

Spring 1988

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Recommended Citation

Popp, J.W., P.E. Matthiae, C.M. Weise and J.A. Reinartz. 1988. Long-term population fluctuations of small mammals at the UWM Field Station. *Field Station Bulletin* 21(1): 10-18

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LONG-TERM POPULATION FLUCTUATIONS OF SMALL MAMMALS AT THE UWM FIELD STATION

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ABSTRACT

Population sizes of four small mammals, Peromyscus leucopus, Microtus pennsylvanicus, Blarina brevicauda, and Sorex cinereus, were monitored for over twenty years at the UWM Field Station. P. leucopus had moderate fluctuations in size, but showed no evidence of cyclic or regular fluctuations. M. pennsylvanicus exhibited dramatic fluctuations with cycles of 3-5 years. Neither shrew species appeared to have cyclic fluctuations. The population sizes of the two shrew species were positively correlated with each other. No other significant correlations were found between species. Population sizes were probably influenced by a number of factors including predation, competition and weather.

INTRODUCTION

The population dynamics of small mammals have received considerable attention, primarily because of an interest in the occurrence of regular multiannual or cyclic population fluctuations (Krebs and Myers, 1974; Keith and Windberg, 1978; Taitt and Krebs, 1985; Hanski, 1987; Lidicker, 1988; Ostfield, 1988). Despite this interest, long-term studies (twenty years or longer) of fluctuations of small mammal population sizes are relatively rare. Here, we report on annual population size fluctuations over a twenty-two year period of four small mammal species at the UWM Field Station; two rodents (Rodentia): Peromyscus leucopus (white-footed mouse), Microtus pennsylvanicus (meadow vole); and two insectivores (Insectivora): Blarina brevicauda (short-tailed shrew), and Sorex cinereus (masked shrew).

Peromyscus leucopus is a habitat generalist, being found in habitats ranging from grasslands to mature forest (Adler and Wilson, 1987), however, the species shows a preference for wooded habitats with complex vertical structure, including a definite shrub layer and fallen trees, stumps and logs (M'Closkey and Lajoie, 1975; Kaufman, et al., 1983). White-footed mouse populations have traditionally been thought to be relatively stable (Terman, 1968). Recent studies indicate, however, that populations of Peromyscus leucopus may exhibit

large fluctuations in population size (Sexton, et al., 1982; Wolff, 1985; Vessey, 1987); these studies include reports of fluctuations of over 10-fold (Sexton, et al., 1982; Vessey, 1987). Some authors have suggested that the observed fluctuations may reflect regular or cyclic fluctuations similar to those reported for microtine rodents (Wolff, 1985).

Population cycles are most commonly associated with microtine rodents (Lidicker, 1988) and have been reported for meadow voles in a number of studies (see Taitt and Krebs, 1985). Many populations are characterized by large fluctuations in size, with distinct peak and crash years. M. pennsylvanicus is found mostly in low-land fields and meadows.

The short-tailed shrew (Blarina brevicauda) has broad habitat requirements, being found in habitats ranging from forest to wet grassy areas (Jackson, 1961; Miller and Getz, 1977). Population sizes may vary greatly from year to year (Jackson, 1961) and crashes may occur requiring several years for recovery (Ozoga and Verme, 1969). During peak years B. brevicauda may be the most abundant small mammal in an area (Jackson, 1961). The masked shrew (Sorex cinereus) can be found in moist areas, primarily in forests or marshes. S. cinereus appears to maintain relatively stable population sizes (Jackson, 1961).

Two small mammals that are common at the Field Station; the eastern chipmunk (Tamias striatus) and the thirteen-lined ground squirrel (Spermophilus tridecemlineatus) are not discussed here because the trapping methods used, in particular trap size, were not appropriate for these species. Two other small rodents are also present at the Field Station; the jumping mouse (Zapus hudsonius) is present but uncommon, and the red-backed vole (Clethrionomys gapperi) is restricted to the bog where its population sizes are not known.

