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Correlating small mammal abundance to climatic variation over twenty years

Jennifer Deitloff,* Matthew R. Falcy, John D. Krenz, and Brock R. McMillan

Department of Biology, Auburn University, Auburn, AL 36849, USA (JD)
Department of Biological Sciences, Minnesota State University, Mankato, MN 56001, USA (JD, JDK, BRM)
Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA (MRF)
Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602-5253, USA (BRM)

* *Correspondent: jenneyd@auburn.edu*

Little is known about abundance–climate relationships for animals because few long-term field studies address the issue. We present results from a 20-year study of abundance of *Peromyscus leucopus* (white-footed mouse) and *Microtus pennsylvanicus* (meadow vole). *P. leucopus* exhibited a biennial cycle with an overall population increase. *M. pennsylvanicus* did not exhibit a population cycle, and population size declined. We attribute long-term changes in abundance of both species to succession from grass-dominated to tree-dominated vegetation. The only significant association we found between abundance of either species over 20 years and 4 climate variables was a positive relationship between *M. pennsylvanicus* and summer precipitation. However, all but 1 of the potential abundance–climate relationships were significant when temporal subsets of the original data were analyzed. Weak associations may exist between climate and abundance that are contingent upon other unidentified factors, which further suggests that abundance–climate correlations are sensitive to the particular time frame of a study. DOI: 10.1644/08-MAMM-A-267R.1.

Key words: long-term studies, meadow vole, *Microtus pennsylvanicus*, *Peromyscus leucopus*, population size, precipitation, snow depth, temperature, weather, white-footed mouse

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Ecologists continue to debate the relative importance of factors that influence or potentially determine population size. Populations can be affected by density-dependent factors such as disease transmission and availability of space and food (Dennis and Taper 1994; Hansson 1996; Lewellen and Vessey 1998a; Vessey 1987). Density-independent factors also can impact population size (Andrewartha and Birch 1954; Marinat 1987). For example, severe weather events can cause direct mortality, and long-term climatic patterns can affect populations indirectly by influencing the abundance of resources, competitors, and predators (Berryman et al. 1987). Understanding how climatic variation affects population size is a necessary prerequisite for predicting the impacts of environmental change. Populations that are affected strongly by climate are often more difficult to predict (Hastings et al. 1993) and manage (Allen et al. 1993; Ginzburg et al. 1990; Stacey and Taper 1992).

Many climatic factors can influence changes in population size of small mammals. These fluctuations can be the result of changes in fecundity or survival. For example, climate can limit seasonal breeding (Kalcounis-Rueppell et al. 2002) and affect daily activity levels (Vickery and Bider 1981). During winter, many small mammals are active under snow cover. Snow cover can provide protection from predators (Hansson 1987) and from harsh temperatures (Zonov 1982). However, severe winter conditions can reduce availability of food (Hansen et al. 1999; Hansson 1987) and decrease health of individuals (Stokes et al. 2001). Also, in summer, extremely hot temperatures have been correlated negatively with population size (Lewellen and Vessey 1998b). Furthermore, precipitation can affect population size indirectly by changing food availability (Bergallo and Magnusson 1999; Wolff 1996). Factors that are critical for persistence of individuals might change between seasons or years (McMillan et al. 2005). Thus, climate can impact population dynamics of small mammals in numerous ways.

This study focuses on the impacts of climate on the abundance of *Microtus pennsylvanicus* (meadow vole) and *Peromyscus leucopus* (white-footed mouse). *M. pennsylvanicus* is a very prolific mammal. Females become sexually mature within 30 days of birth and can produce litters every 3

weeks, with observed litter sizes ranging from 1 to 11 individuals and mean litter size estimated at 4.0–6.2 individuals (Hamilton 1941; Kott and Robinson 1963; Tamarin 1977). *M. pennsylvanicus* is found primarily in open grasslands where it feeds on most species of grasses, sedges, and herbaceous plants. It also scavenges on animal remains and girdles woody vegetation (Reich 1981).

