THE IDENTIFICATION AND DISTRIBUTION
OF TWO SPECIES OF PEROMYSCUS
IN SOUTHEASTERN ONTARIO

by

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A thesis submitted in partial fulfilment of the requirements for the degree of
MASTER OF SCIENCE
in the Department of Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
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ABSTRACT

One hundred and sixty-nine mice of *Peromyscus leucopus* noveboracensis and *Peromyscus maniculatus* gracilis were examined for characters to best separate them. Each species was obtained from an area in Ontario where it was known to be the only one present. An additional 12 mice of both species were obtained from an area of sympatry. The best characters found to separate them were, in order of importance: ear length, interparietal length, tail length, skull length, and rostral length. Although ear length and interparietal length separated most of the individuals, there were still individuals that could not be separated. The two species were found to be completely separable, using either one of two indices:

\[
\text{Ear length} \times \text{tail length} \times \text{interparietal length} \div \text{skull length}
\]

or,

\[
\text{Ear length} \times \text{tail length} \times \text{interparietal length} \div \text{rostral length}
\]

With skull length, *P. l. noveboracensis* has an index value of 2.57-4.09 and *P. m. gracilis* has an index value of 4.26-7.90. With rostral length, *P. l. noveboracensis* has an index value of 7.39-12.50 and *P. m. gracilis* has an index value of 12.83-22.77.

Six crossbreeding experiments were attempted between *P. l. noveboracensis* and four subspecies of *P. maniculatus*. The animals were kept together for periods ranging from 71 days to over a year. No offspring resulted. Three pairs of *P. leucopus* and four pairs of *P. maniculatus* were kept for the same periods of time in the same room, as a control. One pair of *leucopus* produced two litters, another pair produced one, and the third pair, none. Two pairs of *maniculatus* produced one litter each and the
two pairs, none.

P. m. gracilis was not as excitable or nervous as P. l. noveboracensis and was therefore easier to handle.

Although the ranges of P. l. noveboracensis and P. m. gracilis differ, the mice meet in a zone of overlap where they occur sympatrically. Correlations were made between the ranges of the mice and vegetation, food preference, temperature tolerance, water requirement, morphology, color of pelage, and behavior. P. m. gracilis was found to occur in coniferous and P. l. noveboracensis in deciduous vegetation. No correlation was found between the ranges of the mice and food preference, temperature tolerance, water requirement, morphology, and color of pelage. Correlation between the ranges of the mice and their behavior was doubtful.

Preliminary tests were made of the ability of one species to discriminate between its odor and that of the other species. Results showed that a mouse entered more often and stayed longer in a chamber containing the odor of its own species. A chamber containing odor of either species was preferred to the control chamber without odor.

We accept this thesis as conforming to the required standard
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THE IDENTIFICATION AND DISTRIBUTION OF TWO SPECIES OF
PEROMYSCUS IN SOUTHEASTERN ONTARIO.

INTRODUCTION

The aims of this study were to find differences between
Peromyscus leucopus noveboracensis (Fischer) and Peromyscus
maniculatus gracilis (LeConte) to separate them accurately and
to determine whether these differences could be used to explain
their distribution.

P. m. gracilis and P. l. noveboracensis are two species of
mice of the Family Cricetidae that are extremely similar in
appearance and often occur sympatrically (Rutter, 1951; Klein,
1959; Cameron, 1956; Connor, 1960; Waters, 1960).

Confusion in identification of maniculatus and leucopus
has long been a topic of conversation and study (Downing,
personal communication; Rutter, 1951; Waters, 1960).
Misidentification of these species extends throughout the area
where they occur or are thought to occur. Waters (1962) cites
an example of misidentification in southern New England where
Hall and Kelson (1959) extended the range of P. m. gracilis into
northeastern Connecticut on the basis of a single specimen.
Waters has examined this specimen and has concluded that it is
not gracilis but rather a young adult P. l. noveboracensis.

The taxonomy of these two species is further confused by
the wide range of characteristics that have been used to separate
them. The mice are generally described as follows.

Peromyscus maniculatus gracilis (LeConte). The deer mouse
is found in cold, moist places, or deep, mostly coniferous woods (Osgood, 1909). It is of medium size, with a tail longer than or equal to the length of the body (Burt and Grossenheider, 1952). The pelage color is fulvous to cinnamon-brown on the sides and greyish across the shoulders and top of the head. The darker colored dorsal streak in most *gracilis* is not distinct or is lacking in the region of the rump (Standfield, 1950). The underparts and feet are white. The sharply bicolor tail is brownish above and white below and is generally thought of as being more densely haired than that of *leucopus*. The palatine slits are long and nearly parallel-sided. Many animals have preauricular white hairs (Osgood, 1909).

*Peromyscus leucopus noveboracensis* (Fischer). The wood mouse prefers dryer, more open country or deciduous woods (Osgood, 1909). It is similar in size and color to *gracilis* but the tail is shorter than or equal to the body length (Burt and Grossenheider, 1952). The darker dorsal streak extends to the base of the tail (Standfield, 1950). The tail is less distinctly bicolor and more sparsely haired than that of *gracilis*. The palatine slits are narrower at the ends than in the middle. No preauricular white hairs are present (Osgood, 1909).

Workers have separated *leucopus* and *gracilis* in a variety of ways. Osgood (1909, P. 43) found *gracilis* to be similar to *leucopus* except that the braincase was narrower, the nasals were longer, the maxillaries less bulging in front of the infraorbital foramen, the anterior part of the zygomatic was lighter, palatine slits were longer and more nearly parallel-sided and
the molar teeth were smaller.

Rand (1945) relied mainly on skull characters to separate *leucopus* from *maniculatus*. According to him, *maniculatus* was a mouse seven and one-half inches long, with a slender rostrum and long straight slits in the palate. *Leucopus* was seven inches long and had a tapered rostrum and shorter, curved slits in the palate.

Burt (1948) states that *gracilis* differs from *leucopus* in that the anterior border of the zygomatic plate does not cover the infraorbital foramen when viewed from the side. Standfield (1950) found that the shape of the palatine slits was a good means of separating all *maniculatus* from *leucopus*. In the former, the outer sides of the foramina are parallel to each other, curving in abruptly at their anterior ends. In the latter, there is a gradual curving in of the sides of the foramina. The methods of separation of Burt and Standfield are difficult to use because they are subjective.

Burt and Grossenheider (1952) admit that these mice are difficult to tell apart, but say that they can be separated on the basis of their tail lengths.

Cameron (1956) says that the tail length of *leucopus* is usually less than one-half the total length and that *maniculatus* has a tail length that is usually greater than one-half the total length.

Waters (1960, pp. 33-34) used a more elaborate system of identifying these species. His method depends on a number of skull characters. In *maniculatus* the tympanic bulla is relatively flatter and longer, the temporal portion of the zygomatic arch is more widely flaring and the maxillary portion less widely
flaring, the sphenoids are flatter, and the post cranial curvature is greater. In _leucopus_, the supraoccipital region is more protrusive and the palatine foramina have a more pronounced lateral curve. He concludes by saying that, "Relatively few individuals could not be assigned to the correct species on the basis of these criteria." This same author achieved a separation of the species by graphing body length against skull length, tail length against zygomatic width.

Rutter (personal communication) uses a variety of characters to separate the mice. These include "whiteness" of the neck region, shape of the anterior portion of the zygomatic arch when viewed from above, shape of the anterior palatine foramina, and position of the posterior palatine foramina with respect to the cheek teeth.

In summary, a variety of methods have been used to separate _leucopus_ and _maniculatus_. Most of the above are subjective methods that are difficult to use. Some require elaborate preparation of the skull before they can be applied. None of the methods considered completely separated the two populations of mice used in this study. That so many different characters are used to identify the mice indicates the need for better, more quantitative methods of separation in order to end the apparent confusion.

The similarities between _leucopus_ and _maniculatus_ in appearance, measurements, and reproductive biology are so great that they could easily be considered as two subspecies of one species. Both are seasonally polyestrous and breed from March or April to
October or November (Burt, 1940; Jackson, 1952; Hall and Kelson, 1959; Waters, 1960). Svihla (1932) found the gestation period of *leucopus* to be 22-37 days and that of *maniculatus* to be 22-35 days. Litter sizes of both are approximately the same: *leucopus* (young/litter): 4.09 ± 0.08, Svihla (1932); 4.26 (range 2-6), Burt (1940); 4.14 ± 0.08, Jackson (1952); 4.10-4.72, Davis (1956); 5.00 (range 3-7), Hall and Kelson (1959); 5.17 ± 0.29 - 5.20 ± 0.36, Bendell (1959); 4.3 (range 1-8), Connor (1960). *maniculatus* (young/litter): 4.04 ± 0.03, Svihla (1932); 5.33, Beer et al (1957); 5.00 (range 1-8), Hall and Kelson (1959); 5.1 (range 3-7), Connor (1960).

Despite these similarities, *leucopus* and *maniculatus* are valid species. They do not interbreed in nature, even in areas where they both occur. In these areas they can still be told apart by experts (Hall and Kelson, 1959). Breeding experiments have shown that they also do not interbreed in the laboratory (Dice, 1931, 1933, 1937a; Waters, 1960).

**Breeding Experiments**

A number of investigators (including myself) have conducted interbreeding experiments in the laboratory to test the validity of the two species. Dice (1937a) found that 12 subspecies of *leucopus* were interfertile in the laboratory and both male and female hybrids were also fertile. This same author (1931, 1933) found that no offspring resulted from 69 attempted hybridizations of various species of *leucopus* and *maniculatus*. All *gracilis X noveboracensis* hybridizations were failures. Waters (1960) attempted to hybridize four *noveboracensis* with four *gracilis* with
similar results. He also observed that there had been no apparent sexual interest or activity between the mice of these pairs. As a control, Waters crossed 10 pairs of *noveboracensis*. Five $F_1$ and one $F_2$ litters resulted. My own experiments will be discussed later.

**Other Species of *Peromyscus* in Southeastern Ontario**

The only other form of *Peromyscus* in southeastern Ontario is *P. m. bairdii* (Hoy and Kennicott), the prairie deer mouse. Saunders (1907, 1908, 1913) recorded the eastward movement of the prairie deer mouse as it began its range extension across southern Ontario. As it is smaller in size than the other two forms and therefore readily separated from them, I shall not consider this mouse in the present study.

**Distribution of *leucopus* and *maniculatus***

While *leucopus* and *maniculatus* are exceedingly similar in many respects, they have different ranges. The search for differences between the species was not only to separate them but to find how the distribution of each form was determined.

Many accounts have been given of the distribution of these mice. Osgood's (1909) distribution maps of *gracilis* and *noveboracensis* in Ontario show that *gracilis* occupies the area east of the Great Lakes up to the border of Quebec, while *noveboracensis* is restricted to southern Ontario. Hall and Kelson (1959) give distribution maps of both species.

The general distribution of *leucopus* and *maniculatus* indicates that they occupy separate ranges. They meet in an area of sympatry which extends from approximately 44°45' to
approximately 45°30' (Rutter, 1951).

Osgood (1909), and Cross and Dymond (1929) noted a correlation between vegetation and distribution in these species. Klein (1960) commented on this tendency toward ecological separation of *leucopus* and *maniculatus*. He could not find reasons for this separation but suggested that it was perhaps due to differences in microclimate.

Many attempts have been made to correlate other factors such as differences in food preference, temperature tolerance, and water requirement with the distribution of the two species. Kinds of food eaten by the mice were reported by Dice (1922), Cogshall (1928), Burt (1940), Hamilton (1941), Jackson (1952), Cameron (1956), Williams (1959), Connor (1960), Getz (1961), and Howard (1961). Foods eaten included various seeds, nuts, insects, arachnids, fruits, fungi, green vegetation, roots, and molluscs. Being omnivorous, the mice apparently eat whatever foods are most abundant and easy to obtain. No differences in food preference are known for *gracilis* and *noveboracensis* (Klein, 1960). Thus food does not appear to be a factor governing the distribution of these mice.