METHODS

This study was conducted between 1966 and 1987 at the University of Wisconsin-Milwaukee Field Station, Ozaukee County, Wisconsin. Live-trapping was done on two 0.56 ha grids. The grid consisted of 25 trap stations in a 5 x 5 array. From 1966 to 1979, two Sherman type traps were placed on the ground at each station; from 1980 on, two Longworth traps were used at each station. Trapping was conducted in September or early October of each year. One grid was located in an old growth, upland forest dominated by sugar maple (Acer saccharum), white ash (Fraxinus americana), American beech (Fagus grandifolia), and shagbark hickory (Carya ovata) (Dunnum, 1972). The other grid was located on an abandoned agricultural field. For the upland woods site only limited trapping was done in 1980 and insufficient data were collected for analysis in 1985 because of heavy trap raiding by raccoons (Procyon lotor). For the field site only limited trapping was done in 1980-81 and no trapping was done in 1987.

P. leucopus was commonly trapped at the upland site and M. pennsylvanicus at the old field site. Populations sizes for these two species were estimated

using the Bayesian approach of Gazey and Staley (1986). Two measures were used to test for regular or cyclic fluctuations (Henttonen, et al., 1985). The first measure is the standard deviation of logarithmic population densities (\underline{s}) (Lewontin, 1966; Williamson, 1972). Henttonen et al., (1985) have shown that a value of \underline{s} greater than 0.5 is a good indicator of cyclic fluctuations in microtine populations. The second measure involves the use of time series analysis, in particular frequency domain or spectral analysis. Frequency domain analysis uses a sum of sine waves of different frequencies to describe a time series. If cyclic fluctuations occurred it would be apparent from some frequencies contributing much more to the description than others (see Henttonen et al., 1985 for a more detailed explanation). Frequency domain analysis was done using the BMDP univariate spectral analysis program (Dixon, 1981).

The two shrew species were trapped at both grids, but were not abundant enough to estimate population sizes. The number of individuals trapped per 100 trap nights was used as an index of shrew abundance. Values of \underline{s} were calculated for both species.

RESULTS

White-footed mouse

Population sizes of Peromyscus leucopus exhibited moderate fluctuations (Fig. 1). The greatest continuous increase in population size was between 1976 and 1978, when a 3.2 fold increase occurred (peak population size/previous low size). Annual changes in population size (higher population size/lower population size) ranged from 1.0 to 2.9 (mean = 1.8, SD = 0.66). There was no evidence for cyclic or regular fluctuations. The value of \underline{s} was 0.18 which is well below the 0.5 used by Henttonen, et al. (1985) to distinguish cyclic populations. In addition, the contribution of each wavelength range to the total spectral variance did not differ greatly (Table 1).

Meadow vole

Populations of M. pennsylvanicus showed dramatic fluctuations in size (Fig. 2). The greatest increase in population size (from 0 to 80) occurred

Table 1. Results of spectral analysis of the population fluctuations of Peromyscus leucopus and Microtus pennsylvanicus. Values for each wavelength range represent the percentage each range contributes to the total spectral variance.

Species	Wavelength ranges (yrs)				
	<2.5	2.5-3.5	3.5-5.5	5.5-10	>10
<u>P. leucopus</u>	23.7	30.2	21.8	11.7	12.6
<u>M. pennsylvanicus</u>	3.5	15.7	59.8	12.2	8.8

between 1972 and 1973. Annual changes in population size ranged from 1.0 to 7.9 with a mean of 5.6 (SD = 8.1). This measure probably underestimates mean annual changes, since years in which population size was zero were not included. Unlike P. leucopus there was evidence for cyclic population fluctuations in the population of M. pennsylvanicus. The value of \underline{s} was 0.58, which indicates a cyclic population and the spectral analysis suggested population cycles with a 3-5 year periodicity (Table 1).

