MODELING POPULATION VARIATION IN PEROMYSCUS LEUCOPUS: AN EXPLORATORY ANALYSIS

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Time-series analysis was applied in an exploratory analysis of density estimates for Peromyscus leucopus obtained over 9 years by weekly nest-box checks supplemented by live trapping. We developed a model that quantified the relationship between population density in a given month and density 1 month prior (1st-order autocorrelation), 12 months prior (seasonal effects), and 36 months prior (multiannual effects). The remaining variation was examined to determine the influence of stochastic variations in parameters of weather. In order of importance, predictors of density in a given month were density in the previous month (60.4% of variance explained), seasonality (6.1%), and multiannual effects (7.0%). Of the remaining 26.5% of variance, 3.4% was due to two weather factors; deviation from mean precipitation with a 5-month lag and high temperature with a 2-month lag. The population of P. leucopus was relatively resilient to abiotic effects over the 9 years. Quantitative models of this type are rare in the literature because gathering and adequately analyzing long-term ecological data is a demanding task. However, quantitative descriptions of variations in population density are essential to assessment of the relative importance of various mechanisms contributing to population regulation.

Key words: Peromyscus leucopus, demography, population variation, time-series analysis, abiotic factors, population cycles

Population dynamics of Peromyscus are believed to be relatively simple, lacking the multiannual fluctuations seen, for example, in arvicoline rodents (e.g., Adler and Tamarin, 1984; Adler and Wilson, 1987; Batzli, 1977; Kaufman and Kaufman, 1989; Terman, 1968; Van Horne, 1981). However, there is recent recognition that some populations of Peromyscus fluctuate widely and sometimes with predictable frequency (Drost and Fellers, 1991; Krohne et al., 1988; Linzey and Kesner, 1991; Sexton et al., 1982; Wolff 1985, 1993), albeit with lower amplitude than well-described multiannual fluctuations of arvicolines. Recognition that population regulation in cricetine and arvicoline rodents may not be fundamentally different (Sandell et al., 1991) is reflected in recent studies asking such questions as whether the “Chitty effect” (large-bodied morphs in peak populations of arvicolines) is demonstrated by populations of Peromyscus (Wolff, 1993).

Assessment of relative importance of various mechanisms contributing to population regulation requires adequate quantitative descriptions of major components of density variation. Statistical techniques such as time-series analysis can provide powerful tools for exploration of temporal variation in density of Peromyscus. These techniques have only occasionally been applied to data from natural populations of small mammals (Brown and Heske, 1990a; Framstad et al., 1993; Garsd and Howard, 1981, 1982; Henttonen et al., 1985; Hornfeldt, 1994). Further, the techniques often cannot be used because they require datasets that are both long (≥50 data points recommended) and continuous (Box and Jenkins, 1976). Despite a relative wealth of information on density variations in Peromyscus, no long-term density records have
been subjected to these types of exploratory analyses.

Weekly year-round sampling of a population of *Peromyscus leucopus* in western Pennsylvania has provided a database of sufficient duration and quality to initiate exploratory analysis of population variation using time-series analysis. We used Box-Jenkins, ARIMA, time-series analysis to determine the relative effects of biotic and abiotic processes on variation in density of this population.

**Materials and Methods**

The study site encompasses an 8.8-ha area located in Yellow Creek State Park, ca. 20 km E Indiana, Indiana Co., Pennsylvania. It is bounded on the north and west by a road and lake, on the south by a farm and cultivated fields, and is separated from an area of similar habitat to the east by a narrow wooded ravine. A fencerow with trees and heavy underbrush separates the study area from an adjoining cultivated field. The area extends from slightly above lakeshore level (396.3 m) to the top of a ridge overlooking the lake (422.1 m).

The most recent habitat disturbance occurred in 1975 when the vegetation of the entire area was cut to within 15 cm of ground level. At present, vegetation includes a heavy cover of grasses and forbs, shrubs that frequently form dense thickets (silky dogwood, *Cornus amomum*; sumac, *Rhus typhina*), and a few large trees (most commonly dogwood, *Cornus florida*; apple, *Pyrus malus*).

