

Myers, P., B. L. Lundrigan, and B. Vande Kopple. 2005. Climate change and the distribution of *Peromyscus* in Michigan—is global warming already having an impact? pp. 101-125 in E. A. Lacey and P. Myers, eds. *Mammalian Diversification: from Chromosomes to Phylogeography*. University of California Publications in Zoology.

## **Climate Change and the Distribution of *Peromyscus* in Michigan: Is Global Warming Already Having an Impact?**

---

Philip Myers, Barbara L. Lundrigan, and Robert Vande Kopple

Two species of *Peromyscus*, the woodland deer mouse (*P. maniculatus gracilis*) and the white-footed mouse (*P. leucopus*), are found together in the forests of the northern Lower Peninsula of Michigan. Deer mice have become rare and their rate of decline appears to be accelerating. The relative abundance of *gracilis* in this area, measured as % *gracilis* in collections of *Peromyscus*, has declined from over 40% before 1931 to around 6% in 2003, and in detailed recent studies at one site, from over 50% of *Peromyscus* captures before 1996 to less than 10% in 2003. Numbers of *leucopus* at the University of Michigan Biological Station, northern Lower Peninsula, are related to the length of the winter (measured as the date of ice break-up); it appears that few *leucopus* survive long winters (when ice breaks up in late April or early May). We suggest that a recent tendency for winters to end early (revealed for this area by 100+ years of ice break-up records for Grand Traverse Bay, Lake Michigan) may be responsible for the decline in *gracilis* populations.

### ECOLOGY OF *PEROMYSCUS* IN MICHIGAN

Two species of long-tailed, forest-dwelling *Peromyscus* occur together over large areas of the northeastern United States and along the Appalachian Mountains. *Peromyscus leucopus* (the white-footed mouse) is broadly distributed in the eastern and central United States, from southernmost Canada to the Yucatan peninsula and from the Atlantic coast to the western Great Plains. *Peromyscus maniculatus* (the deer mouse) consists of a complex of long-tailed forest and short-tailed grassland “subspecies,” which are sometimes found in different habitats of the same region without evidence of interbreeding. Members of this species occur throughout much of the United States and in southern Canada north to Hudson’s Bay. Where *leucopus* and long-tailed *maniculatus* occur together, the 2 species may be very similar in appearance and difficult to distinguish, both in the field and in the laboratory (Smith and Speller, 1970; Feldhamer et al., 1983; Long and Long, 1993; Rich et al., 1996; Bruseo et al., 1999).

In Michigan, the forest-dwelling *maniculatus* is *Peromyscus maniculatus gracilis*. It has been found throughout the state’s Upper Peninsula and in the northern half of the Lower Peninsula (Figure 1a). Much of the range of *gracilis* lies to the north of Michigan, in Ontario and Quebec. *Peromyscus leucopus*, in contrast, is at the northern

limits of its range in this region and in Michigan is restricted to the Lower Peninsula and southernmost Upper Peninsula (Figure 1b). Where *gracilis* and *leucopus* overlap in Michigan, they are both very similar morphologically and are often captured in the same habitats.

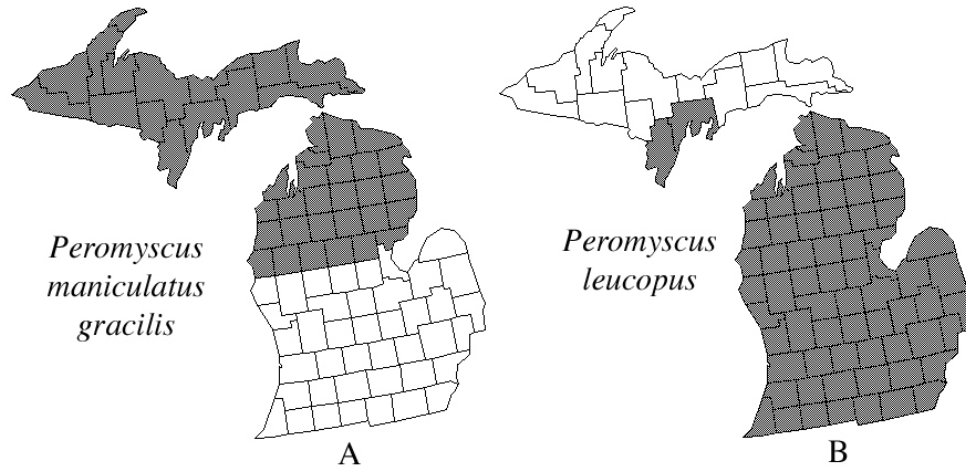


Figure 1. Distribution of *Peromyscus maniculatus gracilis* (a) and *Peromyscus leucopus* (b) in Michigan. Modified from Baker (1983).

Because of their similarity in appearance and habitat use, these two species have been the subject of a number of ecological investigations. Interactions between *leucopus* and *Peromyscus maniculatus nubiterrae* (an Appalachian representative of the forest *maniculatus* complex), for example, have been studied intensively where the two occur together in the mountains of Virginia (Wolff and Hurlbutt, 1982; Wolff et al., 1983; Barry et al., 1984; Wolff, 1985a,b; Wolff et al., 1985; Cranford and Maly, 1986; Wolff, 1986; Wolff and Durr, 1986; Harney and Dueser, 1987; Graves et al., 1988; Dooley and Dueser, 1990). In a summary, Wolff (1985b) reported that *leucopus* and *nubiterrae* "interact ecologically as a single species, though they do not interbreed." Wolff further suggested (1996) that the coexistence of the two species may depend on differences in their winter adaptations, which cause one species (*leucopus*) to flourish when winters are mild and the other (*maniculatus*) to predominate when winters are harsh.

In this paper, we show that the population of *gracilis* in the northern Lower Peninsula of Michigan has declined dramatically since the beginning of the 20<sup>th</sup> century, when the first extensive surveys of the small mammals of this region were carried out. We combine these observations with data from a recent program of regular censuses of small mammal populations in northern Michigan to suggest that *leucopus* may be sensitive to particular aspects of winter weather. We argue that changes in climate over the last century, but especially in the last 20 years, have favored *leucopus* and may be responsible for their increase in abundance relative to *gracilis*.

#### ESTIMATING THE RELATIVE ABUNDANCE OF *PEROMYSCUS MANICULATUS GRACILIS* AND *PEROMYSCUS LEUCOPUS*

Trapping surveys provided data concerning the abundance of *Peromyscus*. For records prior to 1985, we relied on specimens and field notes in Museum collections. More recent records were based on our own observations.

Historical records of trapping surveys are difficult to interpret. Even when field notes are available, the reasons why a collector trapped at a particular place are seldom apparent. Habitat descriptions are often absent or are too sketchy to be useful. Further, collectors may not preserve representatives of each species in the ratio in which they were captured. Rare species may be favored, juveniles discarded, and research interests in one species or another may lead to their over-representation in a collection.

Nevertheless, field notes and specimens preserved in collections are usually the only source of information available on the composition of past communities. Extensive collections from Michigan, often with accompanying field notes, are present in the University of Michigan Museum of Zoology and the Michigan State University Museum. They are the work of many collectors. While each collection undoubtedly reflects the interests and biases of the researchers who contributed to it, we shall assume that, in the aggregate, these materials provide a reasonable picture of the composition of small mammal communities in northern Michigan in the past and present.

