temperature at which noveboracensis from all test groups rested (19.5°C) was not much lower than that for the gracilis (20.0°C). There was also no clear pattern of difference in the lower limit of the zone at which either species normally rested after adaptation to different environments. There were also no significant changes between the highest temperatures at which resting occurred. The gracilis rested at temperatures averaging up to 35.8°C, 2°C higher than the average for noveboracensis. This slight difference does agree with the higher mean selected temperatures of gracilis. The zones of resting do not appear to vary seasonally, however, while selected temperatures do.

C. Nesting Behavior

Table 10 shows the mean nest quality indices (NQI) for nests built by mice exposed singly in either 2°C or 22°C constant temperature rooms. They had previously been acclimated for at least 2 months in these same rooms. Figure 9 gives an example of some nest types used in estimating NQI. Table 10 shows that there was no difference in nest-building between noveboracensis kept at 22°C and those at 2°C. Female noveboracensis built slightly better nests in the cold, while males built better ones in the warmer room. In the case of gracilis, in both sexes the cold-acclimated (and tested) mice built much better nests than the warm-acclimated ones. This difference showed up in the first day of experiments and remained relatively constant until the experiments were stopped after 3 days. The cold-acclimated gracilis built better nests than the cold-acclimated noveboracensis, but with the warm-acclimated mice, this relationship was reversed.

Table 11 shows the results of a second experimental series similar to that of Table 10 with the exception that in a number of cases mice were tested at 2°C after prior acclimation to 22°C or vice versa. Table 11 shows that the warm-acclimated noveboracensis built better nests than cold-acclimated noveboracensis both in the warm and cold tests. In contrast to this, all the gracilis built better nests in

Table 10. Nest Quality Indices (NQI) for nests built by mice exposed singly to the temperatures at which they had been acclimated. NQI's vary from 1, for the best quality, to 6 for no nest (see Fig. 6 and 9). Nests were evaluated after 3 days of experimentation.

Species and Sex	Acclimated and Tested at 2°C			Acclimated and Tested at 22°C		
	mean NQI	range	n	mean NQI	range	n
<u>noveboracensis</u>						
♂♂	3.05	2 - 5	5	2.50	1 - 5	5
♀♀	2.15	1 - 5	5	2.90	1 - 5	5
♂♂ + ♀♀	2.60	1 - 5	10	2.70	1 - 5	10
<u>gracilis</u>						
♂♂	1.50	1 - 3	4	5.00	4 - 6	4
♀♀	2.15	1 - 4	5	3.65	2 - 5	5
♂♂ + ♀♀	1.83	1 - 4	9	4.33	2 - 6	9

Fig. 9. Examples of nests built by Peromyscus.
A, NQI=1; B, NQI=3; C, NQI=5

Fig. 9. Examples of nests built by Peromyscus.
A, NQI=1; B, NQI=3; C, NQI=5

Table 11. NQI for nests built by single mice after acclimation to and during exposure to cold (2°C) or warm (22°C) constant temperatures. Mice were given 3 days to build nests before evaluation.

Acclimation Conditions	Test Conditions	♂♂			♀♀			Both Sexes Mean NQI
		Mean NQI	Range	n	Mean NQI	Range	n	
<u>noveboracensis</u>								
cold	cold	3.8	2-6	5	2.3	1-4	5	3.1
cold	warm	4.7	3-6	3	3.5	2-5	3	4.1
warm	warm	2.0	1-6	5	2.0	1-6	5	2.0
warm	cold	2.5	1-4	3	2.5	1-5	4	2.5
<u>gracilis</u>								
cold	cold	1.7	1-3	4	2.0	1-3	5	1.9
cold	warm	5.0	4-6	3	3.0	1-5	4	4.0
warm	warm	5.3	4-6	4	3.0	2-6	5	4.2
warm	cold	3.0	1-4	5	2.0	1-3	3	2.5

the cold tests independent of the temperature at which they had been acclimated. Also the cold-acclimated gracilis built much better nests in the cold test than the warm-acclimated ones. The only major interspecific differences were between the cold-acclimated, cold-tested mice, with gracilis building much better nests, and between the warm-acclimated, warm-tested animals with noveboracensis building the better nests.

