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# Factors Influencing Persistence of White-footed Mice

Brock R. McMillan

Glennis A. Kaufman

Donald W. Kaufman

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**BROCK R. MCMILLAN[1], GLENNIS A. KAUFMAN,**
**and DONALD W. KAUFMAN**

Division of Biology, Kansas State University, Manhattan, KS 66506

**ABSTRACT** -- We examined factors that potentially influenced persistence of the white-footed mouse (*Peromyscus leucopus*) during 1981 to 1988 at Konza Prairie Biological Station, Kansas. We predicted that both abiotic (e.g., precipitation and temperature) and biotic (e.g., availability of food and density of conspecifics) factors would influence persistence of individuals at the study site. Persistence of individual white-footed mice on the study site differed among years and seasons. White-footed mice that were first captured in summer or in autumn persisted longer than those first captured in spring. Young females (less than 20 g) had greater persistence than young males, whereas old males (greater than or equal to 25 g) had greater persistence than old females. Persistence of white-footed mice captured in summer, autumn, and spring was related to abundance of white-footed mice, to production of seeds by woody plants, and to precipitation during March-May, respectively. Ambient temperature had no influence on persistence. We suggest that biotic and abiotic factors that influence persistence of white-footed mice are local in scale and that they affect persistence differentially at different times of the year.

**Key words:** *Peromyscus leucopus*, persistence, survival, white-footed mouse.

Food has been suggested as a limiting resource that affects density and dynamics of populations and population-level processes of small mammals. Generally, densities of small mammals are related directly to availability of food (Boutin 1990). Increases in abundance of small mammals related to increased quantities of food should result from immigration, reproduction, and increased

[1]Department of Biological Sciences, Minnesota State University, Mankato, MN 56001. E-mail address: brock.mcmillan@mnsu.edu

survival.   Densities of the white-footed mouse (*Peromyscus leucopus*) in spring
and summer were correlated positively with availability of food, primarily mast,
during the previous winter (Miller and Getz 1977, Hansen and Batzli 1979, Wolff
1989, Kaufman et al. 1995, Elkington et al. 1996, Ostfeld et al. 1996, Wolff 1996,
Jones et al. 1998).    Increased densities in spring and summer resulted from
increased reproduction and earlier onset of reproduction (Hansen and Batzli 1978,
Hansen and Batzli 1979, Wolff 1996, Jones et al. 1998).   In addition, Jones et al.
(1998) asserted that white-footed mice have greater over-winter survival in mast
years, but provided no supportive data.   In support of greater survival, Wolff
(1993) found more old white-footed mice in his study population in two of three
springs following autumns with large mast crops.

No consistent relationship between survival and availability of food is
evident for small mammals (Boutin 1990), especially white-footed mice.  Survival of
adult white-footed mice increased (e.g., Bendell 1959, Wolff 1993), decreased (e.g.,
Hansen and Batzli 1978, Briggs 1986), or remained unchanged (e.g., Blair 1948,
Hansen and Batzli 1979, Briggs 1986, Wolff 1986) in response to experimental
supplementation of food or a superabundance of natural foods.   The lack of a
consistent pattern of survival in response to food suggests that other biotic or
abiotic factors must be involved.

Biotic factors, other than food, that influence survival of individual white-
footed mice include abundance of conspecifics (Rintamaa et al. 1976, Miller and
Getz 1977) and sex or age of individuals (Snyder 1956, Adler and Tamarin 1984,
Millar 1984, Schug et al. 1991). Abiotic factors that might influence survival in the
white-footed mouse and other terrestrial small mammals include ambient tempera-
ture and amount of precipitation (Lewellen and Vessey 1998). For example, extreme
temperatures in winter and summer might thermally stress mice, whereas drought
and flooding might cause direct mortality or alter quality of the habitat. Except for
flooding (Batzli 1977), we found no studies that have examined the influence of
abiotic factors on survival of white-footed mice, probably because collection of
long-term data generally is needed to discern such patterns.

Long-term studies are essential to examine processes that have high annual
variability (Franklin 1989). Demographic characteristics of populations of white-footed
mice and other small mammals typically have high inter-annual and intra-annual
variability, especially in temperate regions (Sexton et al. 1982, Tilman 1989, Krohne and
Burgin 1990, Lewellen and Vessey 1998). However, the vast majority of demographic
analyses of small mammals have been for short-term studies (less than three years).
Short-term approaches might be misleading due to rare or episodic events (e.g.,
disease, wildfire, and extremes in precipitation, temperature, and production of seeds;
Franklin 1989, Tilman 1989). Variability in response variables due to a range of variation
in environmental factors typically is considered as noise in short-term studies;
however, long-term approaches enable the use of patterns of environmental variability
to suggest causal relationships in nature.