Sealander (1951) suggested that the northward distribution of small mammals might be limited by winter temperature. Klein (1959) felt that the occurrence of *maniculatus* at higher altitudes than *leucopus* indicated that temperature plays a great role in their distribution. He also suggested (1960) that differences in soil temperature might also be a factor. Howard (1951), and Eskridge and Udall (1955) found that both species
could withstand freezing temperatures provided that sufficient food was available.

Lindeborg (1952) found that leucopus and maniculatus have a similar reaction to limited amounts of water. Neither could survive on 0.2 cc./day and at 0.4 cc./day, each lost weight. Chenoweth (1917) concluded that although leucopus seemed to be able to adapt to different moist environments, evaporation was an important factor in its distribution. When leucopus was kept on a restricted water diet (Chew, 1951), most water conservation was effected by a reduction in urine volume. Evaporation was reduced and became the greatest path of water loss. An average of 39% of the amount of water normally drunk ad libitum was required in order to maintain normal weight. If less water than this was given, the food intake decreased and the animal lost weight. Dice (1922) found that water was not the factor limiting leucopus and bairdii to their respective environments. Klein's (1959) study of water intake of leucopus and gracilis showed that both used about the same amount of water: leucopus: 0.43 cc./gram body weight or 7.6 cc./individual/day; gracilis: 0.42 cc./gram body weight or 7.4 cc./individual/day.

Recently I obtained a copy of the trapping records of Peromyscus in Ontario from the Royal Ontario Museum of Zoology. I shall use these data in preference to all other because they are the most up to date records of the two species in south-eastern Ontario. In addition, I correlate distribution with
Rowe's (1959) new description of the vegetation of Ontario. Numerous studies have shown that the form of an animal is related to its distribution (Palmgren, 1932; Robbins, 1932; Lack, 1944; Horner, 1954). In this study I shall try to correlate the differences I find between the species in form and color with their distribution.

Interspecific interaction of some sort might explain the distribution and also the failure of the two species to interbreed in the laboratory. Studies of the behavior and interaction of these species with each other or with other animals have been made by Dice (1922), Svihla (1932), King (1958), Foster (1959), Klein (1959), and Sheppe (1961). Sheppe concluded that the restricted habitat distribution of *P. oreas* and *P. maniculatus* in their zone of sympatry may result in part from interspecific competition. Since mammals operate in a world of odor (as opposed to the highly visual world of birds), and since these particular mammals are nocturnal, it seemed possible that *leucopus* and *maniculatus* might react to one another by smell. The avoidance of one species by the other might explain their distribution and sexual isolation. Therefore, experiments were conducted to test the reactions of each species to its own and to the other species' odor.

**Summary of the Problem**

Two very similar species of *Peromyscus*, *P. l. noveboracensis* and *P. m. gracilis*, occur in southeastern Ontario. These species occupy different ranges but occur sympatrically where these
ranges overlap. The problem is to find differences between the species in order to separate them and to determine whether these differences could be used to explain their distribution.
THE TAXONOMIC SEPARATION OF PEROMYSCUS LEUCOPUS NOVEBORACENSIS
AND PEROMYSCUS MANICULATUS GRACILIS

MATERIALS AND METHODS

Collection of Specimens

Most of the specimens used in this study came from two areas in Ontario, one near Kingston and the other near Lake of Two Rivers, Algonquin Park. According to maps of Osgood (1909), and Downing (1948), only P. l. noveboracensis occurs in the area around Kingston. The mice from this area fit the description for the species (Osgood, 1909; Burt, 1940; Waters, 1960). Extensive collecting of mice near Lake of Two Rivers (Wildlife Research Station, Lake Sasajewan) has yielded only P. m. gracilis (with the exception of a single specimen from the Joe Lake area, Algonquin Park, tentatively identified as P. l. noveboracensis (Downing, personal communication)). Mice from this area fit the description for the species (Osgood, 1909; Burt and Grossenheider, 1952; Waters, 1960).

The specimens of leucopus were trapped by Dr. J. F. Bendell and Mr. S. M. Teeple during 1956, 1958, and 1959, and sent to me in 10% formalin. This group of 120 adult, subadult, and juvenile mice consisted of 59 males and 61 females. I also received 17 live specimens of leucopus (12 males and 5 females) early in 1961 from Mr. S. M. Teeple.

I collected 157 adult and subadult P. m. gracilis (67 males and 90 females) near Lake of Two Rivers, Algonquin Park. Collecting was done by snap-trapping early in the fall of 1961.
These animals were aged, sexed, weighed, and measured shortly after trapping and were transported to the University of British Columbia in 10% formalin. Seven live *gracilis* (5 males and 2 females) were brought back to the University of British Columbia from Algonquin Park.

Specimens of *P. m. gracilis* were obtained from the Royal Ontario Museum of Zoology through the kindness of Dr. R. L. Peterson and Mr. S. Downing. These included 61 male and 39 female mice trapped in Algonquin Park.

All specimens mentioned thus far were trapped in areas reported to contain only *P. l. noveboracensis* or *P. m. gracilis*. Dr. D. A. Smith sent a collection of 12 mice (6 males and 6 females) from areas near Cloyne, Frontenac County and Calabogie, Renfrew County. In these areas, the mice occur sympatrically and are therefore more difficult to separate.

**Preparation of Specimens**

All mice except those from the Royal Ontario Museum of Zoology and from Dr. D. A. Smith were prepared for study in the following way. Animals in formalin were rinsed with water and damp dried. Freshly killed animals were used without further preparation. The animals were aged, sexed, and weighed. Specimens of *leucopus* were weighed with stomach contents removed, but time limitation prevented a similar procedure to be followed for *maniculatus*. Body, tail, ear, and hind foot lengths were measured. The baculum was removed, mounted immediately on a glass slide under a piece of cellulose tape or embedded in clear glue, and measured. The skull was removed, partially cleaned,
and skull length, rostral length, interparietal length, and interparietal width were measured. The shape of the anterior palatine foramina was noted. Finally, the pelage was examined for color and texture. Only skull measurements were made on specimens from the Royal Ontario Museum of Zoology and from Dr. D. A. Smith. Body measurements of these mice were taken directly from accompanying museum labels.

Features Selected for Measurement

Features were selected on the basis of ease of measurement and use by other workers in the separation of the species (Osgood, 1909; Dice, 1932, 1937(b); Blair, 1941; Burt and Grossenheider, 1952). These were: skull length, rostral length, ear length, body length, tail length, baculum length, and baculum width. I also measured interparietal length and width. Interparietal length and width have not been used extensively for comparison of Peromyscus, but examination of the skulls of both species led me to believe that these measurements (especially interparietal length) differed consistently between the species.

The following measurements were taken:

Total Skull Length (Fig. 1(a)): The longest length of the skull; from the anterior edge of the nasals to the posterior edge of the occipitals.

Rostral Length (Fig. 1(b)): The distance from the anterior edge of the upper incisor to the anterior edge of the first upper premolar.

Hind Foot Length (Fig. 1(c)): The distance from the back of the heel to the end of the longest claw.
Figure 1. MEASUREMENTS MADE

A. TOTAL SKULL LENGTH  B. ROSTRAL LENGTH  C. HIND FOOT LENGTH  D. EAR LENGTH  E. INTERPARIETAL WIDTH  F. INTERPARIETAL LENGTH  G. BODY LENGTH  H. TAIL LENGTH
Ear Length (Fig. 1(d)): The distance from the bottom of the notch of the ear to the tip of the ear.

Interparietal Width (Fig. 1(e)): The shortest distance across the interparietal bone, taken at the point where the mid-sagittal suture meets the interparietal bone.

Interparietal Length (Fig. 1(f)): The greatest length of the interparietal bone.

Body Length (Fig. 1(g)) and Tail Length (Fig. 1(h)): The body and tail lengths were obtained by placing the relaxed animal on a piece of cardboard on which a straight line had been ruled. The nose, base of the tail and tip of the tail were placed on the line. Pins were placed at the tip of the nose, base of the tail, and end of the tail (excluding the tail tip hairs). The mouse was then removed and the distance between the pins along the straight line was measured.

Weight: The mice were weighed to the nearest tenth of a gram. *Leucopus* specimens were weighed with stomach contents removed. Shortage of time did not permit *maniculatus* to be weighed with stomach contents taken out.

Baculum Length: The greatest length of the baculum (os penis).

Baculum Width: The greatest width of the basal portion of the baculum.

These last two measurements are not shown in Fig. 1 because they are applicable only to male animals.
Number of Animals Used

The mice were aged by pelage color (Collins, 1923) and relative amount of tooth wear (Hooper, 1957). Of the 157 *maniculatus* that I trapped, 25 could not be assigned with certainty to either the adult or subadult category and for this reason were not used. Of the remaining 132 specimens, 31 animals were lacking one or more of the measurements taken (usually because of a broken skull or mutilated tail). These animals also were not used in the present study. Thus, out of 157 specimens of *maniculatus*, a total of 101 specimens were used for all comparisons.

Of the 120 *leucopus*, 3 animals were subadults and 2 were juveniles. These numbers were hardly sufficient to use in a comparative study and were therefore omitted. Of the remaining 115 animals, 47 were lacking one or more measurement. Thus a total of 68 *leucopus* were used for all comparisons except for the indices where an additional 24 animals were included.

Methods of Data Analysis

Histograms and bar diagrams were plotted of all measurements (except baculum length and width) and weights taken. Each bar diagram shows the total range of measurements by a horizontal line, the mean by a vertical line, one standard deviation on each side of the mean by an "open" rectangle, and two standard errors on each side of the mean by a "solid" rectangle.

The "t" test for comparisons of groups with unequal numbers of samples in each (Larkin, personal communication), at the 5% level of significance was used to measure differences between
the species in the size of parts. Parts tested included ear length, body length, tail length, skull length, rostral length, and interparietal length. The "t" value was also used to express the amount of difference between parts of each species.

From the study of the form of *leucopus* and *maniculatus*, it became clear that no one part separated the animals well. However, each species showed a group of characters that tended to differ between the species. To show these tendencies, measurement polygons of adult animals of each sex were constructed. These polygons consisted of 8 axes on which the average measurements (in mm.) of 8 body parts were plotted. Each polygon represents an average animal of each sex and species of mouse.

**Experiments in Interbreeding**

Breeding experiments between *leucopus* and *maniculatus* were conducted. Six mixed pairs of *leucopus* and *maniculatus*, 3 pairs of *leucopus*, and 4 pairs of *maniculatus* were kept together for periods ranging from 71 days to over a year. The animals were housed in 2 gallon glass aquaria and were provided with sawdust and cotton batting for nest material. Food was in pellet form (U. B. C. ration #6-61) and water was provided in gravity water bottles inserted through the wire tops of the aquaria.

**Factors Influencing Distribution**

Correlation was made between the distribution of *leucopus* and *maniculatus* and vegetation, temperature tolerance, food preference, water requirement, morphology, color of pelage, and behavior. This was done from recent information in the literature.
Details of the method of analysis will be presented later.

**Experiments in Odor Discrimination**

Experiments were conducted to test odor discrimination between *leucopus* and *maniculatus*. For this part of the work, I designed and constructed an odor discrimination apparatus (olfactometer). Details of the method of analysis of odor discrimination between the mice will be presented in a later section on olfaction.
The measurements of *P. l. noveboracensis* and *P. m. gracilis* were compared to find those useful in the separation of the species. To do this, the measurements of a part were compared for each sex and available ages of a species. The measurements were compared on the same scale by histograms and bar diagrams (Dice and Leraas, 1936, as modified by Hubbs and Hubbs, 1953). These data are presented for weight in Fig. 2(a,b); hind foot length in Fig. 3 and Fig. 5(a); ear length in Fig. 4 and Fig. 5(b); body length in Fig. 6(a,b); tail length in Fig. 7(a,b); interparietal width in Fig. 8 and Fig. 10(a); interparietal length in Fig. 9 and Fig. 10(b); skull length in Fig. 11 and Fig. 13(a); and rostral length in Fig. 12 and Fig. 13(b). Figures to the left of each histogram and bar diagram indicate the number of animals being compared. Letters to the right of each histogram and bar diagram indicate the species, sex, and age of the animals used (L = *P. l. noveboracensis*, M = *P. m. gracilis*, ♂ = male, ♀ = female, A = adult, S = subadult). Data plotted in the bar diagrams are presented in the Appendix (Table I).