An additional problem in estimating abundances of *gracilis* and *leucopus* is that these two mice are sometimes very difficult to distinguish, especially in the field. To be certain that we could identify the taxa correctly in northern Michigan, we examined 223 specimens from Michigan whose identity had been confirmed by allozymes (Meagher, 1995). We found that the following field characteristics were useful for distinguishing most Michigan specimens: ear length (longer in *gracilis*); sharpness of the zone of transition between pale and dark areas of the bicolored tail (always sharply distinct in *gracilis*, variable in *leucopus*); degree of hairiness of the tail (longer hairs in *gracilis*); and color of the throat and upper chest (usually white to the base in *leucopus* vs. hairs with a gray base in *gracilis*). No single characteristic

worked without error, but when considered together, these characteristics resulted in identifications concordant with electrophoretic evidence in almost all cases. Using these criteria, we re-identified all museum specimens included here. We excluded records based strictly on the field notes of early collectors (i.e., where the mice were not collected) because we could not confirm identifications. We included, however, mice captured and released in our own surveys (described below), because we had the advantage of having examined the electrophoretically-identified specimens before we went into the field.

We documented the relative abundance of *gracilis* and *leucopus* as the ratio  $(\#gracilis)/(\#gracilis+leucopus)$  rather than reporting the actual number of mice captured. We chose not to rely on absolute numbers because trapping effort varied from survey to survey and was often not recorded, and because seasonal fluctuations in population levels of both species were often extreme and would have confounded comparisons of collections made at different times of year. Relative abundance will be misleading if methods used in early surveys (e.g., type of trap, bait, habitats trapped) differed from those used recently and if those methods were biased towards one species. Relative abundance might also be misleading with respect to the absolute abundance of *gracilis* if the total number of *Peromyscus* captured has changed significantly over the last century. There is no evidence that either is the case.

To the museum records, we have added a number of trapping surveys in the area of overlap in the northern Lower Peninsula. The goals of these surveys and the details of the methods used often differed, but they usually involved setting lines of Sherman live-traps, typically a mixture of large and small sizes, and running them for 1 to 3 nights. The number of traps set varied from 30 to over 500. Traps were baited with oats. Trapping was completed by us, by graduate and undergraduate students, and by volunteers. Trappers recorded the identity of each individual captured and its sex, weight, and reproductive condition. We marked each mouse temporarily by clipping a small patch of fur from its rump. Identifications were made by ourselves or by students that we had trained. From 1985 to 2002, we conducted surveys at 118 localities in this region, for a total of over 30,000 trap-nights. Initially, we chose localities that we believed would provide a representation of the diversity of mammals in the area. More recently, we have focused more attention on habitats that we know are used by the less common *gracilis*, as we attempt to find remaining populations of that species.

Records were summarized by county. This was done because very few *Peromyscus* were recorded from many of the individual collection sites, resulting in exaggerated differences in relative abundance unless sites were combined. Counties provided a convenient and unbiased basis for pooling data. Counties with <10 *Peromyscus* captured during a given trapping period were not included in subsequent analyses.

### Census Trapping

To examine yearly and seasonal patterns of *Peromyscus* abundance with more precision than was possible with the general survey data, in 1989 we began a biannual census of small mammals at the University of Michigan Biological Station (UMBS), Cheboygan and Emmet Counties, near the northern tip of the Lower Peninsula (Figure 2). Three trap-lines, selected to sample 3 dominant habitat types in the area, were laid out and permanently marked:

(1) Colonial Point: 45° 29.43'N, 84° 41.12'W; mature northern hardwoods with open understory; dominant tree species in the vicinity of the trap-line include sugar and red maple (*Acer saccharum*, *Acer rubrum*), red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), and white pine (*Pinus strobus*).

(2) Burn Plot: 45° 33.65'N, 84° 42.08'W; mixed hardwoods and pines; understory predominantly huckleberry (*Gaylussacia baccata*) and ground cover bracken fern (*Pteridium aquilinum*), blueberries (*Vaccinium* sp.), and lichens; dominant tree species in the vicinity of the trap-line include red maple, red oak, aspen (*Populus grandidentata*), white pine, and red pine (*Pinus resinosa*).

(3) Reese's Swamp: 45° 32.87'N, 84° 39.92'W; boreal conifers with ground cover of sphagnum, maple seedlings, and a variety of forbs; dominant tree species in the vicinity of the trap-line include northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), red maple, and yellow and white birch (*Betula alleghaniensis*, *B. papyrifera*).

Each trap-line consists of 20 trapping stations. At each station, 1 large (9 cm x 8 cm x 23 cm) and 2 small (6.5 cm x 5 cm x 16 cm) Sherman traps are set and baited with oats. Trap stations are separated by approximately 25 m (Colonial Point), 20 m (Burn Plot), and 15 m (Reese's Swamp). Each line is trapped for 3 days and nights in early May (before the first litters of the spring are weaned) and again in late September (after weaning of the last litters of the summer).

In addition to these standardized censuses, in 1996 we began regular sampling near the Black River in the Pigeon River State Forest (Otsego Co., 45° 07'N, 84° 25'W; Figure 2), an area that had also been trapped in 1989, 1991, 1992, and 1993 using a protocol similar to the one described above. This area was chosen for additional sampling because of the presence of large numbers of *gracilis*. Approximately 100 traps (small Shermans) are deployed during each trapping session. They are placed in 2 parallel lines of 50 traps each. Because these trap-lines are on public land, they are not permanently marked. The trap-lines always begin at the same points and follow the same compass directions. Traps are placed at intervals of 5-7 m, baited with oats, and run for 1-2 nights during May and September. The trap-lines lie in deciduous forest. Tree species present are primarily sugar maple and American beech, with some red oak and white birch also present. The understory is open and consists primarily of maple and beech seedlings.

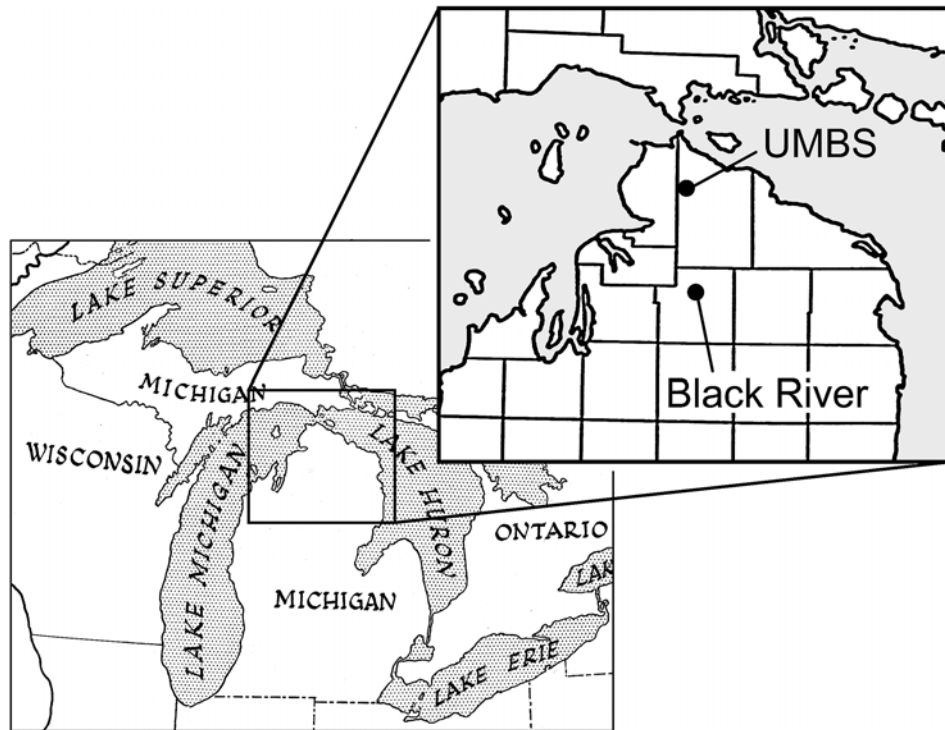


Figure 2. Location of study sites for *Peromyscus leucopus* and *P. maniculatus gracilis* in Michigan.