In 1981, we initiated a study to assess temporal variability in abundance of white-footed mice in forested habitats on the Konza Prairie Biological Station in northeastern Kansas. The magnitude of temporal variation in abundance of white-footed mice at that site (Kaufman et al. 1995) was typical of variation observed in other populations of the white-footed mouse (e.g., Krohne et al. 1988, Krohne and Burgin 1990, Wolff 1996, Lewellen and Vessey 1998). Our seasonal monitoring of abundance of white-footed mice precluded any assessment of mortality and dispersal, but there is little dispersal by adult white-footed mice (Burt 1940) and we could examine length of persistence of individuals on the study site. We hypothesized that factors influencing abundance also would influence persistence. That is, we predicted that precipitation, availability of food (primarily mast production in autumn), and density of conspecifics would influence persistence. More specifically, we expected that persistence of adult white-footed mice would be related positively to production of mast and negatively to density and that precipitation could have either a positive or negative effect on persistence.

## MATERIALS AND METHODS

We sampled small mammals at a wooded site from autumn 1981 to spring 1988 on Konza Prairie Biological Station near Manhattan, Kansas (detailed description in Kaufman et al. 1995). Woody habitats in this region of the tallgrass prairie are sparse and typically associated with streams or rocky outcrops formed by exposed layers of limestone. Therefore, the woody habitats are narrow strips of woodland bordered by native tallgrass prairie on the sides. We established four traplines to sample the linear habitats along the south fork of the King's Creek drainage (T11S, R8E, SW1/4 Section 18, Riley County). Two lines were in gallery forest associated with an ephemeral stream and two were along adjacent limestone outcrops. All traplines were located within an area of about 1 km² and likely were sampling the same population of white-footed mice. Woody vegetation associated with limestone outcrops was rough-leaved dogwood (*Cornus drummondii*), redbud (*Cercis canadensis*), smooth sumac (*Rhus glabra*), aromatic sumac (*R. aromatica*), and bur oak (*Quercus macrocarpa*), whereas gallery forest was dominated by bur oak, chinquapin oak (*Q. muhlenbergii*), hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), and buckbrush (*Symphoricarpos orbiculatus*).

Each trapline consisted of 20 stations with a 15-m interval between stations. Two large Sherman live-traps (7.6 x 8.9 x 22.9 cm) were placed at each station. We simultaneously sampled small mammals on all traplines for four consecutive nights during summer, autumn, and spring of each year (autumn 1981-spring 1988). Summer, autumn, and spring samplings typically were conducted in July, October, and March, respectively. At first capture, all

individuals were toe-clipped with a unique number. Species, age based on coloration of pelage, sex, mass to the nearest 0.5 g, and reproductive condition were recorded for each capture during each sampling period. At initial capture, each individual was assigned to a body mass category that was related roughly with age (Hansen and Batzli 1978, Wolff 1993, McMillan et al. 1997). Categories of body mass were less than 20.0 g (juveniles and subadults), 20.5 to 25.0 g (young adults), and 25.5 to 30.0 g and greater than 30 g (combined to comprise old adults). Sampling years were from summer through the following spring (e.g., sampling year 1982 consisted of summer 1982, autumn 1982, and spring 1983) as this corresponded to the growing season for vegetation; spring sampling occurred before vegetation began to grow.

Herein, we will use the term persistence to refer to length of time individuals remained in the population. We defined persistence as the number of sampling periods that each individual white-footed mouse was present at our site. Animals captured for the first time during sample-year 1987 (last year of the study) were excluded from analyses of persistence because we did not know how long individuals remained on the sites after the study ended. Because all traplines were sampling the same population, we pooled data from all four traplines and used the individual mouse as the experimental unit.

Production of seeds in gallery forest was estimated by Briggs et al. (1989) concurrent with our small mammal study. Open-topped collectors (0.25 x 0.25 x 0.50 m) collected particulate matter greater than 1 mm$^2$ and were open at 1 m above the forest floor (Briggs et al., 1989). Sixty collectors were placed at random locations in the gallery forest in September 1981 (Briggs et al. 1989). Trapped litter was collected at least monthly for the duration of the study. Amount of seed fall (g/m$^2$) was calculated for April to September and October to March from October 1981 through March 1988. Mean values of seed fall used for our analysis (taken from Briggs et al. 1989) were 2, 6, 28, 22, 5, and 17 g/m$^2$ during April to September from 1982 to 1987, and was 22, 12, 17, 1, 23, 3, and 38 g/m$^2$ during October to March from 1981/82 to 1987/88.