Microtus pennsylvanicus is sometimes found in sympatry with *P. leucopus*. *P. leucopus* feeds primarily on insects and seeds (Lackey et al. 1985) and prefers woody habitats (Iverson et al. 1967; Yahner 1982), thus coexistence with *M. pennsylvanicus* may be attributed to differing dietary preferences. In northern North America *P. leucopus* reaches sexual maturity in 44 days and produces an average of 4.3–5.0 individuals per litter with a gestation period of 3–5 weeks (Lackey et al. 1985). The rapid reproductive rates and population turnover times (typically <1 year for both species—Hamilton 1937; McMillan et al. 1997) make these species particularly amenable to the study of the relationship between abundance and climatic variation.

The temporal scale of a field study can influence which components of climate are found to affect population abundance. Long-term studies should be more effective at detecting weak associations because of increased sample size. Alternatively, effects of climate on demography might be very short term (Lewellen and Vessey 1998b), and seasonal averages taken over many years might mask short-term effects (Kalcounis-Rueppell et al. 2002). We used a 20-year data set to examine potential effects that climate has on populations of *P. leucopus* and *M. pennsylvanicus*. We also studied subsets of this data set to determine whether different time periods (duration and start date) revealed different trends.

The purpose of this study was to examine potential effects of climatic variation on population abundance of *P. leucopus* and *M. pennsylvanicus*. Because of contrary results from previous studies (mentioned above), we examined the relationship between abundance and several climatic variables. We hypothesized that fall abundance was influenced by climatic conditions from the previous winter and summer. We also explored the consequences of using shorter studies to understand abundance–climate relationships by comparing results obtained from analysis of subsets of our data with the full data set. We expected that the long-term studies would be better at detecting long-term trends in fluctuations of population size due to climatic conditions.

Materials and Methods

Small mammals were trapped on the Minnesota State University campus in Mankato, Minnesota (northeastern corner of the study site was 44°08.382′N, 93°59.940′W) from late September to early October each year from 1978 to 1997. Sherman traps (13 × 13 × 22 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were baited with a mixture of oats and peanut butter. From 1978 through 1986 we used a trapping grid measuring 40 × 60 m with 35 traps spaced 10 m apart. From 1987 through 1997 grid size changed to a square arrangement of 60 × 60 m with 25 traps spaced 15 m apart. Although the size of our trapping grid was relatively small, it expanded throughout the region that contained woody vegetation and was surrounded by Kentucky bluegrass (*Poa pratensis*). Therefore, the trapping grid likely captured an isolated population. Over the entire study we checked traps twice daily (morning and evening) and rebaited traps when needed. For each animal captured we recorded species and age and marked each with a unique toe-clip pattern within each year. If animals were recaptured, the above data were recorded again for that capture. Capture rates were too low to implement procedures for estimating population size with standard mark–recapture models (Otis et al. 1978). Furthermore, because the number of traps used changed in 1987, each year we calculated abundances of each species as the total number of unique individuals captured divided by the number of traps used that year. All animals were captured by using standard trapping methods. At the initiation of this study no published guidelines existed for capturing and handling small mammals. However, recommended methods for handling mammals were published by the American Society of Mammalogists during data collection (ad hoc Committee for Animal Care Guidelines 1985), and the methods used for this study were consistent with those recommendations. Alternatives to the methods used (e.g., toe-clipping) are suggested in current guidelines of the American Society of Mammalogists (Gannon et al. 2007), and we no longer employ such methods.

The plant community on the site transitioned from grass-dominated toward woodland over the 20 years this study was conducted. Therefore, we needed to account for any possible changes in abundance due to habitat change so as to not mask potential effects of weather on population abundance. This was accomplished by including a time factor of year (hereafter referred to as ''year'') in a multiple regression analysis of abundance on climatic factors. Visual inspection of abundance data for *P. leucopus* suggested that populations might have fluctuated biennially. As for habitat change, we wanted to test statistically for fluctuations and, if significant, remove them from further analyses on effects of climate on abundance. Because our data were collected once a year, we were able to model a cycle by creating a vector of dummy variables consisting of alternating 0s and 1s, corresponding to trough and peak years, respectively. We added this cycle as an additional factor in the overall analysis (see below).

We obtained climate data from the National Weather Service station (National Weather Service 2002) station located in Mankato, Minnesota, (44°09′N, 94°01′W). The climate factors that we used were snow depth, winter temperature, summer precipitation, and summer temperature. Snow depth was defined as mean daily maximum snow depth during December, January, and February. We defined winter temperature as mean daily low during December, January, February, and March. Summer precipitation was defined as mean daily precipitation during April, May, June, and July. Summer temperature was defined as mean daily high during June, July, and August.