The qualitative results of nesting experiments using paired mice are shown in Table 12, which indicates that the female pairs built better nests in both species. Eedy (1969) found that with white mice, grouping of females led to a much greater increase in their survival over that of single females than grouping did among males. This sex difference, in both cases, appears to have been due to fighting and other behaviors of the males not conducive to huddling or nesting. Within the noveboracensis the warm-acclimated mice built better nests than the cold-acclimated mice in both test temperatures. In gracilis the exact opposite occurred. Also after either cold- or warm-acclimation, gracilis built better nests than noveboracensis in the cold test environment. From this, and the results in Table 11, it appears that gracilis change their behavior in reaction to the test environment much more quickly than noveboracensis. Cold acclimation or a cold test environment enhances this difference.

Table 12. Nest Quality Indices (NQI) of nests built by Peromyscus in experiments with 2 mice in each cage. NQI's were assessed after 3 days of experimentation.

Acclimation Conditions	Test Conditions	2 ♂♂			1 ♂♂ + 1 ♀♀			2 ♀♀		
		Mean NQI	Range	n	Mean NQI	Range	n	Mean NQI	Range	n
<u>noveboracensis</u>										
cold	cold	4.0	3-5	2	2.0	1-3	3	2.0	1-3	3
cold	warm	4.0	3-5	2	3.5	3-5	3	3.0	3	2
warm	warm	2.3	1-5	4	2.3	1-3	3	2.7	1-4	3
warm	cold	2.8	1-4	3	3.0	2-4	2	2.1	1-4	4
<u>gracilis</u>										
cold	cold	2.3	1-3	3	2.0	1-3	3	2.0	1-3	3
cold	warm	3.0	2-4	2	2.5	1-4	3	2.5	1-3	4
warm	warm	3.7	2-5	4	4.0	3-5	2	2.7	2-4	3
warm	cold	2.0	1-3	3	2.0	2	2	1.5	1-2	2

Results of the experiments investigating quantities of nesting material used by single mice in the warm or cold test environments are shown in Table 13. On the average gracilis in all combinations of acclimation and test temperatures used as much or more terylene than noveboracensis. In the case of the cold-acclimated, cold-tested gracilis, the mean amount used was much higher than that used by any other test group of either form. The noveboracensis used the most terylene in the warm test environment while the gracilis showed the opposite behavior. The females used more terylene than the males in all cases except the cold-acclimated, cold-tested gracilis where both sexes usually used most of the available nesting material by the third day.

The quantitative results using paired mice are shown in Table 14. In all cases the two mice used more terylene on the average than the single animals previously discussed. In both species the female pairs built much larger nests than either pair in which a male was included. The gracilis in all cases used more terylene than the noveboracensis. The cold-tested gracilis used the most terylene (7.3 - 11.0 g.) of any group while the warm-acclimated and warm-tested noveboracensis built nests averaging 3.1 g, little different from the 4.4 g average of nests built by cold-acclimated cold-tested noveboracensis, much the same as in the single mouse experiments and as in

Table 13. Weights (g) of terylene batting taken from container and used as nesting material by single mice after acclimation to and during exposure to either cold (2°C) or warm (22°C) constant temperature rooms. Eleven g was the maximum that an animal could use. Experiments were run for 3 days each.

Acclimation Conditions	Test Conditions	Weight (g)		Terylene used by	
		♂♂ n	♀♀ n	♂♂ + ♀♀	
<u>noveboracensis</u>					
cold	cold	1.4 5	2.4 5	1.9	
cold	warm	0.6 3	5.5 3	3.1	
warm	warm	2.6 5	4.2 5	3.4	
warm	cold	2.6 3	4.2 4	3.4	
<u>gracilis</u>					
cold	cold	9.1 4	8.1 5	6.2	
cold	warm	0 3	3.9 4	2.0	
warm	warm	4.0 4	4.5 5	4.3	
warm	cold	2.4 5	3.9 3	3.1	

Table 14. Weights (g) of terylene used by paired mice to build nests. Quantities were assessed after 3 days of experimentation.

Acclimation Conditions	Test Conditions	2 ♂♂	Weight (g)	1 ♂♂ + 1 ♀♀	2 ♂♂	n
<u>noveboracensis</u>						
cold	cold	1.1	2	8.5	3	3
cold	warm	0.4	2	3.4	3	2
warm	warm	6.3	4	4.5	3	3
warm	cold	4.9	3	8.5	2	4
<u>gracilis</u>						
cold	cold	7.3	3	11.0	3	3
cold	warm	4.6	2	11.0	3	4
warm	warm	1.6	4	9.5	2	3
warm	cold	8.1	3	11.0	2	2

the single mouse experiments and as in the qualitative tests.