We obtained climatic data from the Kansas Agricultural Experiment Station for Manhattan, which is located about 15 km north of our study area. Mean annual precipitation during our study was 91.2 ± 7.2 cm ($\bar{x}$ ± SE), which is slightly higher, but consistent with the 50-year mean (83 cm). Annual precipitation during the study ranged from 51.3 to 112.3 cm. Likewise, the range of seasonal precipitation also was high (spring: 27.3 to 39.8 cm; summer: 14.5 to 43.7 cm; and winter: 14.5 to 48.0 cm). Mean annual temperature was 13.0 ± 0.2° C and ranged from 11.7 to 14.2° C during our study. Range of mean temperatures within a season among years was similar (spring: 4.7 to 7.7° C; summer: 18.1 to 20.0° C; and winter: -8.0 to -3.8° C). Amounts of precipitation and temperatures used in our analyses were summarized in Kaufman et al. (1995).

We used analysis of variance (PROC GLM; SAS Institute, Inc. 1988) to test for effects of and interactions among season, year, and sex and body mass

categories on persistence. To avoid pseudoreplication (Hurlbert 1984), we used only data from initial capture of each individual for our analysis.

We used multiple-regression analyses to test for relationships between mean persistence of individuals and abiotic and biotic factors. Abiotic and biotic factors considered for analysis of persistence of summer-captured white-footed mice were mean minimum temperature, mean maximum temperature, mean temperature of the warmest month, overall mean temperature, precipitation during June to August, abundance of white-footed mice during the summer sampling period, and seed fall during April to September. Similarly, factors considered for analysis of persistence of autumn-captured white-footed mice were average minimum temperature, average maximum temperature, average temperature of the coldest month, overall average temperature, precipitation during December-February, abundance of mice during the autumn sampling period, and seed fall during October-March. For analysis of persistence of spring-captured white-footed mice, factors considered were mean minimum temperature, mean maximum temperature, mean temperature of the coldest month, overall mean temperature, precipitation during March to May, abundance of white-footed mice during the spring sampling period, and seed fall during both October to March and April to September. For multiple-regression analyses, we used all individuals captured 'during each season instead of only mice first captured during a given season for our seasonal analyses.

Most white-footed mice captured during our study were present only for one or two sampling periods. Moreover, few white-footed mice (less than 6%) persisted on our sites for greater than or equal to one year (McMillan et al. 1997); therefore, we assumed that values for seasonal persistence among years (e.g., summer 1981 versus summer 1982) were independent. In addition, we hypothesized that factors influencing persistence were not continuous throughout the year. If factors influencing persistence did change within a year, then even our seasonal sampling periods were independent. Our results are presented as $\bar{x} \pm SE$ and level of significance for all tests was P less than or equal to 0.05.

## RESULTS

Individual white-footed mice (n = 866) persisted, on average, $0.62 \pm 0.004$ sampling periods after their initial capture. Variability in persistence was great as some individuals were captured only during the initial sampling period, whereas others were captured for up to nine consecutive sampling periods (McMillan et al. 1997). Two temporal factors that significantly influenced persistence of individuals included season of first capture (F = 6.81, d.f. = 2, 849, P $\leq$ 0.01) and year of first capture (F = 4.84, d.f. = 5, 849, P $\leq$ 0.01). Persistence values of mice first captured in summer $(0.75 \pm 0.07)$ and autumn, $(0.64 \pm 0.05)$, which did not differ, were greater than for those individuals first captured in spring $(0.45 \pm 0.07)$. The mean time

intervals between sampling periods were not equal (summer to autumn, autumn to spring, and spring to summer intervals were 3.5, 4.5, and 4 months, respectively). When persistence values were adjusted for differences in interval between sampling periods, results were not different from non-adjusted values. The mean persistence of individual white-footed mice ranged from a low of 0.34 ± 0.13 sampling periods in 1984 to a high of 0.81 ± 0.08 sampling periods in 1985.

Persistence of autumn-captured mice varied significantly among years with a low of 0.26 ± 0.16 sampling periods in 1984 and a high of 0.87 ± 0.11 sampling periods in 1985 (F = 3.58, d.f. = 5, 398, P ≤ 0.01). Persistence of mice captured in spring and summer exhibited similar yearly patterns of variation, but these patterns were not significantly different among years for either season.