A stepwise regression was used to test for associations between abundances of *P. leucopus* and *M. pennsylvanicus* with the 4 climate variables defined above. Thus, for both *P. leucopus* and *M. pennsylvanicus* we performed separate stepwise regression of abundance on year (to account for successional change in habitat), biennial cycle, snow depth, winter temperature, summer precipitation, and summer temperature. Our data were annually censused populations, which potentially contain an autocorrelation structure not fully modeled by the year and cycle terms. If so, the ensuing error terms would violate regression analysis assumptions. We therefore examined plots of the residuals against time but found no evidence for lack of independence. We also were interested in the possibility of delayed population responses to climate, so we also conducted the analysis with 1- and 2-year time lags. This resulted in no significant association between abundance and any of the climate variables.

We also were interested in evaluating how these results change with shorter intervals. Therefore, we divided the data sets for both species into multiple subsets, where each subset constitutes what would have been observed if the study had been conducted over a shorter time period with different starting dates. We considered all possible subsets that were at least 3 years long. For each species this resulted in 171 unique subsets of the original 20-year data set. A stepwise multiple regression was performed on each of the 342 (171 for each species) subsets by using SAS 9.1 (SAS Institute Inc. 2002). We did not make adjustments for nonindependence among data subsets because our goal was not to use data subsets to generate a single estimate of weather effects on abundance; rather, we wished to generate results that would have been produced by shorter-term studies and to compare these to results we found for the entire 20-year data set. This provides insight into how sensitively results depend on the particular period over which the study is conducted and the duration of the study.

Results

The mean ($\bar{X} \pm SD$) abundance of *P. leucopus* (number of animals per trap per year) was 0.088 ± 0.058, and mean abundance of *M. pennsylvanicus* was 0.638 ± 0.498. For the complete 20-year data set only year and the biennial cycle (among year, biennial cycle, and 4 climate variables) were significantly related to abundance of *P. leucopus* ($R^2 = 0.64$; $F_{2,17} = 15.04$, $P_{\text{model}} = 0.002$, $P_{\text{year}} = 0.004$, $P_{\text{cycle}} = 0.003$; Fig. 1a). The 4 climate variables were not significant predictors of abundance of *P. leucopus*. Abundance of *M. pennsylvanicus* was significantly related to year and summer precipitation ($R^2 = 0.56$, $F_{2,17} = 10.9$, $P_{\text{model}} = 0.0009$, $P_{\text{year}} = 0.015$, $P_{\text{summer precipitation}} = 0.004$; Fig. 1b). The biennial cycle and the other 3 climate variables were not significantly related to abundance of *M. pennsylvanicus*.

We then conducted further stepwise regressions on subsets of the 20-year data set. This yielded mixed results. Of 171 data subsets of the *P. leucopus* data, year and biennial cycle were significant in 45 and 109 subsets, respectively (Table 1). Although none of the weather factors were significant in the complete 20-year data set, snow depth was significantly related to *P. leucopus* in 19 subsets, winter temperature was related in 7 subsets, summer precipitation was related in 6 subsets, and summer temperature was related in 11 subsets. In addition, the sign of the relationship was not consistent for all weather variables. For example, winter temperature was related positively to abundance of *P. leucopus* 3 times and related negatively 4 times.

When subsets of the abundance of *M. pennsylvanicus* were analyzed, the results were variable as well (Table 2). Year and summer precipitation were significantly related to abundance in 56 and 68 subsets, respectively, of 171. Factors that were not significant in the 20-year data set of *M. pennsylvanicus* were rarely significant in the subsets: biennial cycle appears 4 times, snow depth appeared once, winter temperature appeared twice, and summer temperature never appeared as significant. Because we performed 171 tests for each species, we expected to obtain approximately 8.6 spurious correlations of each factor at $\alpha = 0.05$. The observed number of significant correlations is much different than this expectation for some of the weather factors (Table 3). Some of the correlations shown in Tables 1 and 2 may be spurious, but our goal was to understand what the results would have been if subsets of our data were examined rather than to suggest that all of these correlations are biologically significant.