#### Mast Data

Acorns have been shown to be an important food resource for *leucopus* in northern New York (Elkinton et al., 1996; Ostfeld et al., 1996). To examine the effects of oak masting on mouse populations in Michigan, we identified years of significant mast production (1988-present) using data from field notes and from the Michigan Department of Natural Resources.

#### Climate Data

Dates when ice leaves Grand Traverse Bay were obtained from the Traverse City Chamber of Commerce. All other climatic data were recorded at a weather station at UMBS, located within 10 km of the UMBS census sites and approximately 54 km NNW of the Black River site.

## DATA ANALYSIS

Analysis of climatic data is problematic because of the large number of climate descriptors available. With a sufficient number of data points, one could record as many weather variables as possible and use multivariate statistical techniques to explore and reduce the variable set. Alternatively, one could carry out a series of univariate tests and adjust significance levels to take into account the number of tests performed. With only 15 points for each spring and autumn (representing the 15 years of UMBS census data), neither approach was feasible. Instead, for these preliminary and exploratory analyses, we chose seven variables that integrate different aspects of the climate experienced by small mammals. We searched for possible effects of winter weather (October-April) on spring populations, and summer weather (May-September) on autumn populations. To represent summer weather, we included total rainfall, total number of cooling degree days (defined as 65°F subtracted from the mean temperature for each day, summed over all days from May 1 through September 30), and the greatest number of consecutive days with no rainfall. For winter weather, we used the total snowfall, the number of heating degree days (defined as the mean temperature for each day subtracted from 65°F, summed over all days from October 1 through April 30), and the minimum winter soil temperature measured at a depth of 50 cm (not available for one year). As an indication of the length of the winter, we used the dates on which ice forms (ice formation) and leaves (ice break-up) Douglas Lake, a large (1520 ha) lake that adjoins UMBS and lies within 10 km of each census site.

Because we did not attempt to adjust significance levels to reflect the number of tests, the patterns reported here should be viewed with caution. Nevertheless, because long-term data such as these are rare and difficult to obtain yet are essential for understanding population processes (Inchausti and Halley, 2001), we present our results to date to point out trends and to encourage and focus future research. Nonparametric statistical tests (Siegel, 1956) were used in the analysis of climatic data.

## RESULTS

Are populations of *Peromyscus maniculatus gracilis* declining in the northern Lower Peninsula of Michigan? To examine long-term changes in the relative numbers of *gracilis* and *leucopus*, we divided our records (including general surveys, plus census data from UMBS and Black River) into four time periods, 1901-1930, 1931-1960, 1961-1990, and 1991-2002. For each period, we calculated the %*gracilis* from records for each county within the known range of *gracilis* in the Lower Peninsula. This analysis indicates that the relative abundance of *gracilis* in the northern Lower

Peninsula has declined sharply over the last century (Figure 3; ANOVA,  $df = 3,27$ ,  $p = 0.044$ ).

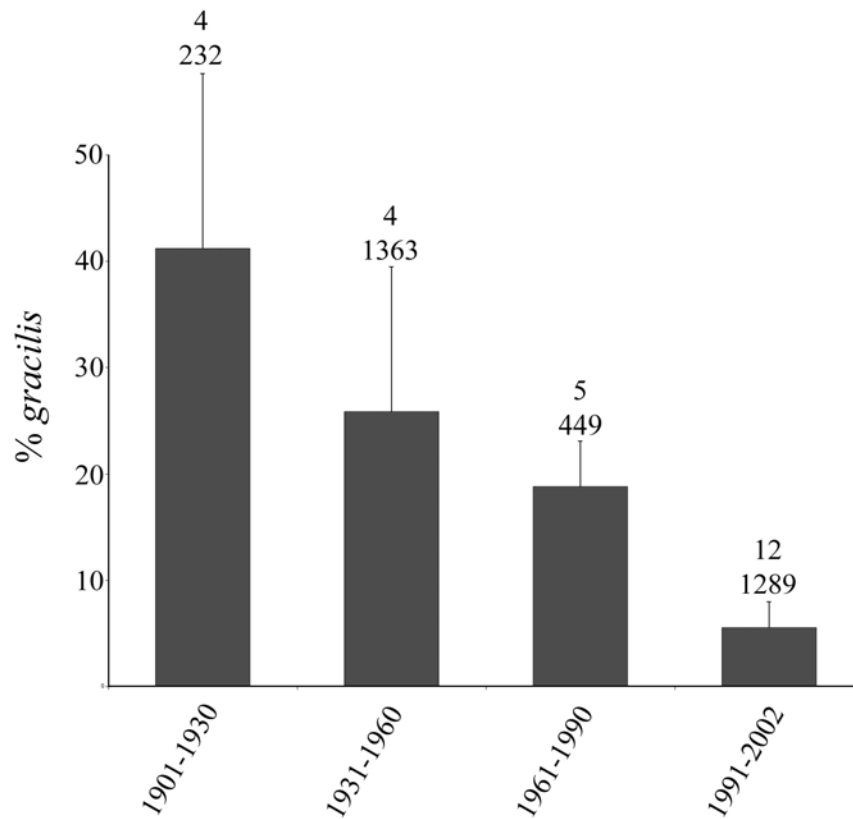


Figure 3. Decline in relative abundance of *P. m. gracilis* in the northern Lower Peninsula of Michigan. The Y-axis shows the relative abundance of *gracilis*, calculated for each time period as the number of *gracilis* captured divided by the total number of *Peromyscus* (*gracilis* + *leucopus*) captured. The error bar represents 1 SE. The upper number above each error bar is the number of counties from which  $\geq 10$  mice were obtained; the second number is the number of *Peromyscus* (*leucopus* + *gracilis*) in the sample.



Records from UMBS and the Black River provided a more detailed account of recent changes in the relative abundance of *gracilis* and *leucopus*. At UMBS, a few *gracilis* were captured early in the census period, but, by 1993, *gracilis* had disappeared entirely. Both species continued to coexist, however, at the Black River site. Here, we trapped at irregular intervals in 1989, 1991, 1992, and 1993; during that time period, between 50% and 87% of the *Peromyscus* captured were *gracilis*. In 1996, we began a program of biannual trapping at the Black River site (as at UMBS). In the first year of that census, the relative abundance of *gracilis* was similar to previous years (73%), but since 1996, it has fallen sharply to less than 10% (Figure 4).

What are the correlates of fluctuations in *Peromyscus leucopus* populations? At UMBS, 15 years of census data allowed us to examine population fluctuations in light of detailed weather records made very near the census sites. Information on masting patterns was also available. Because *gracilis* was last recorded in 1993, we were unable to study changes in its populations. We could, however, examine records of *leucopus* captures to ask whether the number of animals present in autumn or spring censuses was related to climate or acorn availability.