Sex and body mass of individuals at first capture interacted to significantly influence persistence such that persistence differed significantly between female and male white-footed mice in different categories of body mass (Fig. 1; F = 3.63, d.f. = 3, 849, P ≤ 0.05). Specifically, small females (less than or equal to 25 g) persisted on our study sites longer than small males, whereas large males (greater than 25 g) persisted longer than large females (Fig. 1).
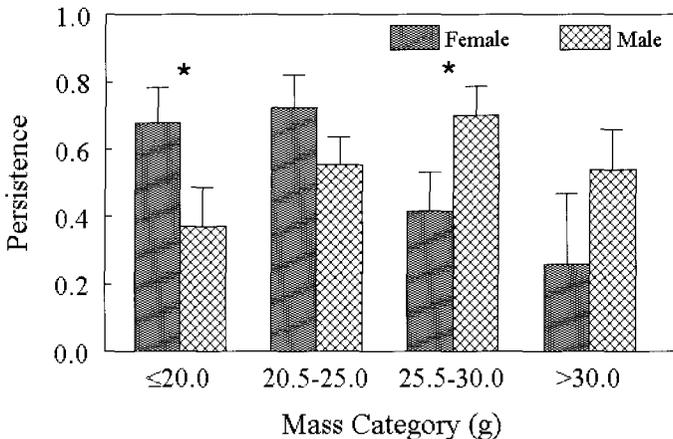


**Figure 1.** Mean persistence (± SE) of male and female white-footed mice (*Peromyscus leucopus*) in woody habitats on Konza Prairie Biological Station, Manhattan, Kansas during 1981 to 1988. Individuals were assigned to body mass categories based on mass at first capture. Values of persistence represent the number of sampling periods that individual white-footed mice were present on study sites after initial capture (1 is equal to about 4 months). An asterisk indicates a significant difference between persistence of female and male white-footed mice at P ≤ 0.05.

Persistence of individual white-footed mice captured during our seasonal sampling periods was related to only one of the many abiotic or biotic factors examined during each season and the factor related to persistence differed among seasons. Persistence of individual white-footed mice first captured during summer was related negatively to abundance during the same sampling period ($R^2$ = 0.70, d.f. = 5, P ≤ 0.05). Overwinter persistence of white-footed mice first captured during autumn was related strongly and positively to seed fall during October to March ($R^2$ = 0.96, d.f. = 5, P ≤ 0.01). Persistence of individual white-footed mice first captured during spring was related negatively to amount of precipitation during March to May ($R^2$ = 0.65, d.f. = 5, P ≤ 0.05).

## DISCUSSION

White-footed mice typically were present for only one or two sampling periods (less than one year), a pattern that was consistent with past studies (Blair 1948, Snyder 1956, Miller and Getz 1977, Schug et al. 1991). Persistence varied greatly among individuals as a few white-footed mice were present for one to two years (four to seven sampling periods) and one male remained for greater than three years (nine sampling periods; McMillan et al. 1997). Further, persistence varied significantly among years and seasons, which also was consistent with past studies of white-footed mice (Blair 1948, Snyder 1956, Miller and Getz 1977, Schug et al. 1991).

Persistence of individuals first captured during spring was significantly lower than for those first captured during summer or autumn. This difference likely resulted from dispersal of young during late spring and early summer (Burt 1940, Goundie and Vessey 1986). Further, persistence in spring was related negatively to amount of precipitation in spring. One possible explanation for this pattern is that white-footed mice likely were more active aboveground during this time; young mice were dispersing, adult males were searching for mates, and adult females were meeting higher energetic demands of reproduction. White-footed mice would be more exposed to extreme environmental conditions and potentially could experi-ence higher mortality when the amount of precipitation is high than when it is low. Possibly deaths, dispersal, or both caused by flooding of belowground burrows were greater during springs with high precipitation than in those springs with low precipitation.

Persistence of females and males differed among categories of body mass. Small females persisted longer on our site than did small males. This difference likely was caused by differences in dispersal tendencies between the two groups; that is, young males are more likely to disperse and move greater distances than young females (Burt 1940, Krohne et al. 1984, Wolff 1985, Goundie and Vessey 1986, Wolff 1989, Keane 1990). However, in contrast to both Wolff (1985) and

Miller and Getz (1977), but consistent with Adler and Tamarin (1984), intermediate-sized and large males persisted longer than females of similar sizes. Little dispersal is thought to occur after establishment of residency by males and females (Burt 1940, Goundie and Vessey 1986), a pattern that is inconsistent with differential persistence among adult males and females. We suggest that decreased persistence by large females might be due to higher mortality that results from higher cost of reproduction for females as compared to males (Wolff 1989).