Discussion

Peromyscus leucopus and *M. pennsylvanicus* remained sympatric on our study site throughout the 20-year study. During this period the study site underwent successional change from grass to tree-dominated vegetation. We observed a concurrent increase in abundance of *P. leucopus* and decrease in abundance of *M. pennsylvanicus*, which is consistent with previous findings on habitat preferences (Grant 1971; Hamilton and Whitaker 1979; McMillan and Kaufman 1994) and competitive interactions (Bowker and Pearson 1975; Reich 1981). Because our study is observational, we cannot determine if the observed difference in population trends can be explained by succession-induced alteration of competitive interactions or a fundamental difference in habitat preference.

Effects of climate on abundance can be mediated by many factors. Short-term weather extremes lasting a few days can be ameliorated or exploited by altering behaviors (Kalcounis-Rueppell et al. 2002). For example, some small mammals increase activity during rainfall, presumably because rainfall inhibits predation (Vickery and Bider 1981). However, scaling short-term behavioral responses to long-term demographic patterns is not simple because optimal behaviors are often state-dependent (Clark and Mangel 2000). Thus, rain should suppress activity of a predator only until its risk of starvation outweighs the risks of foraging in the rain. Longer-term climatic conditions are known to affect foraging patterns and social interactions (Madison 1984; Spencer 1984; Stebbins

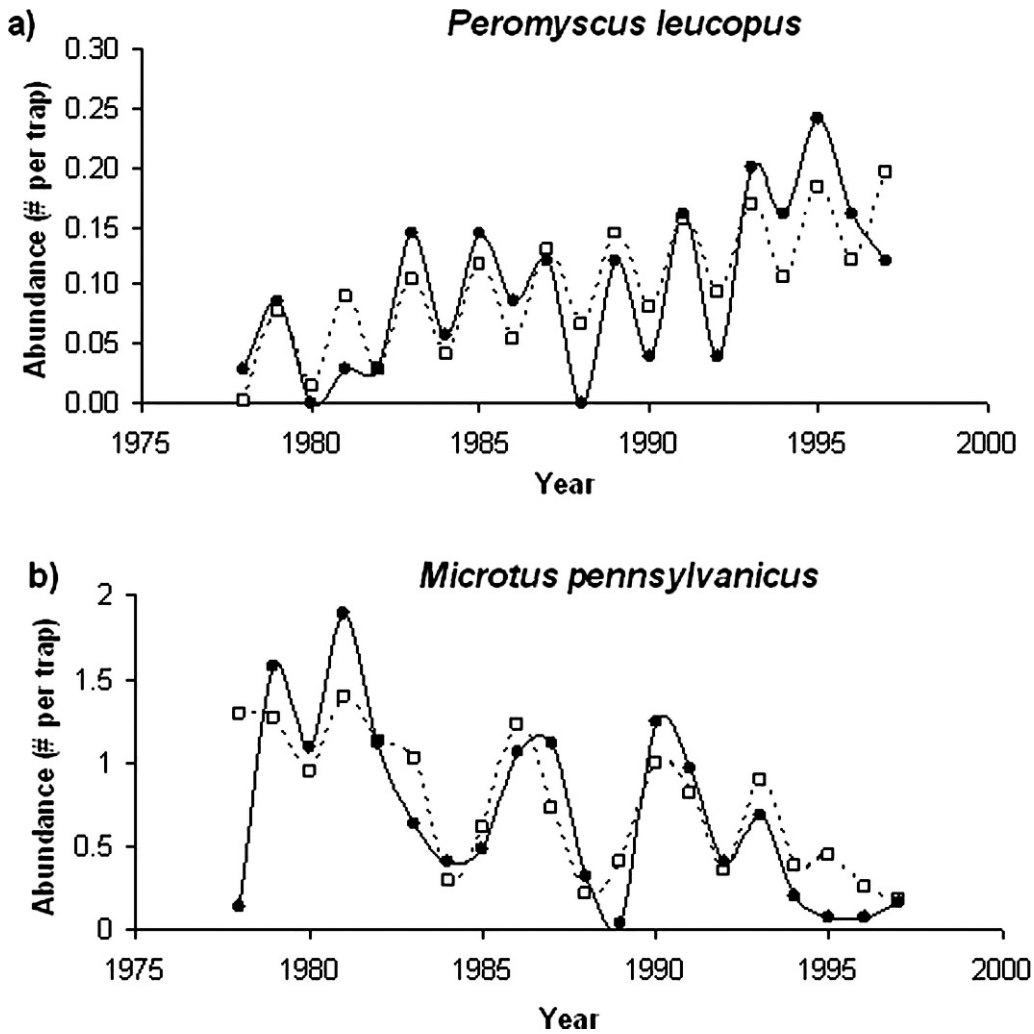

Fig. 1.—Abundance (circle, solid line) of a) *Peromyscus leucopus* and b) *Microtus pennsylvanicus* observed at the study site during 1978–1997. For both species the predicted abundance (open square, dashed line), using the factors of year (successional change) and summer precipitation, is presented for comparison.