From the results of the nesting experiments it appears that the gracilis were better nest-builders than the noveboracensis. Also cold acclimation causes a greater enhancement of this behavior in the gracilis than in the noveboracensis acclimated in similar manner. The cold-acclimated gracilis always built better nests than the warm-acclimated. However, the actual test environment appeared to be more important than the type of prior acclimation. The warm-acclimated and cold-tested gracilis built better nests than the cold-acclimated, warm-tested gracilis. Noveboracensis did not show this relationship as clearly. In fact they often built better nests in the warm test environment. It seemed almost as if they did not know how to react to the cold temperatures.

These results are exactly the same as those found for temperature selection, in that the gracilis showed behavior better adapted to a severe cold climate. The gracilis also reacted more quickly to the cold temperatures and a more marked change in their behavior was caused by acclimation.

In all cases two mice built a better nest than just one. This in addition to heat conservation, which is augmented by huddling in mice, shows why Peromyscus would have

an advantage if they built communal nests in the winter. Howard (1951) working with P. m. bairdii and P. l. noveboracensis, and Gebczynska and Gebczynski (1971) and Meese (1971) all working with Clethrionomys glareolus have indicated that both huddling and nest-building lower the energy requirements of the mice, especially in cold weather. This can greatly enhance the chances of survival. It has been noted by various authors that Peromyscus tend to aggregate in nature to build winter nests (see Hart, 1971:13).

The females in the present experiment tended to build better nests than the males. Also a male present in the paired animal experiments tended to disrupt nesting behavior. This finding is contrary to the results of Layne (1969) and Wolfe (1970) who found no differences in nest-building between sexes. It also differs from the lack of sexual differences found in temperature selection studies. It must be noted that Eedy (1969) found survival differences between grouped male and grouped female laboratory white mice in the cold; these differences were attributed to the better huddling behavior of the females. If one sex builds better nests it would seem to be most advantageous for it to be the females since, to them, a good nest-building ability would mean the survival of their young in summer as well as of themselves in winter.

Various authors have found differences in nesting behavior between species of Peromyscus. Wolfe (1970) felt that burrowers need not build as good nests as surface-dwellers. However, Smith and Speller (1970) concluded that although both species used both burrows and arboreal nests, noveboracensis were perhaps more arboreal and less reliant on burrows than gracilis. Layne (1969) concluded that good nesting ability allows mice to inhabit a wider variety of habitats. This could be true as, although noveboracensis have a greater geographic range, the gracilis seem to have extended their range into the more northern, cooler, damper, conifer types of macrohabitat which have a much greater seasonal variation. Miles (1965) commented that gracilis would be better explorers in a new area and consequently would find the best nest sites more quickly than the poorly exploratory noveboracensis. He also found that noveboracensis showed a higher degree of intraspecific aggression which would detract from communal nesting.

Temperature-induced changes in nesting behavior have been investigated before. Thorne (1958) stated that P. maniculatus osgoodi built much poorer nests in the summer than in the winter. He also found that nesting behavior was almost eliminated at test temperatures of 33°C, while at temperatures of 8°C, both the utilization of paper towels present and the quality of nest built were much higher than at warm test environments, much as in the present study.

Other authors agree that rodents build better nests when kept in a cold environment (Kinder, 1927; Sealander, 1952).

The present study is the only one I know in which interspecific differences in the ways in which nesting behavior changed after acclimation to cold or warm temperatures and during exposure to cold or warm temperatures were tested. The results of this part of the study agree in principle with the results expressed by other authors and with those found in the other sections of this study.

GENERAL DISCUSSION

Weather can have a very important effect on the population regulation of small mammals. Ehrlich et al. (1972) reported that populations of deermice and other small mammals had still not recovered the second summer after a severe spring took an above average death toll. They considered that in some cases local populations of animals and plants can be pushed into extinction by unusually severe weather. In a north temperate climate, large fluctuations in temperature are quite normal. Species of animals would be under selective pressure to evolve methods of adapting quickly to escape drastic reductions in population or even local extinction caused by severe or fluctuating weather.