Data were gathered from 1984 to 1993 with each sampling year extending from September through August. Two methods were used for monitoring populations. First, 36 bluebird boxes were monitored weekly (16,848 box-checks). Boxes were distributed throughout the study area at ca. 60-m intervals, although intervals between adjoining boxes ranged from 30 to 90 m (Linzey and Kesner, 1991). Boxes were assumed to draw mice from within a 15-m radius and, collectively, to sample 2.54 ha. Box-checks have several advantages over more traditional live-trapping techniques for studies of populations. Box-checks are less invasive in both the short term (no trap confinement) and long term (no trap deaths or lowering of survival rates for trapped animals), year-round monitoring is possible in all weather, and the ease of box-checks allows for fine-grain sampling with minimal investment. However, for our population, probability of capture with box-checks was low ($P = 0.288$) and varied seasonally. Low probabilities of capture render population estimators unreliable (Boulanger and Krebs, 1994; Montgomery, 1987; Seber, 1986); therefore, we supplemented our box-checks with live trapping.

Trapping dates were as follows: year 1, 29 August, 28–30 September, 26–29 October, 15–18 December, 23 April–3 May; year 2, 18–21 October, 5–8 April, 29 April–1 May, 5–12 June; year 3, 2–7 September, 30 September–5 October, 1–9 November, 26 April–1 May, 11–16 June; year 4, 10–17 September, 5–11 May, 4–9 July; year 5, 31 August–6 September, 2–12 October, 9–14 May, 27 July–2 August; year 6, 7–12 September, 30 April–11 May, 17–23 July; year 7, 7–13 September, 9–17 October, 12–17 May, 17–25 July; year 8, 13–19 September, 11–26 October, 9–16 May; year 9, 12–22 September, 5–13 May. Trapping effort ranged from 5,345 trap-nights (year 1) to 1,944 trap-nights (year 9). Trapping through May 1986 employed a 300-station grid (10-m spacing) in the upper elevation portion of the study area and a 147-station grid in the lower elevation portion. In this method, the area directly enclosed by traps was 5.72 ha and not all bluebird boxes were included within the grids. Starting in June 1986, the design was changed to a box-centered pattern in which an array of nine traps was set in a three by three pattern at 10-m intervals, with the center trap at the bluebird box. Using this design and assuming that the traps sampled the area within 5 m of the array, the area directly sampled by traps totaled 3.24 ha. For both designs, one small (5.1 by 6.4 by 16.5 cm) Sherman live-trap baited with whole oats was placed per station, traps were checked and closed each morning, reopened each afternoon, and trapping sessions extended over 3 sequential nights (weather permitting).

Live trapping revealed that in April, October, and November the fraction of mice trapped and also captured in boxes in the same month was 0.21 (total trap captures = 42), 0.22 (260), and 0.30 (73), respectively; values for June, July, and August were 0.04 (48), 0.04 (240), and 0.00 (17), respectively. It is apparent that in summer months, some trappable animals are box-shy, perhaps because temperatures in boxes can be
high during these months (mean high temperature for boxes for June through August over the 9 years was 35°C). When data from trapping are added to box-capture data, the probability of capture increases slightly over the entire year (from a mean of 0.288 to 0.317), but increases dramatically in months of heaviest trapping effort (in May, the probability of capture increased from 0.117 to 0.339 with the addition of trapping data; in July, the increase was from 0.078 to 0.232). The use of several sampling techniques or the varying of sampling intensity over time can alter the probability of capture either within or between sampling periods (Jolly and Dickson, 1983; Montgomery, 1987) and, therefore, is generally inappropriate. However, in this case, the use of several sampling methods increased the probability of capture (especially for heavily trapped summer months) and reduced capture heterogeneity across months, thereby improving the reliability of density estimates.