1984), but the demographic consequences of climate-induced alteration of behavior remains difficult to predict.

Using the entire 20-year data set we found that populations of *P. leucopus* do not seem to fluctuate with the climatic variables that we examined. However, populations of *M. pennsylvanicus* correlated with summer precipitation. The 2nd hypothesis that we examined was that long-term studies are better at detecting correlations with fluctuations of population size and climatic variables. Analysis of subsets of our 20-year data set created results equivalent to what would have been generated if the study had been carried out over shorter intervals beginning at different times. This provides insight into how sensitive correlations between abundance and weather are to the particular interval of time over which sampling is performed. Although we expect some spurious associations, we found that results for *P. leucopus* were very sensitive to the time frame used. The results we found in the entire 20-year data set were found only in 26 of 171 possible subsets. For example, there were 8 possible 13-year data sets within the complete data set, and just 3 of these would have returned the same results as the 20-year study. Similarly, results for the 20-year data set of *M. pennsylvanicus* would have been found in only 29 of the 171 possible shorter subsets, and just 1 of the possible 8 subsets of 13 years repeats the results from the 20-year study.

The sensitivity of correlations to time period suggests that the influence of weather might be mediated by other factors. As a hypothetical example, snow depth might have had a significant effect on abundance of *P. leucopus* over the entire 20-year data set if disease, predator abundance, or any other influential factor also had been measured. McMillan et al. (2005) suggested that the relative influence of factors driving population dynamics can change from year to year and can depend on time of year. In addition, others have suggested that biologically critical factors are not always statically significant (Nester 1996). For example, we can speculate that snow depth was significant in 18 of the data subsets because other factors were relatively inconsequential at those times. The factors that were significant most often in these subsets also were significant in the stepwise regression when all the data were used. Long-term data sets might capture

Table 1.—Stepwise regression results for all possible data subsets from 3 to 20 years in duration. Column headings are the starting date (year) of subsets, and row headings represent the number of years included in each subset. Within each cell, numbers represent which factor was significantly related ($P < 0.05$) to abundance of white-footed mouse (*Peromyscus leucopus*; 1 = year [successional change]; 2 = cycle; 3 = snow depth; 4 = winter temperature; 5 = summer precipitation; 6 = summer temperature). Negative relationships were indicated by a minus sign (−) followed by the number of the related factor. Cells showing a dash (—) represent a subset where none of the factors were significantly related to abundance of *P. leucopus*.

No. years	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
20	1, 2																	
19	1, 2	1, 2																
18	1, 2	1, 2	1, 2															
17	1, 2	1, 2	1, 2	1, 2														
16	1, 2	1, 2	1, 2	1, 2, 3	1, 2													
15	2	1, 2, 3	1, 2	1, 2	1, 2	2												
14	2	2, 3	2, 3	1, 2	1, 2	1, 2	2											
13	2	2	2	2, 3	2	1, 2	1, 2, 3	2										
12	2	2	2	2	2	2, −6	1, 2	1, 2, 3	2									
11	2	2	2	2	2	2	2, −6	1, 2, 3	1, 2, 3	1								
10	1, 2	2	2	2	2	2	2	2	1, 2, 3	2	—							
9	—	1	2	—	2	2, −6	2	2, 5	2, −4, −6	1, 2	1, 2	—						
8	—	1	1	—	2, 3	2, −6	2	2	2, 5	1	1, 2, −4	1	—					
7	—	—	2	—	2, 3	2, −6	2, −6	2	2, 5	1, 2	1, −4	2, −4, 6	1	—				
6	—	—	—	—	2	2, 4, −6	2, −6	2, −6	2	2	1, 2	—	1	—	—			
5	2	—	—	—	2	2	—	3	3	2	2	2	—	—	2	−3, 5		
4	3	—	—	—	2	2	—	—	—	2	1	2	2	5	—	4	−3	
3	3	—	—	—	4	2	—	−5	—	2	—	—	2	—	—	—	2	−3

the effects of abiotic influences on populations; however, short-term studies might reveal factors that could be critical to short-lived species. Therefore, we concluded that time period affects the conclusions drawn about which factors influence population size. Our results suggested that climate is a critical, yet elusive, determinant of changes in population size of small mammals.