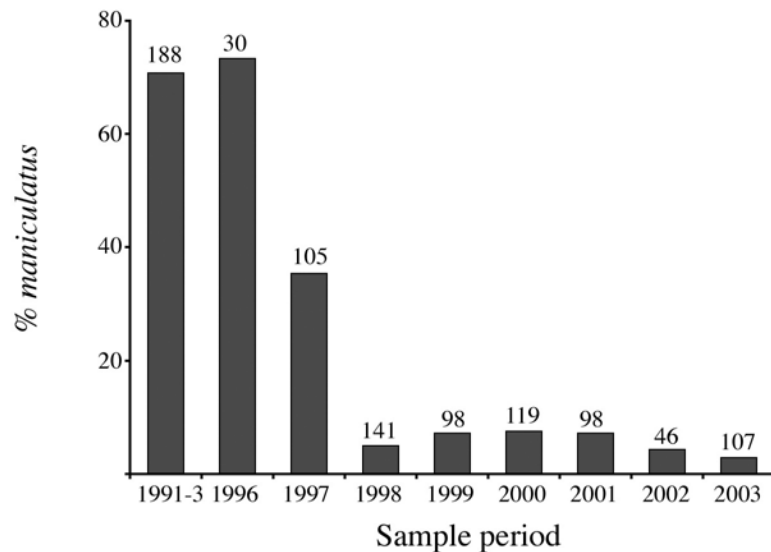


Figure 4. Decline in relative abundance of *P. m. gracilis* in the Black River area in Otsego Co., Michigan. Numbers above the bars indicate total number of *Peromyscus* (*leucopus* + *gracilis*) in the sample; data for 1991-1993 are combined due to small sample sizes for most years. The Y-axis is the same as in Figure. 3.

The abundance of *leucopus* at UMBS varied seasonally and yearly (Figure 5). Not surprisingly, spring populations were always equal to or smaller than populations in the preceding autumn and were usually considerably smaller. Autumn populations ranged from 10 animals in 1996 to 100 in 1993; spring populations fluctuated between 0 mice (1996, 2000) and 22 mice (1990).

Five of the 15 census years were years of substantial mast production (Figure 5). The number of mice captured was unrelated to oak masting. For example, both high (e.g., 1989) and low (e.g., 1996) *leucopus* populations came during the autumns of mast years (the time of year when the acorns drop). Similarly, populations in the spring following a mast were sometimes relatively high (e.g., 1990) and sometimes low (e.g., 1996).

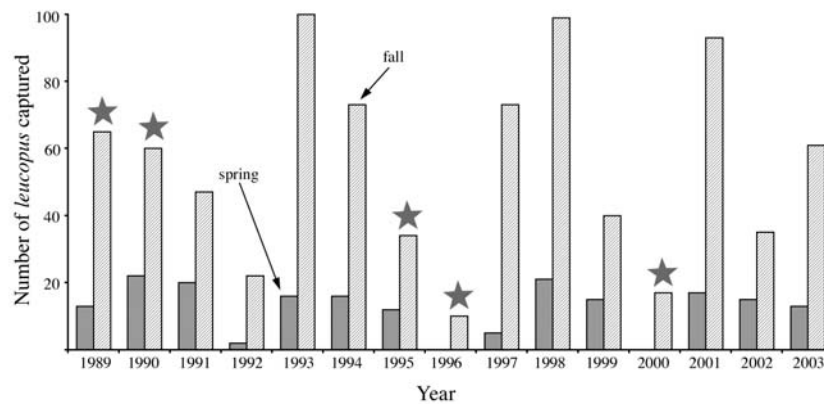


Figure 5. Number of *P. leucopus* captured in semi-annual censuses of small mammals at the University of Michigan Biological Station (UMBS), northern Lower Peninsula. Spring (May) samples are indicated by solid bars; autumn (September) samples by hatched bars. Years of high acorn production are marked by stars.

With respect to climate, northern Michigan experienced a very unusual rainstorm on Jan 1-2, 2000. The hard and prolonged rain collapsed the subnivean space and coated downed branches and tree trunks with a thick layer of ice. *Peromyscus leucopus*, like many other non-hibernating small mammals, relies on these structures for travel and foraging during the winter months. Heavy over-winter mortality in species such as *leucopus*, *Clethrionomys gapperi* (red backed vole), and soricids (*Sorex cinereus*, *Blarina brevicauda*), all of which were characterized by extremely low abundance in spring 2000, was probably a result of this rare storm. We have therefore treated the spring census results of that year as an outlier,

labeling them in the following figures and removing them from the statistical analyses of spring populations that follow.

Population size of *leucopus* in the autumn (at the end of the breeding season) was strongly related to the number of mice in the preceding spring (Spearman's rho = 0.65,  $N = 15$ ,  $p < 0.01$ ; Figure 6d). It was unrelated to total summer rainfall (Spearman's rho = 0.11,  $N = 15$ ,  $p = 0.69$ ), total number of cooling degree days (Spearman's rho = 0.15,  $N = 15$ ,  $p = 0.59$ ), or the maximum number of consecutive days with no rainfall (Spearman's rho = -0.30,  $N = 15$ ,  $p = 0.28$ ; Figure 6a-c).

In the spring census, the number of *leucopus* recorded was not related to the number of mice present during the preceding autumn census (Spearman's rho = 0.23,  $N = 15$ ,  $p = 0.45$ ; Figure 7d). It was also uncorrelated with total snowfall during the preceding winter (Spearman's rho = -0.32,  $N = 14$ ,  $p = 0.27$ ), number of heating degree days (Spearman's rho = -0.38,  $N = 14$ ,  $p = 0.19$ ), and minimum soil temperature at a depth of 50 cm (Spearman's rho = -0.05,  $N = 12$ ,  $p = 0.88$ ; Figure 7a-c). Similarly, mouse population size was unrelated to the date ice formed on Douglas Lake (Spearman's rho = 0.30,  $N = 14$ ,  $p = 0.30$ ; Figure 8a). The population size of *leucopus* was, however, correlated with the date of ice break-up (Spearman's rho = -0.63,  $N = 14$ ,  $p = 0.02$ ; Figure 8b). When ice lasted late into spring (late April or early May), few *leucopus* survived the winter. When ice left early, in late March or early April, *leucopus* populations were at high levels. The date ice left the lake appeared to be more strongly related to population size than the overall length of the winter (number of days ice covered the lake; Spearman's rho = -0.44,  $N = 14$ ,  $p = 0.12$ ; Figure 8c).

## DISCUSSION

In the northern Lower Peninsula, *Peromyscus maniculatus gracilis* is now strikingly less common relative to *leucopus* than it was at the beginning of the 20<sup>th</sup> century. A similar trend has been reported in northern Wisconsin by Long (1996). Over 40% of the *Peromyscus* in collections made in this region of Michigan before 1931 were *gracilis*. Today, that number is less than 6%. Further, because our recent efforts have been aimed at discovering *gracilis* populations and have concentrated on the habitats favored by that species, we strongly suspect that even this number over-represents the frequency of *gracilis*. The population of *gracilis* in northern Lower Michigan has been isolated from other *gracilis* populations for several thousand years and has evolved to become distinct both genetically and morphologically (Meagher, 1995, 1999; Lundrigan, Myers and Meagher, unpublished). The extinction of this unique population is a very real possibility.