Non-trappable juveniles (<10 g) were not included in density estimates. Monthly data used in population modeling represent means of weekly data, with population density estimated by the minimum-number-known-alive (MNA) method. We recognize that Jolly-Seber population-estimation techniques are superior to the negatively biased MNA method (Hillborn and Krebs, 1992; Pollack et al., 1990; Yoccoz et al., 1993). However, our data did not meet the assumptions of the Jolly-Seber method. Mean probability of capture for our population was 0.317, whereas Jolly-Seber estimates are considered invalid if the probability of capture is <0.5 (Pollock et al., 1990; Seber, 1982). Accurate Jolly-Seber estimates require >10 animals per sampling period (Krebs et al., 1986; Pollock et al., 1990; Seber, 1982), but 55 of 108 months in our study had sample sizes <10. Further, highly significant (P < 0.01) chi-square goodness-of-fit measures revealed that our data did not fit the Jolly-Seber model (Program Jolly—Hines, 1991).

Box-Jenkins ARIMA time-series analysis incorporates a family of techniques specifically designed to handle autocorrelated data. ARIMA includes autoregressive (i.e., modeling density as a linear function of previous density plus error), integrative (i.e., modeling density as a past density; more commonly referred to as differencing), and moving average (i.e., modeling density as a linear function of previous error terms) components. The first step in ARIMA is to achieve normality and the second is to assure stationarity (i.e., remove trends or seasonality) of the data series (McCleary and Hay, 1980; Pankratz, 1983; Poole, 1978). The remaining pattern in the data is then modeled by autoregressive or moving average functions. ARIMA modeling is an exploratory, iterative process aided by reference to autocorrelation functions (ACFs = plots of autocorrelations for various lags), partial autocorrelation functions (PACFs = plots of the partial autocorrelations for various lags), and spectral density functions (SDFs = plots of the dominant frequencies of the periodicities in the data—Gottman, 1981). The parsimony of the model is judged by its simplicity, the variance explained, and measures such as the Akaike information criterion (a measure of autoregressive model fit) and Schwartz Bayesian criterion (a measure of general model fit). The residual from a successful ARIMA model should be normal, homoscedastic, and lack autocorrelation (Gottman, 1981; SPSS, Inc., 1990). In addition, any moving-average components will have unique solutions only if a set of invertibility conditions (algebraically equivalent to the stationarity requirement for autoregressive components) are met (Pankratz, 1983).

ARIMA modeling as outlined above was applied to both density and monthly weather data; high temperature, low temperature, mean high temperature, mean low temperature, deviation from mean monthly temperature (derived from a 1961–1990 database), total precipitation, and deviation from mean precipitation (derived from a 1961–1990 database). Weather data were recorded at the Indiana 3SE (Two Lick Creek) Weather Station located 8.8 km NW of the study site. SPSS Trends was used for ARIMA modeling (SPSS, Inc., 1990). Residuals from the ARIMA model of density were then cross-correlated with residuals from ARIMA models of weather data at time lags of up to 7 months to determine the extent to which weather might explain residual density. Multiple regression was used to explore any suggested relationships between residual density and residual weather data.

RESULTS

A total of 1,795 animals was captured 5,760 times with 618, 299, 546, 1,257, 236, 651, 851, 574, and 728 total captures for
FIG. 1.—The thin line plots the square root of density (mice/ha) with time (September 1984–August 1993). The smoothness of the plot suggests an autocorrelation between months (lag 1). The plot also suggests a seasonal cycle (highest densities for each year tend to be in November) and to a lesser extent suggests a multiannual cycle (peaks in 1984, 1987, 1990, and 1992). The thick line plots the residual from the ARIMA (1,1,0)(0,1,1) model of density against time to allow assessment of the effectiveness of the model in removing components from the data.

years 1 through 9, respectively. Population fluctuations during the 9 years revealed a seasonal cycle in density and suggested a 3-year multiannual cycle (Fig. 1). In each year, the population peaked in late autumn and early winter, declined during early spring, and reached lowest levels in midsummer. Comparing years, the highest mean density (28.5 mice/ha) occurred during year 4 (1987–1988) and the lowest (7.4 mice/ha) occurred during year 5 (1988–1989), with densities ranging from a peak of 57.5/ha (November 1987) to a low of 1.2 mice/ha (July and August 1986).

Density was nonnormal, heteroscedastic across years, and autocorrelated. When the data series was subjected to a square-root transformation, the result was normal and homoscedastic. In the following, density refers to the transformed values.