White-footed mice captured during summer persisted for less time when summer abundance was high than when it was low. This relationship was consistent with a trend for a high level of dispersal by adults when densities are high and vice versa (Krohne et al. 1984). However, this pattern was apparent only for persistence of our summer-caught white-footed mice and not for spring or autumn-caught white-footed mice. If persistence were related directly to density, we would expect the highest relationship to occur in the season with the highest densities of white-footed mice, which was autumn. One possible cause for the persistence-density relationship in summer, but not in autumn, might be related to a greater likelihood of natal dispersal in summer than autumn; young white-footed mice present in autumn often overwinter in the natal den and disperse in spring (Wolff and Durr 1986). Additionally, mortality due to predation might be higher in summer than winter (*P. maniculatus*; Kaufman 1990), but we have no observations from our study site to support this conjecture.

Persistence of white-footed mice captured in autumn was related to seeds produced in forested habitats during October to March. Differences in seed production explained 96% of the variability in persistence of autumn-captured mice. Consistent with the observed effect of food on persistence in autumn, abundance of white-footed mice in spring on our sites was related positively to amount of seed fall from the previous October to March period (Kaufman et al., 1995). However, we found no relationship between seed fall in October to March and persistence of spring-captured white-footed mice. The increased abundance during summers following mast years (Ostfeld et al. 1996, Jones et al. 1998) likely is due to both increased abundance in spring (Kaufman et al. 1995) and increased reproduction in spring (Hansen and Batzli 1978, Hansen and Batzli 1979, Wolff 1996, Jones et al. 1998), but not directly related to autumn mast.

From our results, it seems probable that studies examining effects of supplemental food on persistence of white-footed mice at different times of the year would yield differing results as has been the case. For example, supplemental food applied during April to October likely would not increase persistence when natural foods are abundant. In contrast, supplemental food supplied during November to March likely would increase persistence during periods of low levels of natural foods. Consistent with these predictions, persistence of adult white-footed mice either was unaffected or decreased when food was supplied from spring to autumn (Blair 1948, Hansen and Batzli 1978, Briggs 1986, Wolff 1986). Further, the only study that supplemented food

to over wintering populations of white-footed mice found a corresponding increase in the persistence of individual adults (Bendell 1959).

Multiple factors influenced overall persistence of white-footed mice on Konza Prairie, but our study suggested that one factor might predominate in its influence on persistence at any given time of the year. We acknowledge the oversimplification of this statement, but it might be instructive in furthering our understanding of conflicting results among studies. For example, studies that examine one factor (e.g., food, density, or precipitation) during one season within a single year or among several years might find a relationship with persistence, whereas studies using similar methods during other seasons might find none. Based on our data, the only abiotic factor of consequence was precipitation in spring, which was related negatively to persistence of individuals captured in spring. In contrast, biotic factors, such as abundance of white-footed mice and production of seeds in the gallery forest, were the factors that were related to persistence of summer-captured and autumn-captured white-footed mice, respectively. We suggest that factors that influence persistence of white-footed mice are local on a landscape level and vary on a temporal scale that is less than a year in length. Therefore, studies designed to examine factors expected to influence demographic characteristics, such as persistence and abundance in populations of small mammals, should be approached by assessing seasonal variation rather than on an annual basis.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Adler, G. H., and R. H. Tamarin. 1984. Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. Canadian Journal of Zoology 62:58-64.

Batzli, G. O. 1977. Population dynamics of the white-footed mouse in flood-plain and upland forest. American Midland Naturalist 97:18-32.

Bendell, J. F. 1959. Food as a control of a population of white-footed mice, *Peromyscus leucopus noveboracensis* (Fischer). Canadian Journal of Zoology 37:173-209.

Blair, W. F. 1948. Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. American Midland Naturalist 40:395-416.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68:203-220.

Briggs, J. M. 1986. Supplemental food and two island populations of *Peromyscus leucopus*. Journal of Mammalogy 67:474-480.

Briggs, J. M., T. R. Seastedt, and D. J. Gibson. 1989. Comparative analysis of temporal and spatial variability in above-ground production in a deciduous forest and prairie. Holarctic Ecology 12:130-136.

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Miscellaneous Publications of the Museum of Zoology, University of Michigan 45:1-58.