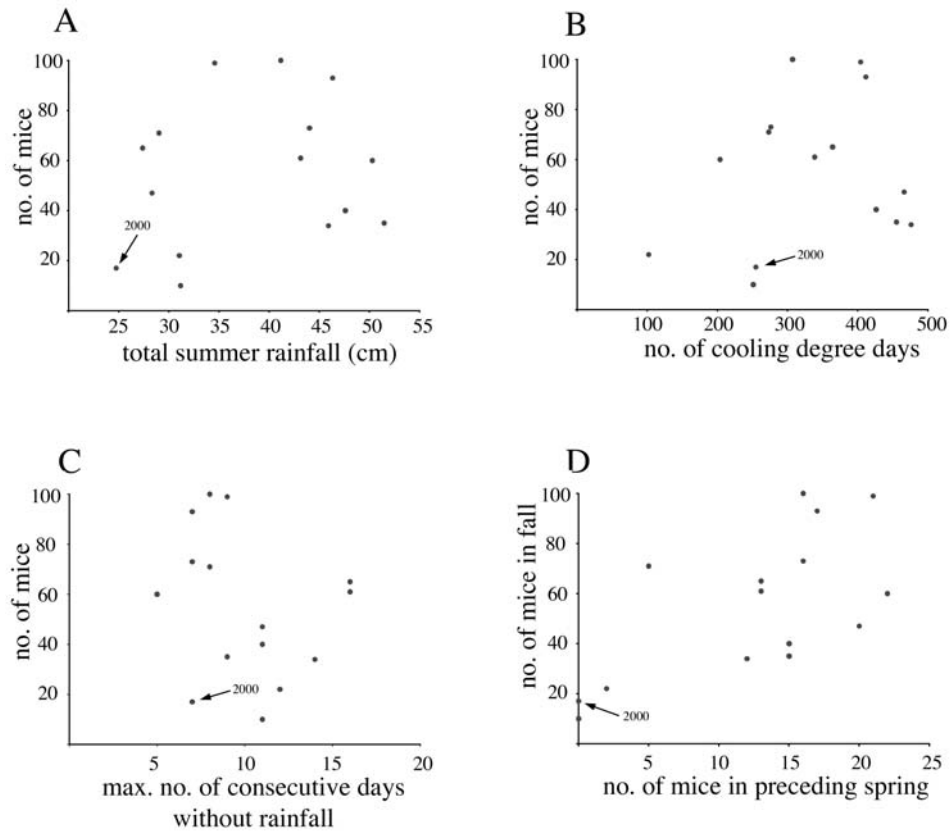


Figure 6. Number of *P. leucopus* captured in each autumn sample at the UMBS (Y axis) vs. (a) total summer (May-September) rainfall, (b) total number of cooling degree days during the summer months, (c) maximum number of consecutive days during the summer with no rainfall, and (d) number of *leucopus* captured during the preceding spring.

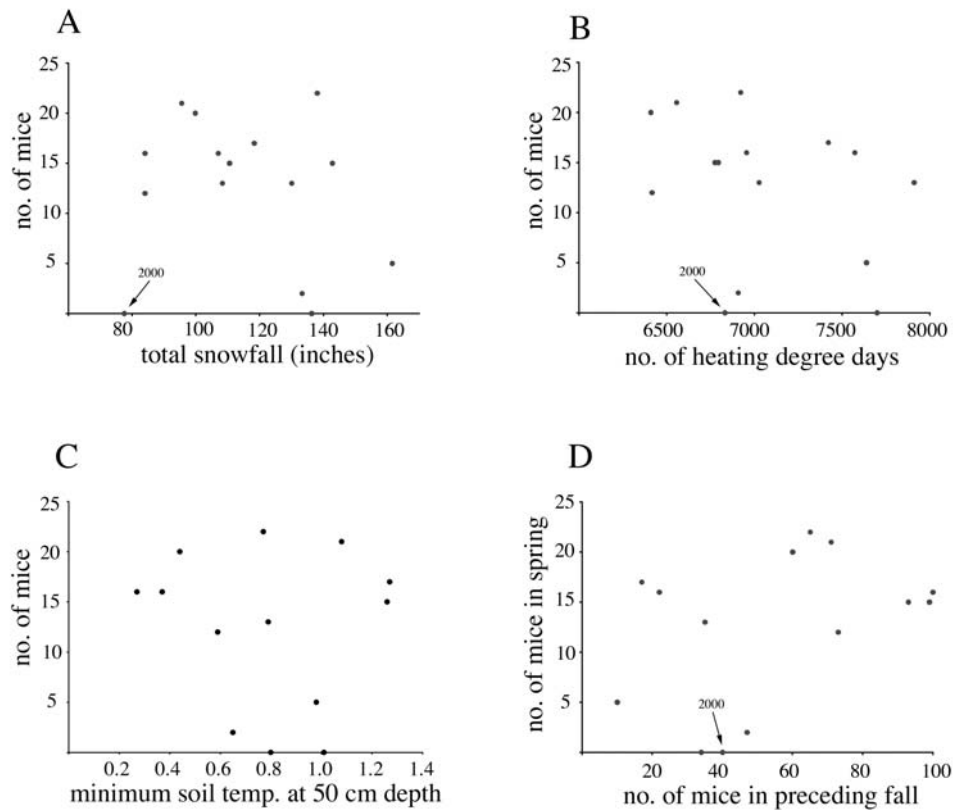


Figure 7. Number of *P. leucopus* captured in each spring sample at UMBS (Y axis) vs. (a) total snowfall during the preceding winter (October-April), (b) total number of heating degree days during the winter months, (c) minimum temperature reached at a soil depth of 50 cm during the winter months, and (d) number of *leucopus* captured during the preceding autumn.

Forest habitats in the northern Lower Peninsula have changed considerably over the last century (Whitney, 1987). Can these changes explain the loss of *gracilis* from this area? *Peromyscus maniculatus gracilis*, like *leucopus*, is found in a variety of habitats and, in the Great Lakes region, *gracilis* is often reported to prefer cooler, more boreal microhabitats (e.g., Dice, 1925; Hooper, 1942; Long, 1996). In the Lower Peninsula, we have found it to be strongly associated with forests, especially northern hardwoods (sugar maple, beech, white and yellow birch) or mixed hardwoods and hemlock (*Tsuga canadensis*), balsam fir, white pine, and red pine.

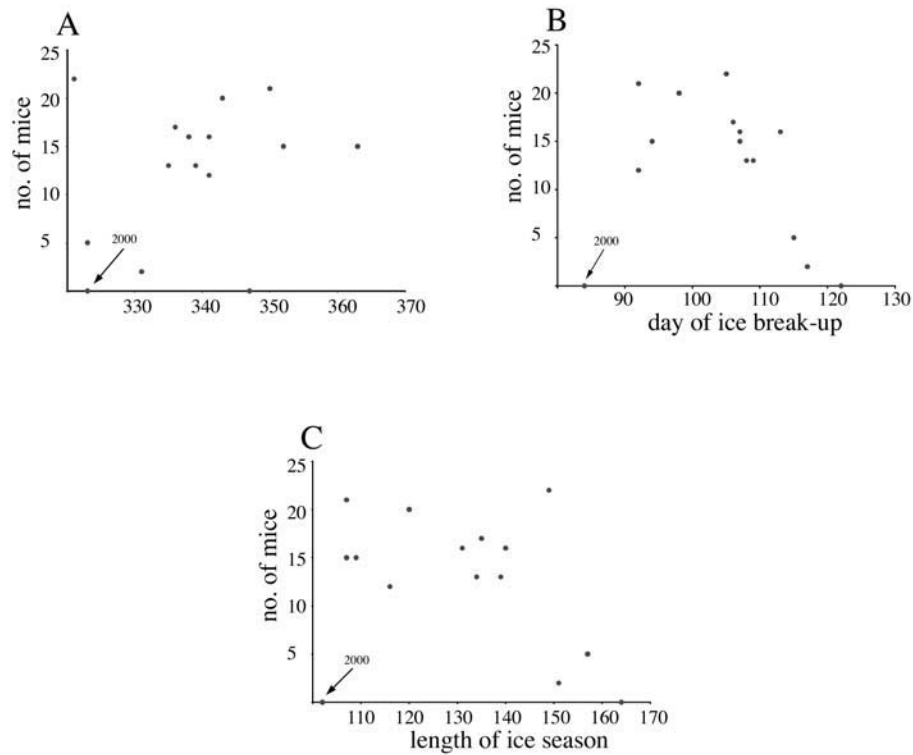


Figure 8. Number of *P. leucopus* captured in each spring sample at UMBS (Y axis) vs. (a) day of the year on which ice first covered Douglas Lake (UMBS) in the preceding winter, (b) day of the year on which the ice covering Douglas Lake broke up, (c) total number of days ice covered Douglas Lake.