The slight upward trend in the plot of density (Fig. 1), the linear decay evident in the ACF of density (i.e., autocorrelation of 0.794 at lag 1, 0.612 at lag 2, 0.399 at lag 3; Fig. 2a), and the peak at zero frequency (period = infinity) in the spectral-density function (SDF) of density (Fig. 3a) all indicate regular differencing (subtraction of density at time t−1 from density at time t) is necessary to achieve stationarity. Similarly, density plotted over time (Fig. 1), the linear decay from lag 12 (autocorrelation = 0.437) through lag 24 (0.324) and lag 36 (0.248) seen in the ACF of the regularly differenced series (Fig. 2b), and a peak at period 12 in the SDF of the regularly differenced series (Fig. 3b) support the need for seasonal differencing (subtracting regularly differenced density at time t−12 from regularly differenced density at time t).

Analysis of the stationary data series suggested that some additional modeling was necessary. An ACF and PACF of the fully differenced series revealed significant autocorrelations at lag 12 (−0.283 in the ACF, −0.331 in the PACF; Fig. 2c). Further, the plot of density over time (Fig. 1) hints at a multiannual (36 month) cycle, whereas the SDF of the fully differenced series (Fig. 3c) shows a peak at a period of 36 months.
FIG. 2.—a, Autocorrelation function (ACF) for density (plot of the correlation between density at time \( t \) with past densities at various lags) with \( \pm 2 \) SE indicated by broken lines. Note the high autocorrelation at lag 1. b, ACF of density after subtraction of density at time \( t - 1 \) (regular differencing). With the removal of autocorrelation at lag 1, the seasonal component (peaks at 12, 24, and 36 month lags) is evident. c, ACF of density after subtraction of density at times \( t - 1 \) and \( t - 12 \) (lags 1 and 12, the latter is referred to as seasonal differencing).
Fig. 3.—a, Spectral-density function (SDF) of density (plot of the relative dominance (log periodogram) of the frequencies of any periodicities in the density data). The x-axis is labeled with the period of the plotted frequency rather than the frequency itself for clarity. Note the dominant period at infinity (0.0 frequency) reflecting the presence of a lag-1 autocorrelation and trend in the data. b, SDF of density at time \( t \) after subtraction of density at time \( t-1 \) (regular differencing). A seasonal component (peak at period 12) is now apparent. c, SDF of density after subtraction of density at time \( t-1 \) and density at \( t-12 \) (seasonal differencing). With removal of dominant components, a 36-month periodicity is suggested.
Table 1.—Weather variables evaluated in this study, transformations necessary to achieve normality and homoscedasticity, the ARIMA necessary to remove any trends or seasonality from the data, and remaining autocorrelations as an indicator of the success of the ARIMA.

<table>
<thead>
<tr>
<th>Monthly weather variable</th>
<th>Transformation</th>
<th>ARIMA</th>
<th>Significant autocorrelations remaining after ARIMA (lag)</th>
</tr>
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<tbody>
<tr>
<td>High temperature</td>
<td>×³</td>
<td>(1,0,0)(1,1,0)</td>
<td>none</td>
</tr>
<tr>
<td>Low temperature</td>
<td>×¹.⁵</td>
<td>(1,0,0)(0,1,1)</td>
<td>none</td>
</tr>
<tr>
<td>Mean high temperature</td>
<td>none</td>
<td>(0,0,0)(1,1,0)</td>
<td>none</td>
</tr>
<tr>
<td>Mean low temperature</td>
<td>×¹.⁵</td>
<td>(0,0,0)(1,1,0)</td>
<td>none</td>
</tr>
<tr>
<td>Deviation from normal temper</td>
<td>(× + 13)⁰.⁹</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Total precipitation</td>
<td>ln(×)</td>
<td>(0,0,0)(1,0,0)</td>
<td>-0.207(11)</td>
</tr>
<tr>
<td>Deviation from normal precip</td>
<td>ln(×)</td>
<td></td>
<td>none</td>
</tr>
</tbody>
</table>