The gracilis appear to have evolved efficient thermoregulatory behavior patterns and an ability to change them seasonally. These appear to give this form a definite survival advantage over noveboracensis when living in a more severe, cooler climate. This genetic behavioral difference is very important to the mice in determining their geographic distribution. In northern areas gracilis inhabit forest habitats similar to those selected by noveboracensis in the south. Although gracilis have been trapped in the same dry hardwood forests as noveboracensis in some of the areas in which the two species overlap, they are more often associated

with cooler, damper, coniferous habitats in this region. This leads one to speculate that without the climatic restrictions, noveboracensis would be able to outcompete gracilis in the north as it appears they are doing in the south. Smith and Speller (1970) suggested that noveboracensis may be the better competitor and that gracilis only manages to live in the same area when the population of the former is kept low by some other factor. Evidence is, however, quite inconclusive.

The evolutionary difference giving gracilis better behavioral thermoregulation for a colder macroclimate appears from the present discussion to have occurred after the mice had extended their range into the more northern areas. Other differences such as better exploratory behavior, physiological thermoregulatory ability, or a combination of the numerous minor variations between the two species have allowed variations in geographical distribution to occur. Now that it has occurred though, further evolution of behavior to compensate for the cold macroclimate has given the gracilis a decided advantage over the noveboracensis both in survival in these northern regions and in extension of its range into more unfavorable macrohabitats in the overlap area. Didow (1972) found that even within the subspecies noveboracensis, the northern forms exhibited a greater cold resistance than those from the south in both summer and winter. He also stated (p.iii): "Interrelations

of ambient temperature, metabolic failure time, and maximal heat production rate were directly related to previous thermal conditioning of the mice and their geographic distribution". He further stated that behavior was one of the major differences that gave northern animals a heat conservation advantage over those from the south.

The behavioral differences in seasonal activity, temperature selection and nest-building of the two species complement each other. The gracilis "prefer" warmer microhabitats, and build better nests than the noveboracensis. These differences are accentuated by exposure to cold, or the arrival of the winter season. In the winter gracilis also seem to decrease their surface activity to a greater extent than noveboracensis. All these factors would lead to increased energy conservation at a time of year when food is hard to find, and energy can be spent extremely rapidly by the unnecessary over-utilization of physiological thermoregulatory methods.

CONCLUSIONS

- 1) When studied in a temperature gradient apparatus, Peromyscus maniculatus gracilis selected higher temperatures than P. leucopus noveboracensis.
- 2) The gracilis built better nests than leucopus.
- 3) Both these differences may be looked upon as behavioral preadaptations advantageous to mice living in a cooler, more severe macroclimate. The gracilis would thus have an advantage in more northern or cooler habitats. These adaptations may in this case have important bearing on the geographic distribution of the 2 subspecies.
- 4) Both these behavioral differences were more pronounced after the mice had been exposed to low controlled temperatures (2°C) in the laboratory or to cold seasons outdoors. This means that gracilis show a much greater adaptation of their behavior to the cold seasons than noveboracensis.
- 5) The gracilis were also more difficult to trap in the winter than noveboracensis, perhaps because they engage in less surface activity and spend more time in their nests at this time of the year.

- 6) Within each subspecies the more northern mice selected higher mean temperatures and showed a greater reduction in winter activity.
- 7) Mean selected temperatures were higher after the mice had been stressed for at least 2 months by exposure to low temperatures (2°C) or to high relative humidity (90-95%). They even changed owing to excitation of the mice after some changes in handling or experimental techniques.
- 8) Fall seasonal changes in temperature selection appear to occur prior to the winter changes in climate for which they compensate. Preadaptation clues may be shortened photoperiod, differences in available foods, or even cooler night temperatures in the fall.

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APPENDIX I: The Identity of the Quebec Peromyscus.

The Quebec Peromyscus were caught in woodland areas in the Saguenay River basin (see methods IB(4)) within the range mapped by Hall and Kelson (1959) for P. m. gracilis (see Fig. 1). However, apparently the only previous records of Peromyscus being trapped from the Quebec areas used in this study are those of Osgood (1909). He examined specimens from Lac aux Sables, Godbout, Lac Edouard, and La Malbaie. The first place could not be positively identified, while the others were 290 km northeast, 120 km southwest and 160 km southeast respectively of the major Quebec trapping area of this study. Other references to the distribution of gracilis in this area can be traced back to Osgood's records. In an attempt to clarify the subspecies situation, study skins and skulls of our mice from Quebec were compared with specimens of gracilis caught in the Ottawa area, and P. m. maniculatus trapped north of Lake Superior.