The effect of formalin preservation on length of body parts was investigated by Lanko (1960). This preliminary study found no significant differences between measurements taken before and after immersion for 30 days in 10% formalin. Therefore, the use of preserved material would not affect any comparisons made with mice that had been measured when freshly killed.
Weight

The weights of *leucopus* and *maniculatus* were compared. *Leucopus* tends to be heavier than *maniculatus*. Although *leucopus* specimens were weighed minus stomach contents, their weights overlap and even exceed those of *maniculatus*. Examination of Fig. 2(a,b) shows that weight gives no clear separation of *leucopus* and *maniculatus*. The weights of adult male and female *leucopus* were not significantly different. The same was true for the weights of adult male and female *maniculatus* and subadult male and female *maniculatus*. Adult *leucopus* and adult *maniculatus* weights did not differ significantly. Weights of subadult *maniculatus* differed more from those of adult *leucopus* than they did from those of adult *maniculatus*.

Hind foot length

Hind foot lengths have been used to separate species of *Peromyscus*. McCarley (1954) found hind foot length to be the best character to separate *P. leucopus* and *P. gossypinus*. Examination of Figs. 3 and 5(a) shows that its usefulness in separating *P. l. noveboracensis* and *P. m. gracilis* is limited. Adult male and female *leucopus* do not differ significantly in the length of hind foot. Male adult *maniculatus* have a slightly longer, though not significantly longer, hind foot than adult female *maniculatus*. The ranges of hind foot length of subadult male and female *maniculatus* were the same and did not differ significantly from the hind foot lengths of adult *maniculatus*. Some parts (eg. body length) of subadult *maniculatus* are smaller than those of the adult, others are not. For example, subadult
Figure 2(a). Histograms of weights of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.

Figures to the left of each histogram indicate the number of animals being compared. Letters to the right of each histogram indicate the species and age of the animals being compared.

L = *P. l. noveboracensis*
M = *P. m. gracilis*
A = Adult
S = Subadult

(This legend will be used in all histograms)
Figure 2(a). WEIGHT (GMS.)
Figure 2(b). Bar diagrams of weights of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.

The total range of measurements is shown by a horizontal line, the mean by a vertical line, one standard deviation on each side of the mean by an "open" rectangle, and two standard errors on each side of the mean by a "solid" rectangle.

Figures to the left of each bar diagram indicate the number of animals being compared. Letters to the right of each bar diagram indicate the species and age of the animals being compared.

*L = P. l. noveboracensis*

*M = P. m. gracilis*

*A = Adult*

*S = Subadult*

(This legend will be used in all bar diagrams)
Figure 2(b). WEIGHT (GMS.)
Figure 3. Histograms of hind foot lengths of 
P. l. novoiberacensis and P. m. gracilis
by sex and age.
Figure 3. HIND FOOT LENGTH (MM.)
hind foot lengths are the same as those of the adults. Perhaps the early attainment of adult size is necessary for adeptness in climbing or running.

**Ear length**

Ear length has been used as an aid to separating these species. Cameron (1956) pointed out that *leucopus* has shorter ears than *maniculatus*. My data (Figs. 4 and 5(b)), show that *leucopus* does have shorter ears and that they are significantly shorter than those of *maniculatus*. The ear lengths of adult male and female *leucopus* do not differ significantly from each other. Neither do those of adult male and female *maniculatus* and subadult male and female *maniculatus*. Ear lengths of subadult *maniculatus* do not differ significantly from those of adult *maniculatus*. Hence full ear length is attained early in life. Perhaps the early attainment of adult ear length, like hind foot length has some adaptive significance. Ear length was the most highly significantly different character found and most nearly separated these species of mice.

**Body length**

Body lengths were compared to assess their usefulness in separating the two species. *Leucopus* tends to have a shorter body length than *maniculatus*. No significant differences were found between male and female adults and male and female subadults of either species. Body lengths of subadult *maniculatus* were significantly different from those of adult *maniculatus*. Since adult body length is not attained by subadult animals, it may
Figure 4. Histograms of ear lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Figure 4. EAR LENGTH (MM.)
Figure 5(a). Bar diagrams of hind foot lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.

Figure 5(b). Bar diagrams of ear lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Figure 5(a). HIND FOOT LENGTH (MM.)

Figure 5(b). EAR LENGTH (MM.)
Figure 6(a). Histograms of body lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Figure 6(a). BODY LENGTH (MM.)
Figure 6(b). Bar diagrams of body lengths of 

$P. \ l. \ noveboracensis$ and $P. \ m. \ gracilis$

by sex and age.
Figure 6(b).  BODY LENGTH (MM.)
not have as much adaptive significance as hind foot length or ear length. Although body lengths of adult *leucopus* and adult *maniculatus* were found to be significantly different, the wide range of measurement in any one group (for example, adult female *maniculatus*) make it useless in the separation of these species.

**Tail length**

Investigators have often used tail length as an aid to separating these two species. Burt and Grossenheider (1952) admit they are difficult to tell apart, but give the following as a fairly good means of separation: *P. l. n.*: tail length shorter than 3 3/5 inches (9.15 cms.); *P. m. g.*: tail length longer than 3 3/5 inches (9.15 cms.). This method, however, does not completely separate the mice used in this study. Of 120 *noveboracensis*, 9 have tails longer than 9.15 cms.; of 157 *gracilis* (Algonquin Park), 136 have tails shorter than 9.15 cms.; and of 100 *gracilis* (R.O.M.Z. loan), 78 have tails shorter than 9.15 cms.

Cameron (1956) says that the tail length of *leucopus* is usually less than one-half the total length and that *maniculatus* has a tail length that is usually greater than one-half the total length. This method does not completely separate the specimens used here. Of 120 *leucopus*, 119 have a tail length less than one-half the total length; of 157 *maniculatus* (Algonquin Park), 69 have a tail length greater than one-half the total length; and of 100 *maniculatus* (R.O.M.Z. loan), 27 have a tail length greater than one-half the total length. Neither of the above methods is substantiated by my data.
Figure 7(a). Histograms of tail lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Figure 7(a). TAIL LENGTH (MM.)
Figure 7(b). Bar diagrams of tail lengths of

P. l. noveboracensis and P. m. gracilis

by sex and age.
Figure 7(b). TAIL LENGTH (MM.)
Comparisons of tail lengths of *leucopus* and *maniculatus* are shown in Fig. 7(a,b). No significant differences in tail length were found between the sexes of each age group of each species. Tail lengths of adult *leucopus* were significantly different from those of adult and subadult *maniculatus*. Subadult *maniculatus* tended to have shorter tails than adult *maniculatus*. Although there was great overlap in length of tail between *leucopus* and *maniculatus*, this character appears to have some value in the separation of the two.

**Interparietal width**

Interparietal widths of *leucopus* and *maniculatus* were examined for possible differences. Graphic presentation of interparietal widths (Figs. 8 and 10(a)), shows that the measurements for both species overlap too greatly for this character to be of taxonomic value.

**Interparietal length**

The interparietal length has been used by Hoffmeister (1951), and Cockrum (1954), for comparisons of species of *Peromyscus*. These authors found that the length of the interparietal changes very little with age and that it does not differ between sexes. My data (Figs. 9 and 10(b)) show that it does not differ significantly between the sexes and ages of *maniculatus* and the sexes of *leucopus*. *Leucopus* has a significantly shorter interparietal length than *maniculatus*. Interparietal length is a good character for separating most animals of the two species.
Figure 8. Histograms of interparietal widths of

*P. l. noveboracensis* and *P. m. gracilis* by

sex and age.
Figure 8.

INTERPARIETAL WIDTH (MM)

NUMBER OF INDIVIDUALS

M. ♀ (S)
M. ♂ (S)
M. ♀ (A)
M. ♂ (A)
L. ♀ (A)
L. ♂ (A)
Figure 9. Histograms of interparietal lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Figure 9. INTERPARIETAL LENGTH (MM.)
Figure 10(a). Bar diagrams of interparietal widths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.

Figure 10(b). Bar diagrams of interparietal lengths of *P. l. noveboracensis* and *P. m. gracilis* by sex and age.
Fig. 10(a). INTERPARIETAL WIDTH (MM.)

Fig. 10(b). INTERPARIETAL LENGTH (MM.)
Skull length

The lengths of skulls of leucopus and maniculatus were examined for possible specific differences (Figs. 11 and 13(a)). Leucopus has a significantly longer skull than maniculatus, although there was great overlap of measurement. Subadult maniculatus tended to have shorter skulls than adult maniculatus. No significant differences in skull length were found between the sexes of adult leucopus, adult maniculatus, and subadult maniculatus. Skull length is useful in the separation of the mice.

Rostral length

Comparisons were made of rostral lengths of leucopus and maniculatus (Figs. 12 and 13(b)). Leucopus tended to have a longer rostrum than maniculatus. Subadult maniculatus had a shorter rostrum than adult maniculatus. No significant differences in rostral length were found between the sexes of adult leucopus, adult maniculatus and subadult maniculatus. There was a greater difference between the species in skull length than in rostral length. This character is useful as an aid to the separation of the mice.

Baculum length

The length of the baculum has been used by many authors to distinguish between genera and species of Peromyscus. Blair (1942) found no marked qualitative differences between the bacula of the maniculatus and leucopus species groups. Hooper (1958) reported the mean value for baculum length in leucopus to be 9.0 mms. and in maniculatus, 8.3 mms. Burt (1960) questioned the
Figure 11. Histograms of skull lengths of *P. l. novboracensis* and *P. m. gracilis* by sex and age.
Figure 11. SKULL LENGTH (MM.)
Figure 12. Histograms of rostral lengths of \textit{P. l. noveboracensis} and \textit{P. m. gracilis} by sex and age.
Figure 13(a). Bar diagrams of skull lengths of

P. l. noveboracensis and P. m. gracilis by
sex and age.

Figure 13(b). Bar diagrams of rostral lengths of

P. l. noveboracensis and P. m. gracilis by
sex and age.
Figure 13(a). **SKULL LENGTH (MM.)**

![Graph showing skull length for different species and genders.]

Figure 13(b). **ROSTRAL LENGTH (MM.)**

![Graph showing rostral length for different species and genders.]

taxonomic value of the baculum in *Peromyscus* except for the separation of subgenera. He found the mean value for the length of the baculum of *leucopus* to be 9.5 mms. (range, 8.1-10.9 mms.), and of *maniculatus* to be 9.3 mms. (range, 8.7-9.8 mms.). These values are so similar that their taxonomic usefulness is negligible.

My data show that the lengths of the bacula of adult *leucopus* and *maniculatus* lie in the same size range. *Leucopus* averaged 8.9 mms. for 39 individuals (range, 5.3-11.3 mms.), and *maniculatus* averaged 8.1 mms. for 19 individuals (range, 6.0-10.0 mms.). Burt's statement (1960, P. 54), that (the baculum length of), "*P. m. gracilis*, for instance, is well within the size range of *leucopus*." is supported by my data. Baculum length is not a good character for the separation of these species.

In summary, graphic comparison shows that ear length and interparietal length are the best characters to use in the separation of *P. l. noveboracensis* and *P. m. gracilis*. Neither of these measurements differ significantly between subadult and adult animals of the one species. Tail length is the next best character, followed by skull length, rostral length, and hind foot length. Body length and interparietal width overlap too greatly to be of any value.

**The Separation of *leucopus* and *maniculatus* using Morphological Characters**

Comparison of parts of mice showed that some measurements differed more than others between species. To select the measurements most useful in separating the species, "t" values
were calculated to show the degree of difference between measurements. No significant differences, at the 5% level, were found between the sexes of adult *leucopus*, adult *maniculatus*, and sub-adult *maniculatus* for all measurements compared. The parts compared between species, and their "t" values, are arranged in a decreasing order of difference in the following table:

Table 1. Degree of difference between body parts of *leucopus* and *maniculatus* as shown by "t" values.