The benefits of our relatively long-term data are offset partially by the relatively restricted spatial scale over which abundance was measured. Because too few captures were made to estimate population size with mark–recapture estimation techniques, we used the number of unique animals captured per trap as a proxy for population size. Thus, we were

Table 2.—Stepwise regression results for all possible data subsets from 3 to 20 years in duration. Column headings are the starting date (year) of subsets and row headings represent the number of years included in each subset. Within each cell, numbers represent which factor was significantly related ($P < 0.05$) to abundance of meadow vole (*Microtus pennsylvanicus*; 1 = year [successional change]; 2 = cycle; 3 = snow depth; 4 = winter temperature; 5 = summer precipitation; 6 = summer temperature). Negative relationships were indicated by a minus sign (−) followed by the number of the related factor. Cells showing a dash (—) represent a subset where none of the factors were significantly related to abundance of *M. pennsylvanicus*.

No. years	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
20	−1, 5																	
19	−1, 5	−1, 5																
18	5	−1, 5	−1, 5															
17	—	−1, 5	−1, 5	−1, 5														
16	−1	−1, 5	−1, 5	−1, 5	−1, 5													
15	−1	5	5	−1, 5	5	5												
14	5	−1	−1	−1	−1	—	5											
13	5	−1	−1, 5	−1	−1	−1	—	5										
12	—	−1, 5	−1, 5	−1, 5	−1, 5	−1, 5	−1	5	−1, 5									
11	—	−1, 5	−1, 5	−1, 5	5	5	−1, 4	—	5	5								
10	—	−1, 5	−1, 5	−1, 5	5	5	—	−1, 4	5	5	−1							
9	—	−1	5	5	5	5	5	—	−1	—	−1, −2	−1						
8	—	5	—	5	—	5	5	5	—	—	−1	1	−1					
7	—	−1	—	—	5	—	5	5	5	—	—	−1	−1, 5	−1, 3				
6	—	—	—	—	—	5	—	—	—	—	—	—	−1, 5	−1	—			
5	—	—	—	−1	—	—	—	—	—	—	5	—	−1, 5	5	—	5		
4	—	—	—	−1	—	−2	−2	—	—	—	—	5	—	5	—	—	—	
3	—	—	2	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—

Table 3.—Values are the number of times the given factor was significantly associated with abundance of each species (*Peromyscus leucopus* [white-footed mouse] and *Microtus pennsylvanicus* [meadow vole]). With 171 analyses performed for each species, 8.6 spurious associations were expected using $\alpha = 0.05$. If spurious associations are distributed binomially, no more than 14 are expected at $\alpha = 0.05$.

Factor	*P. leucopus*	*M. pennsylvanicus*
Year	45	56
Cycle	109	4
Snow depth	19	1
Winter temperature	7	2
Summer precipitation	6	68
Summer temperature	11	0

unable to determine how much error exists in our index of population size. However, we do believe that this is a real representation of what is occurring in this relatively isolated population because the area of the trapping grid covered the majority of the wooded region. Nonetheless, we assume that the process operating on our sample grids is reflective of the process operating across a larger spatial scale because we have no a priori reason to assume otherwise.

The 20-year data set revealed that abundance of *P. leucopus* cycled biennially and was related positively to year (successional change) and that abundance of *M. pennsylvanicus* is related positively to summer precipitation and related negatively to year (successional change). The analysis of subsets revealed that results from the 20-year data set were not repeated frequently with shorter-term studies, suggesting that weak associations between abundance and climate can be contingent upon other unidentified factors. Our results further suggest that relatively long-term studies might be necessary to characterize relationships between abundance and climate. Even if a study (short-term or long-term) does not reveal a significant relationship, this does not necessarily mean those factors are unimportant biologically; it simply may be that those relationships are masked by other processes.

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