*Peromyscus leucopus* can also be found in these habitats, sometimes in high numbers. Unlike Lower Peninsula *gracilis*, *leucopus* is also abundant at the edges of fields or even in areas that have been recently logged (*gracilis* is often found in these habitats in parts of the Upper Peninsula where *leucopus* is absent). All of northern Michigan was logged at the end of the 19<sup>th</sup> and beginning of the 20<sup>th</sup> centuries and much of the area was subsequently burned in a series of fires that followed logging. Forest habitats largely disappeared. Our early records from this area document collecting soon after logging was completed, yet they contain a high proportion of

*gracilis*. Since that time, logging has continued in a more controlled fashion and forests have regenerated to a considerable extent. Based on current knowledge of the habitat preferences of these two species, we would expect conditions for *gracilis* to be improving, not deteriorating.

Additional evidence that the apparent replacement of *gracilis* by *leucopus* is not related to forest regeneration comes from the Black River site. The abundance of *gracilis* at that site has fallen sharply during the last 10 years, yet neither the plant communities nor any other aspect of the habitat has changed appreciably.

With respect to the abundance of *leucopus* at UMBS, the number of years of census data is small. Any statistical analysis of the correlates of mouse population size must be viewed with caution, particularly when, as is the case here, several potential correlates were examined. Nevertheless, even with just 15 census samples, some variables were clearly unrelated to mouse number, while for others, a relationship appeared to emerge.

Oak mastings had little if any effect on mouse populations at UMBS, in contrast to its strong influence on *leucopus* populations in New York (Elkinton et al., 1996; Ostfeld et al., 1996). Also, the summer temperature and rainfall variables tested here had no detectable effect. Of the summer variables we examined, the only one affecting population size in the autumn was the number of mice captured during the preceding spring.

The winter pattern was quite different. Autumn population levels had no detectable effect on population levels in the succeeding spring, suggesting that events during the winter months were critical for determining spring (and by correlation, subsequent autumn) population levels. *Peromyscus leucopus* is at the very northern limit of its distribution in this region and it would not be surprising if populations of this species were especially vulnerable to harsh winter weather. Variables such as number of heating degree days and total snowfall, however, bore no relationship to the number of mice remaining in the spring.

Winters in the northern Lower Peninsula are long, as well as cold and snowy. Winter conditions often extend into late April or even early May. Length of winter is difficult to define and even harder to measure. We chose to use dates of ice formation and ice break-up on nearby Douglas Lake to represent the beginning and end of winter conditions, because these dates integrate temperature, snowfall, and other aspects of local weather (Anderson et al., 1996) and because they have been recorded consistently over the years of the study. The number of *leucopus* that successfully over-wintered appeared to be strongly related to the date of ice break-up, slightly less strongly related to the number of days between ice formation and break-up, and unrelated to the date of ice formation. Prolonged winters were always followed by low numbers of *leucopus* in the spring. Shorter winters appear to be more favorable and are generally followed by larger spring populations. Alternatively, they permit other factors to come into play (for example, the unusual rainstorm in January 2000).

Long (1996), reporting on long-term observations of *Peromyscus* populations in Wisconsin, also proposed that winter weather had a greater impact on populations of *leucopus* than on populations of *gracilis*. He suggested that temperature and snow depth might be critical factors (a combination of low temperature and lack of snow being detrimental; see also Long, 1973). Based on reports that *maniculatus nubiterrae* tends to nest in trees during the winter, while *leucopus* tends to move its nests underground (Wolff and Hurlbutt, 1982; Wolff and Durr, 1986), Long (1996) argued that *leucopus* might be more susceptible than *gracilis* to deep frost during severe winters, and that deep frosts were the result of cold temperatures occurring when the ground was unprotected by snow. We found no relationship, however, between the minimum soil temperature reached during the winter and *leucopus* population size the following spring.

*Peromyscus leucopus* is abundant in southern Michigan, where members of the species begin breeding in March in most years (Baker, 1983). The onset of breeding is probably at least partially determined by photoperiod, and this mechanism is under direct genetic control (Heideman and Bronson, 1991; Heideman et al., 1999). Breeding is a risky and expensive process. One possible explanation for the relationship between winter length and *leucopus* survival reported here is that the timing of breeding in the northern Lower Peninsula, at the northern fringe of the species' range, is influenced by gene flow from southern populations for which a March onset of reproduction is more appropriate. When winter ends early, mice breed successfully. When it ends late, breeding begins before resources are available to sustain the breeding process. If this hypothesis is correct, then (1) winter mortality in *leucopus* populations in the northern Lower Peninsula should be most severe in late winter or early spring, and (2) breeding activity of *leucopus* should begin in March or early April, regardless of weather. We hope to examine both predictions in the future.

#### Climate and *Peromyscus maniculatus gracilis*

Does weather, especially winter weather, affect *gracilis* in the same way that it affects *leucopus*? Field data on breeding and mortality patterns from the northern Lower Peninsula are lacking. In other areas, however, it has been shown that *gracilis* and the similar *nubiterrae* make better use of torpor than *leucopus* to survive particularly difficult conditions (Tannenbaum and Pivorun, 1988; Pierce and Vogt, 1993; Wolff, 1996). Pierce and Vogt (1993) showed that *gracilis* builds nests that are better insulated than those of *leucopus*, *gracilis* hoards greater quantities of food, and *gracilis* is more likely to go out of breeding condition during the winter months. Unfortunately, these studies involved comparing *gracilis* or *nubiterrae* with *leucopus* from milder climates rather than from syntopic populations. Based on field studies of the two species where they occur together, Wolff (1996) suggested that climatic variation may contribute to the coexistence of these two taxa. *Peromyscus leucopus*



should thrive when winters are mild, and *gracilis* populations should rebound when winters are harsh. At UMBS, *leucopus* populations behaved as predicted by Wolff; the number of *leucopus* was high following short winters and low when winters were prolonged. What about *gracilis* populations?

By 1993 *gracilis* had disappeared from the area around the census sites at UMBS. The species still persists, however, at the Black River site. Comparing the number of *gracilis* trapped at the Black River site to climatic conditions was not possible because weather records comparable to those for UMBS were not available, spring samples were available for only seven years, and the number of individuals captured has generally been very low. Nevertheless, we can predict that if *leucopus* consistently experiences higher winter mortality than *gracilis* but recovers during the breeding season, the relative abundance of *gracilis* at the site should be high in the spring and low in the autumn. This was consistently true despite substantial year-to-year variation in the number of individuals of each species captured (resulting from both population fluctuation and from differences in trapping effort; Figure 9).