<table>
<thead>
<tr>
<th>Parts Compared</th>
<th>&quot;t&quot; Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ear length</td>
<td>51.436</td>
</tr>
<tr>
<td>Tail length</td>
<td>49.352</td>
</tr>
<tr>
<td>Interparietal length</td>
<td>19.308</td>
</tr>
<tr>
<td>Body length</td>
<td>10.987</td>
</tr>
<tr>
<td>Skull length</td>
<td>7.326</td>
</tr>
<tr>
<td>Rostral length</td>
<td>3.722</td>
</tr>
</tbody>
</table>

The "t" values in Table 1 are all significant at the 5% level and represent comparisons of body parts of adults of both sexes of *leucopus* with those of adults of both sexes of *maniculatus*. A complete summary of all "t" tests calculated is given in the Appendix (Table II). Table 1 indicates that *leucopus* and *maniculatus* are significantly different in all comparisons for which "t" was calculated. The greatest divergence between the forms was in those characters that possessed the largest "t" values. Length of ear possesses the largest "t" value but is not satisfactory, when used alone, to separate *leucopus* and *maniculatus* because the ranges of measurement for the two species overlap. Hence, while ear length separates the species statistically, in practice, it does not separate all the individuals. The above table also shows that these mice differ
significantly in a number of characteristics. If these
classified characteristics are considered at the same time, a total
difference may be seen between the species. This is done in
Fig. 14(a,b), the measurement polygon.

The measurement polygon expresses a number of characteristics
simultaneously. Each polygon is a "picture" of an average
animal, based on the mean values of 8 measurements. Examination
of Fig. 14(b) reveals that there is considerably more similarity
between polygons A and B and C and D than there is between A and
C or D or between B and C or D. The polygons clearly show that
*leucopus* has a shorter average interparietal width, ear length,
body length, tail length, interparietal length, and hind foot
length, while its average skull length and rostral length are
longer than comparable average values for *maniculatus*.

The Character Index for the Separation of *leucopus* and *maniculatus*

While polygons express total average features, they are not
a convenient way to separate the species. Also, I have no
measure of the goodness of fit of a species to a polygon. At
the moment, all that can be said is that a mouse is either a
*leucopus* or a *maniculatus* depending upon which polygon it
resembles most.

Another way of making use of a number of tendencies in each
species to separate them is by the use of the character index.
The term "character index" was proposed by Hubbs and Whitlock
(1929), who found the need for a simple mathematical expression
of several differential features. These indices have been used
successfully in fish systematics for the separation of closely
Figure 14(a). Key to measurement polygons of *P. l. niveboracensis* and *P. m. gracilis*. One average measurement (in mms.) is plotted on each radius.

E. L. = ear length  
B. L. = body length  
T. L. = tail length  
SK. L. = skull length  
R. L. = rostral length  
I. L. = interparietal length  
H. F. L. = hind foot length  
I. W. = interparietal width  
(This legend applies to Figure 14(b))
Figure 14(a).

MEASUREMENT POLYGON KEY
Figure 14(b). Measurement polygons of *P. l. noveboracensis* and *P. m. gracilis*. Average measurements for each group of animals are plotted on each radius.

A. = adult male *P. l. noveboracensis*  
B. = adult female *P. l. noveboracensis*  
C. = adult male *P. m. gracilis*  
D. = adult female *P. m. gracilis*
Figure 14(b). Measurement polygons of $P_l n$ and $P_m g$. 

A. $P_{lN} \sigma$ (A)  
B. $P_{lN} \varphi$ (A)  
C. $P_{mG} \sigma$ (A)  
D. $P_{mG} \varphi$ (A)
allied forms by Schultz (1937), Schultz and Welander (1934), Hubbs and Kuromuma (1941), and Hubbs et al (1943). Davenport (1935) used simple indices to compare proportions of animals. Moreau and Southern (1957) used the index, tail/wing X 100, to show geographical variation in shrikes. Cameron (1958) found that the index, mean skull height/mean rostral length, separated black bears of Newfoundland from those of the mainland.

The pros and cons of using character indices for comparisons of species and subspecies of animals are discussed by Ginsburg (1939) and Hubbs et al (1943). Hubbs et al (P. 5), strongly defend the use of character indices by saying that, "no arithmetic combination of characters, however, can bring out differences which do not exist, so long as we apply the identical character-index formula to both types being compared.". They further state (P. 6), that, "we have been informed by statisticians that such values as standard deviation, standard error, and the like may legitimately be computed for an array of the indices, provided that each of the combined characters presents in itself an approximately normal frequency distribution.".

The main criticism against the use of character indices is concerned with the determination of species and subspecies (Ginsburg, 1939). This author points out that the degree of difference between individuals of two populations depends on the characters selected and on the manipulations performed. These indices should not, therefore, be used to determine whether two populations are subspecies of one species or are separate species.

Ginsburg's criticisms are valid and worthy of consideration. However, they do not apply to the problem I am trying to solve
with character indices. The animals used in this study are known to be separate species on the basis of their breeding biology and I wish only to be able to separate them by some quantitative rather than qualitative method.

Of the characters compared graphically and statistically, ear length, interparietal length, and tail length were found to be the measurements differing most between the two species. These characters were shorter in *leucopus* than in *maniculatus*. If these three measurements were multiplied together for each individual of each species, the resultant indices for *leucopus* would be smaller than those for *maniculatus*. To further increase the difference between the two species, division of these indices by another measurement that was longer in *leucopus* than in *maniculatus* would give even smaller indices for *leucopus* and comparably larger ones for *maniculatus*. Both rostral length and skull length filled this requirement and each was used as part of a character index. The resulting indices were:

I. \[ \text{ear length} \times \text{tail length} \times \text{interparietal length} \div \text{skull length} \]

II. \[ \text{ear length} \times \text{tail length} \times \text{interparietal length} \div \text{rostral length} \]

Although each of these indices was found to completely separate *leucopus* and *maniculatus*, both are given here because specimens collected by snap trapping are often damaged and one of the necessary measurements, such as skull length, might be unobtainable. In this example, index II could be used rather than index I.
Tests of Indices

If an index is to be of value, it should be easily calculated and separate all ages and sexes of forms to which it may be applied. The indices were tested by calculating values for all animals used in the study. Histograms and bar diagrams of the values for each species, sex, and age group were plotted (Figs. 15, 16, 17(a,b)). Also included in the tests (but not graphed) were data for mice from the Royal Ontario Museum of Zoology and from Osgood (1909, pp. 260-61, 263-64). A summary of data plotted in bar diagrams for each species, sex, and age group is given in the Appendix (Table III). The indices for each species were compared by "t" test and found significantly different at the 5% level for mice from all areas.

It has already been shown that sex had no effect on measurements. Although subadult mice tend to have smaller parts, Figs. 15, 16, and 17(a,b) show that age does not affect the values of the indices calculated for all age groups examined. Since the values of the indices are not affected by sex or age, data for each species can be combined. Combined data of the indices are presented in Table 2.

Table 2. Means and ranges of combined data of the character indices of leucopus and maniculatus.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Source</th>
<th>Index I Mean</th>
<th>Index I Range</th>
<th>Index II Mean</th>
<th>Index II Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>leucopus</td>
<td>92</td>
<td>L. Opin., Perth Rd.</td>
<td>3.41</td>
<td>2.57-4.09</td>
<td>10.45</td>
<td>7.39-12.50</td>
</tr>
<tr>
<td>leucopus</td>
<td>10</td>
<td>Osgood</td>
<td>3.49</td>
<td>------------</td>
<td>---</td>
<td>------------</td>
</tr>
<tr>
<td>maniculatus</td>
<td>10</td>
<td>Osgood</td>
<td>5.75</td>
<td>5.69-5.83</td>
<td>---</td>
<td>------------</td>
</tr>
</tbody>
</table>
Figure 15. Histograms of the index (I),

E.L. X T.L. X I.L., for P. l. noveboracensis
SK.L.
and P. m. gracilis by sex and age.

E. L. = ear length
T. L. = tail length
I. L. = interparietal length
SK. L. = skull length
NUMBER OF INDIVIDUALS

INDEX: E.L. X T.L. X L.L.

Figure 15.
Figure 16. Histograms of the index (II),

E.L. X T.L. X I.L., for P. l. nibleboracensis
and P. m. gracilis by sex and age.

E. L= ear length
T. L= tail length
I. L= interparietal length
R. L= rostral length
Figure 17(a). Bar diagrams of the index (I),

\[ E.L. \times T.L. \times I.L. \], for \( P. l. \) \textit{noveboracensis} \( \text{SK.L.} \)

and \( P. m. \) \textit{gracilis} by sex and age.

(Legend as in Figure 15)

Figure 17(b). Bar diagrams of the index (II),

\[ E.L. \times T.L. \times I.L. \], for \( P. l. \) \textit{noveboracensis} \( \text{R.L.} \)

and \( P. m. \) \textit{gracilis} by sex and age.

(Legend as in Figure 16)
Fig. 17(a). INDEX: \( \frac{E.L \times T.L. \times I.L.}{S.K.L.} \)

Fig. 17(b). INDEX: \( \frac{E.L \times T.L. \times I.L.}{R.L.} \)
Table 2 shows that means and ranges of character indices calculated for *leucopus* differ from those calculated for *maniculatus*. "t" tests and bar diagrams (Fig. 17(a,b)) show that all *leucopus* indices differ significantly from all *maniculatus* indices. Hence, the character indices completely separate *leucopus* and *maniculatus* of all ages and sexes that were examined. A mouse with an index I of 2.57-4.09 is *leucopus* and one with an index I of 4.26-7.90 is *maniculatus*. A mouse with an index II of 7.39-12.50 is *leucopus* and one with an index II of 12.83-22.77 is *maniculatus*.

Although Osgood (1909) measured ear lengths from dried specimens, the values for indices calculated from his data fall within the ranges of each species index derived from my data. The shrinkage of pinnae is apparently not sufficient to greatly alter the value of the index.

**Test of the Indices on Mice From an Area of Sympathy**

The indices worked to separate mice from areas and samples that were chosen to represent "good" *leucopus* and *maniculatus*. If the mice are not good species, they might blend in areas of sympathy. Also, it is in areas of overlap of range that geography is of no assistance in the identification of a specimen. Thus, the final and perhaps most critical test of the indices was to apply them to mice caught in the area of sympathy of *leucopus* and *maniculatus* in Ontario.

Twelve mice from areas of sympathy were sent to me by Dr. D. A. Smith of Carleton University, Ottawa. Almost all were captured two and one-half miles north of Cloyne, Frontenac
County. Two were captured five miles northwest of Calabogie, Renfrew County. Calculation of indices I and II for these mice completely separated them into two groups. Four specimens were clearly referable to *leucopus* (index I: range 3.35-3.93; index II: range, 10.56-12.38) and 8 specimens were clearly referable to *manticulus* (index I: 4.39-6.01; index II: 13.36-18.61). This test again indicates that the indices are valid methods for the separation of *P. l. novoeracensis* and *P. m. gracilis* in southeastern Ontario.

**Summary of the Indices**

Indices have been shown to be valid tools for separating closely related, difficult to separate species. Indices were formulated that completely separate *P. l. novoeracensis* and *P. m. gracilis* on a quantitative basis. These indices are:

I. \( \text{ear length} \times \text{tail length} \times \text{interparietal length} \times \frac{\text{skull length}}{\text{rostral length}} \)

II. \( \text{ear length} \times \text{tail length} \times \text{interparietal length} \times \frac{\text{skull length}}{\text{rostral length}} \)

These indices completely separate the two species regardless of sex and age. For index I, values ranging from 2.57 to 4.09 are indicative of *leucopus*, while values ranging from 4.26 to 7.90 are indicative of *manticulus*. For index II, values ranging from 7.39 to 12.50 are indicative of *leucopus*, while values ranging from 12.83 to 22.77 are indicative of *manticulus*.