Our Quebec specimens could not be distinguished from either group of museum specimens. In fact, attempts to separate series of gracilis and maniculatus from well within the ranges for these subspecies (Hall and Kelson, 1959) using the distinguishing characters of Osgood (1909) were unsuccessful. Although he claimed that maniculatus had shorter tails, more slate grey coloration on the back,

and broader, flatter crania, careful examination of the specimens showed that individuals of both nominal subspecies showed the complete range of characters of the other. No distinguishing subspecific characteristics could be discerned. It appears that the validity of the races maniculatus and gracilis requires critical evaluation. In the meantime, for convenience, the Quebec Peromyscus used in this study have been referred to as P. m. gracilis to conform with current usage.

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TEMPERATURE SELECTION

WRIGHT

Exp. _____ In _____
 Animal _____ Sex _____
 Species _____ Region _____
 Grad. Type _____

Operator W. Eedy
 Date _____
 Time in _____
 Start _____

attack _____

CAUGHT
BORN

AT

end

move

sit

groom

rest

feces

L

R

Time	Pos	Obs.	Time	Pos.	Obs.	Time	Pos	Obs
1			21			41		
2			22			42		
3			23			43		
4			24			44		
5								
6								
7								
8								
9								
10								
11			31			51		
12			32			52		
13			33			53		
14			34			54		
15			35			55		
16			36			56		
17			37			57		
18			38			58		
19			39			59		
20			40			60		

APPENDIX II

The chart used to record temperatures at which mice rested and their behavior during temperature selection studies. Various other parameters were also recorded.

Temperatures:

R1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____, H _____

L1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____,

R1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____, H _____

L1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____,

R1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____, H _____

L1 _____, 2 _____, 3 _____, 4 _____, 5 _____, 6 _____, 7 _____, 8 _____,

1 5 9 13 17 21 25 29

APPENDIX III: Statistical Procedures Used

1. Mean ± 2 (Standard Error of Mean) This was the standard way used to describe the selected temperature values of each experimental group. The mean for the group was calculated from the total number of observations (60 per mouse) of all of the mice in the treatment group. The standard error of mean was calculated using a computer program modified from Kemeny and Kurtz (1968).

The statistic of $\pm 2 S_{\bar{x}}$ is an estimate of the 95% confidence interval of the mean which is approximately $t(.05)$ for the appropriate degrees of freedom multiplied times the standard error of mean. As the number of degrees of freedom gets larger (always more than 9 in the current study) the $t(.05)$ value approaches a value of 1.96. The 95% confidence interval is the range about a mean in which there is a probability of 0.95 that another mean that is statistically equal to the former will be found (Steel and Torrie, 1960).

2. Analysis of Variance To compare two mean temperatures selected by different experimental treatment groups of mice an analysis of variance was used. In this, the sums of squares were calculated for differences between observations within each animal, between mice within each treatment group, and between treatment groups. F-ratios were calculated to determine whether the variation between

treatment groups was significantly greater than that either between the mice, or between the different observations for each mouse. The probabilities greater than 0.05 were considered as being due to chance. Methods and tables were taken from Steel and Torrie (1960) and Ostle (1963).

3. Analysis of Variance by the Method of Fitting Constants (Unbalanced Data)

This was performed on the results of temperature selection of the two subspecies, each trapped near the northern and southern limits of its geographic range, and in each case after laboratory acclimation to high and low constant temperatures, and also after natural acclimatization to summer and winter outside environments. The first statistical test used in this method adjusted each term for all of the other variables. A second or hierarchical test was also used in which each term was only adjusted for those that followed it, but this was felt to be less useful for interpretation of the data than the first method. Environmental covariates were incorporated either singly or in groups and the analysis reconsidered; this enabled some consideration of their effect.

Variables used in this calculation were: species, sexes within each species, type of adaptation (laboratory vs. field), exposure temperature within each type (warm vs. cold), and the areas from which the mice originated.

The effects of interactions were computed between species and adaptation type, between species and adaptation temperature, and between sexes, temperature and adaptation type.

Covariates investigated were relative humidity, photoperiod, minimal temperature, and average temperature, all calculated as the mean of daily values for 3 weeks prior to temperature selection experiments.

Computer programs and time for these calculations were by courtesy of the Canada Department of Agriculture, Central Experimental Farm, Ottawa.

4. Correlation Coefficients Correlation coefficients and their F-ratios were calculated using a modified version of the LINREG computer program from Kemeny and Kurtz (1968). Tables and largest allowable probability of chance variation are the same as in the analysis of variance previously mentioned.