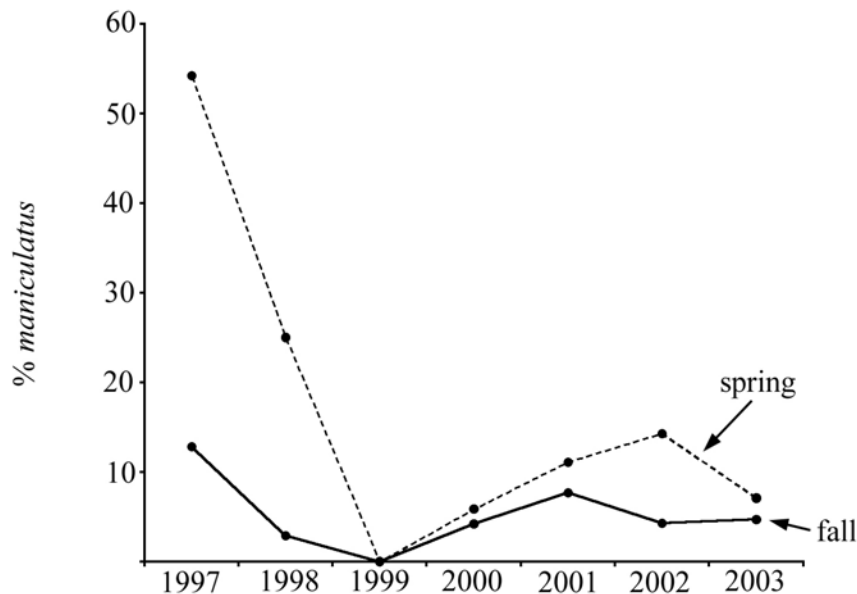


Figure 9. Spring (dashed line) and autumn (solid line) abundance for *P. m. gracilis* at the Black River Study site. Sample sizes (spring/fall): 1997 63/90; 1998 13/200; 1999 72/26; 2000 23/91; 2001 22/135; 2002 26/64; 2003 28/335.

We hypothesize that recent climatic warming may be responsible for the decline in *gracilis* relative to *leucopus* in northern Michigan. In accord with Wolff (1996) and Long (1996), we suggest that *gracilis* survives better than *leucopus* when winters are long and harsh, that *leucopus* has an as-of-yet unknown competitive or reproductive advantage when spring comes early, and that the two species coexist despite their ecological and morphological similarity because of year-to-year variation in the severity of winter. To explain the long-term decline in *gracilis* populations described at the beginning of this paper, however, winters must be shorter now than they were earlier in this century. Further, the Black River data suggest that warming has recently accelerated. Is this the case?

The UMBS ice break-up data do not go far enough back in time to allow us to address this question. A much larger dataset is available, however, for Grand Traverse Bay, on Lake Michigan approximately 100 km SSW of UMBS, where break-up dates have been recorded for over 100 years (Figure 10a). A general decline in break-up date is evident, but there is considerable year-to-year variability. To make long-term trends more obvious, we calculated for each year the average of the break-up date for that year and the preceding 9 years (Figure 10b). These 10-year running averages reveal a striking pattern. During the 20<sup>th</sup> century, the average time of ice break-up decreased gradually from around the 90<sup>th</sup> day of the year in the early 1900's to approximately the 75<sup>th</sup> day of the year in the early 1970's. Since the early 1970's, the average date of break-up has fallen to about day 50 in 2001. The rapid decline of the last 3 decades has been due largely to an increase in the number of years in which ice did not form on the bay (these years were assigned a value of 0, or ice break-up on January 1, for this analysis). Clearly, ice break-up data suggest that winters in this region are ending earlier than in the past.

On average, the earth's climate has warmed 0.3-0.6° C over the last century (Intergovernmental Panel on Climate Change, 1996). This change has not been uniformly distributed. Some areas have experienced much greater warming, while some have actually become cooler (op. cit.). Precipitation patterns have also been altered. Most models predict even greater changes over the next century.

A growing number of studies, like this one in northern Michigan, suggest that recent changes in climate have already had an effect on the organisms inhabiting Earth (McCarty, 2001; Walther et al., 2002). This is true both at the level of individual species (studies showing change in mammal populations include Frey, 1992; Hersteinsson and Macdonald, 1992; Post et al., 1999; Inouye et al., 2000) and at the level of entire communities (e.g., Brown et al., 1997). Taken individually, at best these studies provide evidence of a correlation between climate change and alterations of the biological attributes of species (e.g., distributions, breeding phenology, community structure). Causation is extremely difficult to establish. Nevertheless, as the number of studies that report concordant biological and

climate changes grows, the case for global warming as a causal element becomes increasingly compelling.

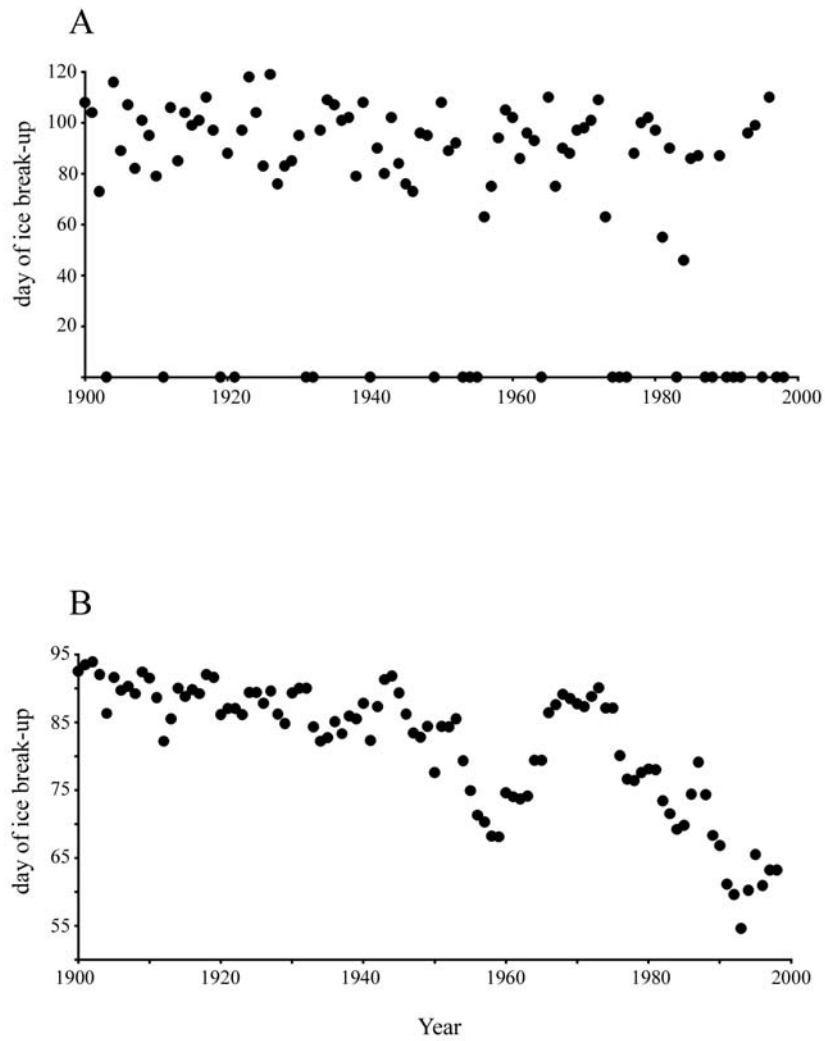


Figure 10. (a) Day of ice break-up on Grand Traverse Bay, Michigan. Years during which continuous ice did not form are recorded as break-up occurring on day 0 (Jan. 1). (b) Day of ice break-up on Grand Traverse Bay, each year calculated as the average of that year and the preceding 9 years.