The indices are simple and easy to use quantitative methods for the separation of *P. l. novoeracensis* and *P. m. gracilis*. The indices separated *novoeracensis* and *gracilis* from areas of sympatry and areas of allopatry.
Results of Crossbreeding

Crossbreeding experiments between *P. leucopus* and *P. maniculatus* were attempted in the laboratory. Results of the experiments are summarized in the Appendix (Table IV). Four of the 17 live *leucopus* received early in 1961 were paired with local *maniculatus* (*P. m. austerus*, *P. m. oreas*, and *P. m. spp.* from Mandarte Island, British Columbia). These mice have been paired for over a year and have not littered. Two control pairs of *leucopus* produced a total of three litters. One control pair of each of the above subspecies of local *maniculatus* produced a total of two litters (*P. m. oreas* failed to breed).

Two mixed pairs (*P. m. g.♂ X P. l. n.♀*), (*P. m. g.♀ X P. l. n.♂*) of mice were placed in separate cages on February 17, 1962. The mice have been in breeding condition but have not littered. One pair of *leucopus* and one pair of *maniculatus* were placed in separate cages on the same date, in the same room, to be used as controls. No litters have resulted from these pairs.

The negative results obtained by the attempted crossbreeding of *leucopus* and *maniculatus* support those of Dice (1931, 1933, 1937), and Waters (1960). The fact that pairs of *leucopus* and *maniculatus*, chosen at random from groups of mice caught in the same areas and kept in similar cages in the same room, produced litters, indicates that something other than laboratory conditions apparently inhibits interbreeding between the two species.
From my work and the experiments of others, it appears that *leucopus* will not mate with *maniculatus* in captivity. The block to interbreeding may be morphological, behavioral, or physiological, and perhaps linked with sight or smell.

The smell of a strange male may be an exteroceptive block to pregnancy in white mice (Bruce and Parrott, 1960). These workers found that single or successive pregnancies in the same female could be blocked by the introduction of a strange male, particularly a male of a different strain from the stud male, near or with the female. These inhibitory effects were abolished in mice from which the olfactory bulbs had been removed.

Perhaps the females of either *leucopus* or *maniculatus*, when mated with animals of the other species, react in much the same way. The odor of the strange male could be a more or less permanent inhibitor to pregnancy. Hence, species odor might play a role in reproductive isolation and speciation in mammals in general and *leucopus* and *maniculatus* in particular. I will present my own results on the role of odor in interspecies reaction in a later section of this report.
THE DISTRIBUTION OF PEROMYSCUS LEUCOPUS NOVEBORACENSIS AND PEROMYSCUS MANICULATUS GRACILIS

Differences between P. l. noveboracensis and P. m. gracilis were investigated not only to find a method of separating them but also to see if differences found could be used to explain their distribution. Attempts will be made to relate the distribution of the mice with environmental factors, morphology, color of pelage, behavior, and species interaction.

History of Distribution of Peromyscus

Knowledge of the history of distribution of species of the genus Peromyscus in eastern North America might provide an explanation for their present range. Waters (1960) reviews the post-Wisconsin redistribution of mice of this genus and speculates on the sequence of events leading to speciation and subsequent development of exclusive ranges. He presents evidence that the genus Peromyscus reached the eastern United States during the early Pleistocene. It is probable that the frequent shifts and alternation of climate and vegetation during the glacial and interglacial periods of the Pleistocene also caused Peromyscus to shift frequently, resulting in highly variable species of mice in eastern North America.

Waters proposes that toward the end of the Pleistocene, an incipient population of P. maniculatus occupied the higher elevations of the southern half of the Appalachians, while an incipient P. leucopus population occupied the lower elevations to the east, south, and west of this area. His data indicate
that a genetic divergence took place in the incipient *P. leucopus* population during the late Pleistocene and resulted in forms with either strongly or weakly bicolored tails.

Waters correlates the northward movement of *maniculatus* and *leucopus* with botanical data derived from Braun (1950). According to this author, spruce was the first forest component to move northward, following the retreat of the Wisconsin ice cap. Oaks, at first associated with pines, moved in after the spruce. *Maniculatus* moved north with the expanding spruce forest, before *leucopus*. *Leucopus* began to move northward with the expansion of oak forests, the population west of the Appalachians spreading throughout the midwest, that east of the Appalachians spreading along the Atlantic coastal plain. Thus, *maniculatus* was associated with coniferous and *leucopus* with deciduous forest. The present relationship of these species with the vegetation of Ontario will be discussed later.

In summary, Waters feels that the species and subspecies of *Peromyscus* are probably limited to their present day ranges by characteristics developed through the late Pleistocene and during their post-Wisconsin movement northward.

**Present Distribution of *Peromyscus* in Ontario**

The present distribution of the two species has been outlined by several authors (Osgood, 1909; Hall and Kelson, 1959). For this study, I obtained trapping records of *Peromyscus* in Ontario from the Royal Ontario Museum of Zoology. These data are presented in Fig. 18(a,b,c) and indicate where *Peromyscus* have been trapped up to 1960-61. Also included in these figures are data I have
Figure 18(a). Map of Counties and Districts of southeastern Ontario.

1. Essex  18. Peel  
3. Lambton 20. Dufferin 
5. Middlesex 22. Durham 
8. Brant   25. Bruce 
10. Welland 27. Simcoe 
11. Lincoln 28. Victoria 
12. Wentworth 29. Peterborough 
13. Waterloo 30. Hastings 
15. Halton  32. Frontenac 
16. Huron   33. Leeds 
17. Wellington  34. Grenville 
18. Peel    35. Dundas 
20. Dufferin 37. Glengarry 
22. Durham  39. Russell 
23. Northumberland 40. Carleton 
24. Prince Edward 41. Lenarck 
25. Bruce   42. Haliburton 
26. Grey    43. Muskoka 
27. Simcoe  44. Parry Sound 
28. Victoria 45. Renfrew 
29. Peterborough 46. Manitoulin 
30. Hastings 47. Nipissing 
31. Lennox and Addington 48. Algoma 
32. Frontenac 49. Sudbury 
33. Leeds    50. Timiskaming 

(This legend also applies to Figures 18(b) and 18(c))
Fig. 18(a). COUNTIES AND DISTRICTS
OF SOUTH-EASTERN ONTARIO
Figure 18(b). Range of *P. l. noveboracensis* in southeastern Ontario, taken primarily from R.O.M.Z. trapping records. The stippled areas indicate record(s) of animal(s) tentatively identified as *P. l. noveboracensis*. The black areas indicate counties or districts where *noveboracensis* has been trapped.
Figure 18(b).

RANGE OF P. L. NOVEBORACENSIS
IN SOUTH-EASTERN ONTARIO.

(ROMZ. FILES)
Figure 18(c). Range of *P. m. gracilis* in south-eastern Ontario, taken primarily from R.O.M.Z. trapping records. The stippled areas indicate record(s) of animal(s) tentatively identified as *P. m. gracilis*. The black areas indicate counties or districts where *gracilis* has been trapped.
Figure 18(c).

RANGE OF P. M. GRACILIS IN SOUTH-EASTERN ONTARIO

(R.O.M.Z. FILES)
obtained from published faunal surveys for portions of Ontario (Wright and Simpson, 1920; Snyder and Logier, 1930; Davis, 1931; Snyder and Logier, 1931; Clarke, 1933; Snyder et al, 1941; Jameson, 1943; Rand, 1945; Warburton, 1949; Brown and Lanning, 1954; Rutter, 1959).

The distributions of *P. l. noveboracensis* and *P. m. gracilis* shown in fig. 18(b,c) are only rough approximations because: (1) Trapping records for the whole of southeastern Ontario are incomplete, (2) Many specimens are only tentatively identified, and (3) Trapping records were mapped by counties and districts, not by site of capture.

Osgood's (1909, p. 114, frontispiece) distribution maps of *P. l. noveboracensis* and *P. m. gracilis* in Ontario showed that *gracilis* occupied the area east of the Great Lakes up to the border of Quebec, while *noveboracensis* was restricted to southern Ontario. Recent data (Rutter, 1951; R.O.M.Z. trapping records), show that the ranges of the two species have changed slightly; *gracilis* has moved its southern boundary northward, while *noveboracensis* has extended its northern boundary further north.

**Correlation of Ranges of Mice with Vegetation**

The distributions of the mice can be roughly correlated with types of vegetation. Osgood (1909), and Cross and Dymond (1929) noted that *gracilis* preferred the colder, more moist places, or deep, mostly coniferous woods, while *leucopus* preferred the warmer, dryer, more open country, or deciduous woods.

The changes in distributions of the mice, since 1909, can also be roughly correlated with changes in types of vegetation.
Since 1909, considerable settlement has taken place in southern Ontario and much of the native vegetation has been removed. Settlement has spread northward and conifer forest has been cleared. These clearings encouraged the growth of deciduous trees of the conifer-hardwood subclimax. *Gracilis* has withdrawn its range northward, presumably following the receding border of coniferous forest where it prefers to live. *Leucopus* has extended its range northward, presumably following the expansion of hardwood forest.

The association of *maniculatus* with coniferous forest and *leucopus* with deciduous forest was recently reported by Klein (1959). He found *maniculatus* to be positively associated with plants of the hemlock-white pine-northern hardwoods forest region and avoided plants of the oak-chestnut forest region. *Leucopus* was positively associated with plants of the oak-chestnut forest region and avoided plants of the hemlock-white pine-northern hardwoods forest region.

Further evidence for the association of *leucopus* and *maniculatus* with forest regions can be shown by comparing their ranges with the forest regions of southeastern Ontario. The forest regions of Ontario are well known and have recently been redescribed by Rowe (1959). Comparing the ranges of *leucopus* and *maniculatus* a map of forest regions of southeastern Ontario (fig. 19) shows several correlations. The range of *maniculatus* lies primarily in the coniferous forest region while that of *leucopus* lies in the deciduous forest region. The area where their ranges overlap coincides with the coniferous-deciduous forest transition zone. Further, correlation with the principle
Figure 19. Forest regions of southeastern Ontario (after Rowe, 1959).

1. Deciduous forest region
   Niagara section

2-10, 12. Great Lakes-St. Lawrence forest region
   2. Huron-Ontario section
   3. Georgian Bay section
   4. Algonquin-Pontiac section
   5. Middle Ottawa section
   6. Upper St. Lawrence section
   7. Algonquin-Pontiac section
   8. Sudbury-North Bay section
   9. Timagami section
  10. Algoma section
  12. Haileybury clay section

11. Boreal forest region
   Missinaibi-Cabonga section
Figure 19.  FOREST REGIONS OF SOUTH-EASTERN ONTARIO

(AFTER ROWE, 1959)
trees in each region shows that the range of *maniculatus* is associated with trees such as spruce, pine, aspen, and birch, while that of *leucopus* is associated with sugar maple and beech. From the evidence presented here, I conclude that *maniculatus* is associated with regions of coniferous forest growth and *leucopus* with regions of deciduous forest growth.

Examination of fig. 18(b) reveals a somewhat discontinuous distribution for *gracilis* along the southeastern edge of Lake Huron, at the south end of Lake Erie, and along the northern edge of Lake Ontario. Perhaps *gracilis* is present in these areas in relic stands of coniferous forest.

**Relationship of Ranges of Mice to Food, Temperature and Water**

Correlations between vegetation and distribution may only be superficial and not causal factors. Other factors such as food, temperature, and water may be the ones governing the distributions of these mice. The foods eaten by *leucopus* and *maniculatus* were mentioned by Dice (1922), Cogshall (1928), Burt (1940), Hamilton (1941), Jackson (1952), Cameron (1956), Williams (1959), Connor (1960), Getz (1961), and Howard (1961). Both species ate a variety of foods including seeds, nuts, insects, arachnids, fruit, fungi, green vegetation, roots, and molluscs. No apparent differences in food preference were exhibited. Food is not clearly related to the distribution of these mice.