Masked and short-tailed shrews

Both shrews showed considerable year to year variation in the index of population size (Fig. 3). Annual changes in the index of population size ranged from 1.3 to 10 for S. cinereus (mean = 3.5, SD = 2.4) and from 1.0 to 6.0 for B. brevicauda (mean = 2.8, SD = 1.5). These results indicate that the two shrews show greater annual variation in population size than P. leucopus, but less variation than M. pennsylvanicus. This suggestion is supported by the values of \underline{s} for the shrews which are intermediate between P. leucopus and M. pennsylvanicus (\underline{s} = 0.40 for Sorex and \underline{s} = 0.31 for Blarina).

Table 2. Correlation coefficients (r) between estimated population sizes (P. leucopus and M. pennsylvanicus) or population size indexes (S. cinereus and B. brevicauda) for the four species under study.

	<u>M. pennsylvanicus</u>	<u>S. cinereus</u>	<u>B. brevicauda</u>
<u>P. leucopus</u>	0.25	0.23	0.39
<u>M. pennsylvanicus</u>		-0.12	-0.16
<u>S. cinereus</u>			0.52*

*, $p < 0.05$

Correlations between species

To test whether species exhibited similar patterns of population size fluctuations, correlation coefficients were calculated between the population size estimates of each species (Table 2). A positive correlation between the sizes of the two shrew populations, was the only significant correlation found.

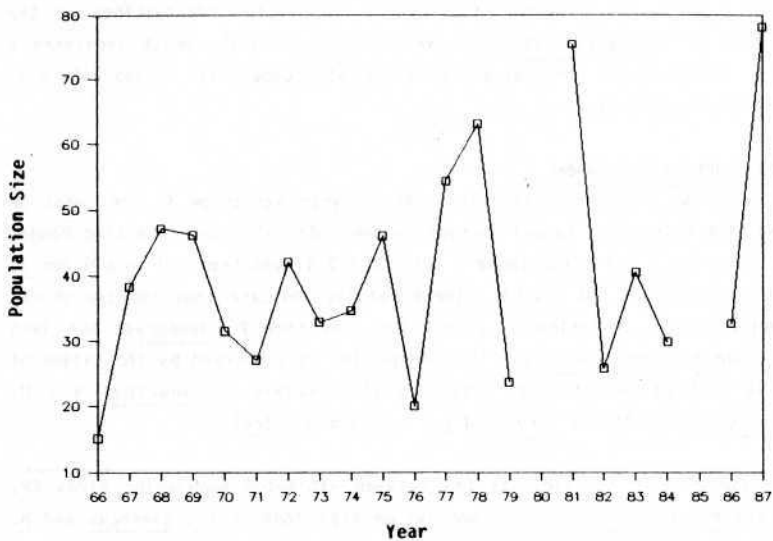


Figure 1. Fluctuations in size of the Peromyscus leucopus population.

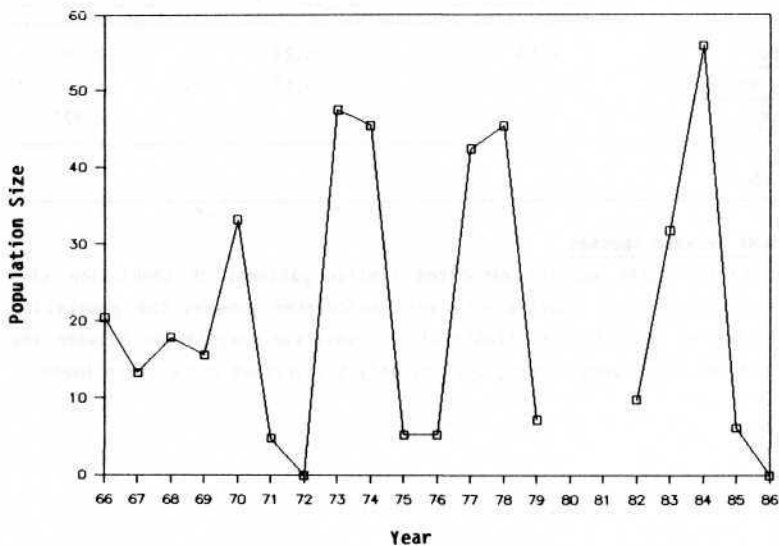


Figure 2. Fluctuations in size of the Microtus pennsylvanicus population.