## ACKNOWLEDGMENTS

We are grateful to Jim Patton for his unflagging encouragement and, in particular, for his enthusiasm for an extraordinarily wide variety of research endeavors having to do with mammals. Field surveys were supported in part by a grant from the Michigan Nongame Wildlife Fund, Michigan Department of Natural Resources. The University of Michigan Biological Station has sponsored 14 years of small-mammal censusing; we are very grateful to UMBS and especially to its director during this period, Jim Teeri, for his strong encouragement, support, and advice. Glen Matthews (Michigan Department of Natural Resources) generously gave us information on oak masting, and the Traverse City Chamber of Commerce provided its remarkable records of dates of ice formation and break-up on Grand Traverse Bay. John Megahan gave valuable assistance with figures. Many students and friends have participated in field surveys; they include Rebecca Anderson, Andrew Bunker, Guillermo D'Elia, Toni Gorog, Nedra Klein, Eladio Marquez, Rosa Moscarello, Carol Patton, Jim Patton, Sally Petrella, Dave Storer, Robert Storer, Jerry Svendsen, and the Field Mammalogy class (Biology 453) at UMBS.

## LITERATURE CITED

- Anderson, W. L., D. M. Robertson, and J. J. Magnuson  
1996 Evidence of recent warming and El Nino-related variations in ice breakup of Wisconsin lakes. *Limnology and Oceanography* 41:815-821.
- Baker, R. H.  
1983 *Michigan Mammals*. Michigan State University Press, East Lansing, MI., 642 pp.
- Barry, R. E., Jr., M. A. Botje, and L. B. Grantham  
1984 Vertical stratification of *Peromyscus leucopus* and *P. maniculatus* in southwestern Virginia. *Journal of Mammalogy* 65:145-148.
- Brown, J. H., T. J. Valone, and C. G. Curtin  
1997 Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Science of America* 94:9729-9733.
- Bruseo, J. A., S. H. Vessey, and J. S. Graham  
1999 Discrimination between *Peromyscus leucopus noveboracensis* and *Peromyscus maniculatus nubiterrae* in the field. *Acta Theriologica* 44:151-160.

- Cranford, J. A., and M. S. Maly  
1986 Habitat associations among small mammals in an old-field community on Butt Mountain Virginia, USA. *Virginia Journal of Science* 37:172-176.
- Dice, L. R.  
1925 A survey of mammals of Charlevoix County, Michigan and vicinity. *Occasional Papers of the University of Michigan Museum of Zoology* 159:1-33.
- Dooley, J. L., Jr., and R. D. Dueser  
1990 An experimental examination of nest-site segregation by two *Peromyscus* species. *Ecology* 71:788-796.
- Elkinton, J. S., W. M. Healy, J. B. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold  
1996 Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77:2332-2342.
- Feldhamer, G.A., J. E. Gates, and J. H. Howard  
1983 Field identification of *Peromyscus maniculatus* and *P. leucopus* in Maryland: reliability of morphological comparisons. *Acta Theriologica* 28:417-423.
- Frey, J. K.  
1992 Response of a mammalian faunal element to climatic changes. *Journal of Mammalogy* 73:43-50.
- Graves, S., J. Maldonado, and J. O. Wolff  
1988 Use of ground and arboreal microhabitats by *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 66:277-278.
- Harney, B. A., and R. D. Dueser.  
1987 Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. *Ecology* 68:1084-1091.
- Heideman, P. D., and F. H. Bronson  
1991 Characteristics of a genetic polymorphism for reproductive photoresponsiveness in the white-footed mouse (*Peromyscus leucopus*). *Biology of Reproduction* 44:1189-1196.

Heideman, P. D., T. A. Bruno, J. W. Singley, and J. V. Smedley

- 1999 Genetic variation in photoperiodism in *Peromyscus leucopus*: geographic variation in an alternative life-history strategy. *Journal of Mammalogy*, 80:1232-1242.

Hersteinsson, P., and D. W. Macdonald

- 1992 Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* 64:505-515.

Hooper, E. T.

- 1942 An effect on the *Peromyscus* rassenkreis of land utilization in Michigan. *Journal of Mammalogy* 23:193-196.

Inchausti, P., and J. Halley

- 2001 Investigating long-term ecological variability using the Global Population Dynamics Database. *Science* 293:643-650.

Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye

- 2000 Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Science of America* 97:1630-1633.

Intergovernmental Panel on Climate Change

- 1996 Climate change 1995: the science of climate change. Contribution of working group 1 to the second assessment report of the IPCC. Cambridge University Press, New York, 572 pp.

Long, C. A.

- 1973 Reproduction in the white-footed mouse at the northern limits of its geographic range. *Southwestern Naturalist* 18:11-20.

- 1996 Ecological replacement of the deer mouse, *Peromyscus maniculatus*, by the white-footed mouse, *P. leucopus*, in the Great Lakes Region. *Canadian Field-Naturalist* 110:271-277.

Long, C. A., and J. E. Long

- 1993 Discriminant analysis of geographic variation in long-tailed deer mice from northern Wisconsin and Upper Michigan. *Transactions of the Wisconsin Academy of Arts, Sciences, and Letters* 81:107-116.

McCarty, J. P

- 2001 Ecological consequences of recent climate change. *Conservation Biology* 15:320-331.

Meagher, S.A

- 1995 Ecology, genetics, and evolution of deer mice (*Peromyscus maniculatus gracilis*) and a parasitic nematode (*Capillaria hepatica*). Ph.D. thesis, University of Michigan, 117 pp.

- 1999 Genetic diversity and *Capillaria hepatica* (Nematoda), prevalence in Michigan deer mouse populations. *Evolution* 53:1318-1324.

Ostfeld, R. S., C. G. Jones, J. O. Wolff

- 1996 Of mice and mast. *Bioscience* 46:323-330.

Pierce, S. S., and F. D. Vogt

- 1993 Winter acclimatization in *Peromyscus maniculatus gracilis*, *P. leucopus noveboracensis*, and *P. l. leucopus*. *Journal of Mammalogy* 74:665-677.

Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren

- 1999 Ecosystem consequences of wolf behavioral response to climate. *Nature* 401:905-907.

Rich, S. M., C. W. Kilpatrick, J. L. Shippee, and K. L. Crowell

- 1996 Morphological differentiation and identification of *Peromyscus leucopus* and *Peromyscus maniculatus* in northeastern North America. *Journal of Mammalogy* 77:985-991.

Siegel, S.

- 1956 *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, Inc., New York, 312 pp.

Smith, D. A., and S. W. Speller

- 1970 The distribution and behavior of *Peromyscus maniculatus gracilis* and *Peromyscus leucopus noveboracensis* (Rodentia: Cricetidae) in a southeastern Ontario woodlot. *Canadian Journal of Zoology* 48:1187-1199.

Tannenbaum, M. G., and E. B. Pivorun

1988. Seasonal study of daily torpor in southeastern *Peromyscus maniculatus* and *Peromyscus leucopus* from mountains and foothills. *Physiological Zoology* 61:10-16.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebe, J.-M. Fromentin, O. Hough-Guldberg, and F. Bairlein.

- 2002 Ecological responses to recent climate change. *Nature* 416:389-395.

Whitney, G. G.

- 1987 An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology* 75:667-684.

Wolff, J. O.

- 1985a Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 63:1548-1555.

- 1985b. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 63:2657-2662.

- 1986 Life history strategies of white-footed mice (*Peromyscus leucopus*). *Virginia Journal of Science* 37:208-220.

- 1996 Coexistence of white-footed mice and deer mice may be mediated by fluctuating environmental conditions. *Oecologia* 108:529-533.

Wolff, J. O., and B. Hurlbutt.

- 1982 Day refuges of *Peromyscus leucopus* and *Peromyscus maniculatus*. *Journal of Mammalogy* 63:666-668.

Wolff, J. O., M. H. Freeberg, and R. D. Deuser

- 1983 Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). *Behavioral Ecology and Sociobiology* 12:237-242.

Wolff, J. O., R. D. Dueser, and K. S. Berry

- 1985 Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. *Journal of Mammalogy* 66:795-798.