Temperature tolerances of *leucopus* and *maniculatus* might be factors influencing their distribution. However, Howard (1951) and Eskridge and Udall (1955), found that both species could
withstand freezing temperatures provided sufficient food was available. Sealander (1952) showed that *P. leucopus* could endure temperatures from +35 to -25°C. Getz (1961) concluded that temperatures had no obvious influence upon the local distribution of *P. leucopus*. High temperatures probably do not affect the mice because of their nocturnal behavior.

Perhaps the availability of food during the winter differs for each species and this governs their respective distributions. No data are available on their ability to survive this critical period under conditions of winter temperature, provided with selected kinds and amounts of food.

From the evidence above, I conclude that there is little difference in temperature tolerance between *leucopus* and *maniculatus*. Thus temperature, by itself, does not appear to be a factor determining their distributions.

The water requirements of the two species might influence their distribution. Lindeborg (1952) observed that *leucopus* and *maniculatus* displayed similar reactions to limited amounts of water. Neither could survive on 0.2 cc./day and both lost weight on 0.4 cc./day. Klein (1959) showed that both species used about the same amount of water: *leucopus*, 0.43 cc./gram body weight or 7.6 cc./individual/day; *gracilis*, 0.42 cc./gram body weight or 7.4 cc./individual/day. These studies indicate that water requirements for *leucopus* and *maniculatus* are not appreciably different. This factor does not appear responsible for their distributions.
The Morphology and Pelage Color of the Mice as an Explanation of Distribution

Differences in morphology and color of pelage between the two species might be correlated with differences in distributions. Dice (1940) suggested that correlation of tail length and hind foot length with type of environment might essentially be a correlation with behavior. Longer-tailed mice, for example, are usually found in heavily forested areas (Fox, 1948), and this in turn might be correlated with semi-arboreal behavior. Horner (1954) demonstrated that semi-arboreal Peromyscus were significantly better than terrestrial Peromyscus in their ability to climb artificial tree trunks and cross gaps of varying widths. She also showed that the long tail was an adaptive structure which facilitated semi-arboreal existence.

Although P. maniculatus has a longer tail than P. leucopus, both are known to be semi-arboreal (Chenoweth, 1917; Burt, 1940; Blair, 1950; Linduska, 1950; Horner, 1954; Connor, 1960). Horner (1954) classified both P. l. noveboracensis and P. m. gracilis as being semi-arboreal and detected little difference between them in climbing performances. I observed both species climbing glass drinking tubes and cage walls with equal facility. Since no difference in the climbing abilities of maniculatus over leucopus have been found, I conclude that the slightly longer tail of maniculatus is not causally related to its distribution.

Correlation between size of other body parts and the distribution of either species can only be suggested. For example, the slightly longer rostral length of leucopus might
provide more leverage for eating large, hard foods such as nuts that are commonly found in its range. However, this is only conjecture and I have found no supporting data on Peromyscus in the literature.

Similar morphological differences for food handling have been observed for birds (Robbins, 1932; Lack, 1944, 1947). Lack (1947) considers that the marked difference in size of beaks of the Galapagos finches is an adaptation for taking foods of different size.

The pelage color of mammals tends to be positively correlated with the color of the soil surface. Dice (1940) demonstrated this correlation between soil color and color of pelage of Peromyscus and gave further evidence (1947) of its protective function. The colors of pelage of noveboracensis and gracilis are nearly identical, although the former tends to be more brightly colored. Brighter pelage may have a protective function in the autumn when leaves in deciduous forests become highly colored. Gracilis, with its less brightly colored pelage might gain more protection in the less brightly colored coniferous forests. Differences in pelage color between the two species, however, are so slight that I find it hard to be convinced that this is of importance in the distribution of these forms.

Behavior of the Mice as a Cause of Distribution

Differences in behavior between leucopus and maniculatus might be factors influencing their distribution. For this reason, they were observed at every opportunity in the laboratory. Both species were good climbers and readily climbed the glass
drinking tubes on gravity water bottles in their cages.

When I cleaned out cages, occasionally an animal would escape. Escapees of each species tended to behave differently. *Maniculatus* moved comparatively slowly and appeared to be uncertain about which direction to go. *Leucopus* ran quickly as soon as it had escaped from the cage. Horner (1954) also noted that *leucopus* moved more quickly and unhesitatingly than *maniculatus*. This difference in approach to a new situation could be related to the speed at which the animal is capable of travelling, or to some inherited factor related to its normal habitat. *Leucopus* has been found to be the faster of the two on the ground (Layne and Benton, 1954). These investigators found that *leucopus* could travel at 8.46 feet/second (range, 6.9-10.0 feet/second), while *maniculatus* could travel only 6.4 feet/second (range, 6.2-6.6 feet/second).

The two species of *Peromyscus* reacted differently to handling. *P. l. noveboracensis* was difficult to catch and would run and jump rapidly around the cage. *P. m. gracilis* was fairly easily approached and often came out to investigate the opening of the cage door. Svihla (1932) found *leucopus* to be more excitable and difficult to handle than *P. m. bairdii*. Horner (1954) and Foster (1959) reported that *gracilis* was more easily handled than *bairdii*. I found differences in the behavior of *leucopus* and *maniculatus*. *Leucopus* was the more highly excitable and faster moving of the two forms.

*Leucopus* as mentioned above, is considered by many workers to be the more enterprising, less habitat-restricted mouse
Perhaps the enterprise and greater speed of *leucopus* reflects its wide choice of habitats. *Maniculatus* is less enterprising and slower of movement than *leucopus* and this may be related to its presence in more homogeneous habitats. Whether this behavior of each form is cause or effect of the vegetation in which they occur is unknown.

**Interaction Between Species as a Cause of Distribution**

The role of species interaction in distribution has been examined by Dice (1922), Klein (1959), and Sheppe (1961). Klein (1959) reported that although there was some ecological separation of *leucopus* and *maniculatus*, no evidence was present to suggest that behavioral factors, such as interspecific antagonism, played a part in determining the local distribution of the forms. Interaction may not only prevent sympatric species from interbreeding, but it might also restrict their distribution in local areas. Sheppe (1961) found that *P. oreas* and *P. maniculatus* have more restricted habitat preferences in the area of sympatry than where each occurs alone. The restriction of habitat distribution was attributed, in part, to interspecific competition. Interspecific interaction may or may not influence distribution.

Klein (1959) found no antagonism or cannibalism resulted from keeping *leucopus* and *maniculatus* together. He observed that their initial response to each other was one of caution, but soon they could be found huddling together. In my crossbreeding experiments, mixed pairs of both species lived amicably and no antagonism
between the two was evident. Unfortunately, insufficient numbers of live animals were available to test antagonism between two pairs (one pair of each species) during the breeding season. Perhaps at that time of the year, antagonism plays a large role in keeping the species apart. An experiment with one pair of leucopus kept in the same cage as two successive pairs of local maniculatus, gave interesting observations. In both instances, the female of the pair of maniculatus was found dead. The dead animals were not eaten but were mutilated, and the blood-spattered cage gave evidence that the dead animals had moved about before they had succumbed. These deaths occurred several months after both pairs had been placed in the cage and, at no time was antagonism shown between the animals. The dead animals had been bitten about the ears and the tails were badly chewed. Neither the pair of leucopus nor the male maniculatus showed evidence of having fought. No explanation for this behavior has been found. Burt (1940) reported that the female leucopus holds a definite territory in the breeding season and is antagonistic to other leucopus females. However, both maniculatus females were killed in mid-winter.

Intraspecific antagonism was evident in cages containing only leucopus. In one cage, four males were discovered starting to eat the warm carcass of their female litter mate. The dead animal had a badly chewed tail and neck. In another cage, three of seven male leucopus were found huddled in the corner of the cage farthest from the nest. All had raw, stubby, swollen tails, and would not enter the nest even when prodded. The other four leucopus were not injured. Reasons for antagonism in leucopus
are unknown.

Only one instance of antagonism was noted among *maniculatus*. A female *P. m. austerus* killed and partly ate her three litter mates. Further investigation revealed that lack of food had prompted the cannibalism.

**Interaction Between Species by Odor**

Interaction between the two forms could be responsible for their differences in distribution and ability to live sympatrically, still retaining separate identity. Moore (1961) reported that there was evidence to support the role of olfaction in the sexual isolation of *P. maniculatus* and *P. polionotus*. Because *noveboracensis* and *gracilis* occur sympatrically, and are not known to interbreed where they do, it seemed plausible that odor discrimination might be involved in their apparent sexual isolation. To test this, plans were drawn up for an odor discrimination apparatus (olfactometer).

**Apparatus for Testing Recognition of Odor**

Certain specifications had to be considered in the design of the olfactometer. Firstly, it should be as light-proof and air-tight as possible to prevent external stimuli from affecting results. Secondly, it should present the animal with a number of choices, each of which could equally be taken. Thirdly, some method of recording the animal's movement within the apparatus must be incorporated in the design of the apparatus. Fourthly, the suspected odor must be readily obtainable and in a form that could be used in the apparatus.

After consideration of these specifications, a testing
chamber was constructed (Fig. 20). The apparatus consisted of a central chamber with moveable doors connecting to three radiating arms. It was constructed entirely of sheet metal and was made as air-tight and light-impervious as possible. The three radiating arms were spaced equidistantly to give the animals an equal opportunity to enter any one of them. Three arms were chosen because there were two species odors to test and the third could be used as a control.

The problem of recording the activity of an animal in a metal container was solved by having a moveable joint in the middle of each arm. A projecting piece of metal (writer) was soldered onto the end of each arm. The writer traced a record of the movement of the animal in the end of the arm, on a piece of smoked kymograph paper.

Selection of a source of odor was a problem because Peromyscus have a number of glands (eg. anal, preputial, clitoral) which could be responsible for a species-specific odor and, almost nothing is known about their function. Mammals are known to use odor for sexual attraction, territory and home range marking, and possibly for protection (Bourlière, 1956, pp. 103-107, 225-230). Hediger (1949, from Bourlière, 1956) reported the use of urine and faeces by the male pygmy hippopotamus in marking its territory. The ease of obtaining urine and faeces, and the knowledge that it is used by mammals in the marking of territories and trails, made this the choice for a source of odor.

The apparatus was set up as in Fig. 20(B). Soiled paper cage lining was placed in two of the three arms. The third arm was used as the control and contained only clean paper cage lining.
Figure 20. Diagram of odor discrimination apparatus (olfactometer).

A. Plan of apparatus as seen from above.

B. Side view of apparatus in operation.
Figure 20.

ODOR DISCRIMINATION APPARATUS
A mouse (tester) was then placed in the central chamber for 10-15 minutes to allow it to become accustomed to the apparatus. Each experiment was run at the same time of day (5:30 P.M.) and for the same length of time (one hour). No animal was used for more than a single experiment.

To start an experiment, three kymographs "attached" to the ends of the arms were turned on and doors leading from the central chamber to the arms were opened. Entrance of the mouse into the ends of the arms was recorded as a "dip" on the kymograph paper. The initial movement of the mouse was usually recorded as a series of rapid visits to each arm. Gradually the mouse would settle down and tend to remain longer in one of the arms.

Results of Tests with the Olfactometer

These preliminary experiments were run to test the design of the apparatus and to see if mice do respond to their own or other species odors. Seven experiments were done and the results are given in the Appendix (Table V). A summary of the results is given in Table 3.

Table 3. Results of odor discrimination experiments.

<table>
<thead>
<tr>
<th>Expt. No.</th>
<th>Tester</th>
<th>Odor</th>
<th>No. of Times Entered Arm</th>
<th>% of Total Time in Arms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>ΨP.л.n.</td>
<td>Control</td>
<td>4</td>
<td>5.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ψ and ΨF.m.g.</td>
<td>6</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ψ and ΨF.л.n.</td>
<td>10 *</td>
<td>83.1 *</td>
</tr>
<tr>
<td>2.</td>
<td>ΨF.m.g.</td>
<td>Residual control</td>
<td>7 *</td>
<td>18.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual Ψ and ΨF.m.g.</td>
<td>6</td>
<td>44.0 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual Ψ and ΨF.л.n.</td>
<td>6</td>
<td>37.5</td>
</tr>
</tbody>
</table>
### Table 3 (cont'd). Results of odor discrimination experiments.