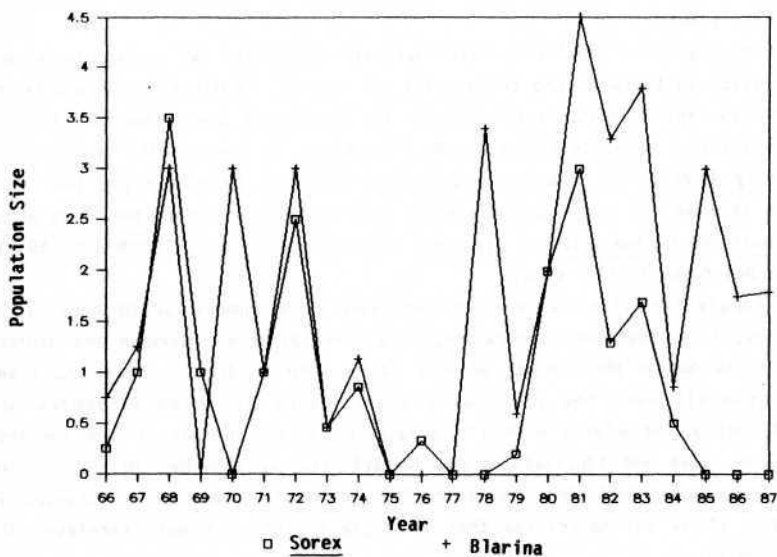


Figure 3. Fluctuations in the index of population size of Sorex cinerus and Blarina brevicauda.

DISCUSSION

The P. leucopus population under study exhibited moderate fluctuations in population size. The fluctuations were, however, not as great as recently reported for other populations (Sexton, et al., 1982; Vessey, 1987). The fluctuations observed in this population showed no evidence of being regular or cyclic and probably reflect annual changes in population size rather than multiannual cycles. The value of s from this study (0.18) was within the range of values previously reported for this species. Values reported have ranged from 0.07 to 0.56, with most values between 0.16 and 0.27 (Ostfeld, 1988). The P. leucopus fluctuations appear to be greater during the second half of the study period; this may be due to the effects of an ice storm which occurred at the study site during March of 1976. The ice storm changed the habitat of P. leucopus, which could have had large effects on its population dynamics. This aspect is currently under further investigation.

The size fluctuations of M. pennsylvanicus showed clear evidence for cycles of 3-5 years. The value of s from this study was higher than the values reported for five populations by Ostfeld (1988). In fact, only two of five populations of M. pennsylvanicus exceeded 0.5 and another recent, long-term study found little evidence of multiannual cycles (Getz, et al., 1987). There appears,

therefore, to be much interpopulation variation in the occurrence and degree of multiannual population cycles, which may also be true for other microtine species (Lidicker, 1988).

The degree of population size fluctuations for the two shrew species was intermediate to those of the two species of rodents. Neither shrew population appeared to exhibit multiannual cycles. The indexes of population size for the two species were positively correlated, in contrast to the results of Platt and Blakeley (1973) who found a negative relationship between these two shrew species in Iowa. A positive correlation between the population densities of B. brevicauda and P. leucopus has also been reported in Illinois (Lindeborg, 1941), but was not found in this study.

Population sizes were also compared to a number of meteorological variables, including mean temperature, total precipitation, maximum and minimum temperatures during three month periods (Jan. - March, April - June, etc.) and total snowfall over the previous winter. None of these variables was significantly correlated with the population sizes for any of the species. Population sizes and fluctuations may be affected by a number of interacting factors, such as predation, intraspecific competition, weather or changes in habitat. It is not surprising that a single factor does not correlate with population size.

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