Elkington, J. S., W. M. Healy, J. P. 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.

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. Pp. 3-19 *in* Long-term studies in ecology: approaches and alternatives (G. E. Likens, editor). Springer-Verlag, New York, New York.

Goundie, T. R., and S. H. Vessey. 1986. Survival and dispersal of young white-footed mice born in nest boxes. Journal of Mammalogy 67:53-60.

Hansen, L. P., and G. O. Batzli. 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Canadian Journal of Zoology 56:2530-2541.

Hansen, L. P., and G. O. Batzli. 1979. Influence of supplemental food on local populations of *Peromyscus leucopus*. Journal of Mammalogy 60:335-342.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279:1023-1026.

Kaufman, D. W., G. A. Kaufman, and E. J. Finck. 1995. Temporal variation in abundance of *Peromyscus leucopus* in wooded habitats of eastern Kansas. American Midland Naturalist 133:7-17.

Kaufman, G. A. 1990. Population ecology, social organization, and mating systems in the deer mouse (*Peromyscus maniculatus bairdii*) in mixed-grass prairie in Kansas. Ph.D. Dissertation, Kansas State University, Manhattan.

Keane, B. 1990. Dispersal and inbreeding avoidance in the white-footed mouse, *Peromyscus leucopus*. Animal Behaviour 40:143-152.

Krohne, D. T., and A. B. Burgin. 1990. The scale of demographic heterogeneity in a population of Peromyscus leucopus. Oecologia 82:97-101.

Krohne, D. T., B. A. Dubbs, and R. Baccus. 1984. An analysis of dispersal of an unmanipulated population of *Peromyscus leucopus*. American Midland Naturalist 112:146-156.

Krohne, D. T., J. F, Merritt, S. H. Vessey, and J. O. Wolff. 1988. Comparative demography of forest *Peromyscus*. Canadian Journal of Zoology 66:2170-2176.

Lewellen, R. H., and S. H. Vessey. 1998. The effect of density dependence and weather on population size of a polyvoltine species. Ecological Monographs 68:571-594.

McMillan, B. R., G. A. Kaufman, and D. W. Kaufman. 1997. A case of senescence for the white-footed mouse? Southwestern Naturalist 42:236-237.

Millar, J. S. 1984. Reproduction and survival of Peromyscus in seasonal environments. Pp. 253-266 *in* Winter ecology of small mammals (J. Merritt, editor). Special Publication 10, Carnegie Museum of Natural History.

Miller, D. H., and L. L. Getz. 1977. Comparisons of population dynamics of Peromyscus and Clethrionomys in New England. Journal of Mammalogy 58:1-16.

Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast: ecological connection in eastern deciduous forests. BioScience 46:323-330.

Rintamaa, D. L., P. A. Mazur, and S. H. Vessey. 1976. Reproduction during two annual cycles in a population of *Peromyscus leucopus noveboracensis*. Journal of Mammalogy 57:593-595.

SAS Institute, Inc. 1988. SAS/STAT user's guide. SAS Institute Inc., Cary, North Carolina.

Schug, M. D., S. H. Vessey, and A. I. Korytko. 1991. Longevity and survival in a population of white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 72:360-366.

Sexton, O. J., J. F. Douglas, R. R. Bloye, and A. Pesce. 1982. Thirteen-fold change in population size of *Peromyscus leucopus*. Canadian Journal of Zoology 60:2224-2225.

Snyder, D. P. 1956. Survival rates, longevity, and population fluctuations in the white-footed mouse, *Peromyscus leucopus*, in southeastern Michigan. Miscellaneous Publication of the Museum of Zoology, University of Michigan 95:1-33.

Tilman, D. 1989. Ecological experimentation: strengths and conceptual problems. Pp. 136-157 *in* Long-term studies in ecology: approaches and alternatives (G. E. Likens, editor). Springer-Verlag, New York, New York.

Wolff, J. O. 1985. Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. Canadian Journal of Zoology 63:1548-1555.

Wolff, J. O. 1986. The effects of food on midsummer demography of white-footed mice, *Peromyscus leucopus*. Canadian Journal of Zoology 64:855-858.

Wolff, J. O. 1989. Social behavior. Pp. 271-291 *in* Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland and J.N. Layne, editors). Texas Tech University Press, Lubbock.

Wolff, J. O. 1993. Does the "Chitty effect" occur in *Peromyscus*? Journal of Mammalogy 74:846-851.

Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy 77:850-856.

Wolff, J. O., and D. S. Durr. 1986. Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 67:409-411.