<table>
<thead>
<tr>
<th>Expt. No.</th>
<th>Tester</th>
<th>Odor</th>
<th>No. of Times Entered Arm</th>
<th>% of Total Time in Arms</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.</td>
<td>$\sigma^P.m.g.$</td>
<td>Control</td>
<td>28</td>
<td>44.0 *</td>
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<td></td>
<td>$\sigma$ and $\varphi^P.m.g.$</td>
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<td>33 *</td>
<td>25.0</td>
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<td></td>
<td>$\sigma$ and $\varphi^P.l.n.$</td>
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<td>23</td>
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<tr>
<td>4.</td>
<td>$\varphi^P.m.g.$</td>
<td>Control</td>
<td>31 *</td>
<td>62.6 *</td>
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<td>$\sigma$ and $\varphi^P.m.g.$</td>
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<td>15.9</td>
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<td></td>
<td>$\sigma$ and $\varphi^P.l.n.$</td>
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<td>21.5</td>
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<tr>
<td>5.</td>
<td>$\varphi^P.l.n.$</td>
<td>Control</td>
<td>30 *</td>
<td>85.3 *</td>
</tr>
<tr>
<td></td>
<td>$\varphi^P.m.g.$</td>
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<td>22</td>
<td>4.6</td>
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<tr>
<td></td>
<td>$\varphi^P.m.g.$</td>
<td></td>
<td>25</td>
<td>10.1</td>
</tr>
<tr>
<td>6.</td>
<td>$\varphi^P.l.n.$</td>
<td>Control</td>
<td>11</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>$\sigma$ and $\varphi^P.m.g.$</td>
<td></td>
<td>18</td>
<td>20.8</td>
</tr>
<tr>
<td></td>
<td>$\sigma$ and $\varphi^P.l.n.$</td>
<td></td>
<td>31 *</td>
<td>73.8 *</td>
</tr>
<tr>
<td>7.</td>
<td>$\varphi^P.m.g.$</td>
<td>Control</td>
<td>20</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>$\varphi^P.m.g.$</td>
<td></td>
<td>31 *</td>
<td>79.3 *</td>
</tr>
<tr>
<td></td>
<td>$\sigma$ and $\varphi^P.l.n.$</td>
<td></td>
<td>22</td>
<td>16.7</td>
</tr>
</tbody>
</table>

* denotes the greatest number of times any arm was entered and the greatest % of total time spent in any arm.

Although this odor discrimination experiment was intended to be only a preliminary study and few tests were run, I believe the above results are worthy of comment. Since the tester was used only once, no bias was incurred by having the animal follow a learned path. The tests were run early in January and none of the mice used were in breeding condition. This rules out possible changes in response to odor caused by animals being in estrus. The residual odor test (no. 2) was conducted to find out how effectively the apparatus had been cleaned. In this test, only clean paper cage lining was placed at the end of each arm. It was decided that although results showed some residual odor
was present in the arms, it would not greatly alter the following results provided each arm was consistently used for the same odor.

Generally, the tester entered most often and/or stayed longest in the arm containing its own species odor (experiments no. 1, 2, 3, 6, 7). Exceptions to this are experiments 4 and 5 where the animals entered more often and stayed longer in the control. No explanation is offered for experiment 4, but in experiment 5, the animal appeared to be avoiding the arms which both contained the odor of the other species. Perhaps there is an active avoidance of the other species in nature by odor?

Another generalization that can be made is that the testers appeared to prefer arms containing an odor to the arm used as a control (experiments no. 1, 2, 6, 7). Why this is so is not known.

The possibilities of testing species interaction by odor discrimination are only beginning to be realized. The results thus far indicate: (1) The apparatus works and (2) There seems to be measurable odor discrimination in the mice. Continuation of these experiments promises to give valuable results which may hold the key to sexual isolation in sympatric species and perhaps a clue to patterns of distribution in closely related species.
SUMMARY

1. The aims of this study were: (1) to investigate morphological differences between two similar species of mice, *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis*, to find a method of separating them, and (2) to determine whether morphological or other differences found between the two species could be used to explain their distribution.

2. Most mice used in this study came from areas in Ontario where each was known to occur alone. Samples of *leucopus* came from areas near Kingston and *maniculatus* from Algonquin Park. The only exception is the sample from the area of sympatry (Renfrew and Frontenac Counties).

3. The measurements of 169 mice of both species were analyzed graphically and statistically to find a method to separate them. The characters evaluated were: weight, hind foot length, ear length, body length, tail length, interparietal width, interparietal length, skull length, and rostral length.

4. No one character was useful in separating the two forms. From an evaluation of the differences in size of parts of the mice, indices were developed which completely separated *leucopus* and *maniculatus* of all sexes and ages examined. These indices were: 

   \[ \text{ear length} \times \text{tail length} \times \text{interparietal length} \text{ or } \frac{\text{skull length}}{\text{ear length} \times \text{tail length} \times \text{interparietal length}} \]

   \[ \text{ear length} \times \text{tail length} \times \text{interparietal length} \times \text{rostral length} \]

5. The indices completely separated a sample of 12 *leucopus* and *maniculatus* trapped in the zone of sympatry.

6. Breeding experiments were conducted to see if the two species would interbreed. Four mixed pairs of *leucopus* and local
maniculatus were kept together for over a year and did not produce offspring. Two control pairs of leucopus produced a total of three litters and three control pairs of maniculatus produced a total of two litters (P. m. oreas failed to breed). No litters resulted from two mixed pairs of P. m. gracilis and P. l. noveboracensis kept together for 71 days. One pair of noveboracensis and one pair of gracilis (controls), kept together for the same length of time, failed to reproduce.

7. The distribution of P. l. noveboracensis and P. m. gracilis in Ontario was redescribed using recent data.

8. An attempt was made to explain the distribution of each species on the basis of factors such as vegetation, food preference, temperature tolerance, water requirement, morphology, color of pelage, and behavior. Maniculatus was found to occur in coniferous and leucopus in deciduous vegetation. No correlation was found between the ranges of the mice and food preference, temperature tolerance, water requirement, morphology, and color of pelage. Correlation between their ranges and behavior was doubtful.

9. Interaction between the species was investigated as a cause of distribution. Experiments were conducted in an olfactometer with the odor of mice. The purpose was to investigate interaction between mice by olfaction. Preliminary work suggested that the mice responded to the odor of other mice. A mouse entered more often and stayed longer in a chamber containing the odor of its own species. A chamber containing odor was preferred to the control chamber without odor.
APPENDIX

Table I.

Measurement data plotted in bar diagrams (in mms.).

<table>
<thead>
<tr>
<th></th>
<th>Ear L.</th>
<th>Body L.</th>
<th>Tail L.</th>
<th>Skull L.</th>
<th>Rostral L.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Adult</strong></td>
<td>Range</td>
<td>15.0-17.3</td>
<td>73.4-96.4</td>
<td>62.1-88.2</td>
<td>25.1-28.0</td>
</tr>
<tr>
<td><strong>♂P. l. n.</strong></td>
<td>Mean</td>
<td>16.2</td>
<td>85.5</td>
<td>74.9</td>
<td>26.4</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.67</td>
<td>5.30</td>
<td>5.70</td>
<td>0.68</td>
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<tr>
<td></td>
<td>N =35</td>
<td>2 S.E. 0.22</td>
<td>1.80</td>
<td>1.94</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Adult</strong></td>
<td>Range</td>
<td>14.8-17.5</td>
<td>76.5-96.0</td>
<td>61.2-86.9</td>
<td>25.0-27.9</td>
</tr>
<tr>
<td><strong>♀P. l. n.</strong></td>
<td>Mean</td>
<td>16.0</td>
<td>86.4</td>
<td>74.0</td>
<td>26.4</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.69</td>
<td>5.50</td>
<td>6.40</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>N =33</td>
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<td>1.92</td>
<td>2.20</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Adult</strong></td>
<td>Range</td>
<td>17.0-20.9</td>
<td>80.6-97.4</td>
<td>76.2-97.2</td>
<td>24.6-27.0</td>
</tr>
<tr>
<td><strong>♂P. m. g.</strong></td>
<td>Mean</td>
<td>18.8</td>
<td>88.6</td>
<td>86.8</td>
<td>25.9</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.85</td>
<td>4.60</td>
<td>5.80</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>N =22</td>
<td>2 S.E. 0.38</td>
<td>2.10</td>
<td>2.60</td>
<td>0.28</td>
</tr>
<tr>
<td><strong>Adult</strong></td>
<td>Range</td>
<td>17.0-20.4</td>
<td>72.5-101.0</td>
<td>69.5-105.5</td>
<td>24.3-27.9</td>
</tr>
<tr>
<td><strong>♀P. m. g.</strong></td>
<td>Mean</td>
<td>19.0</td>
<td>89.2</td>
<td>86.8</td>
<td>25.7</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.76</td>
<td>6.30</td>
<td>8.90</td>
<td>0.76</td>
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<td></td>
<td>N =31</td>
<td>2 S.E. 0.28</td>
<td>2.40</td>
<td>4.00</td>
<td>0.28</td>
</tr>
<tr>
<td><strong>Subad.</strong></td>
<td>Range</td>
<td>17.4-20.1</td>
<td>75.0-86.0</td>
<td>66.8-97.0</td>
<td>24.0-26.1</td>
</tr>
<tr>
<td><strong>♂P. m. g.</strong></td>
<td>Mean</td>
<td>18.6</td>
<td>82.5</td>
<td>81.8</td>
<td>25.3</td>
</tr>
<tr>
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<td>0.54</td>
</tr>
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<td>1.38</td>
<td>3.00</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Subad.</strong></td>
<td>Range</td>
<td>17.5-20.1</td>
<td>79.4-89.2</td>
<td>75.1-90.9</td>
<td>24.1-26.1</td>
</tr>
<tr>
<td><strong>♀P. m. g.</strong></td>
<td>Mean</td>
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<td>83.2</td>
<td>82.3</td>
<td>25.1</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.82</td>
<td>2.99</td>
<td>4.45</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>N =26</td>
<td>2 S.E. 0.32</td>
<td>1.18</td>
<td>1.74</td>
<td>0.20</td>
</tr>
</tbody>
</table>
Table I. (Continued)

Measurement data plotted in bar diagrams (in mms.).