Of several models investigated, the most parsimonious was ARIMA (1,1,0)(0,1,1) (in ARIMA notation the numerals in the first set of parentheses signifies the order of regular autoregressive, regular differencing, and regular moving-average components of the model, respectively; those in the second set of parentheses signify the order of seasonal autoregressive, seasonal differencing, and seasonal moving-average components, respectively). All ARIMA coefficients added significantly to the model, which also possessed the smallest standard error of the estimate, Akaike Information Criterion, Schwartz Bayesian Criterion, and residual variance of any model evaluated. The residuals were normal, homoscedastic, and not autocorrelated (Fig. 1). The PACF of the residual revealed a barely significant correlation at lag 30; however, the expectation that two of the 36 correlations in the PACF would be significant at $P < 0.05$ by chance alone and the lack of any discernible pattern in either the ACF or PACF supports the interpretation that the residual is stochastic. However, a SDF of the residual shows a peak at frequency 0.028 (36 months), suggesting that the 36-month cycle was not totally removed from the data.

The next step in the analysis was to determine if any weather variables correlated with the residual from the ARIMA model. Transformations were necessary to achieve normal and homoscedastic weather data, and we applied ARIMA models to eliminate trends and seasonality (Table 1). ARIMA models were chosen using ACFs and SDFs of weather variables and evaluated using goodness-of-fit criteria as described for density. All ARIMA coefficients added significantly to the models and ACFs of all residuals were nonsignificant with the exception of an autocorrelation at lag 11 for the residual from total monthly precipitation (Table 1). However, this latter residual had only one significant autocorrelation (out of 36 possible) and the ACF did not possess a pattern as evidenced by a nonsignificant Box-Ljung statistic. ARIMA weather residuals were normal and homoscedastic. The transformed deviation from normal monthly temperature did not require an ARIMA, but was heteroscedastic over months. Further attempts at transformation were unsuccessful in removing heteroscedasticity from this variable.

Residuals from the ARIMA model of density were then cross-correlated with each of the residuals from ARIMA models of weather data. Four significant cross-correlations were found with density at time t; high temperature at t−2 ($r = -0.225$) and t+4 ($r = -0.302$), total precipitation at t−5 ($r = 0.235$), and deviation from normal precipitation at t−5 ($r = 0.301$). With a total of 98 comparisons, some spurious significant correlations (e.g., correlation of density at time t with high temperature at time t+4; i.e., 4 months later) would be expected by chance. Thus, further evaluation of the significance of observed correlations must be based on their biological interpretations.
ARIMA residuals of total precipitation correlate with those of deviation from normal precipitation ($r = 0.836, P < 0.001$); therefore, correlation of density at time $t-5$ with these two variables can be represented by one of them. Multiple regression was used to determine the degree to which high temperature (HT) at $t-2$ and deviation from normal precipitation (DP) at $t-5$ might explain density. The regression had a multiple $r = 0.368$, with both independent variables entering significantly (HT, $P = 0.041$; DP, $P = 0.004$). Lack of correlation between HT and DP ($r = -0.070$) indicated that their contributions to the regression are largely independent. The residual from the multiple regression was normal and homoscedastic. The residual did have a significant autocorrelation at lag 34 ($r = 0.165$), but the Box-Ljung statistic was non-significant, the PACF had no significant correlations, and the Durbin-Watson statistic of 2.113 for the regression further suggested the residual was not autocorrelated.

**DISCUSSION**

The best predictors of density in a given month were density from the previous month (explaining 60.4% of the variance of transformed density) and density 12 months prior (6.1%, Table 2). The lack of an exact estimate of variance explained by multianual effects (a maximum of 7.0%) was due to adding a first-order regular autoregression to the model (to eliminate autocorrelation from the residual) and to our inability to isolate this component from that representing the 36-month cycle (first-order seasonal moving average). Because ≥10 repetitions of a cycle are needed to assure detection by SDF analysis (Jassby and Powell, 1990), the data were not sufficient to allow total modeling of this component. Although speculation about mechanisms producing this cycle is premature, the data provide additional evidence of regular multianual fluctuations in *P. leucopus*. Continued study of this population, together with additional long-term studies from other areas, are needed to confirm this pattern.

After removal of monthly, seasonal, and multianual processes via our ARIMA model, the residuals were stationary, normal, homoscedastic, and, with the possible exception of a component of the multianual process, did not contain deterministic elements (Fig. 1). The remaining 26.5% of variance appears to be stochastic. Cross-correlation analysis between abiotic variables and the residual from the ARIMA model suggests that an additional 3.4% of population variance is due to two weather factors. Deviation from mean precipitation is correlated positively with density variations 5 months later (1.1% of total variance, based on semipartial correlation) and high temperature is correlated negatively with density variations two months later (2.2% of total variance, based on semipartial correlation). Thus, the total population model accounts for 76.9% of population variation (Table 2).

Comparison with results from the literature is difficult, because published studies vary in length, sampling techniques, sam-

<table>
<thead>
<tr>
<th>Model component</th>
<th>Percentage of variance explained</th>
<th>Percentage of variance explained by semipartial correlations</th>
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<tbody>
<tr>
<td>Monthly resilience</td>
<td>60.4</td>
<td></td>
</tr>
<tr>
<td>Seasonality</td>
<td>6.1</td>
<td></td>
</tr>
<tr>
<td>Multiannual</td>
<td>7.0</td>
<td></td>
</tr>
<tr>
<td>Weather</td>
<td>3.4</td>
<td></td>
</tr>
<tr>
<td>Deviation from normal precipitation</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>High temperature</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>76.9</td>
<td></td>
</tr>
</tbody>
</table>
pling frequency, density estimates, and methods of analysis. These differences preclude strict comparisons with our study. We are aware of only two long-term studies of rodents that compared weather and population dynamics and measured density on a time scale similar to ours. Garsd and Howard (1982) monitored Microtus californicus bimonthly and found significant relationships between September–October captures and maximum August soil temperature ($r^2 = 0.52$ and 0.56 for two monitored areas, $P < 0.01$) and between March–April and July–August captures and solar variables ($r^2$-values between 0.21 and 0.26, $P < 0.05$). Twigg and Kay (1994) reported $r^2 = 0.38$ ($P < 0.01$) when they regressed 3-month mean minimum temperatures on abundance of Mus domesticus. Clearly the population of P. leucopus studied here did not respond to weather variations to the same degree. However, demonstrations that precipitation and high temperature influence survivorship and reproductive abilities of small rodents in field situations (Best and Hoditschek, 1986; Myers et al., 1985; Pinter, 1988) suggest the possibility that the small (3.4%) weather effects seen here have short-term biological significance.

The overall consequence of unusual weather events to population patterns may be diminished by the fact that the impact of such events is situational (i.e., dependent upon an interaction between season of occurrence and status of the population). For example, although the overall correlation with precipitation was positive in our study, winter precipitation shows a higher frequency of negative relationships to density 5 months later (Table 3). Positive relationships (predominant in spring, summer, and autumn) may reflect the positive impact of precipitation on food resources, reproductive capabilities, and overwinter survival. Negative relationships associated with winter precipitation may relate to ground saturation and subsequent impacts on mortality. This speculative discussion is meant to illustrate the conditions under which abiotic effects can impact populations of P. leucopus. Similar ad hoc analysis of the impact of high temperature could be performed. However, we wish to emphasize that such impacts, although possibly important in a given season or year, are barely perceptible over a 9-year period.

Long-term studies of weather and annual or semi-annual estimates of rodent populations suggest that the effects of weather can vary greatly. For example, Ostbye et al. (1989) found a significant relationship between an autumn population index for Lemmus lemmus and precipitation in July and temperature in September ($r^2 = 0.58$, $P < 0.01$). However, they found no relationship between the same variables when their index represented aggregations of populations of lemmings from a larger area. Framstad et al. (1993) were unable to find any relationships between density of L. lemmus and weather and concluded that both their investigations and those of Ostbye et al. (1989) did not indicate any consistent relationships between weather and density. Other studies have found relationships of varying magnitude between population densities of rodents, temperature ($r^2$ from 0.08 to 0.43—Garsd and Howard, 1981; Hornfeldt, 1994; Pucek et al., 1993), precipitation ($r^2$ from 0.09 to 0.91—Drost and Fellers, 1991;
Hornfeldt, 1994; Pinter, 1988; Pucek et al., 1993), and snow cover (r² from 0.06 to 0.67—Hornfeldt, 1994; Pucek et al., 1993). The large number of weather variables analyzed across these studies, some with small effect, suggests that not all of these statistically significant findings have biological importance.