<table>
<thead>
<tr>
<th></th>
<th>Int. L.*</th>
<th>Int. W.</th>
<th>Weight (gms.)</th>
<th>Hind Foot L.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Range</td>
<td>6.8-9.0</td>
<td>2.1-3.4</td>
<td>15.10-31.25</td>
<td>19.4-22.0</td>
</tr>
<tr>
<td>μP.l.n. Mean</td>
<td>7.5</td>
<td>2.9</td>
<td>20.7</td>
<td>20.5</td>
</tr>
<tr>
<td>1 S.D.</td>
<td>0.51</td>
<td>0.33</td>
<td>3.26</td>
<td>0.70</td>
</tr>
<tr>
<td>N=35</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 S.E.</td>
<td>0.17</td>
<td>0.11</td>
<td>1.10</td>
<td>0.24</td>
</tr>
<tr>
<td>Adult Range</td>
<td>6.8-8.3</td>
<td>2.0-3.6</td>
<td>13.16-25.46</td>
<td>18.4-22.0</td>
</tr>
<tr>
<td>μP.l.n. Mean</td>
<td>7.5</td>
<td>2.8</td>
<td>19.3</td>
<td>20.3</td>
</tr>
<tr>
<td>1 S.D.</td>
<td>0.42</td>
<td>0.36</td>
<td>1.04</td>
<td>0.76</td>
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<td></td>
<td></td>
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<td>2 S.E.</td>
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<td>0.13</td>
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<td>Adult Range</td>
<td>8.1-9.8</td>
<td>2.3-3.9</td>
<td>15.13-24.27</td>
<td>20.5-22.2</td>
</tr>
<tr>
<td>μP.m.g. Mean</td>
<td>9.2</td>
<td>3.1</td>
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<td>21.3</td>
</tr>
<tr>
<td>1 S.D.</td>
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<td>0.33</td>
<td>2.43</td>
<td>0.53</td>
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<td></td>
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<td>0.15</td>
<td>1.10</td>
<td>0.24</td>
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<tr>
<td>Adult Range</td>
<td>7.9-9.9</td>
<td>2.5-3.9</td>
<td>13.39-23.92</td>
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</tr>
<tr>
<td>μP.m.g. Mean</td>
<td>9.1</td>
<td>3.0</td>
<td>18.9</td>
<td>21.0</td>
</tr>
<tr>
<td>1 S.D.</td>
<td>0.38</td>
<td>0.27</td>
<td>3.04</td>
<td>0.52</td>
</tr>
<tr>
<td>N=31</td>
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<td></td>
</tr>
<tr>
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<td>0.05</td>
<td>1.08</td>
<td>0.19</td>
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<td>Subad. Range</td>
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<td>12.13-19.79</td>
<td>20.0-22.2</td>
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<tr>
<td>μP.m.g. Mean</td>
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<td>3.1</td>
<td>16.1</td>
<td>21.0</td>
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<td>1 S.D.</td>
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<td>0.26</td>
<td>1.68</td>
<td>0.65</td>
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<td>N=22</td>
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</tr>
<tr>
<td>2 S.E.</td>
<td>0.17</td>
<td>0.12</td>
<td>0.76</td>
<td>0.30</td>
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<tr>
<td>Subad. Range</td>
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<td>2.5-3.3</td>
<td>13.18-18.81</td>
<td>20.0-21.8</td>
</tr>
<tr>
<td>μP.m.g. Mean</td>
<td>9.0</td>
<td>3.0</td>
<td>16.2</td>
<td>21.0</td>
</tr>
<tr>
<td>1 S.D.</td>
<td>0.36</td>
<td>0.25</td>
<td>1.49</td>
<td>0.49</td>
</tr>
<tr>
<td>N=26</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 S.E.</td>
<td>0.14</td>
<td>0.05</td>
<td>0.58</td>
<td>0.19</td>
</tr>
</tbody>
</table>

* interparietal length, interparietal width.
Table II.

"t" values calculated in comparisons of body parts

<table>
<thead>
<tr>
<th>Animals Compared</th>
<th>Ear L.</th>
<th>Body L.</th>
<th>Tail L.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ad. $\varphi$ P. l.n. x Ad. $\varphi$ P. m.g. N = 22</td>
<td>14.534</td>
<td>3.441</td>
<td>14.399</td>
</tr>
<tr>
<td>Ad. $\varphi$ P. l.n. x Ad. + Subad. $\varphi$ P. m.g. N = 57</td>
<td>23.925</td>
<td>0.582</td>
<td>19.458</td>
</tr>
<tr>
<td>Ad. $\varphi$ P. l.n. x Ad. + Subad. $\varphi$ P. m.g. N = 31</td>
<td>20.532</td>
<td>3.881</td>
<td>19.328</td>
</tr>
<tr>
<td>Ad. + Subad. $\varphi$ P. m.g. N = 57</td>
<td>9.492</td>
<td>0.221</td>
<td>25.164</td>
</tr>
<tr>
<td>Ad. + Subad. $\varphi$ P. m.g. N = 53</td>
<td>51.436</td>
<td>10.987</td>
<td>49.352</td>
</tr>
<tr>
<td>Ad. $\varphi$ P. l.n. x Ad. $\varphi$ P. l.n. N = 33</td>
<td>1.664</td>
<td>1.400</td>
<td>1.611</td>
</tr>
<tr>
<td>Ad. $\varphi$ P. m.g. N = 31</td>
<td>0.071</td>
<td>0.595</td>
<td>0.000</td>
</tr>
<tr>
<td>Subad. $\varphi$ P. m.g. x Subad. $\varphi$ P. m.g. N = 26</td>
<td>0.415</td>
<td>0.651</td>
<td>0.471</td>
</tr>
<tr>
<td>Ad. + Subad. $\varphi$ P. m.g. N = 57</td>
<td>1.778</td>
<td>1.967</td>
<td>1.425</td>
</tr>
</tbody>
</table>

** P ≤ 0.005
*** P ≤ 0.001
Table II. (Continued)

"t" values calculated in Comparisons of body parts.

<table>
<thead>
<tr>
<th>Animals Compared</th>
<th>Skull L.</th>
<th>Rostral L.</th>
<th>Int. L. (f)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ad. (\sigma) P.l.n. (N=35) X Ad. (\sigma) P.m.g. (N=22)</td>
<td>1.840</td>
<td>1.682</td>
<td>19.051</td>
</tr>
<tr>
<td>Ad. (\sigma) P.l.n. (N=35) X Ad. + Subad. (\sigma) P.m.g. (N=44)</td>
<td>5.136</td>
<td>6.088</td>
<td>30.096</td>
</tr>
<tr>
<td>Ad. (\varphi) P.l.n. (N=33) X Ad. (\varphi) P.m.g. (N=31)</td>
<td>3.269</td>
<td>0.461</td>
<td>23.278</td>
</tr>
<tr>
<td>Ad. (\varphi) P.l.n. (N=33) X Ad. + Subad. (\varphi) P.m.g. (N=57)</td>
<td>7.410</td>
<td>4.738</td>
<td>34.782</td>
</tr>
<tr>
<td>Ad. (\sigma) + (\varphi) P.l.n. (N=68) X Ad. (\sigma) + (\varphi) P.m.g. (N=53)</td>
<td>7.326</td>
<td>3.722</td>
<td>19.308</td>
</tr>
<tr>
<td>Ad. (\sigma) P.l.n. (N=35) X Ad. (\varphi) P.l.n. (N=33)</td>
<td>0.000</td>
<td>0.787</td>
<td>0.356</td>
</tr>
<tr>
<td>Ad. (\sigma) P.m.g. (N=22) X Ad. (\varphi) P.m.g. (N=31)</td>
<td>0.684</td>
<td>0.000</td>
<td>0.484</td>
</tr>
<tr>
<td>Subad. (\sigma) P.m.g. (N=22) X Subad. (\varphi) P.m.g. (N=26)</td>
<td>0.606</td>
<td>0.940</td>
<td>0.517</td>
</tr>
<tr>
<td>Ad. + Subad. (\sigma) P.m.g. (N=44) X Ad. (\varphi) Subad. (\varphi) P.m.g. (N=57)</td>
<td>1.898</td>
<td>1.445</td>
<td>0.085</td>
</tr>
</tbody>
</table>

\(f\) interparietal length

** \(P \leq 0.005\)

*** \(P \leq 0.001\)
Table III.

Data plotted in bar diagrams of indices.

<table>
<thead>
<tr>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SK.L.</td>
<td>R.L.</td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>2.66-4.09</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>3.45</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.125</td>
</tr>
<tr>
<td>dP.l.n.</td>
<td>N = 46</td>
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</tr>
<tr>
<td>Adult</td>
<td>Range</td>
<td>2.57-4.01</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>3.37</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.119</td>
</tr>
<tr>
<td>Adult</td>
<td>Range</td>
<td>4.83-7.00</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>5.77</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.250</td>
</tr>
<tr>
<td>dP.m.g.</td>
<td>N = 22</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>Range</td>
<td>4.54-7.14</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>5.80</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.228</td>
</tr>
<tr>
<td>Subad.</td>
<td>Range</td>
<td>4.26-6.50</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>5.39</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.264</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>5.52</td>
</tr>
<tr>
<td></td>
<td>1 S.D.</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>2 S.E.</td>
<td>0.149</td>
</tr>
</tbody>
</table>

* E.L. = ear length, T.L. = tail length, I.L. = interparietal length, SK.L. = skull length.
Table IV.

Breeding data.

<table>
<thead>
<tr>
<th>Length of Time Paired</th>
<th>Pairs</th>
<th>No. of Litters</th>
<th>No. in Litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>67 days</td>
<td>P. l. n.♂ x P. l. n.♀</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>73 days</td>
<td>P. l. n.♂ x P. l. n.♀</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. m. o.♂ x P. l. n.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. m. a.♂ x P. l. n.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. l. n.♂ x P. m. a.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. l. n.♂ x P. m. spp.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. m. o.♂ x P. m. o.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. m. a.♂ x P. m. a.♀</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>365+ days</td>
<td>P. m. spp.♂ x P. m. spp.♀</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>71+ days</td>
<td>P. l. n.♂ x P. l. n.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>71+ days</td>
<td>P. l. n.♂ x P. m. g.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>71+ days</td>
<td>P. m. g.♂ x P. m. g.♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>71+ days</td>
<td>P. m. g.♂ x P. l. n.♀</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

P. l. n. = P. leucopus noveboracensis
P. m. o. = P. maniculatus oreas
P. m. a. = P. maniculatus austerus
P. m. g. = P. maniculatus gracilis
P. m. spp. = P. maniculatus (Mandarte Island, British Columbia)
Table V.

Results of odor discrimination experiments.

<table>
<thead>
<tr>
<th>Expt. No.</th>
<th>Tester</th>
<th>Odor</th>
<th>No. times Entered</th>
<th>Minutes Spent in Arm</th>
<th>% of Total Time in Arms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>♀P.l.n.</td>
<td>Control</td>
<td>4</td>
<td>1.2</td>
<td>5.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.m.g.</td>
<td>6</td>
<td>2.7</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.l.n.</td>
<td>10 *</td>
<td>19.1 *</td>
<td>83.1 *</td>
</tr>
<tr>
<td>2.</td>
<td>♂P.m.g.</td>
<td>Residual control</td>
<td>7 *</td>
<td>0.7</td>
<td>18.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual ♀and ♀P.m.g.</td>
<td>6</td>
<td>1.6 *</td>
<td>44.0 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual ♀and ♀P.l.n.</td>
<td>6</td>
<td>1.3</td>
<td>37.5</td>
</tr>
<tr>
<td>3.</td>
<td>♂P.m.g.</td>
<td>Control</td>
<td>28</td>
<td>5.7 *</td>
<td>44.0 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.m.g.</td>
<td>33 *</td>
<td>3.3</td>
<td>25.0</td>
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<tr>
<td></td>
<td></td>
<td>♀and ♀P.l.n.</td>
<td>23</td>
<td>4.0</td>
<td>31.0</td>
</tr>
<tr>
<td>4.</td>
<td>♀P.m.g.</td>
<td>Control</td>
<td>31 *</td>
<td>31.5 *</td>
<td>62.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.m.g.</td>
<td>25</td>
<td>8.0</td>
<td>15.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.l.n.</td>
<td>30</td>
<td>10.8</td>
<td>21.5</td>
</tr>
<tr>
<td>5.</td>
<td>♀P.l.n.</td>
<td>Control</td>
<td>30 *</td>
<td>42.3 *</td>
<td>85.3 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀P.m.g.</td>
<td>22</td>
<td>2.3</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀P.l.n.</td>
<td>25</td>
<td>5.0</td>
<td>10.1</td>
</tr>
<tr>
<td>6.</td>
<td>♂P.l.n.</td>
<td>Control</td>
<td>11</td>
<td>0.5</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.m.g.</td>
<td>18</td>
<td>2.1</td>
<td>20.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.l.n.</td>
<td>31 *</td>
<td>7.4 *</td>
<td>73.8 *</td>
</tr>
<tr>
<td>7.</td>
<td>♀P.m.g.</td>
<td>Control</td>
<td>20</td>
<td>1.8</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀P.m.g.</td>
<td>31 *</td>
<td>36.2 *</td>
<td>79.3 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀and ♀P.l.n.</td>
<td>22</td>
<td>7.6</td>
<td>16.7</td>
</tr>
</tbody>
</table>

* denotes the greatest number of times any arm was entered, the greatest number of minutes spent in one of the three arms, and the greatest % of total time spent in any arm.
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