To allow comparison, we analyzed the relationship between annual means of our monthly density and weather variables. We discovered one significant relationship, a negative correlation between density and total precipitation (r² = 0.45, P < 0.05). The negative impact of total precipitation might vary seasonally (e.g., early spring precipitation might impact survival of overwintered mice); however, we were unable to uncover any seasonal effects. Our confidence in the validity of the correlation would increase if, as in the studies by Garsd and Howard (1981, 1982) examining the relationship between density and soil temperature, the effect was evident at several temporal scales. Analysis at semi-annual and quarterly scales (with seasonal effects removed from both density and precipitation data) failed to reveal significant relationships. Moreover, at the monthly scale (Table 2) a significant positive relationship exists between density and precipitation. A low sample size (9) and our inability to discover a meaningful biological explanation suggest that this correlation may be spurious.

A relationship between density and weather could reflect direct impacts on natality or mortality or result from lagged indirect effects via changes in food or cover. The study of direct effects requires a temporal scale suited to detect the relatively immediate impacts of weather (weekly or monthly for small rodents), although even immediate impacts, if large enough, might be detectable at larger temporal scales. The study of lagged indirect effects could be attempted at larger time scales. However, because the impact of indirect effects of weather might be greater in certain seasons (at least in strongly seasonal environments), the scale of study must allow for a fine scale dissection of the relationship to reveal biological significance. Given the potential generation times of small rodents (weeks to months), a monthly sampling scale may allow the most efficient detection of both direct and indirect effects of abiotic variables.

In summary, weather was not a major determinant of population density of P. leucopus during this study and the significant relationships found (although perhaps important in the short-term) do not warrant extensive ad hoc analyses. The literature suggests some rodent populations do respond to weather, but the sampling frequency of these studies generally does not allow for detailed analysis of the biological significance of these observations. Only Garsd and Howard (1982), Twigg and Kay (1994), and this study have analyzed weather and density on the most appropriate temporal scale for small rodents. These studies suggest that the impact of weather varies tremendously. Further understanding of the impact of abiotic factors on population dynamics of small rodents must await additional appropriately designed studies.

The gathering and analysis of long-term ecological data is demanding. Time-series analysis requires large continuous samples (n > 50) and minimally four (for ACF analysis—Box and Jenkins, 1976) to 10 (for SDF analysis—Jassby and Powell, 1990) repetitions of any lag or cycle of interest. Although our understanding of population dynamics can benefit from carefully designed, short-term experiments, there are cogent reasons for the frequently expressed call for more long-term studies. For example, Magnuson (1990) noted that the significance of short-term studies often is invisible without a larger scale view and that larger scales are essential to detect the lagged effects prevalent in ecological systems. There is evidence that unusual events are assigned greater (often unjustified) significance in short-term studies (Weather-
head, 1986). If our study had been shorter and had included a winter when high precipitation resulted in increased overwinter mortality, the relatively low impact of this situational effect on long-term population patterns would not have been recognized. Further, interspecific interactions known to influence population dynamics can vary over time and space (Bronstein, 1994). For example, Heske et al. (1994) recently replicated a study confirming the critical (keystone) status of kangaroo rats (Dipodomys) as competitors and potential population regulators of five other granivorous rodents (Brown and Heske, 1990b; Brown and Munger, 1985). Under experimental conditions on localized plots (small patch size), they were able to demonstrate a negative correlation between densities of species of Dipodomys and those of their competitors. However, time-series analysis of 10 years of data from a larger area exhibited positive correlations between densities of species pairs, leading to the conclusion that community dynamics were more influenced by responses of individual species to environmental variations than to the competition evident at smaller scales (Brown and Heske, 1990a). Results cannot be extrapolated without confirmation that phenomena influencing populations at smaller spatial or temporal scales will have similar effects at larger scales.

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LITERATURE CITED


HENSTONEN, H., A. D. MCGUIRE, AND L. HANSSON. 1985. Comparisons of amplitudes and frequencies...


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